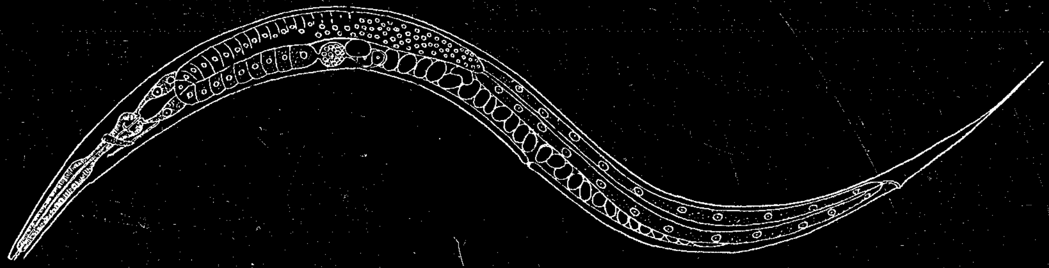
# Free-Living Marine Nematodes of the Sevastopol Area



TRANSLATED FROM RUSSIAN

ISRAEL PROGRAM FOR SCIENTIFIC TRANSLATIONS

TRUDY OSOBOI ZOOLOGICHESKOI LABORATORII I SEVASTOPOL'SKOI
BIOLOGICHESKOI STANTSII ROSSIISKOI AKADEMII NAUK
Transactions of the Zoological Laboratory and the Sevastopol Biological Station
of the Russian Academy of Sciences

Series II No. 4

## I. N. Filip'ev

# FREE-LIVING MARINE NEMATODES OF THE SEVASTOPOL AREA

(Svobodnozhivushchiya morskiya nematody okrestnostei Sevastopolya)

Issue I

(Read at the meeting of the Department of Physics and Mathematics
on 26 November, 1914)

Tipografiya Rossiiskoi Akademii Nauk
Petrograd 1918

Translated from Russian

Israel Program for Scientific Translations
Jerusalem 1968

IPSI Cat. No 1921

Translated by M. Raveh

Printed in Jerusalem by S. Monson
Binding: Wiener Bindery Ltd., Jerusalem

# Table of Contents

This publication constitutes the taxonomic part of my study. Under the present conditions it is by no means clear when the second part of the work, which contains anatomical, biological, and zoogeographical conclusions, will appear. It may be within one year or it may be in five.

Although the printing of this part began in 1916, it is being published only now. The issue of individual printer's sheets was as follows:

1 – April, 1916
2 – 4 – May, 1916
5 – 9 – September, 1916
10 – 11 – January, 1917
12 – 13 – April, 1917
14 – February, 1917
15 – 17 – April, 1917
18 – February, 1918
19 – September, 1917
20 – 22 – March, 1918.

I have tried as far as possible to make use of the most recent papers which reached me while the book was in press, and have made additions to the proofs. For this reason data from several papers by Steiner, Cobb, Southern, etc., are not encountered in the first pages. All the appendices will be given at the end of the book, where a bibliographical list and explanation of the tables will also appear.

14 (1) March, 1918
Zootomy Department,
Petrograd University

I. Filip'ev

## TRANSLATOR'S NOTE

In his descriptions of the species the author of this book refers to and makes great use of drawings. Unfortunately, the part of the book containing the drawings of the species was not available at the time of translation, so that the translator has been obliged to rely largely on his imagination, which for the description of complicated organs and their disposition may not always have been adequate.

The references to the drawings have nevertheless been retained in the translation so that the reader who acquires a copy of the original Russian book will have no difficulty in relating the written description to the drawings. To this end, the Russian page numbers have been reproduced in the left-hand margin of the translation.

The Russian original contains sections on the general comparative morphology of free-living and parasitic nematodes, as well as Appendices. These also were not available for translation.

## iii FOREWORD

Nine momentous years have passed since I embarked upon this work. A world war has begun and ended, Russia has been shaken by revolution, a civil war has run its course. The last event cut me off in the south, far from Petrograd.

The study was completed and in press as early as 1917, and the first part appeared in the autumn of 1918. The second part is being published only now. For three years it was impossible for me to correct the proofs (from April, 1918), and matters came to a standstill. A deficiency in the work is the scant reference to the most recent literature; from the early days of the war the flow of foreign scientific papers to us was poor. Even in 1918 at best only the news of the appearance of a publication reached us while the paper itself remained inaccessible. It seemed advisable not to make use of the two or three papers which I have recently been able to obtain. Therefore, the second part of the study also relates, strictly speaking, to 1918 and not to 1921, which is the date printed on the cover. The paper by Steiner, "Untersuchungen über den allgemeinen Bauplan des Nematodenkörpers," published in Zoologische Jahrbücher, Abtheilung für Anatomie und Ontogenie, Band 43, 1919, which judging by its title and author is a very important work, could not be employed in the second part. Many papers by Steiner, Cobb, Southern, Micoletzky (1914 – 1917) are utilized for the taxonomic part only in the Appendix.

iv The dates of appearance of individual printer's sheets are as follows:

1 – April, 1916
2 – 4 – May, 1916
5 – 9 – September, 1916
10 – 11 – January, 1917
12 – 13 – April, 1917
14 – February, 1917
15 – 17 – April, 1917
18 – February, 1918
19 – September, 1917
20 – 22 – March, 1918
23 – 24 – March, 1918
25 – 26 – July, 1918
27 – December, 1918
28 – 32 – October, 1921
33 – 39 – December, 1921.

The first part (sheets 1 – 22) was published in November, 1918, and the second part appears now.

At this point I state my debt of thanks to those whose help made the publication of this book possible: S. A. Zernov, former head of the Sevastopol Biological Station of the Russian Academy of Sciences, Professor of the Petrovskaya [Razumovskaya] Academy, for his aid in collecting material and for the guidance which I obtained following his preliminary work; the recently deceased Academician V. V. Zalenskii, who as Director of the Sevastopol station presented this study to the Academy; S. F. Ol'denburg, Permanent Secretary of the Russian Academy of Sciences, who always met the requirements of printing; V. V. Nordgeim, Director of the technical section of the Academic Press, to whose mighty efforts the "peacetime" appearance of this book is due and through whose consideration the printing of the end of the second part was speedily accomplished while I was engaged in Petrograd; I. A. Orbeli, who accelerated the printing; the Praesidium of the Sevastopol Agricultural Institute, which commissioned the study.

Petrograd,
1 December, 1921

I. N. Filip'ev
Professor at the Sevastopol
Agricultural Institute

## 1 *INTRODUCTION*

While parasitic nematodes have for a long time attracted the attention of research workers and many data on them collected and widely published by numerous scientists have by now accumulated, the free-living nematodes have until recently been neglected. The monograph by de Man (1884) is basic for the study of terrestrial and freshwater nematodes, and the elaboration of this fauna has for some time been the aim of certain scientists in the countries of Central Europe. Since 1876 Holland has been the center for investigations of de Man, whose name will be frequently cited in subsequent pages. In Germany this fauna has been studied since the 1870's, in Hungary since the 1890's, and in Denmark in recent years. A fairly large number of different free-living nematodes have been found. Switzerland has taken the leading place recently; this country has witnessed a general development in hydrobiology, and many young scientists in various fields have devoted themselves to the study of nematodes. Outside Europe the work of Cobb in Australia alone has demonstrated the cosmopolitan nature of the fauna of terrestrial and freshwater nematodes. Thus, even at this point we find ourselves dealing with the beginning of the **taxonomic study** of nematode fauna. Unfortunately, such widespread interest has not been shown in the study of the anatomy, which up to now has been halting.

2 The situation is entirely otherwise for the sea. Several scientists have have been working in this sphere, many species have been described, frequently with great and accurate detail, the anatomy of many genera has been elaborated highly satisfactorily. However, there is hardly any study* that has even attempted to deal exhaustively with all the nematode fauna of a given marine region. No expedition has made a large collection of nematodes; at best they include in their reports the description of a dozen species, but this is most unusual.

The second failing in the current position is that although a fairly large number of genera have been described, and although the accumulation of material is adequate, no author has so far attempted to establish the natural groupings of the genera or to unite them in families and subfamilies.**

At first my interest in free-living nematodes was centered upon their anatomy. With the intention of studying this I collected and preserved nematodes while still a student at Naples in the summer of 1909. For various reasons these pursuits were interrupted before they had produced any results. In 1911, while at the Villefranche Zoological Station,

---

* With the exception of the paper by Savel'ev for the Kola Gulf (1912), which, however, has not yet been published in its entirety.

** If we do not consider de Man's attempt (1876), which he himself later regarded as outdated (1884).

I renewed my studies of nematodes and began working on vital staining of the nervous system with methylene blue. In the winter of 1911 – 1912 I continued in this occupation at Sevastopol, where I came across a very rich and suitable collection of material. Processing this material in the summers of 1912 and 1913, I in passing became acquainted with the nematode fauna of the Black Sea, which I collected from various facies. My familiarity with the literature assured me of the poor development of 3 the taxonomy and faunistics of the free-living marine nematodes, and this induced me to undertake the fullest possible elaboration of the nematode fauna of the environs of Sevastopol. This study, then, must be seen as a purely systematic work; its primary aim is to provide a picture of the Black Sea nematode fauna, albeit an approximate one. The account is still far from complete, and indeed could not be completed by the efforts of a single individual in the course of two or three years. Another aim is to establish a basis for the natural grouping of free-living nematodes in families and subfamilies. Here I have for the present hardly entered into phylogenetic considerations but have endeavored to extract from the general confused mass of genera those which bear similar features, sometimes pausing only when small, but completely homogeneous, groups have been created. This system also, of course, must still be subjected to changes and additions. Many genera which for the most part have been inadequately described by previous authors had to be omitted.

The systematic nature of the work also explains why I have paid scant attention to many data which are interesting from the general anatomical point of view, but which have little bearing upon taxonomy. However, it was always necessary to study closely the small features and details that are so important in identifying species.

In conclusion I venture to express my sincere appreciation of those who assisted me in my work: M. M. Davydov, F. A. Snichakov, and T. E. Timofeev in Villefranche, L. I. Yakubova in Sevastopol, and particularly S. A. Zernov, who always supplied material willingly and helped me with his wide knowledge of the facies of the environs of Sevastopol.

4

## *MATERIALS AND METHODS OF RESEARCH*

The methods used for collecting nematodes were the usual ones, which makes it unnecessary to describe them in detail. The nematodes were caught with a drag, a trawl, or a plankton net over water plants (Zernov's Zostera plankton). Another suitable method was raising bottom muck or extracting small animals from it. N. L. Girshman particulary recommends the use of the sledge trawl, with which he obtained very good results in collecting ostracodes; however, I had no occasion to use it. It should only be noted that when the bottom is loose – algae and particularly coarse sand and shells – a drag with a fine mesh bag should be used, since otherwise the muck may be washed out, especially when the bag is raised from great depths, and only a few nematodes may remain. I was impressed of this at Murmansk, where I collected shells from mud on two successive occasions from the same place, once using a coarse-mesh bag and the second time using a sack with a fine bag.

In every facies nematodes are encountered to a greater or lesser degree. However, it is very time consuming and unproductive to select them directly from the sand or plants that have been raised; other methods are required to obtain them en masse. These are in part based on biological principles and in part on the mechanical sorting of bottom samples by size and specific weight.

### *A. Biological methods of selection*

a) Primarily we make use of the habit of many animals of crawling along the side of a vessel to the surface of the water. For this purpose algae (Cystoseira, Fucus, etc.) are placed in a glass vessel with a vertical edge; as soon as the water becomes fairly calm an entire fauna 5 of small animals will swim or crawl to the edge of the vessel at the surface of the water. The animals include Copepoda, ticks, Infusoria, Rhabdocoela, Polychaeta, Nemertina, rotifers, and sometimes many nematodes, which may be simply collected with a pipette. In this fashion we succeeded in collecting Cyatholaimus, Leptosomatum, and especially Symplocostoma and various Chromadorini and Spilophorini. This is a good method, since the nematodes are taken undamaged and directly from the water, and are therefore suitable for physiological experiments also. However, only a small amount of material may be obtained in this way.

b) The second method is based on the fact that the cuticle of some free-living nematodes stick to air bubbles once they have come into contact with them, and such nematodes cannot sink back into the water after having risen to the surface (Viscosia, Euchromadora, Spilophorella, etc.). A similar phenomenon is observed with many crustaceans (Cladocera, etc.). To bring this about I shook up the sample, or used a pulverizer to blow air that had been passed through porous stone or carbon into the water, as is done in the aeration of aquaria. The nematodes were collected off the water surface with blotting paper and transferred to a fixative. Good collections were sometimes obtained in this way.

c) If sand, mud, or algae with a large quantity of nematodes are obtained without scavenging, decomposition processes soon take place and the water becomes foul. Under conditions of insufficient oxygen many nematodes emerge and accumulate in piles. The same process is described by Zernov (1913) for saccocirrous sand, where Saccocirrus, Protodrilus, and Triclada emerge and form piles. Exactly the same occurs if sand that has been dirtied with decay products is placed in the vessel. Light-orange piles of Oncholaimus demani Zur Strassen and Capitella capitata of the polychaetes accumulate on the surface of the sand and on the glass. By this means, but with less success, I was able to collect Enoplus from algae at Murmansk. This

6 method is of course suitable only for the more viable nematodes; many of the delicate species perish.

## B. *Mechanical methods of selection*

One of the most simple methods consists of washing various objects—algae, sponges, bryozoa, stones—in a preserving fluid. This method is recommended by Savel'ev (1912) and Shchepot'ev (1908), but in my opinion is good only for the incidental collection of nematodes together with other animals. As Savel'ev (1912) points out, free-living nematodes are always abundant on the bottom of jars containing hydroids, sponges, and bryozoa. However, this method is not recommended for the collector who is specifically interested in nematodes, since on the one hand the nematodes cannot be caught live and on the other an excessive amount of preservative fluid is required; this can very easily be avoided by washing live nematodes out of the substrate.

The procedure for washing nematodes out of the deposit may be broken down into three operations: (1) the separation of the nematodes from the heavier particles (sand, shells, etc.); (2) the separation of the larger but lighter particles (algae); (3) the separation of mud. For the first operation I placed the sand or shells in small amounts into a round vessel 15—20 cm in diameter, shook it vigorously, and poured everything that came to the surface—mud and animals—into another vessel. The process was repeated two or three times with the same sample.

The larger particles were separated by means of a sieve with a mesh diameter of about 0.5 cm. The material was laid in even layers in the sieve and placed under a jet of water. A powerful jet was required since 7 the nematodes wind themselves firmly around the algae, etc., and can be dislodged only by force. At this stage I was kindly assisted by G. A. Klyuge of the Murmansk station, who constructed according to my specifications a small rectangular tray furnished with a metal mesh, under which there was a plate of galvanized iron with a gutter for the stream of water. The sample under inspection was placed on the tray, and the water, having passed through the sieve, ran through the gutter into a vessel placed underneath, or into a finer sieve, as will be explained below.

The separation of mud was a very painstaking operation. For this a sieve consisting of a coarse plankton net—No. 2—sometimes folded double was used. The most convenient height for the walls of the sieve was about 20 cm, and its diameter was about 15 cm. A fine sieve would have clogged up with mud too quickly, while meshes of a larger size would have become strained under the weight of the water and burst at the edges or the network would have frayed. Here too a jet of water strong enough to pass through the bottom and not permit it to become clogged with mud was required. Sometimes even this was not sufficient and the mud had to be continually stirred by hand. It was important not to allow the water to become still for any length of time so as to prevent the nematodes from hooking onto the bottom of the sieve and worming their way through the net. I sometimes lost considerable parts of my collection in this way.

Zernov used different methods in his expedition along the Asia Minor seaboard in 1912, when he collected nematodes at my request. He washed the sand, etc., in a large tub and drew off the turbid water with a sieve of the type described. He obtained much material in this way. The entire sample cannot be processed exhaustively by this method, but it is simple, and gives pure material at once. It may therefore be recommended for expeditions where there is no time for a careful washing, or the sample 8 of bottom muck taken is so large that a great amount of material will be obtained in any case. Zernov's material was not used for this study, and is at the Zoological Museum of the Imperial Academy of Sciences awaiting processing.

If there are large branched objects, such as algae, clusters of mussels, and Lithothamnium, washing is not effective. The objects must be broken up by hand into the smallest pieces possible, which may then be filtered through a sieve. The nematodes are not crushed in the process, as I have frequently had occasion to observe in practice. N. L. Girshman found the same to be true for ostracodes. Stones, both on the surface and embedded in the deposit, should also be washed.

Sand and muddy-sand materials should be first freed of heavy particles. This is because nematodes bury themselves in the mud or sand but do not cling to the grains except when disturbed. There are no points of attachment in the mud, with which the nematodes are initially separated from the heavier particles. However, if sand remains in the sample the disturbed nematodes are able to wrap themselves around the grains, or to anchor themselves to them by means of the secretions of the caudal glands. In this way they can remain in the waste together with the heavy particles.

One of the most laborious operations was the separation of the very fine sand which forms particularly in coastal tidal zones. This sand was too coarse to pass through the net, but too fine for washing, and therefore remained in the sample, clogging it up. The larger grains were first washed out and the smaller ones were filtered through the sieve; the vessel was then shaken and the lighter sediment collected at its center and had to be poured off carefully. The process had to be repeated several times, but each time the sand was agitated more gently than at first as there were no large objects which the nematodes could hook themselves onto and the layer of fine sand was too shallow for them to 9 bury themselves in it.

Thus, the methods of separating nematodes from sediment may be summarized as follows:

a) Algae, bryozoa, hydroids: (1) crushing the material in water; (2) separation of the larger pieces in a sieve; (3) separating the residue and superfluous water in a fine sieve; (4) crushing the large pieces a second time.

b) Sand, mud, shells: (1) washing the heavier particles in a round vessel; (2) filtering through a fine sieve; (3) separating the fine sand if necessary.

After performing these operations one is left with the following: (1) pieces of plants, stalks of hydroids, fragments of bryozoa; (2) a small amount of sand which it is impossible to eliminate; (3) various small animals of many forms: nematodes, polychetes, small mollusks, copepods, ticks.

The bottom muck itself determines which form will dominate. Thus, where the sample is mostly algae and Zostera, the main bulk consists of small pieces of living plants. Oxeas sand yields a large percentage of animals, but the major part of the residue in that case is made up of living and dead filamentous algae. More than half the residue from dead seaweed and coastal sand consists of amphipods. Finally, dirty sand, particularly in winter, yields hardly any pure residue of nematodes and capitellids.

## *FIXATION*

The fixing of nematodes is not difficult, especially for the purpose of taxonomy. Fixation with alcohol is not recommended since the thick cuticle of many nematodes acts as a highly effective semipermeable membrane, and the nematodes shrivel up if brought directly into contact with strong alcohol; if the alcohol is gradually added to the seawater a
10 suspension forms in it which coats the cuticle, while weak alcohol macerates the nematodes. I therefore tried other methods. Dilution in seawater of 1—3% corrosive sublimate gave good results, but I hardly ever applied this means as it is laborious and troublesome, involving washing with iodine, etc. Fixation with formalin proved to be an excellent method, which I shall therefore describe in detail. (1) The sample is washed free of sand, scraps of algae, and mud, filtered through a fine sieve, and placed in a jar of volume 200—300 cc; the sample together with water should fill the jar about half-way. (2) The jar is placed in a water bath and heated to about 40° C (so that it is warm to the touch); at this temperature heat dormancy of the nematodes occurs; they do not die nor does their structure change. In this way it is possible to obtain fully extended nematodes, not rolled into loops and clumps; this greatly facilitates examination and particularly measuring. (3) One-eighth to one-tenth part of commercial 40% non-neutralized formalin is added to the warm water. (4) The nematodes remain in the 4—5% formalin thus obtained for at least 24 hours, and even a longer immersion will not injure them. Nematodes collected on expeditions may, if time is short, be stored in this way until processed at a later date. (5) After having remained for a sufficient period in the formalin the sample is poured into a funnel in which a filter made of a plankton net has been placed, and is washed with fresh water for some time. It is then replaced with a spatula into the vessel, which is filled with pure water. (6) Strong alcohol is gradually added to the water, and with each addition the sample is stirred. The initial strength of the alcohol is 30°, it is then increased to 50°, and finally to 80—90°, at which strength the sample is preserved. It is necessary, however, to replace the alcohol before it becomes stained by the extracts of the algae, or the nematodes also will take on a brown color,
11 which will make examination difficult.

Nematodes should always be studied live in the research. They are easily compressed under the cover glass, and may be turned around by careful movement of the glass with a needle. This cannot always be done with a preparation. For this reason the live specimen facilitates study of the details of organization, particularly of the anterior end, whose structure is complicated and small. Many features are generally better seen on the live specimen than on the preparation, although preparations of nematodes are usually better in this respect than those of many other animals. Here too it is useful to apply heat stiffening to prevent the nematodes from moving. This is done simply by warming the glass over a burner until the nematode ceases to move. After some time it recovers, and then the process is repeated. Unfortunately, for a long time I have not worked with as much live material as could have been wished.

The preparations that were used for taxonomy were mounted almost exclusively in glycerin-gelatin, and only rarely in dammar-lac—for the study of the genital parts of large nematodes. Dammar-lac clears too much and makes the examination of bristles and other small transparent parts difficult.

I made use of a solution recommended by Looss for the transference of the nematodes to the glycerin. The solution is made up of various volumes of 96° alcohol, water, and glycerin. The nematodes are placed in the solution in a saltcellar or watch glass, which is covered with a second watch glass. After 3—10 days the alcohol and water will have evaporated to a large degree, and the glycerin solidifies. The nematodes are then embedded for 24 hours in pure glycerin. The process may be accelerated by placing the glass with the nematodes in a thermostat (in this case, however, the more delicate worms may sometimes become wrinkled). After this they may be placed in the glycerin-gelatin.

Difficulties arise when the preparation is treated with dammar-lac:
12 xylene, and even cedar oil, having saturated the specimen, are able to penetrate deeply into the surrounding mass and form holes, which become filled with xylene vapour, making the specimen opaque. This can be avoided if the specimen is placed in a very nonviscous solution of dammar-lac which then solidifies gradually over several days (as occurs with glycerin). The preparation then has time to become saturated with dammar-lac, and holes do not form.

In addition to these methods I applied more detailed ones. Nematodes were fixed by all possible means. Corrosive sublimate and Carnoy's solution gave good results. It proved useful to add formalin to the corrosive sublimate. In addition I used methylene blue and the silvering method. I therefore only mention briefly that in this study I have virtually omitted the results obtained by these methods; the work is taxonomic, and good whole mounts are sufficient for this.

## *HISTORICAL REVIEW*

I divide the survey of the literature into three periods. The first (introductory) ends with the publication of Bastian's monograph (1865), the second relates to the collected taxonomic material from Bastian to the publication of de Man's work (1884—1893), and the third extends up to the present.

### 1. *The period up to Bastian (1865)*

The first free-living nematode was discovered by Borellus in 1656. This was the vinegar eel, Anguilla aceti (O. F. Müller). Several early microscopists saw and drew it subsequently. O. F. Müller (1773) described and drew some nematodes, including the vinegar eel. He relates all these nematodes, together with bacteria and spirochaetes, to genus 13 Vibrio. In the posthumous edition of his work (1786) we find once more descriptions and drawings of these and other members of Vibrio. They include two marine species—V. gordius and V. anguillula $\gamma$. Anguillula marina. However, it is quite impossible to judge which species Müller had before him, and we can only conjecture concerning V. anguillula $\delta$ A. aceti.

There followed a long interval during which no original observations were published. This terminated only in 1823 with the appearance of Bauer's work. He discusses Vibrio (Tylenchus) tricici, a parasite of wheat, which was discovered as early as 1744 by Needham. The author was particularly struck by the capacity of the larvae to become desiccated and to remain thus for a long period, but to revive when water was supplied. The paper is devoted entirely to this phenomenon. The same matter was touched upon by Dugès three years later. Hemprich and Ehrenberg (1828), and Ehrenberg (1830, 1836) described some species of nematodes including several marine forms. Genera Amblyura, Anguillula, and Enchelidium were created in these papers. However, the descriptions are so incomplete that the only conclusion to be drawn is that the observations were in fact of nematodes. Amblyura is related to the Infusoria, while the other two genera are related to Entozoa. Genus Anguillula remained in the literature since its type A. aceti (O. F. Müller) the vinegar eel was known. Genus Enchelidium, which was established for large-eyed marine nematodes (Ehrenberg observed a lens as well), was restored later by Eberth (1863) and de Man (1878, 1888), also possibly without sufficient grounds. Nordmann (1840) added genus Phanoglene to the second edition of Lamarck's Natural History, but it was so indefinitely characterized that it cannot be considered today.

The first scientist to gain an understanding of the free-living nematodes was Dujardin (1845). He established genera Enoplus, Oncholaimus, Rhabditis, Dorylaimus, which after a rather more accurate definition by later authors entered science, and have remained 14 until the present day. Some of his species also persist. The most distinctive anatomical features of these genera—the structure of the digestive tract, the genital organs, the oral armature—were accurately described by him and in part drawn. He placed them all, together with some parasitic nematodes, into the group "Enopliens," which he characterized as "Nématoides a bouche armée d'une ou plusieurs pièces distinctes (stylet ou mâchoires)."

Quatrefages (1846) attempted to establish a new genus Hemipsilus for marine nematodes possessing hairs. Other forms of Hemipsilus were described by Leuckart (1849) and Grube (1855). In all three cases it is hardly possible to determine what the authors mean. Grube described some freshwater nematodes in 1849. In the same year Professor Chernyia of Kharkov published "Monographie des Essigaelchens," in which he described fairly accurately the internal structure and life-cycle of the vinegar nematode.

In 1850—1851 Diesing published his "Systema helminthum." This is a very painstaking bibliographical list, but does nothing to advance our knowledge. All the preceding literature is listed. Berlin (1853) described Enoplus quadridentatus as a new species. At least four different species which are now related to different genera figure under this name, so that the work has no taxonomic value. The anatomical data are also very doubtful. Leydig (1854) described three species: Oncholaimus (now Diplogaster) rivalis, O. echini, a parasite of Echinus esculentus (it is not known what is meant by this name), and Enoplus tridentatus Dujardin; this is of course not the species of Dujardin, which is a true Enoplus, but probably some form of Cyatholaimus. Leydig described the caudal glands of free-living nematodes for the first time as well as their secretion, by which the nematode is attached to submerged objects. Leidy (1852-1857) described several species, for which he created the new genera Nema, Potamonema and Pontonema, but it is improbable that any of these will be recognized again. M. Schultze (1857) in "Icones Zootomicae" 15 by V. Carus drew three species of nematodes—Diplogaster micans n. g., n. sp., Rhabditis (Chromadora) bioculata n.sp., and Enoplus sp. (some form of Eurystoma). Genus Diplogaster has proved to be completely natural and has remained up to the present in the literature.

Carter (1859) described about ten species of the true genus Urolabes, but it is scarcely possible to recognize them, with few exceptions, because of the diagrammatic nature of the drawings and inadequacy of the descriptions. Enchelidium obtusum Grube (1861) is probably some form of Leptosomatum.

In 1863 a very important work by Eberth appeared. He provided a short anatomical survey, in which amongst other things he noted for the first time the cervical glands, gubernaculum, and development of the eggs in the ovary. In addition he described several new species. A failing of Eberth's study is that in spite of the large amount of material he did not establish new genera, preferring to assign his species to already existing genera—Phanoglene Nordmann, Enchelidium Ehrenberg, Odontobius Roussel, Enoplus and Oncholaimus Dujardin. Phanoglene was a dubious genus without sufficient characterization, and was established erroneously; Odontobius was described from the mucous membrane of the mouth of a whale and has no free-living representatives, while genus Enoplus became a catch-all for multifarious forms of nematodes. The chief advantage of Eberth's work is the excellent drawings which make it possible to recognize most of his species. Some of them are described again in this book.

Claparède's study (1863) contained descriptions of the aberrant nematodes Desmoscolex and Chaetosoma. The short studies by Claus (1863), Mechnikov (1863), and Greeff (1864) touched upon freshwater fauna. With them the first, introductory, period of study of free-living nematodes came to an end. Some data, though few, were accumulated as well as several anatomical facts, and several genera with some tens of species were described; but this was only a mass of raw material, which was to be dealt with most creditably by Bastian (1865).

## 16 *2. The period from Bastian (1865) to de Man (1884–1893)*

Bastian's works on taxonomy (1865) and anatomy (1866) provide a wealth of data for the study of free-living nematodes. Bastian found nematodes everywhere: in fresh water, in all soil samples, in mosses, in the sea. He thus obtained an impressive amount of material, including 100 species that proved to be new. It was Bastian who discerned the feature distinguishing free-living from parasitic nematodes — the lesser development of the genital organs — although in some cases the feature was only of quantitative significance. Bastian also noted many anatomical details. Thus, he frequently saw and drew the ventral [cervical] gland, and the discovery of the lateral [excretory] vessels in Tylenchus and some other free-living genera is due to him. He saw and drew repeatedly the lateral organs [amphids] (cervical markings) in genera Linhomoeus, Theristus, Comesoma, and Cyatholaimus, but did not describe them in detail. He noted the weak regenerative powers of nematodes. He found that the capacity for desiccation of larvae was inherent not only in Tylenchus (Vibrio) tritici but also in the larvae of several other similar genera, which Oerley (1886) subsequently isolated in family Rhabditidae. As for taxonomy, he took all the free-living nematodes for one family, Anguillulidae, in which he established several marine and freshwater genera. The major value of Bastian's work lies here. Almost all 22 of his genera are fully natural groupings with only genera Spilophora and Chromadora containing a great mixture of forms which are, moreover, insufficiently differentiated; Anoplostoma vivipara is wrongly united with Symplocostoma, and Leptosomatum includes two generic types which although similar are clearly distinguishable. In addition, genera
17 Theristus and Tachyhodites are so similar to Monhystera that there was no basis for isolating them; this was done only because of their annulated cuticle. Bastian's second work (1866) is primarily of an anatomical and physiological nature, and covers parasitic nematodes also. Some of the anatomical features mentioned above are described in detail. This study, however, is somewhat superficial. Bastian (like Eberth) did not recognize the nerve ring as a nervous organ, in spite of the fact that he interpreted quite accurately the function of the same organ in parasitic forms. He took the sensory papillae, which are especially visible in species with a thick cuticle (Dorylaimus, Leptosomatum) for pores in the cuticle, and compared them to the ambulacral system in Echinodermata, to which he likened nematodes in general. The lateral excretory vessels were a second feature for comparison, although Bastian himself recognized their replacement by simple cells in certain free-living nematodes, which he quite rightly considered the ancestors of the parasitic forms. Owing to all that has been mentioned, this study, as distinct from "Monograph on the Anguillulidae," had little influence on subsequent literature.

The works appearing between 1866 and 1870 should really be related to the preceding period as in part they deal with aberrant groups that are absent in Bastian's work (Mechnikov, 1867, Greeff, 1869), and in part their authors were unable to take Bastian's study into consideration or overlooked it through carelessness (A. Schneider, 1866, Marion 1870a, b). Mechnikov established a new aberrant genus Rhabdogaster and Greeff established Trichoderma. Genus Eubostrichus Greeff deserves special mention. The author described under this name two marine nematodes possessing some kind of membrane which became detached under pressure. One species (Eu. filiformis) is quite doubtful; the anus is described as being at the end of its tail. The other species is undoubtedly a nematode, but the incomplete description makes it impossible to establish which. This
18 genus, of course, could not be maintained in the literature, and only Certes (1889) described Eubostrichus again. "Monographie der Nematoden," by Schneider, which proved so important for parasitic nematodes, hardly touches upon the free-living forms. The author mentions Anguillula scandens Schneider (Tylenchus tritici Bastian) and numerous forms of Rhabditis (Pelodera and Leptodera Schneider — here Anguillula aceti (O. F. Müller) = Leptodera oxophila Schneider). He places all other freshwater and marine species with numerous muscle cells (Polymyaria Schneider) into genus Enoplus Dujardin. He knew among the marine forms two species that are now related to Thoracostoma, one true Enoplus, and one freshwater form of Dorylaimus.

Marion (1870 a, b) sharply distinguished various genera, paid strict attention to the internal anatomy, and produced fine drawings. This work would have had even greater significance if Marion had not overlooked Bastian's work completely and described some "new" genera that had already been described by Bastian and Eberth. Of the ten genera that he described only Eurystoma, Thoracostoma, Acanthopharynx, and possibly Necticonema, still remain in science, although the priority of genus Rhabdotoderma over the later Euchromadora de Man, 1886 should be restored. All the remaining genera are encountered as synonyms, partly as determined by the author himself in a later notice (1875): Lasiomitus Marion = Enchelidium Ehrenberg, Eberth; Amphistenus Marion = Symplocostoma Bastian; Stenolaimus Marion = Anticoma Bastian (apparently another species of Leptosomatum); Heterocephalus Marion = Phanoderma Bastian; Enoplostoma Marion = Enoplus Dujardin, Bastian. He described under the name Calyptronema paradoxum Marion a moulting nematode, apparently belonging to Enchelidium, whose outer layer of cuticle has become detatched anteriorly but is still supported by the cuticle of the esophagus, forming a hood around the head. In anatomical details Marion first noted the esophageal glands, and worked out in greater detail the structure of the esophagus, observing its musculature; he noted the cutaneous glands in one of the forms of
19 Thoracostoma; he interpreted correctly the significance of the nerve ring, and took note of some nerves that arose from it; he observed the attachment of muscle cell processes to the ring and to the surface of the esophagus; he described in greater detail the structure of the eyes and

noted their nerves; he noted lateral organs in some species and gave an abundance of detail on other systems of organs. However, there are some serious mistakes in the work. An amazing excretory trunk is described, opening at the posterior end; the muscles attached to the posterior end of the esophagus are taken for a dissepiment, while the beginning of the ventral nerve trunk is thought to be a muscular appendage; the structure of the esophagus is quite wrongly explained. The cells of the intestine are for some reason considered to be hepatic; in annulated nematodes a posterior nerve ring at the end of the esophagus is described in place of the normal one (this is probably some muscular or mucosal formation); the muscle layer is described as entire, and no note is taken of the intervals in it made by the rows of epidermal cells (longitudinal lines or fields [chords] of later authors); these cells are described as lying under the muscle layer. No cleavage of eggs is noted in the process of their development. Marion considered it necessary to distinguish sharply between free-living and parasitic nematodes.

In 1873 and 1874 two very important papers by Bütschli appeared; the first deals only with freshwater forms, while the second is concerned primarily with marine forms, collected in the Kiel Firth. The author established the new genera Oxystoma and Odontophora and corrected some errors in taxonomy made by Bastian; Symplocostoma viviparum Bastian is placed in the new genus Anoplostoma, genera Theristus and Tachyhodites are joined with Monhystera, the species in Leptosomatum provided with a cephalic capsule are removed from that genus and isolated under the name Thoracostoma Marion. Bütschli corrected many of Marion's errors, and argued justly against the sharp distinction made by Marion and Bastian between smooth and annulated nematodes, observing for the first time the layer of crossing fibers in Enoplus and others; he noted the general
20 distribution of the lateral organ; he described the ventral nerve trunk, its relationship with the nerve ring at the vulva and on the posterior end; he observed the ganglionated cells around the ring, noted the general distribution of the longitudinal fields, and described the radial fibers of the esophagus. However, he made the error of confusing the esophageal glands that lie in the sectors of the esophagus with the pigmented strips that are located in the angles of the esophageal lumen, i. e., between the sectors. Bütschli's study of 1876 does not touch upon marine nematodes.

The next work on marine nematodes was produced by Villot (1875). It contains some very superficial drawings and descriptions of several species from Brittany. They include the new genus Discophora for Enoplus cirrhatus Eberth; this name, which had been used in biology earlier, must yield to the later Dipletis Cobb. De Man's short study (1878) deals with marine nematodes around Naples. Unfortunately, very few species are described and it contains only fragmentary information on the internal organization.

De Man's study written in Dutch on freshwater and terrestrial nematodes appeared in 1876. This work, which is illustrated with very accurate, if somewhat diagrammatic, drawings, establishes several new genera and species of freshwater nematodes. The papers of 1880—1881 are of a preparatory nature, and the completed work appeared in 1884. This is a large volume, with numerous keys. De Man did not attempt to penetrate especially deeply into the anatomy and hardly deals with it; the main purpose of the work is taxonomic—the erection and redescription of several genera and species. In this respect the study is extraordinarily complete, and later works of various researchers are only an appendix to it. Its deficiencies include the somewhat diagrammatic nature of the drawings and the complete absence of any kind of grouping of genera. The article of 1885 is an appendix to this monograph.

Between 1876 and 1887 several papers by Linstow appeared under very
21 general titles ("Helminthologica," "Helminthologische Beobachtungen," etc.), and are of very varied content. Several free-living forms are described among the various platyhelminths and nematodes. All the descriptions are extremely superficial or simply wrong, and the drawings are very rough and inaccurate, so that it is often impossible to guess the author's intention.

Oerley's study (1880) is a carefully composed bibliographical compilation with keys, in Hungarian. In addition there are some descriptions of old and new species. In a later work (1886) he quite correctly isolated several freshwater and terrestrial genera in family Rhabditiae, which is directly connected with some parasitic nematodes having rhabdiform larvae and is distinguished from the other free-living nematodes. However, the name of this family is incorrect: it should be Anguillulidae, according to the older usage. According to Oerley, this family contains genera Plectus, Cephalobus, Rhabditis, Anguillula, Teratocephalus, Tylenchus, Aphelenchus, and Diplogaster. He gives the bibliographical references to this family with keys.

Reingard (1881) found Desmoscolex in the Black Sea near Odessa, and Levinsen (1881) found Chaetosoma off the coast of Greenland. Müller (1883) established genus Heterodera for the sugar-beet nematode.

### *3. The period from the appearance of de Man's work up to the present*

In 1886 de Man's magnificent study "Anatomische Untersuchungen über freilebende Nordsee-Nematoden" appeared. This book provides a solid basis for the study of the anatomy of marine nematodes. In it de Man propounds in detail, from work on live nematodes, the entire anatomy of Enoplus communis Bastian, Enoplus brevis Bastian, Anticoma pellucida Bastian, Oncholaimus fuscus Bastian, Tripyloides vulgaris n. sp., and Euchromadora vulgaris (Bastian). The work is furnished with numerous excellent and highly
22 accurate drawings. De Man observed the cell structure of the subcuticle [epidermis] and median fields in Anticoma and Enoplus; he discovered the submedian epidermal fields, recognized a universal distribution for the lateral organs (although he incorrectly ascribed an excretory function to them), and described the interesting form of the ventral excretory gland in Enoplus. He was the first to describe accurately the structure of the esophagus with its glands and the muscles

attached to its surface; he described in completely accurate detail the structure of the male and female genital apparatus and distinguished for the first time in the male genital apparatus the vas deferens from the muscular ejaculatory duct. Finally, he was the first to detect and describe the unexplained tubular organ [demanian system] in females of Oncholaimus fuscus Bastian. Among the deficiencies of the study are some erroneous interpretations of the significance of organs (this will be further discussed below), and the absence of any information on the nervous system.

Between 1888 and 1893 de Man published five papers on the taxonomy of marine nematodes which contain many descriptions of new and old genera and species. Almost all the descriptions are highly detailed, the external features and internal organization are examined, and in almost all cases detailed drawings are provided. Without these papers it is impossible to treat of either the taxonomy or anatomy of free-living nematodes.

In these papers the following genera are erected: Halalaimus (1888); Thalassoalaimus (1893), similar to Oxystoma Bütschli; Terschellingia (1888); Araeolaimus (1888); Axonolaimus (1889), from the Monhystera group; Dolicholaimus (1888); Syringolaimus (1888), similar to the freshwater Dorylaimus; Thalassironus, similar to the freshwater Ironus. The group Spilophora — Chromadora Bastian is subjected to detailed processing and these genera are given a new characterization, while several forms are allotted to new genera, which are in addition to Euchromadora (1886), which has already been mentioned: Halichoanolaimus (1888), Hypodontolaimus (1888),
23 Desmodora (1889), Monoposthia (1889); from the Leptosomatum group there are isolated Cylicolaimus (1889) for Lept. magnum Villot; Oncholaimellus (1890), similar to Oncholaimus; from the Enoplus group the author separates Triodontolaimus (1893) (Enoplus acutus Villot); Enoplolaimus (1893); Trefusia (1893), similar to Tripyla; finally, there are the original types Camacolaimus (1890) and Siphonolaimus (1893). These studies will be examined in greater detail in the taxonomic part of the book. Two species of Oncholaimus living in damp earth are mentioned in the short study of 1889.

Strubell's work (1888) deals with the anatomy and reproduction of the sugar-beet nematode. Ritzema Bos (1887—1892), Göldi (1889—1892), and others described several parasites of plants.

In 1888 Cobb's first study was published. In the years that followed (1890—1898) this scientist published several papers dealing with terrestrial, freshwater, and marine nematodes, primarily of Australian fauna. Cobb is always accurate, but brief; he often describes new genera, sometimes from inadequate or poor material.* It is unfortunate that he gives very few drawings; these could have helped to provide the details that are missing from his descriptions. To curtail description he introduces a very convenient formula that expresses the length and width of various parts of the body as percentages of the overall length; I have used this formula throughout this book. I have found and redescribed some of the numerous genera that he established.

Certes (1889) described two aberrant nematodes from Tierra del Fuego that inhabit moss, now related to genus Criconema Hofmänner et Menzel (1914). De Man (1892) described a species of Tylenchus inhabiting galls on fucus.

In 1892 Linstow published several papers on free-living marine nematodes. He described Antarctic nematodes (1892), and published accounts of the worms in "Hamburger Magalhaenischen Sammelreise" (1896) and "Fauna Arctica" (1901); he made a survey of those in the Zoological Museum of
24 the Imperial Academy of Sciences (1903), and those collected by L. Schulze in southwest Africa (1908). The last-named paper has been inaccessible, but I found that all the others are of a general, superficial nature: the author displays a complete lack of familiarity with the literature, confuses genera, makes no distinction between species that are somewhat similar in the collections even if they are related to different genera. After studying the types I was able to determine that in the paper on the nematodes in the Zoological Museum (1903) Linstow drew the head of one species and the tail of another in his description of a new species! I have already dealt with this problem in another work (Filip'ev 1916) and I refer the reader to that source.

In 1894 Zur Strassen published a short study in which he presented a detailed description of the structure of the tubular organ in some forms of Oncholaimus (Metoncholaimus m.), at the same time establishing a new species.

Beginning in 1894 a series of papers was published by the Hungarian scientist Daday dealing with the freshwater fauna of Hungary (1894, 1897), Switzerland (1906, 1911), Central Asia (1902, 1904, 1906, 1908), New Guinea (1899, 1901), South America (1905), East Africa (1910). Daday was erudite in freshwater microfauna, and described together with nematodes rotifers, copepods, ticks, and Protozoa. He established genera Bathylaimus (1905) (which is likely to be renamed since the marine genus Bathylaimus Cobb 1894 already exists), Hoplolaimus (1905), and Pseudochromadora (1901). One of his papers (1901) deals with marine nematodes found at Fiume on the Adriatic Sea; about fifteen species of old and new nematodes are drawn and described here. He made one error in this paper, describing two forms of Eurystoma as Oncholaimus (E. assimile de Man and E. ornatum Eberth).

Plotnikov (1899, 1901) gave some information on the freshwater nematode fauna of Russia.

Two very interesting papers by Maupas appeared in 1899 and 1900, both of them concerned with biological phenomena. In order to obtain much material Maupas made use of the method of cultures. Nematodes from
25 genera Rhabditis, Cephalobus, etc., were grown successfully in an extract of rotten meat. The first paper deals with the phenomenon of molting in nematodes. In all species four molts were observed with five stages — four larval and one adult. The author was able to demonstrate that under unfavorable circumstances the larval case thickens somewhat after the second stage, is separated from the cuticle but not cast off, forming a cyst. Only at this stage can the larvae withstand easily various

---

* Genera Chaolaimus (1893), Fimbria (1894), etc.

external influences by their ability to become desiccated and later revive, which property was long known. The second paper deals with parthenogenesis and hermaphroditism in nematodes. Maupas succeeded in clarifying that in many nematodes sperm are formed before the eggs ripen in the terminal parts of the ovary, and the subsequent generation of genital cells produces eggs that are fertilized by these sperm. In some species there are "rudimentary" males which have sometimes preserved and sometimes lost their sexual instinct, while in others males are completely absent.

The short work by Hallez (1900) contains fairly complete anatomical data on Anguillula aceti (O.F. Müller).

In 1901 Jägerskiöld's very important study appeared. The author described in detail (making use of sections) the anatomy of Cylicolaimus magnus (Villot) and in somewhat less detail Thoracostoma acuticaudatum n. sp., both very large species. He determined the almost complete absence of an epithelial layer in these species (apart from the lateral fields), and the presence of interesting cutaneous glands, and extended to them his data for parasitic nematodes on the structure of the esophagus; he described the structure of the genital organs in detail. It is strange that Jägerskiöld made no conjecture as to the significance of the ganglion cells, which here, as a rule, are ganglia of the diffuse type and lie freely in the body cavity around the esophagus, even though this 26 was known to Bütschli (1874). Two years after Jägerskiöld, Türk published his study (1903) on the same subject. He described the structure of genera Thoracostoma and Cylicolaimus from Naples. In most points his observations fully coincide with those of Jägerskiöld. He described interesting fat (possibly phagocytic) cells in the lateral fields. He correctly interpreted the ganglionic cells in the body cavity around the esophagus, but refrained from making a similar interpretation of the cells at the posterior end. He justly emphasized the complete absence of a body cavity if the specimen was well preserved.

In 1901—1902 Golovin published his study of the phagocytic and excretory organs in nematodes. The author made use of a special method for this research: he vitally stained nematodes, including free-living forms, with neutral red, methylene blue, etc. He even succeeded in fixing the specimens stained in this way and passing them through alcohol in order to wash them in paraffin. The free-living nematodes he used included marine forms from the Black Sea: Oncholaimus vulgaris Bastian (Paroncholaimus zernowi m.), O. (?) fuscus Bastian, Eurystoma assimile de Man, Symplocostoma longicolle Bastian, Anticoma pellucida Bastian (A. pontica m.), Cyatholaimus ocellatus Bastian (demani m.). The phagocytic cells are either joined to the longitudinal lines (Cyatholaimus) or lie scattered in the body cavity (Oncholaimus Symplocostoma, Anticoma). They readily absorb the vital dyes in special vacuoles, thereby taking on the appearance of mulberries. On longer immersion in the dye all the body tissues become stained. Two of the terrestrial nematodes studied (a new genus of Rhabditis and Anguillula aceti O. F. Müller) proved to be somewhat different from the remainder in their physiological properties. Their body fluid was found to possess powerful regenerative properties, as in the parasitic nematodes, and could be stained only by a chemical combination of water-blue and neutral red, applied for the first time by Golovin. After a prolonged immersion in the stain the phagocytic cells in all these nematodes became decolorized and the stain accumulated in the plasma of the ventral and caudal glands. This 27 observation, however, requires verification. The excretory apparatus of Rhabditis is quite different. It consists of two lateral vessels, as in the parasites, in addition to which an accumulation of stain occurs in two more single gland cells distributed in the lateral fields in the tail.

Rouville (1903—1904) made a survey of the marine nematode fauna of the coast at Sète on the Mediterranean and established the new genus Sabatieria. This study appeared as two preparatory reports without drawings and so far has not been published in its final form. Jägerskiöld (1904) turned his attention to some inaccuracies in de Man's description of Hypodontolaimus inaequalis Bastian.

Zur Strassen (1904) described two marine nematodes furnished with an oral spine [spear], which in his opinion constituted a new genus Anthroconema. However, both his species belong to genera described earlier—A. weissmani to Solenolaimus Cobb 1894 (the species also may be identical with Cobb's) and A. sagax to genus Siphonolaimus de Man, 1893 (Chromagaster Cobb, 1894). The main emphasis of the work is upon the detailed description of the central nervous system. This is not of the usual diffuse type, but the individual cells are grouped in clearly isolated ganglia. The ganglia and nerves are accompanied by special "Stütz-" and "Geleitzellen"* of a glial nature (the terms are Goldschmidt's). These cells are unusually strongly developed around the sensory bristles on the body, and are very reminiscent of the "glands" described by Jagerskiöld in Thoracostoma and Cylicolaimus. In addition the muscular development of the lateral fields and black-red color of the intestine are noteworthy.

In the same year de Man published his work on the nematodes of the "Belgia" Antarctic expedition, including in part a revision of Linstow's material (1892, 1896). This extremely painstaking study is similar in its nature to the great monograph of 1886. The work centers upon a 28 detailed description of Enoplus michaelseni Linstow (which proved to be identical with Enoplus atratus Linstow, Thoracostoma antarcticum Linstow, and Thoracostoma setosum Linstow; with the last-named the method of sections was applied, and proved most useful in displaying the structure of the head. However, no particularly notable anatomical data are brought into this study.

Jägerskiöld (1905) established in a short notice a new interesting genus, Bunonema, that inhabits moss.

In 1906 Stewart published his paper on Oncholaimus vulgaris Bastian. This study is less accurate than could have been desired, particularly in respect of its drawings. Stewart recognized the glandular nature of the longitudinal fields and the nervous nature of the cells around the esophagus; he observed an excretory apparatus, independently confirming that described by Golovin; he described special fibrillary tissue in the body cavity (these are probably processes encircling the cells or bits of coagulated body fluid, while the nuclei he describes belong to the epidermis). He noted in the female genital apparatus an interesting

---

* [Supporting and escorting cells.]

gonenteric canal between the intestine and uterus. Finally, he expressed the idea earlier voiced by Jägerskiöld and Golovin, and in a more vague form by Bastian (1866), of the homology of the cervical glands of free-living nematodes and the lateral canals of the parasites.

Retzius (1906), applied silver staining to the cell boundaries in many representatives of the animal kingdom, including nematodes. He was able to distinguish eight characteristic longitudinal rows of cells—three lateral pairs and two median rows—in Enoplus, Oncholaimus, and Thoracostoma.

G. Schneider (1906) described several nematodes from the Gulf of Finland and freshwater forms from Estonia. Cobb (1906, 1909) described terrestrial nematodes from the Hawaiian Islands, and Kati Marcinowski (1906, 1908) several parasites of plants.

29 Rauther (1907) examined the structure of the esophagus and oral cavity in Enoplus, Cylicolaimus, Thoracostoma, and Oncholaimus vulgaris, using the method of sections. He confirmed Jägerskiöld's data and in addition found two special glands in the subventral sectors of the posterior part of the esophagus that are distinct from those of de Man; he described a confluence of the glands under the jaws [gnathi] in Enoplus and nerve cells inside the esophagus and further, an accumulation of intravitam stains on the esophageal gland, which he considered played a part in excretion. He believed that the pigment strips on the esophagus were associated with this also. In a later work (1909) he dealt with the question of the origin of nematodes, linking them with Arthropoda. However, this is not the place to examine his views.

De Man (1907) published a new work of the same type as his fundamental studies of 1888—1893. In it he described new genera: Aegialoalaimus, Cobbia, similar to Monhystera; Parasabatieria and Metalinhomoeus, whose position is evident from the names. Sphaerolaimus hirsutus Bastian is described in more detail than the others. There are many taxonomic features in the work. Two other papers of de Man that appeared in 1907 deal with terrestrial nematodes.

In 1907—1908 several papers by Shchepot'ev appeared on the aberrant genera Chaetosoma, Rhabdogaster, Trichoderma, and Desmoscolex. The author mistakenly neglected to examine living or cleared animals but studied them exclusively either in alcohol or in sections. Because of this Shchepot'ev was unable to determine even the roughest anatomical data, e.g., the position of the nerve ring or the form of the esophagus. Furthermore, the author did not deem it necessary to take note of even the most important literature on free-living nematodes, as a result of which the structure of the head is described most imperfectly, and some kind of scraps are drawn instead of the genital apparatus ( Table 7, Figure 23; Table 11, Figure 22; Table 13, Figure 17 of the Russian edition). Such fragments are drawn throughout on the
30 sections. Shchepot'ev's taxonomic descriptions are also very incomplete and one should, where possible, turn to the old works. All this, of course, decreases the value of his theoretical conclusions also.

Jägerskiöld (1909) compiled a list of freshwater nematode fauna of Germany for "Süsswasserfauna Deutschlands." This compilation is most convenient and may be recommended for original definitions. De Man (1910, 1912, 1913) described several forms of genera Anguillula Ehrenberg and some other saprophages, and new genera related to Diplogaster — Diplogasteroides and Odontopharynx (1912). Ditlevsen (1911) studied nematodes in Denmark, chiefly freshwater and terrestrial, but touched incidentally upon some marine forms, presenting Rhabditis marina Bastian and Oncholaimus oxyuris n. sp. in greater detail. He also described the marine species of Dorylaimus from Greenland. Schwartz (1911—1912) published several short papers on parasites of plants.

Savel'ev's study of the nematodes of Murmansk appeared in 1912. In it the author described briefly but very accurately several new species and the new genus Enoploides, similar to Enoplus Dujardin and Enoplolaimus de Man. These papers are preparatory reports and do not include drawings. Somewhat later in the same year I too published a preparatory report on the structure of the epidermis and nervous system of nematodes. I described, chiefly in Paroncholaimus zernowi m., the composition of the epidermis of eight longitudinal rows of cells, the topography of the nervous system, the sensory, and in part locomotive systems.

Eva Krüger (1913) described the formation of the genital cells in a hermaphroditic form of Rhabditis. Cobb (1912) gave a description of a new species of genus Tricoma Cobb 1894, which is close or even identical to Desmoscolex. In another notice (1913) he perfected his formula by introducing several conventional signs for the form of the lateral organs, the oral cavity [buccal capsule], and the esophagus.
31 I have not followed his example, since these signs complicate the already ponderous formula, and in addition they may be confused in printing, which would entirely denude the formula of its value. Indeed, to prevent this the Journal of the Washington Academy of Sciences, in which this article was printed, reproduced these formulas photographically from the typewritten copy; this too is not always convenient. Most of Cobb's species are limited to the old genera (chiefly Tylenchus and Dorylaimus), which adds detail to our taxonomic knowledge. It is possible that some of them should either be combined, as they are too little distinguished from each other, or be changed to the rank of subgenus.

In 1912 Menzel's first paper on free-living nematodes appeared. Menzel was followed by Hofmänner, Steiner, and Stefanski (1913—1915), who produced a series of papers on the free-living nematodes of the Swiss fauna. Hofmänner and Menzel jointly prepared a compilation of data in 1915. These studies are a later development of a rich Swiss hydrological literature, and therefore they often bear a taxonomic character, hardly touching upon anatomical details. There are also errors. Hofmänner (1914, 1915), for example, unites completely different species: the freshwater Monhystera dubia Bütschli, 1873, apparently even belonging to another genus, is joined with the marine M. setosa Bütschli, 1874; the species that is described under the former name is identical with neither the one nor the other. Some new genera were described in these papers: Criconema Hofmänner and Menzel (1914, 1915)—an original annulated and hairy nematode living in mosses, like Trichoderma, and Demaniella Steiner, 1914, a relation of Diplogaster. In addition some species of the interesting genus Bunonema were once more found and described. Zograf's notice (1913) touches upon this also.

Micoletzky's paper (1914) is of the same nature as the Swiss studies. He described fairly carefully several new and old nematodes found in the 32 Tyrol, paying particular attention to the biology and variation within species. He reduced these data to a series of curves; these clearly indicated that dimensions, both relative and absolute, cannot always serve as good species criteria. Subgenus Parachromadora which he established proved to be an error; one species was affixed to Etholaimus de Man 1880, the other to Achromadora Cobb 1913. The paper by Brakenhoff (1914) is of the same type, dealing with free-living nematodes of northwest Germany. It contains some good drawings.

## *TAXONOMIC SECTION*

### 34 *CLASSIFICATION OF FREE-LIVING NEMATODES*

As was stated in the introduction, the classification of these nematodes is still in a rudimentary state. The majority of textbooks follow Oerley (1886) in distinguishing two families. One is Rhabditidae, or Anguillulidae, and contains the inhabitants of decomposing matter. Its genera are Anguillula, Rhabditis, Tylenchus, Cephalobus, etc. The other family is Enoplidae, which incorporates all the remaining free-living nematodes. In addition the aberrant Chaetosomatidae and Desmoscolecidae* are regarded as special supplements or separate families. Only Perrier (1897)** has attempted to establish an entire system of free-living nematodes on the basis of published data, but this system is unsuccessful and I shall not examine it.

Among the authors who have dealt specifically with the free-living nematodes, only de Man (1876) attempted to give a natural classification of the freshwater genera known to him. He distinguishes eight families: 1) Ironidae (Ironus); 2) Dorylaimidae (Dorylaimus); 3) Tylolaimidae (Tylenchus, Aphelenchus, etc.); 4) Odontosphaeridae (Anguillula, Cephalobus, Plectus, Rhabditis, Diplogaster); 5) Ptychopharyngidae (Spilophora, Chromadora, Cyatholaimus); 6) Tripylidae (Tripyla, Leptolaimus); 7) Monhysteridae (Monhystera, etc.); 8) Odontopharyngidae (Oncholaimus, Mononchus). This system contains several 35 accurate indications as to the grouping of the genera and it is very unfortunate that de Man did not develop it further in any of his later studies.

The isolation of Anguillulidae (Tylolaimidae + Odontosphaeridae de Man, Rhabditidae Oerley 1886) from the other free-living nematodes is undoubtedly warranted. This family consists of degenerate forms, possibly even descendants of parasites that have reverted to the free-living state. This is indicated by their similarity to the rhabdiform larvae of Strongylidae and Angiostomidae (the latter even have a free-living generation living underground). Several other features of their organization point to this also: the lateral vessels, which are always absent in other free-living nematodes, the small number of cells, and their "larval" organization. Many of them are meromyarian.

The remaining free-living nematodes — Enoplidae auct. — are all polymyarian and possess a more or less complete organization. The structure of the female genital organs serves as a distinguishing feature. One family — Monhysteridae — possesses straight, outstretched ovaries, while

---

* See Kholodkovskii, N. A. Kurs zoologii i sravnitel'noi anatomii (A Course in Zoology and Comparative Anatomy), 3rd edition, S. Pb., 1914; Braun, M. Die tierischen Parasiten des Menschen. 2 Aufl. Königsberg 1911; Leunis, J. Synopsis der Tierkunde. 3 Aufl. bearb. v. H. Ludwig. Hannover 1886; Claus-Grobben. Lehrbuch der Zoologie. 2 Aufl. Marburg 1910.

** Traité de Zoologie, Fasc 3, p. 1915.

the others possess reflexed ovaries, which is more primitive. I consider Monhysteridae also a reduced group.

Among the other nematodes I isolate a group of marine and freshwater forms possessing a more complete organization, but with many primitive features. This group is family Enoplidae and contains the largest and best known genera—Enoplus, Oncholaimus, etc. Another group of nematodes, also with complete organization but which followed a different path of development, is Chromadoridae, to which I also relate Chaetosomatidae as a special subfamily. I have for the present left Desmoscolecidae separate, but these may be aberrant relatives of Monhysteridae.

I feel that there are insufficient grounds for making a sharp distinction between free-living and parasitic nematodes. I prefer to consider these
36 families together with others, such as Ascaridae, Strongylidae, etc., which are equally ranked. If, however, some distinction must be made, then Anguillulidae appears to be in a group with the parasites and distinct from the other free-living nematodes.

I thus distinguish the following families of free-living nematodes:

1) **Enoplidae** (p. 23). Typical, sometimes large nematodes. Cuticle almost always smooth. Polymyarian. **Lateral organ cyathiform.** Only Tripyloidini have a special type of spiral lateral organ. **Esophagus attached anteriorly to cuticle** (sometimes this connection is lost). Its musculature anteriorly is never differentiated into specific longitudinal strips. Ovaries reflexed. Uterus bilocular, sometimes with ovejector (rarely only one of its branches). Tip of tail always blunt. Majority of species marine.

2) **Chromadoridae** (p. 131). **Cuticle annulated,** sometimes of complex structure. Polymyarian. **Esophagus not attached to cuticle. Lateral organs externally spiral or degenerate,** rarely rounded or of aberrant form. Tail furnished with terminal tube and therefore appears pointed. Uterus simple. Largely marine.

3) **Desmoscolecidae** (p. 196). Aberrant nematodes **with cuticle consisting of very thick conspicuous annules**; polymyarian. Ovaries probably straight. Marine.

4) **Monhysteridae** (p. 199). Reduced nematodes, mostly small; polymyarian. Lateral organ most often round, although spiral form exists. Tail usually rounded at end. **Ovaries straight.** Marine and freshwater.

5) **Anguillulidae** (p. 251). Reduced nematodes of larval nature. Many of them meromyarian. Majority of genera characterized by esophagus with swelling in middle and having a second enlargement at posterior end. One of these enlargements is a true bulb with a special masticatory [valvular] apparatus inside. In earth and fresh water, most often in
37 rotting matter; very few marine.

1 (10). Many rows of muscle cells in each muscle strip (polymyarian) Esophagus never with swelling in middle.
2 (3). Cuticle bears thick beltlike annules . . . . . . . **3. Desmoscolecidae**
3 (2). Cuticle smooth or annulated without beltlike annules.
4 (5). Lateral organs cyathiform . . . . . . . . . . . . . . **1. Enoplidae** (part.)
5 (4). Lateral organs spiral, circular, or of other form, sometimes absent.
6 (9). Ovaries reflexed.
7 (8). Lateral organs in form of excavated spiral . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **1. Enoplidae** (part.)
8 (7). Lateral organs spiral, large, thin-walled, in form of irregular pouch, sometimes absent. . . . . . . . . . . . . . **2. Chromadoridae**
9 (6). Ovaries straight. Lateral organs often circular . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **4. Monhysteridae**
10 (1). Only few fibers (2—4 rows) in each muscle strip (meromyarian). If polymyarian, esophagus bears two swellings (sometimes bulbs), one in middle, one at end . . . . . . . . . . **5. Anguillulidae**

## I. Family *ENOPLIDAE*

This is an extensive family containing the largest and best known representatives of the free-living nematodes. It includes those with the most complete organization having undergone less reduction than others.

**The cuticle is almost always smooth,** rarely slightly annulated. All are polymyarian. The head structure is varied; there are always six labial papillae, ten (rarely six) cephalic bristles (more rarely papillae). **The lateral organ is almost always cyathiform** and spiral only in Tripyloidini. The structure of the oral cavity is very varied and serves as a feature for subfamily and genus definition.

A distinctive feature is that the **esophagus anteriorly is either closely attached to the cuticle or shows signs of previous attachment,** later lost owing to the development of a large oral [buccal] capsule. The oral cavity, therefore, can never evert outwards, as in some other forms; at most a tooth or spine is protruded. Moreover, the esophageal muscles also are weakly differentiated anteriorly and never form longitudinal strips. **The esophagus never forms a bulb** (only in Symplocostoma hexabulba n. sp. is the posterior end of the esophagus further divided
38 into six bulbs, but it nevertheless maintains the general structure characteristic for the genus). **The ovaries are always reflexed.** The uterus is thin-walled, usually without a common cavity. I enumerate the following nine subfamilies:

1) Leptosomatini (Leptosomatum, Thoracostoma, Phanoderma, etc.,) p. 25.
2) Anticomini (Anticoma, Anoplostoma), p. 41.
3) Oxystomini (Oxystoma, Halalaimus, etc.,) p. 48.
4) Enoplini (Enoplus, Enoploides, Enoplotaimus, Triodontolaimus), p. 52.
5) Oncholaimini (Oncholaimus and the genera separated from it, Pelagonema), p. 75.
6) Enchelidiini (Enchelidium), p. 104.
7) Symplocostomini (Symplocostoma, Eurystoma), p. 109.
8) Dorylaimini (Mononchus, Ironus, Dolicholaimus, Syringolaimus, Tylencholaimus, Dorylaimus. The group Trilobus with several freshwater genera belongs here), p. 125.
9) Tripyloidini (Tripyloides, Bothylaimus), p. 128.

In my opinion, the Leptosomatini constitute the basic group, being the least reduced and specialized, although some specialized function is observed among them.

Some of the simplified members of Anticomini and Oxystomini are similar to the preceding group in general organization. Like Leptosomatini, they may be characterized by an elongated body, particularly at the anterior end. Enoplini are a fairly specialized group, having developed a movable jaw apparatus, and having lost it (Enoplolaimus). Oncholaimini have developed an immovable voluminous oral cavity and a complex labial apparatus. The organization of the more perfected representatives— Paroncholaimus —bears an undoubted resemblance to that of Leptosomatini, while most of the other Oncholaimini are forms that have become reduced for a second time. Enchelidiini and Symplocostomini are somewhat different in general organization; they are closely related to each other, and apparently represent a separate branch. 39 Dorylaimini show some similarity to Leptosomatini, but this is apparently a branch that became detached early and moved to fresh water; Dolicholaimus and Syringolaimus are their marine representatives. The lip structure is very similar in Mononchus, and we can see from this example how the movable spear of Dorylaimus developed from the immovable tooth of the oral cavity. Many other freshwater genera are associated with them, chiefly related to Trilobus. Tripyloides, in spite of its spiral lateral organ, is so similar to the other members of Enoplidae that I include it here also.

1 (2). Lateral organ spiral . . . . . . . . . 9. **Tripyloidini**
2 (1). Lateral organ cyathiform.
3 (4). Head enlarged, upon it anteriorly are six cushionlike elevations on which lie papillae. Bristles usually absent, only papillae. Movable spear in oral cavity; it is either thick-walled with dorsal tooth or very long . . . . . . . . . 8. **Dorylaimini**
4 (3). Anterior part of body of different structure.
5 (6). Three large lips on head, sometimes very large; in mouth three movable jaws with hooks on ends (rarely replaced by homologous immovable parts, in which case labial papillae are replaced by bristles) . . . . . . . . . 4. **Enoplini**
6 (5). Movable jaws absent, labial papillae never in form of bristles.
7 (8). Oral aperture anteriorly enclosed by six platelike lips. Oral cavity wide with thick walls, usually with three teeth . . . . . . . . . 5. **Oncholaimini**
8 (7). Lips absent.
9 (16). Oral cavity wide with thick walls.
10 (11). Teeth in oral cavity, which is widely opened anteriorly, without lips; annular thickenings on its walls . . . . . . 7. **Symplocostomini**
11 (10). Oral cavity without teeth and annular thickenings.
12 (15). Oral cavity gradually expands, its posterior end embraced by esophagus.
13 (14). Cephalic capsule present. Large marine nematodes . . . . . . . . . 1. **Leptosomatini** (Cylicolaimus)
14 (13). Cephalic capsule absent. Small freshwater forms . . . . . . . . . 8. **Dorylaimini** (Trilobus, etc.)
15 (12). Oral cavity widens suddenly and is not embraced by esophagus. Small nematodes. . . . . . . . . . 2. **Anticomini** (Anoplostoma)
16 (9). Oral cavity inconspicuous, hidden inside esophagus or entirely absent.
17 (18). Two cuticular bodies present around anterior end, serving as lens. Esophagus narrows conically anterior to eyes . . . . . . . . . 6. **Enchelidiini**
18 (17). Cuticular bodies absent. Anteriorly, esophagus extensively fused to cuticle.
40 19 (20). Anterior end greatly elongated so that cephalic bristles are divided into two circlets and lateral organs lie far from anterior end . . . . . . . . . 3. **Oxystomini**
20 (19). Anterior end not greatly elongated, cephalic bristles in one circlet, and lateral organs not distant from them.
21 (22). Cuticle thick, oral cavity not isolated; large nematodes . . . . . . . . . 1. **Leptosomatini**
22 (21). Cuticle thin, oral cavity present but inconspicuous and embraced by esophagus; small nematodes . . . . . . . . . 2. **Anticomini**

## 1. Subfamily **Leptosomatini**

These are large or medium-sized nematodes. **The cuticle is thick,** usually with a layer of crossing fibers anteriorly. Six labial papillae and ten cephalic bristles or papillae are present. **The lateral organ is cyathiform with a very small anterior porelike orifice,** leading to the central spherical cavity.

The esophagus is connected directly to the mouth without an oral cavity being formed; only in Cylicolaimus is a true wide oral cavity formed, but even here it is merely a widened part of esophagus, which gradually narrows posteriad. The **cephalic capsule** is attached anteriorly directly to the esophagus; this is a chitinized part of the cuticle on the head. Its development is very varied and may be used to characterize different genera. Teeth, which arise from it in some genera, are always immovable. **Eyes with lens** are usually present. The esophagus is weakly muscular and narrow, as is the intestine. The ovaries are paired and reflexed. The eggs are large. The spicular apparatus is variously developed. I relate the following genera to this subfamily:

1) Leptosomatum Bastian 1865 (see p. 26)
2) Leptosomatides gen. nov., (see p. 33)
3) Deontostoma Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 73; Thoracostoma auct. ex. p. For a survey of species and keys see ibid.
4) Thoracostoma Marion 1870; Leptosomatum ex. p. Bastian 1865: Trans. Linn. Soc. 25, p. 146; Thoracostoma ex. p. Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 25; Bütschli 1874: Abh. Senck. Ges. 9, p. 41; de Man 1888: Mém. Soc. Zool. France 1, p. 21; Jägerskiöld 1901; Svenska Vetensk. Akad. Handl. 35, No. 2, p. 33; Thoracostoma Filipjev 1916: Ann. Mus. Zool. 41 Petrograd 21, p. 82; For a survey of species and keys see ibid.
5) Jägerskiöldia Filipjev 1916: Ann. Mus. Zool. Petrograd 21 p. 83. For survey of species see ibid. Thoracostoma Jägerskiöld

1901 loc. cit., ex p.; Turk 1903: Mitth. Zool. Stat. Neapel 16, p. 284.
6) Cylicolaimus de Man 1889: Mém. Soc. Zool. France 2, p. 1; Jägerskiöld 1901: Svenska Vetensk. Akad. Handlinger, 35, No. 2, p. 7.*
7) Phanoderma Bastian 1865, see p. 35.

1 (8). Tail short, blunt, curved at end.
2 (5). Cephalic capsule present only under anterior surface of head, not passing onto its lateral parts, sometimes hardly developed.
3 (4). Gubernaculum small, adjoining spicules on dorsal side, and not covering their ends, without dorsal process; supplementary bristles in male absent. . . . . . . . . . . . . . **Leptosomatum** Bastian
4 (3). Gubernaculum large, covering ends of spicules, with dorsal process; supplementary bristles well developed . . . . . . . . . . . **Leptosomatides** n. g.
5 (2). Cephalic capsule well developed, extending to lateral parts of head.
6 (7). Cephalic capsule short, only few processes running anteriad from it . . . . . . . . . . . . . . . . . . . . . . . . . . **Deontostoma** Filipjev
7 (6). Cephalic capsule long with powerful **ventral** tooth. . . . . . . . . . . **Thoracostoma** Marion
8 (1). Tail more or less elongate, pointed at end.
9 (10). Cephalic capsule consists of three enlargements opposite three sectors of esophagus that extend posteriad far behind cephalic bristles and unite posterior to them. Spicules slender, long, slightly curved, accessory [copulatory] organ tubular. . . . . . . . . **Phanoderma** Bastian
10 (9). Cephalic capsule consists chiefly of broad ring situated in front of cephalic bristles between groups of which it sometimes sends processes posteriad. Spicules shorter, arched.
11 (12). Oral cavity absent, or if present very narrow. . . . . . . . . . . . . **Jägerskiöldia** Filipjev
12 (11). Oral cavity wide. . . . . . . . . . . . . . . . . . . . . **Cylicolaimus** de Man

42

## Genus LEPTOSOMATUM Bastian 1865

Phanoglene Eberth 1863 (nec Nordmann 1841): Untersuchungen über Nematoden p. 19.
Leptosomatum ex p. Bastian 1865: Trans. Linn. Soc. 25, p. 144.
Stenolaimus ex p. Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 17.
Leptosomatum ex p. Villot 1875: Arch. Z. Exp. (1) 4, p. 457.
Leptosomatum de Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 102.
—— de Man 1893: Mém. Soc. Zool. France 6, p. 102.
—— Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 65.

Type species: L. elongatum Bastian 1865

These are large nematodes with a filiform body, greatly tapering anteriorly and slightly tapering towards the anus, **with a short curved tail. The cuticle is thick**, with layers of crossing fibers. Six labial papillae and ten short cephalic bristles or papillae are present. The lateral organ is circular with a very small anterior orifice. **The oral cavity is absent and** the esophagus is attached directly to the mouth. The internal angles of the sectors of the esophagus are slightly movable anteriorly, resembling lips (de Man). Processes of the **cephalic capsule** join the esophagus anteriorly. The cephalic capsule is very weakly developed, unlike Deontostoma and Thoracostoma and is present only under the anterior surface of the head; only a few processes penetrate from it posteriorly between the cephalic bristles, or they are entirely absent. The cephalic capsule sends a short process anteriad in the dorsal angle of the oral aperture. The two subventral esophageal glands open far anteriorly, while the dorsal gland opens more posteriorly. Between the glands lie small lentiform enlargements of the lumen of the esophagus — depressions on the ventral rays — to which muscles are attached radially. A pair of lateral eyes with lens is present. The esophagus is weakly developed, straight. The cervical gland lies opposite the posterior part of the esophagus, while the cervical pore is preneural. In some species 43 degeneration of the intestine is observed in males. The ovaries are paired, fairly long, and reflexed. The eggs are large, the testes paired, the spicules slightly curved, and plain. The gubernaculum is also plain and small. Supplementary bristles are absent. A preanal gland is present but no accessory organ is formed at the end of its duct. The caudal glands are very long. I found two species in the Black Sea.

Genus Leptosomatum was established by Bastian. Some of the forms he included have remained in this genus, while others were subsequently transferred to genus Thoracostoma Marion. Bütschli (1874) distinguished between these two genera, whereas Villot (1875) erroneously reunited them. The most amazing confusion exists in Linstow's papers (1892—1908); this author consistently confounded the two genera, describing Thoracostoma as Leptosomatum. Sometimes it is impossible to determine the membership of the species that he established. We find a thorough description of the genus in de Man (1893).

Up to now the following species have been described:

1) L. elongatum Bastian 1865: Trans. Linn. Soc. 25, p. 145, Table 12, Figures 156, 157; de Man 1893: Mém. Soc. Zool. France 6, p. 103, Table 6, Figure 9; Syn.: L. gracile Bastian loc. cit., p. 145, Table 12, Figures 158—160: Atlantic Ocean: Falmouth, in sponges.

2) L. tetrophthalmum Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 124. — Murmansk: Pala Inlet, Lake Mogil'noe.

3) L. arcticum Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 66, Table 4, Figure 1 — Murmansk: Vardö; Lithothamnium in Ekaterininskaya Harbor.

---

* Two species: (1) C. magnus (Villot 1875); Leptosomatum m. Villot, Arch. Z. Exp. 4, p. 458, Table 11, Figure 2; Cyl. m. de Man 1889: loc. cit.; p. 2; Jägerskiöld 1901: loc. cit., p. 5; Table 1, Figures 1—5; Table 2; Table 3, Figures 2—4; Table 4, Figures 1—2, 4—11; ? Rauther 1907: Zool. Jahrb. Anat. 23, p. 704, 726. North Sea and Atlantic Ocean: (2) C. jägerskiöldia Türk 1903: Mitt. Zool. Stat. Neapel 16, p. 334. — Naples. It is possible that here should be related Leptosomatum minutum Villot 1875: Arch. Z. Exp. 4, p. 459, Table 11, Figure 3—Roscoff

4) L. bacillatum (Eberth 1863) see p. 28.

5) L. grebnickii Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 68, Table 4, Figure 2: Bering Sea.

6) L. punctatum (Eberth 1863) see p. 31.

7) L. behringicum Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 70, Table 4, Figure 3: Bering Sea.

There is an inadequate description of Phanoglene logissima Eberth 1863 (Unters. über Nematoden p. 21, Table 2, Figure 8. Among corals, Nice) with a more sharply tapering tail than in L. bacillatum. Phanoglene subulata Eberth 1863 (ibid. p. 21, Table 2, Figures 9, 10) with a long pointed tail apparently belongs to another genus. Finally, Leptosomatum australe Linstow 1907 (National Antarctic Expedition (Discovery) 1901–1904 Nat. Hist., Vol. 3; Nematoda, p. 1, Table 1) belongs either to Deontostoma or to Leptosomatides. Linstow's poor description makes it impossible to decide to which. I have not included these three species in the key.

44 1 (2). Cephalic bristles well developed . . . . . . . . **L. punctatum** (Eberth)
2 (1). Cephalic bristles in form of papillae.
3 (4). Diameter of body at eyes is $2^{1}/_{2}$ times diameter of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **L. behringicum** Filipjev
4 (3). This diameter is twice or less that of head.
5 (8). Eyes distant from anterior end by twice diameter of head.
6 (7). Lateral organ 9$\mu$, $^{1}/_{6}$ of diameter of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **L. grebnickii** Filipjev
7 (6). Lateral organ 6$\mu$, $^{1}/_{10}$ of diameter of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **L. arcticum** Filipjev
8 (5). Eyes distant from anterior end by three times diameter of head.
9 (10). Behind main eyes lie two additional pigment spots, as in Enoplus . . . . . . . . . . . . . . . . **L. tetrophthalmum** Saveljev
10 (9). Only two eyes.
11 (12). Lateral organ $^{1}/_{6}$ width of head; head hardly truncated, spherical . . . . . . . . . . . . . . . . . . . . . . . **L. bacillatum** (Eberth)
12 (11). Lateral organ $^{1}/_{10}$ width of head; head greatly flattened anteriorly . . . . . . . . . . . . . . . . . . . . . . . **L. elongatum** Bastian

### 1. **Leptosomatum bacillatum** (Eberth 1863)
(Table 1, Figure 1)

Phanoglene bacillata Eberth 1863: Untersuchungen über Nematoden p. 19, Table 2, Figures 1–4.

Leptosomatum bacillatum de Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 103, Table 8, b – Figure 9a.

Stenolaimus macrosoma Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 17, Table C, Figure 2; (5) 14, Art. 1, p. 10, Table L, Figure 3.

$$\text{♂} = \frac{1.0 \quad 3.2 \quad 11.6 \quad 64.0^{*} \quad 99.0}{0.6 \quad 0.8 \quad 0.9 \quad 1.0 \quad 0.7}\ 9300$$

$$\alpha = 100,\ \beta = 8^{1}/_{2},\ \gamma = 100.$$

$$\text{♀}\ \frac{1.1 \quad 3.6 \quad 13.4 \quad 23.8 \quad 39.3 \quad 57.0 \quad 72.1 \quad 88.8 \quad 99.1}{0.7 \quad 0.9 \quad 1.0 \qquad\qquad 1.3 \qquad\qquad 0.8}\ 8200$$

$$\alpha = 77,\ \beta = 7,\ \gamma = 110.$$

$$\text{♀}\ \frac{1.1 \quad 3.4 \quad 13.2 \quad 47.1 \quad 60.4 \quad 74.1 \quad 99.1}{0.6 \quad 0.9 \quad 1.3 \qquad\qquad 1.4 \qquad\qquad 0.8}\ 8600$$

$$\alpha = 71,\ \beta = 7,\ \gamma = 110.$$

| Dimensions adult ♀ | Cephalic papillae | Anterior margin of lateral organ | Eyes | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 9 | 18 | 75 | 235 | 1,030 |
| Width | 27 | 29 | 55 | 70 | 95 |
| ♂ 9,300$\mu$ | | | | | |
| Length | 11 | 20 | 73 | 280 | 1,090 |
| Width | 32 | 40 | 57 | 80 | 95 |

45 The **body** tapers anteriorly and posteriorly, more anteriorly, so that at the level of the eyes it is twice narrower than at the end of the esophagus and at the level of the cephalic papillae it is four times narrower. The maximum width is slightly more and the width at the anus slightly less than that at the end of the esophagus, as is seen from the formula. The **cuticle** is thick, two-layered, 5 – 6$\mu$ thick; outer layer is about 1$\mu$. A layer of crossing fibers is clearly seen anteriorly. The complete absence of any bristles is characteristic for this species; all are replaced by papillae. A group of 5 – 6 of the latter lies between the anterior end and the eyes.

The **head** is similar to L. elongatum Bastian but is rounded anteriorly and only at the very anterior surface is it slightly truncated; sometimes this is not pronounced. The cephalic papillae hardly rise above the surface of the head, the nerve canals supplying them piercing the cephalic capsule obliquely. The ten cephalic papillae are very small, about $1^{1}/_{2}\mu$, lie regularly, with smooth cuticle surrounding each submedial pair such that they are set in a common depression. The lateral organ in this species is large, occupying $^{1}/_{4}$ to $^{1}/_{5}$ of the diameter of the body at its level. It lies over half the diameter of the head behind the lateral papillae. Its anterior orifice is small ($2^{1}/_{2}\mu$), its length is 8 – 9$\mu$, and width $7^{1}/_{2}\mu$. Its internal cavity is round, a papilla supplied with a bundle of nerve fibers projects into it posteriorly.

The **cephalic capsule** in this species is fairly well developed and consists of shields covering the anterior surface of the head and formed from the inner layer of cuticle. These shields are also observed laterally on the head at the points of attachment of the esophagus. De Man considered these

---

* Anterior end of testis.

shields in L. elongatum Bastian as a skeleton for the lips, an interpretation with which I cannot agree. In the male a cephalic capsule proper is not noted, in conformity with the weak development of the esophagus,
46 but the inner layer of the cuticle, from which the capsule originates, is fully developed. An **oral cavity** is completely absent, the lumen of the esophagus opens directly anteriorly. At the level of the anterior margin of the lateral organ, two depressions with thick chitinized walls lie in the two ventral rays of the esophagus. Some esophageal fibers are attached to the walls and center of the depressions (a—Figure 1a). The dorsal esophageal gland, which is the most developed, opens somewhat posterior to these enlargements. Both ventral glands open more anteriorly and are far less developed than the dorsal.

The **esophagus** is straight and fairly muscular. The **eyes** are quite large, 14 μ long and 11 μ wide, furnished with a large lens, about 5 μ in diameter, whose position is clear from the table given above. The **cervical gland** is large, has an elongated pear shape, and lies half way between the nerve ring and the end of the esophagus. The cervical pore lies half way between the eyes and the nerve ring.

The digestive tract of the one fully adult male that I saw was extremely interesting. The entire tract bore clear signs of degeneration. The esophagus had the appearance of having been treated with caustic potash. (However, there was no possibility of maceration here since all the body musculature and nervous system were very well preserved.) All the esophageal fibers had either disappeared or were preserved only as indistinct remnants. The esophageal gland was highly pigmented (gl. oes.—Figure 1b), its margins were clearly defined only anteriorly, while posteriorly they were unclear and pigment was distributed irregularly in spots over the entire esophagus; this was partially due to the natural branching of the gland and partially to the breakdown of its margins. However, in spite of the deep internal process, the external form of the esophagus remained unchanged. Degeneration of the intestine was even
47 further advanced. Its cells were completely resorbed, and the entire mass consisted of irregular clumps of organic matter with numerous crystals in the form of elongated hexagonals lying between them. A similar phenomenon was described previously by de Man for L. elongatum Bastian.

The **female genital system** is double, with reflexed ovaries that are small compared with the uterus, which occupies $^2/_3$ of the entire genital tract on each side. The oldest eggs measure 250×70 μ, the younger ones being wider; on fertilization the eggs become invested with a shell. Fertilization apparently occurs in females of varying ages with most diverse lengths of genital tract. The later fertilization occurs, the greater the number of eggs that have passed previously into the uterus and the longer, therefore, the genital tract. Thus, a very long uterus packed with eggs and thicker than indicated in the formula sometimes occurs in the unfertilized females. The **ovejector** is well developed and consists of large cells. The **vagina** is about 60 μ long, is thick-walled, and extends across $^2/_5$ of the body diameter.

Two **testes** exist, the posterior by far the shorter; the sperm are very small—$3^1/_2$ μ. The **spicules** are 90 μ long, and smooth as in all Leptosomatum. The manubrium is somewhat rectangular with a thickening in the middle of its posterior half (a—Figure 1d). The **gubernaculum** is short, tubular, about 25 μ long, and lies posterior to the anus. The opening of the gland of the accessory organ, which lacks a chitinized thickening, is preanal. Supplementary papillae are very weakly developed; I could find only a small area behind the anus on which some pores were visible.

The **tail** is conical, its length hardly greater than its width at the base, and the tip curves ventrally. The caudal glands are of the tubular type, run far anteriad from the anal pore (for a distance 10 times the diameter of the body at the anus). In the male they measure 700, 960, and 1,240 μ. The proportions at the posterior end are: length of tail 1.2; spicules 1.4; gubernaculum 0.4; distance from the anus to the accessory organ 1.7.

L. bacillatum was encountered in the following samples: (1) deep sand from Kruglaya Bay 7.12, 7.13, 8.13, adult females and juveniles;
48 (2) mussels from rocks at the station 6.12, adult female; (3) phyllophores 6.12, numerous females; (4) oysters 6.12, juveniles; (5) silt from Artilleriiskaya Bay on Nassarius 6.12, juveniles; (6) coquina at 27 sajenes [1 sajene = 2.134 m] at Georgievskii Monastery 7.12, juveniles; (7) phaseolin mud from Georgievskii Monastery 7.13, male. It was described for the first time from the Mediterranean Sea: Villefranche, among algae (Eberth); Naples (de Man); Sète, canal de Bourdigues (Rouville), Marseilles—"Assez fréquents en février sur les rochers du Pharo, retrouvés aussi à Endoûme et à la jetée de la Joliette en février 1869" (Marion).

## 2. **Leptosomatum punctatum** (Eberth 1863)

(Table 1, Figure 2)

Phanoglene punctata Eberth 1863: Untersuchungen über Nematoden p. 20, Table 2, Figures 5—7.

$$♂\ \frac{1.3\quad 4.4\quad 14.2\quad 45.6\quad 55.9\quad 98.7}{0.7\quad 1.0\quad 1.1\qquad (1.2)\qquad 1{,}0}\ 8010$$

$$\alpha=83,\ \beta=7,\ \gamma=77.$$

$$\text{Immature}\ ♀\ \frac{1.1\quad 4.0\quad 11.4\quad 40.5\quad 47.3\quad 49.1\quad 54.7\quad 64.2\quad 98.7}{0.6\quad 0.9\quad 1.1\qquad\qquad 1.4\qquad\qquad 0.8}\ 8470$$

$$\alpha=70,\ \beta=9,\ \gamma=77.$$

| Dimensions ♂ | Cephalic bristles | Aperture of lateral organ | Eyes | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length ........... | 8 | 27 | 105 | 350 | 1,080 |
| Width ........... | 26 | 35 | 50 | 80 | 95 |

The **body** is filiform, evenly tapering anteriorly and posteriorly. At the level of the eyes its diameter is somewhat more than half the width at the end of the esophagus, and at the level of the cephalic bristles it narrows almost half again. The diameter at the anus is $^{2}/_{3}-{}^{5}/_{6}$ of the maximum diameter of the body, and somewhat less than the diameter at the end of the esophagus.

The **cuticle** is somewhat thicker than in L. bacillatum, up to 6 $\mu$, the outer layer making up almost half its thickness. A characteristic difference from L. bacillatum Eberth is the far greater development of the bristles; here they are not in the form of papillae but are true
49 bristles whose length exceeds their thickness several times. Similar groups of narrower yet not papilliform bristles lie between the anterior end and the eyes, both laterally and along the subventral lines. The bristles are generally larger than the papillae of L. bacillatum.

The **head** (Figure 2a) is somewhat narrower than in L. bacillatum; the eyes lie more posteriorly such that the entire anterior part of body is more elongated. The labial papillae (p. lab. —Figure 2a) are small, shifted further anteriorly than in the forgoing species, and each is set in a hollow, so that on examination from the surface they appear surrounded by small disks. The cephalic bristles here, in conformity with the generally greater development of the bristle armature of the body, also appear as true bristles; their length is 6 $\mu$. The lateral organ, relatively greater (8 $\mu$) than in L. bacillatum, covers $^{1}/_{3.5}$ of the corresponding diameter of the body. Its anterior aperture is smaller still, about 2 $\mu$.

The **internal structure of the head** slightly differs from that of the forgoing species, primarily in the presence of three small pockets in the angles of the mouth anteriorly (a—Figure 2a). The three sectors of the esophagus are also supported by a thickening of the cuticle — rudiments of the cephalic capsule; small processes run inside the esophagus also ("apophyses chitineuses" of de Man, not drawn in the figure). The three esophageal glands are as in the foregoing species, but corresponding to the more elongated anterior end, the aperture of the dorsal gland is shifted further back. The **eyes,** although slightly smaller than in L. bacillatum, are nevertheless fairly large, the pigment cup is about 10 $\mu$, the lens, turned laterally and anteriorly, is about 4 $\mu$. They are shifted far more posteriad. The **esophagus** proper is weakly developed, hardly forming posterior swellings. The **nerve ring** stands perpendicular to it. The **cervical gland** is large, lies half way between nerve ring and beginning of intestine, and occupies about $^{1}/_{3}$ of the internal space. Its duct runs anteriad from the nerve ring, but could not be traced further, nor could the position of the cervical pore be determined.

50 **The female genital organs** are not particularly distinguished from those of foregoing species insofar as can be judged from the single adult female that I found.

The **testes** are long and apparently unpaired. The cells in the vas deferens are very long. The bursal musculature runs anteriad from the anus for five times the length of the tail. The **spicules** (Figure 2d) are not as straight as in L. bacillatum Eberth and its northern relative L. elongatum Bastian; in their basal part they are distinctly S-shaped. They are shorter than in both these species, measuring 65 $\mu$. The spicule plate is fairly well developed; its posterior edge is the thicker. The **gubernaculum** is very small, 20 $\mu$ long, narrow with thin walls. A small preanal thimble-shaped accessory organ is present. The proportions of the posterior end are: length of spicules 1.0; gubernaculum 0.3; length of tail 1.6; distance from anus to accessory organ 1.7. The tail is short, rounded (Figure 2b), longer than in L. bacillatum. The **caudal pore** as drawn in Figure 2c is seen as a space formed by the parting of the two layers of cuticle (b). The fact that cone (a) does not completely fill up the aperture is a postmortem phenomenon.

L. punctatum is encountered together with L. bacillatum in deep sands and in deeper coquina: Kruglaya Bay 7.13, 2 males; coquina at 27 sajenes at Georgievskii Monastery 7.12, immature females and juveniles. This species is encountered less frequently than the foregoing.

Geographical distribution: Mediterranean Sea: Villefranche, among algae (Eberth).

## Genus LEPTOSOMATIDES n. g.

The genus described is intermediate between Leptosomatum and Deontostoma. It resembles the former in the structure of the anterior end: the cephalic capsule is weakly developed and not characterized as a separate morphological structure but is merely a compaction of the
51 inner layer of cuticle. There are enlargements such as these on the internal ventral angles of the esophagus, making small chambers, but the apertures of the esophageal glands are apparently disposed otherwise.

The posterior end of the male, on the other hand, is exactly similar to Deontostoma. The tail is blunt, short, the posterior end somewhat thickened; the spicules have a complex form, as has the gubernaculum that covers them, in that it is provided with two knobs. The supplementary bristles of the male, that in Leptosomatum are hardly developed or entirely undeveloped, are developed here, as in Deontostoma. Subventrally, between the anus and the accessory organ, lie two rows of small regular bristles, while anterior to the accessory organ there are several pairs of particularly well-developed bristles standing on elevations, as in Deontostoma.

Type and so far sole species: Lept. euxina n.sp., described below. Leptosomatum arcticum and Lept. grebnickii, which I have described elsewhere, possibly belong to this genus; this will become clear when their males are found. Leptosomatum australe Linstow (see p. 28) may also be related to this genus.

### 3. **Leptosomatides euxina** n. sp.
(Table 1, Figure 3)

$$♂\ \frac{\quad 1.3^{*}\quad 5.3\quad 16.5\quad 46.3^{**}\quad 51.3^{\dagger}\quad 56.5^{\dagger\dagger}\quad 99.1}{0.4\quad 0.7\quad 1.0\quad 1.0\qquad (1.1)\qquad 1.1}\ 8950$$

Only male known

$\alpha=85,\ \beta=6,\ \gamma=108.$

* Eyes; ** Anterior part of testis; † Beginning of seminal duct; †† Posterior part of testis.

|  | Cephalic bristles | Lateral organ | Eyes | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 11 | 16 | 100 | 470 | 1,800 |
| Width | 35 | 40 | 60 | 85 | 95 |

52 **The body** is filiform, of even thickness, narrows anteriorly $2^1/_2$ times as compared with the maximum diameter of the body. Posterior to midbody the body thickens somewhat, attaining its greatest diameter once more anterior to the anus. The **cuticle** is very thick, smooth, a layer of crossing fibers being observed only anteriorly. The outer layer of the cuticle, about $^1/_3-^1/_4$ of the overall thickness, is hardly differentiated from the inner. From the front its thickness gradually decreases posteriorly, from $7^1/_2$ to 5 μ. There are few bristles; I could observe only definite anterior and posterior groups; the latter will be discussed below. The anterior groups lie between the anterior end and the eyes. There are 9—10 bristles which stand in an irregular longitudinal row (Set.— Figure 3a).

The **head** has a general rounded form, hardly thickened. The labial papillae are hardly noticeable, and are six in number as usual (p. lab.– Figure 3b). The ten cephalic bristles are disposed normally, and are about 3 μ long (Figures 3a, b). The lateral organ is small, only $^1/_8$ of the corresponding diameter of the body; it is considerably smaller than in the Black Sea Leptosomatum, but similar to the lateral organs of L. arcticum and L. grebnickii. It lies almost directly behind the lateral cephalic bristles. It is circular, 5 μ in diameter, with an anterior orifice which is relatively far larger than in Leptosomatum (2 μ).

The **cephalic capsule** is fairly well developed compared with Leptosomatum (Figure 3b). It mainly consists of an arch running parallel to the anterior surface of the head, to which the esophagus is attached (a—Figure 3b). The esophageal lining is a direct continuation of the cephalic capsule. Processes run anteriad along the ventral rays of the esophagus. A similar process is particularly well developed on the dorsal ray (b—Figure 3b), at the end of which it splits up further. In addition the cephalic capsule sends processes posteriad into the sectors of the esophagus (c—Figure 3b); these serve as supports for the esophagus
53 in the lateral parts of the head. The **oral cavity** is absent; only an inconspicuous vestibule is present opening directly to the outside (vest. — Figure 3b). Two enlargements are seen on the ventral rays, as is characteristic for Leptosomatum also; radial muscle fibers of esophagus are attached to these. All three **salivary** [esophageal] **glands** apparently open anterior to the enlargement, the dorsal somewhat posterior to the ventral.

The **eyes** are asymmetrical in the specimen that I found. The pigment cups are about 13 μ long; the lens is deeply set in it and about 4 μ long (Figure 3c). The esophagus is as in all Leptosomatini narrow, only slightly developed posteriorly. A pigment strip lies in it and is particularly developed posteriorly. The **nerve ring** is broad, almost straight. I could not find an excretory gland or its pore, but I do not deny their existence.

The **lateral fields** (very narrow owing to strong development of musculature) consist of elongate cells. Special shiny bodies lie at the sides of the intestine which cannot be confirmed as cells. They have an irregular shape and are highly reminiscent in consistency of the bodies that I saw in the intestine of males of L. bacillatum. The testes are paired, the posterior being more developed. The mature (?) sperm are large—6 μ. The spicular apparatus is identical to that in Deontostoma (Figures 3e, f). The spicules are nonuniform, the left being 110 μ, the right 90 μ. The large left spicule has the following parts: (1) a manubrium, gradually tapering posteriad, about $^2/_5$ of spicule length (a—Figure 3e); (2) a central part, about $^2/_5$ of the total length, on which are observed two irregular flanges extending posteriad and upward (b—Figure 3e). Finally, (3) a terminal part, being $^1/_5$ of the overall length and characterized by two bulges on its dorsal surface, one anterior to the extreme tip. The end of the spicule is blunt, even truncated. The right spicule has a similar form in general but the manubrium is shorter. The **gubernaculum** has the following parts: (1) two knobs of unequal size and uneven form (Figures 3e, d; the right one is smaller, not drawn in figure); (2) a piece covering the
54 terminal parts of the spicules; (3) a part forming a paired horizontal support anterior to the anus (as in Deontostoma arcticum Saveljev) (e—Figure 3e at the side and Figure 3f below). Its total length is 65 μ. Supplementary bristles (Figure 3d) are apparently absent on the tail. A double subventral row of 9—10 supplementary bristles (a—Figure 3d) runs more anteriorly, and anterior to these is another subventral row of 5 pairs of thick bristles (b—Figure 3d), each of which is set on an elevation of cuticle in a pit surrounded by a cuticular disk (Figure 3g). The **accessory organ** sends no chitinized processes internally, but has only lateral wing-like stiffenings, i.e., it is more simply constructed than in Deontostoma. The proportions at the posterior end are: length of spicules: right 1.1, left 1.0; gubernaculum 0.7; length of tail 0.9; distance from anus to accessory organ 1.0. The **tail** is short and blunt. The caudal glands are of tubular type, weakly developed.

Only one male found in the coquina at 27 sajenes at Georgievskii Monastery. 7.12.

## Genus PHANODERMA Bastian 1865

Trans. Linn. Soc. 25, p. 142.
de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 100.
Heterocephalus Marion 1870: Ann. Sci. Nat. Zool (5) 13, Art. 14, p. 18.

Type species: Ph. tuberculatum (Eberth) 1863
(cocksi Bastian 1865)

This small, characteristic genus is distinguished by the following features. The **cuticle** is very thick, and smooth; pores supporting the

nerves that supply the bristles pierce it obliquely; terminal sensory bodies are contained in the cuticle also, as can be seen by the bulge in the cuticular canal. A **cephalic capsule** is present; it mainly consists of **three hollow enlargements opposite the three sectors of the esophagus**
55 **directed anteriad: the two subventral hollows are large and the one dorsal is small.** The external trilobate form of the head also corresponds to these enlargements. Lateral parts of the capsule disposed more posteriorly are also present. The oral cavity is extremely inconspicuous. In the known species an eye with a lens is present. There is an excretory gland. The esophagus in the posterior part consists of separate cells that do not fuse with the syncytium. The ovaries are paired and reflexed. The testes are paired. **The spicules are slender, long, and curved. The gubernaculum is inconspicuous** (if present). **The accessory organ is present in the form of a fairly conspicuous tube. The tail is pointed,** at least twice longer than wide.

The first species of this genus was found by Eberth and described as Enoplus tuberculatus. Bastian established genus Phanoderma in his monograph, in which he included Eberth's species and added two new ones: Ph. albidum and Ph. cocksi, the latter apparently identical with Ph. tuberculatum (Eberth). Marion, not knowing Bastian's work, described genus Phanoderma once again under the name Heterocephalus with species H. laticollis, which proved to be new; in his work on the Neapolitan nematodes, de Man introduced yet another species, Ph. gracile. Since 1878 no new descriptions of Phanoderma have appeared.

Thus, the four authentic species so far known for this genus are as follows:

1) Ph. tuberculatum (Eberth 1863), see p. 37
2) Ph. albidum (Bastian 1865), see p. 39
3) Ph. gracile (de Man 1878), Tijd. Ned. Dierk. Ver. 3, p. 101, Table 8, d—Figure 8a. Naples.
4) Ph. laticolle (Marion 1870); Heterocephalus l.: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 18, Table D. — near Marseilles "en mai, sur les rochers de Pharo, et en juillet a Mallamousque dans l'anse où abordent les pêcheurs... assez fréquents."

In addition, there has been described:

Ph. parvum (Villot 1875); Arch. Zool. Exp. (1) 4, p. 462, Table 11, b—Figure 7a. Roscoff, which is unlikely to be recognized anywhere again. It is also possible that Thoracostoma setigerum (Marion 1871): Ann. Sci. Nat. Zool (5) 14, Art. 1, p. 11, Table L, Figure 1 ("des rochers de la côte sud de l'île de Maïré," around Marseilles) is also related to Phanoderma. I have therefore included this species in the key.

56

1 (8). Tail long, pointed end.
2 (5). Tail 2—3 times longer than wide.
3 (4). Tail twice longer than wide , body narrows fairly sharply to anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Ph. tuberculatum** (Eberth)
4 (3). Tail three times longer than wide, body narrows very gradually to anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Ph. albidum** Bastian
5 (2). Tail 4—5 times longer than wide.
6 (7). Spicules shorter than tail . . . . . . . . . . . . . **Ph. laticolle** (Marion)
7 (6). Spicules same length as tail . . . . . . . . . . . . . **Ph. gracile** de Man
8 (1). Tail short, blunt, hardly longer than wide . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Ph.** (?) **setigerum** Marion

### 4. **Phanoderma tuberculatum** (Eberth 1863)

(Table 1, c—Figure 4a)

Enoplus t. Eberth 1963; Unters. üb. Nematoden, p. 38, Table 4, Figures 1—5.
? Ph. cocksi Bastian 1865: Tr. Linn. Soc. 25, p. 143, Table 11, Figures 151—153.

$$\text{♂}\ (\text{immature})\ \frac{\begin{array}{cccccc} — & 9.9 & 22.4 & 51.5 & 63.4^{*} & 97.0 \end{array}}{\begin{array}{cccccc} 0.7 & 1.4 & 2.8 & & 3.0 & 1.4 \end{array}}\ 3500$$

$$\alpha = 33,\ \beta = 4^1/_2,\ \gamma = 33.$$

$$\text{♀}\ \frac{\begin{array}{ccccccccc} — & 6.2 & 16.7 & 36.5 & 42.7 & 51.3 & 63.1 & 69.4 & 95.8 \end{array}}{\begin{array}{ccccccccc} 0.7 & 1.7 & 2.0 & & & 2.6 & & & 1.5 \end{array}}\ 4900$$

$$\alpha = 33—38,\ \beta = 6,\ \gamma = 24.$$

| Dimensions ♀ | Anterior end | Cephalic bristles | Eyes | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length . . . . . . . . . . | — | 25 | 50 | 305 | 820 |
| Width . . . . . . . . . . . . . . . | 16 | 32 | 45 | 85 | 95 |

Dimensions of ♂ are not given as there were no mature specimens.

The **body** is fairly stout, tapers gradually anteriad and more markedly posteriad; in the male, enlargements are formed in the region of the spicules so that the tapering to the anus is even more pronounced. At the level of the cephalic bristles the body is twice narrower than at the level of the beginning of the esophagus and four times narrower than the maximum body width, the most marked narrowing occurring in the region anterior to the nerve ring. The diameter at the anus is about 60% of the
57 maximum body diameter. The **cuticle** is smooth and thick, $4\,\mu$ anteriorly, $7^1/_2\,\mu$ at midbody, $2\,\mu$ near the caudal end. It is a very characteristic feature that the sensory endings of the bristles lie within the cuticle. Usually they are located in the subcuticle, but here the layer containing them has become cuticularized and a characteristic form is obtained, like that drawn in Figure 5a (for another species). In this species the terminal parts lie even more obliquely. The bristle armature is sparse, the bristles being concentrated anteriorly (laterally between the head and the eye) and posteriorly, particularly in the male; there are very few bristles on the remainder of the body.

The **head** is greatly elongated anteriorly in such a manner that in outline the body has a depression anterior to the cephalic bristles, as can

---

* Back of testis.

be seen from Figure 4a. The labial papillae lie at the extreme ends of the lips on their outer surface, piercing the cephalic capsule obliquely. The cephalic bristles are 16 μ long, relatively longer than in the following species. The lateral organ is 3 μ in diameter, round, and disposed as in Ph. albidum.

The **cephalic capsule** is of complex structure. I refer the reader to the following species and to Figure 4a for a more detailed description.* The vestibule, slight oral cavity, esophagus, esophageal gland, and excretory apparatus are exactly similar to these organs in Ph. albidum. The **eyes** are shifted more anteriad, $1^1/_2$ head lengths from the anterior end, while in Ph. albidum they are almost 3 head lengths from it. The female genital tract is exactly as in the following species. The eggs are 80×150 μ, the shell 5 μ thick. There are two testes, but further details could not be ascertained as all the males were immature. The bursal musculature is well developed, occupying a space $2^1/_2$ times greater than the length of the spicules. The **spicules** are long, slender, their terminal 58 part is arched, the base straight; a manubrium lies on the base and is followed by a more slender part, while at the ends there are some kinds of indentations possibly belonging to the gubernaculum, which I could not distinguish clearly. The spicules are 150 μ long. The **accessory organ** lies at the anterior end of the spicules. This is a fairly long tube with thickened internal margins and a smooth lumen. Its length is about 40 μ. There are several pairs of pre- and postanal bristles lying subventrally.

The **tail** is pointed, twice narrower at the tip than at the base, and clearly different in its form from the tail of Ph. albidum; it is shorter, being only twice longer than wide, the cuticle becomes thin at the end, and its tip is slightly swollen. The caudal glands are either within the tail or extend only slightly anteriad.

The proportions of the posterior end are: length of tail 2.0; width at end 0.3; distance from tip of tail to aperture of accessory organ 2.0; spicules 2.4; accessory organ 0.5.

This species is definitively deepwater. In shallower regions it is replaced by Ph. albidum; the two species are encountered together only in oysters. They were found: in oysters 6.12, male, female, juveniles; coquina of Georgievskii Monastery 7.12, adult female; phyllophore 6.12, many males and females.

I identify this species with that of Eberth not without some hesitation. Eberth's description is quite similar, but the old descriptions did not pretend to any special accuracy, and we must therefore turn to the drawings. Here we find two differences: the caudal glands are extremely large and extend far beyond the tail with indistinct outlines; however, in the tail three small cells are drawn also which, apparently, are also true caudal glands. Apart from this, the posterior bristles in the male are set upon buttonlike elevations. I also observed elevations, but they were by no means as pronounced: this difference should probably be put down to the inadequacy of the drawing. Passing now to Bastian's species Ph. cocksi, we observe a difference in that the cuticle of the tail is 59 drawn thicker, but this is undoubtedly due to an inaccuracy in the drawing. Of course, only further research into the finer details of the Mediterranean and North Sea forms of Phanoderma will be able to solve this problem conclusively. Thus, if my assumptions are correct, the geographical distribution of this species is: Mediterranean Sea — Nice (Eberth); North Sea — "about the roots of Corallines in tide-pools, Falmouth" (Bastian).

### 5. **Phanoderma albidum** Bastian 1865

(Table 1, Figure 5)

Trans. Linn. Soc. 25, p. 143, Table 11, Figures 154, 155.

Only ♀ known

$$♀\ \frac{—\quad 7.6\quad 17.3\quad 33.8\quad 42.7\quad 54.7\quad 62.2\quad 72.0\quad 94.1}{0.7\quad 1.9\quad 2.7\qquad\qquad\qquad 3.0\qquad\qquad\qquad 1.9}\ 3500$$

$\alpha=33,\ \beta=6,\ \gamma=16.$

| | Anterior end | Cephalic bristles | End of cephalic capsule | Eyes | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|---|
| Length | — | 14 | 25 | 35 | 68 | 300 | 750 |
| Width | 14 | 24 | 32 | 40 | | 65 | 75 |

The **body** at its widest part is not narrower than Ph. tuberculatum Eberth, but its more gradual tapering anteriad and posteriad gives this impression initially. It narrows anteriad from the end of the esophagus almost four times, and its maximum width is only slightly greater than the body diameter at the end of the esophagus. The diameter at the anus is $^2/_3$ that of the maximum. The **cuticle** is smooth and two-layered, the outer layer being far thinner than the inner; it is about $^1/_4 - ^1/_5$ of the cuticular thickness, which anteriorly reaches $3^1/_2$ μ, posteriorly about $4^1/_2$ μ. The thinnest part is on the tail (2 μ), which is thinner than in Ph. tuberculatum. The number of bristles is greater than in the preceding species, being particularly numerous in the anterior part of 60 the body (see Figure 5a). Canals containing both the nerve fibers and sensory bodies pass through the cuticle obliquely and have a very characteristic form.* The bristles are of varying lengths, sometimes being very short and papilliform.

The anterior part of the **head** extends anteriad, and it is separated by an annular fissure from the rest of the body. All this part is divided into three lobes in accordance with the internal skeleton, but true lips are not formed. The ventral lobes are connected but the dorsal lobe is separated from the others by deep excavations (Figure 5c). Two labial papillae lie on each lip (d — Figure 5a). The canals of these papillae are slender and

---

* The figure shows indistinctly that the cephalic capsule extends inside the cuticle far backwards, as in Ph. albidum. Its surface is cross-hatched (a — Figure 4a).

* The form of these canals also leads me to suspect that Thoracostoma setigenum Marion is an aberrant form of Phanoderma; see p. 36.

pass obliquely through the skeletal part of the head lying under them (p.lab. — Figure 5b). The usual number of cephalic bristles are present, 9—10$\mu$ long. The lateral organ is very small, about 4$\mu$ in diameter; it lies somewhat ventrally to the lateral bristles. Its aperture is very small and oval.

The **cephalic capsule** has a complex structure. Only in its anterior part is it formed from the modified inner layer of cuticle, which further back remains unchitinized as does the central layer, on which a characteristic longitudinal striping appears (Figure 5d). The anterior part consists in the main of three hollow teeth directed anteriorly and invested with a thick cuticle. These three teeth correspond to the three sectors of the esophagus and are disposed thus: two large teeth are subventral, and one small tooth is on the dorsal line. All three teeth are immovable and hollow. Two oblique chitinized canals that contain the nerves of the labial papillae pierce the cuticle opposite each of the three teeth. The dorsal tooth has a more simple form (Figure 5c) than the indentated ventrals (Figure 5b). Posteriorly the teeth are connected by special cross-pieces. Ventrally this
61 union is effected by deep-set narrow cross-pieces of complex structure (Figure 5b); laterally they are superficial and are wide thickenings of the cephalic capsule, having the outline of a tooth (a — Figure 5d). In general they curve dorsally and ventrally around the lateral organ, while more posteriorly they gradually fade out, fusing with the fine striations that run along the posterior part of the cephalic capsule. There are additional internal cross-pieces. Three special cuticular bodies lie at the base of the dorsal tooth (a — Figure 5c). The internal tube of the esophagus is directly adjacent to the cephalic capsule. Anteriorly it broadens somewhat and forms a small conical oral cavity, while at its most anterior end, between the cephalic lobes, lies a small vestibule (Figure 5c).

Small **eyes** (8$\mu$) lie a short distance behind the end of the oral cavity (Figure 5a). They are square and provided with a small lens. The **esophagus** is fairly thick and has a characteristic structure: its entire posterior part is covered with a membranelike layer of special cells, which are embossed in mounds on the surface. These cells form several rows having the appearance of broken lines. It is probable here that the fusion with the syncytium of the cells that compose the esophagus is incomplete. The internal esophageal tube has fairly thick walls. The esophageal glands open anteriorly into special reservoirs, which in turn open by narrow pores into the lumen of the esophagus at the level of the end of the cephalic bristles (gl. oes. — Figure 5b). The **nerve ring** is not marked by any special feature. The **excretory gland** lies opposite the posterior part of the esophagus; it is quite large, its duct is stout, and it runs anteriorly along the ventral wall to open a short distance behind the eyes (gl.excr. — Figure 5a). The intestine consists of large cells with large nuclei.

The ovaries are paired, reflexed, and fairly large. The eggs ripen singly in their distal ends. The uterus is thick-walled and the ovejector is hardly differentiated from it. The eggs measure 65×135$\mu$, with the shell thickness reaching 5$\mu$.

The two vaginae are thin-walled and run obliquely directly from the gonopore, ending far short of midbody.

62 The **hindgut** is long, approximately $1^1/_2$ times longer than the diameter of the body at the anus. Anterior to its junction with the hindgut the midgut gradually narrows. The **tail** narrows to the end, tapering more slightly in its posterior half, and is not thickened at its posterior tip. It is twice longer than its width at the base, while the width at the end is $4^1/_2$ times less than the length.

Ph. albidum Bastian is by preference an inhabitant of coastal waters, not penetrating to the deeper parts: Cystoseira 5.12, juvenile females, 7.12, 2 adult females, oysters 6.12, juvenile female, mud of Artilleriiskaya Bay 1.12, adult female.

This species is easily differentiated from Ph. tuberculatum Eberth by its longer tail, smaller size, and more gradually tapering end of the body.

Bastian found his Ph. albidum in "small green seaweed from tide-pools, Falmouth" in the English Channel. The identity of the Black Sea species with that of Bastian has still to be confirmed.

## 2. Subfamily **Anticomini**

I incorporate two genera in this subfamily — Anoplostoma Bütschli and Anticoma Bastian. The features that characterize it are as follows. Nematodes of small size, tapering anteriorly and posteriorly, with a thin, smooth cuticle; the lateral organs are cyathiform; there is a slender esophagus lacking a bulb, reflexed ovaries, and eyes are absent. Median fields are not noted; special large fat (?) cells are concentrated in the ventral field. The two genera are greatly differentiated by the structure of the anterior end: in Anticoma the oral cavity is inconspicuous, while in Anoplostoma it is wide with thick walls; in Anticoma the lateral organs lie immediately behind the cephalic bristles; in Anoplostoma they are shifted far back. However, the two genera have many common structural features. This view is also expressed by de Man (1907, p. 49ff).

63 1 (2). Oral cavity very small; lateral organ not far posterior to cephalic bristles; no bursa in male ...... **Anticoma** Bastian p. 41
2 (1). Oral cavity large, prism-shaped, with thick walls; lateral organ lies far behind its posterior margin; bursa present ........................................ **Anoplostoma** Bütschli p. 46

### Genus ANTICOMA Bastian 1865

Odontobius ex p. Eberth 1863: Unters. über Nematoden, p. 27.
Anticoma Bastian 1865: Trans. Linn. Soc. 25, p. 141.
Stenolaimus Marion 1870 ex p.: Ann. Sci. nat. Zool. (5) 13, Art. 14, p. 16.
Anticoma Bütschli 1874: Abh. Senck. Ges. 9, p. 35.
de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 98.
de Man 1886: Anat. Unters., p. 51.
Cobb 1891: Proc. Linn. Soc. NSW 5, p. 765.

Type species: A. pellucida Bastian 1865

This very natural genus is distinguished by the following features. It is small (only one species reaches 7 mm: usually they are no more than $3^{1}/_{2}$ mm). The body tapers greatly anteriorly. The cuticle is thin and smooth. There are ten cephalic bristles. A group of 3—6 cervical bristles lie behind the head in a longitudinal line: this is extremely characteristic for this genus, and also the reason for its name.* The lateral organ is cyathiform. The esophagus is attached anteriorly to the cuticle and there is a large excretory gland. The ovaries are paired and reflexed; the testes are paired. The spicules have a curved upper part and a velum, and the gubernaculum covers their ends. There is a preanal accessory organ in the form of a small tube. The tail is long with a filiform end.

64 The first form of Anticoma was described by Eberth (1863) under the name Odontobius acuminatus n.sp. Soon afterwards Bastian's study (1865) appeared, in which the author established genus Anticoma. Marion (1870), who did not know of Bastian's work, described one aberrant species as Stenolaimus lepturus n.sp. Descriptions of various old and new members of Anticoma were given by Bütschli 1874, Villot 1876, and de Man 1878. De Man (1886) provided a magnificent description of the organization of A. pellucida Bastian with numerous drawings on the basis of live specimens. Cobb (1891) made a compilation of genus Anticoma, in which in addition to the description of a new species from Ceylon he redescribed A. acuminata Eberth and established as synonyms for it A. tyrrhenica de Man 1878 and A. pellucida Bastian 1865 (= limalis Bastian). Cobb is probably right concerning A. tyrrhenica, but A. acuminata and A. pellucida are quite different species and are easily distinguished by the position of the cervical bristles (see Table). In 1901—1902 Golovin in his work on the excretory and phagocytic systems of nematodes touched also upon A. pontica m. (A. pellucida Golowin nec. Bastian et de Man), first found by him in the Black Sea.

Thus, the following species of this genus have so far been described:

1) Ant. acuminata (Eberth 1863) Unters. über Nematoden p. 28, Table 1, Figures 6—9. Nice. — Cobb 1891: Trans. Linn. Soc. NSW 5, p. 765. — Naples, among seaweeds. — Daday 1901: Termész. Füzet. 24, p. 435, Table 21, Figures 1—3. — Fiume, among coastal seaweeds.
2) Ant. similis Cobb 1898: Proc. Linn. Soc. NSW 23, p. 383. — Port Jackson NSW. Sand at low tide. — de Man 1904: Rés. voy. Belgica; Nématodes libres p. 13, Table 4, Figure 4: Baie d'Orange, Tierra del Fuego, on crab.
3) Ant. eberthi Bastian 1865: Trans. Linn. Soc. 25, p. 141, Table 11, Figures 143—145 — Roots of corallina, Falmouth, English Channel. — de Man 1889: Mém. Soc. Zool. France 2, p. 186, Table 5, Figure 3. — Rocks at Penzance, St. Vaast—French and English coasts of English Channel.
4) Ant. trichura Cobb 1898: Proc. Linn. Soc. NSW 23, p. 385 — Sand at low tide, Port Jackson NSW.
5) Ant. lata Cobb 1898: ibid., p. 384, together with preceding.
6) Ant. tyrrhenica de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 99, Table 7, e — Figure 7a — Naples, in seaweed; according to Cobb, a synonym of A. acuminata Eberth.
7) Ant. typica Cobb 1891: Proc. Linn. Soc. NSW 5, p. 768, Figures 1, 2; Ceylon—among seaweed, winter.

65

8) Ant. pellucida Bastian 1865: Trans. Linn. Soc. 25, p. 142, Table 11, Figures 149, 150; de Man 1886; Anat. Untersuch. über freilebende Nordsee-Nematoden p. 53, Tables 9, 10. Syn.: Ant. limalis Bastian 1865: loc. cit.; p. 141, Table 11, Figures 146—148; — Bütschli 1874: Abh. Senck. Ges., 9, p. 35, c — Figure 19a. Northern seas of Europe: English Channel: Falmouth, mud from harbor (Bastian); Roscoff (Villot). North Sea: sea canal on Walcheren Island (de Man); oyster bank at Sylt (Bütschli); Baltic Sea: Kiel Firth, several sajenes (Bütschli); Arctic Ocean — Kola Gulf, Lake Mogil'noe (Savel'ev). Golovin's indications for Sevastopol relate to A. pontica n.sp.
9) Ant. pontica n.sp., see p. 44.
10) Ant. calveti Rouville 1903; 1904: CR. Ass. Franç. Avanc. Sci., p. 788. Sète, canal de Bourdigues, among seaweed.
11) Ant. reflexa Linstow 1896: Ergebn. Hamburger Magalhaenischen Sammelreise 1, No. 7, p. 8, Figures 8, 9. Uschuaia at low tide, roots of seaweed, 1—2 sajenes, October—December. This inadequately described species may not even be Anticoma.
12) Ant. leptura (Marion 1870): Stenolaimus l. Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 16, Table C, Figure 1. — Marseilles — rochers du Pharo — février. May also not be Anticoma.
13) Ant. tenuicaudata Villot 1875: Arch. Z. Exp. (1) 4, p. 462, Table 11. b — Figure 8a — doubtful species, probably not Anticoma, unlikely to be recognized again anywhere — described from Roscoff.

The differences among these species arise from the relative position of the cervical bristles, the lateral organ, the excretory pore, the accessory organ of the male, and the form of the spicules, which are of the slender type, as in A. pontica n.sp. (Figures 6d, e) or of the stout type, as in A. pellucida Bastian (cf. de Man 1886, Table 9, Figure 9). Three insufficiently described species (10, 11, 13) are not included in the key.

1 (2). Some groups of cervical bristles, about 5—7 in each . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **A. leptura** (Marion)
2 (1). Two lateral groups of cervical bristles
3 (4). Large species—7 mm; 5—6 cervical papillae lying $1^{1}/_{2}$ head widths from anterior end; excretory pore near nerve ring; spicules of slender type; accessory organ shifted to anus by one spicule length . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **A. eberthi** Bastian
4 (3). Small species $1^{1}/_{2}$—4 mm.
5 (10). Cervical bristles shifted anteriorly by $1^{1}/_{2}$—2 head widths.

---

* In A. leptura (Marion) there are several of these groups; it may possibly be another genus.

6 (7). Excretory pore lies anterior to cervical bristles, of which there are 4–5 lying $1\frac{1}{2}$ head widths from anterior end; lateral organs half head width from anterior end. Accessory organ lies one spicule length from anus; spicules of slender type ..........
66 ................................. **A. acuminata** (Eberth)

7 (6). Excretory pore lies posterior to cervical bristles; 4 cervical bristles lie 2 head widths from anterior end.

8 (9). Lateral organ shifted very close to cephalic bristles; excretory pore at level of nerve ring, tail beset with bristles. $3\frac{1}{2}$ mm. . . . ................................. **A. trichura** Cobb

9 (8). Lateral organ lies half head posterior to cephalic bristles; excretory pore lies half way between head and nerve ring; tail bare; spicules are $1\frac{1}{2}$ times diameter of body at anus, of stout type; accessory organ lies $1\frac{1}{2}$ spicule lengths from anus; $2\frac{1}{2}$ mm ................................. **A. lata** Cobb

10 (5). Cervical bristles shifted by $2\frac{1}{3}$–3 head widths from anterior end.

11 (12). Species insufficiently described: $1\frac{1}{2}$mm; 3–4 cervical bristles; spicules slender; accessory organ $1\frac{1}{2}$ spicule lengths from anus (probably a young A. acuminata Eberth). ............... ................................. **A. tyrrhenica** de Man

12 (11). Features otherwise.

13 (14). Excretory pore near nerve ring; 1.3 mm; lateral organ lies one head length from anterior end; 4 cervical bristles; spicules of slender type; accessory organ removed from their base ...... ................................. **A. typica** Cobb

14 (13). Excretory pore anterior to cervical bristles; 2–3 mm long; lateral organ half head length from anterior end; 5–6 cervical bristles.

15 (18). Excretory pore posterior to lateral organ.

16 (17). Excretory pore $1\frac{1}{2}$ head widths from cephalic bristles; cervical bristles 3 head lengths from anterior end; spicules of slender type; accessory organ almost 2 spicule lengths anterior to anus. ................................. **A. pellucida** Bastian

17 (16). Excretory pore $1\frac{1}{2}$ head widths from cephalic bristles; cervical bristles $2\frac{1}{2}$ head lengths from anterior end; spicules of slender type; accessory organ hardly shifted from their base ........ ................................. **A. pontica** n. sp.

18 (15). Excretory pore at level of lateral organ; cervical bristles $2\frac{1}{2}$ head lengths from anterior end; male unknown ............ ................................. **A. similis** Cobb

### 6. Anticoma **pontica** n. sp.
(Table 2, Figure 6)

$$♀\ \frac{-\quad 8.6\quad 16.7\quad 33.0\quad 39.3\quad 46.1\quad 53.3\quad 60.3\quad 88.0}{0.6\quad 1.8\quad 2.0\qquad\qquad 2.5\qquad\qquad 1.5}\ 2560$$

$$\alpha=40;\ \beta=6;\ \gamma=8$$

$$♂\ \frac{-\quad 8.8\quad 18.4\quad 28.0\quad 40.1\quad 49.7\quad 91.2}{0.7\quad 2.0\quad 2.7\qquad (3.1)\qquad 2.3}\ 2300$$

$$\alpha=32;\ \beta=5\frac{1}{2};\ \gamma=11$$

| Dimensions adult ♀ | Cephalic bristles | Lateral organ | Excretory pore | Cervical bristles | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length .............. | 7 | 10 | 22 | 40 | 160 | 340 |
| Width .............. | 14 | 17 | 17 | 22 | 40 | 45 |

67 The **body** tapers evenly anteriorly and posteriorly, most markedly anteriorly in the esophageal region and posteriorly in the region behind the genital tract. In the male the diameter at the anus is relatively thicker. From the end of the esophagus anteriorly the body narrows more than twofold and posterior to the anus it narrows less than twofold. The **cuticle** is thin, about 1 μ, smooth, and layers are not observed. The bristles on the body are true bristles but there are very few.

The **head** is rounded and slightly flattened (Figure 6a). The cervical papillae are well developed, set upon low elevations, and encircled by a fold of cuticle. The ten cephalic bristles are somewhat shorter and thicker than in A. pellucida, 7 μ long, or about half the head width. The lateral organ is cyathiform with a transverse slit, widest in the middle, while in A. pellucida the widest part is anterior and it tapers posteriorly. Its width and length are 4 μ, $\frac{1}{4}$ of the corresponding width of the body. The five cervical bristles lie three head widths from the anterior end somewhat irregularly (s.cerv. – Figure 6a).

The **cephalic capsule** is rudimentary and serves for the attachment of the esophagus anteriorly. The **oral cavity** is very small; when the esophagus is relaxed it is completely inconspicuous. In Figure 6b, for example, it is visible, while in Figure 6a it is virtually absent.

The **esophagus** is smooth, thin, weakly muscular, about half the thickness of the body, gradually tapering posteriorly. The esophageal glands open more posteriorly than in A. pellucida, opposite the lateral organ; the aperture of the dorsal gland is shifted more posteriorly (gl. oes. – Figure 6a). The nerve ring is broad and flat.

The **cervical gland** lies opposite the posterior part of the esophagus on the left, measuring about 70×25 μ; its duct is very long, terminating $1\frac{1}{2}$ head widths behind the cephalic bristles, anterior to the cervical bristles. The end of the duct before the pore is somewhat modified, appearing
68 more compact and shiny. The **intestine** is thin-walled, composed of small cells.

The ovaries are reflexed and short, with numerous oocytes. The oviduct proceeds from the ovary, is well developed, with muscle cells and wrinkled epithelium; it is inserted somewhat into the uterus, as described by de Man (1886) for A. pellucida Bastian. The latter organ is thin-walled. The eggs measure 70×45 μ.

Two **testes** are present. There are some large cells around the posterior part of the body (glands?). The **spicules** are 80–85 μ (e – Figure 6d), slender, with a swelling near the beginning and tapering evenly to the end. A thin plate is attached to the concave surface of the spicule. The **gubernaculum** has a broad base, pointed at the end, and envelops the ends of the spicules (30 μ). The preanal accessory organ consists of a short tube (16 μ). Some bristles are observed at various points on the posterior end of the body.

The tail of the female is relatively longer (Figure 6c) owing to its far smaller width at the anus. The length is 8.0$\mu$, and the width at the end is $^1/_6$ of that. The tail tapers only for half its length, after which it is evenly narrow. The hindgut is small and thin-walled. The caudal glands are accommodated within the tail. The proportions at the posterior end of the male are: length of spicules 1.4; gubernaculum 0.5; tail 4.0, its width at the end 0.1; distance from anus to accessory organ 2.1.

A. pontica is a very common nematode distributed on all superficial facies but also encountered more deeply. Cystoseira 7.12, adult male, female, and juveniles; rocks near Georgievskii Monastery 7.12, juvenile; rock algae 7.12, adult female; mussels from rocks under the station 6.12, many immature specimens; coastal shingle at Georgievskii Monastery 7.12, 1 female; slimy sand from Grafskaya Pier 7.13, 1 female, immature; Zostera 5.12, many specimens; Potamogeton from Streletskaya Bay 3.10, S. Zernov, many; oxeas sand at Georgievskii Monastery 7.13, few juveniles; sand, 27 sajenes at the same place, many juveniles; algae on oxeas sand of Kruglaya Bay 6.12, many adults; mud from Artilleriiskaya Bay on
69 Nassarius, many 7.15, 7.13.

As is seen from the key, this species is most similar to A. pellucida Bastian, but differs from it in several minor features. Golovin's indication that A. pellucida is encountered in Sevastopol "on mussels, frequently in winter, rarely in summer," relates to A. pontica.

## Genus ANOPLOSTOMA Bütschli 1874

Symplocostoma pp. Bastian 1865: Trans. Linn. Soc. 25, p. 132.
An. p.p. Bütschli 1874: Abh. Senck. Ges. 9, p. 36.
" " de Man 1889: Mém. Soc. Zool. France 1, p. 17.
An. de Man 1907: Mém. Soc. Zool. France 20, p. 49.

Type species: An. viviparum (Bastian 1865) Bütschli 1874

This genus is distinguished by the following features. It has small dimensions and the body tapers greatly to the ends. Ten cephalic bristles are disposed in two circlets, the anterior of four large submedial and two small lateral bristles and the posterior of four small submedian bristles. The lateral organ is cyathiform, removed far posteriorly. The oral cavity is large, prism-shaped with thick walls, and devoid of teeth. Eyes are absent. There are cervical bristles, as in Anticoma, but not so regularly disposed. The ovaries are paired and reflexed. The testes are paired. There are two slender spicules with a gubernaculum. A bursa with papillae is present in the male.

The first species of this genus was described by Bastian (1865) and related to Symplocostoma. Bütschli (1874) correctly differentiated it from Symplocostoma but incorrectly related his An. spinosum to that genus. De Man (1890) transferred An. spinosum Bütschli to the new genus Axonolaimus.

Thus, only three species are known for this genus:

1) A. viviparum (Bastian 1865), see p. 47.
2) A. blanchardi de Man 1888: Mém. Soc. Zool. France 1, p. 18, Table 2, Figure 10; Walcheren Island on the coast of Holland, mud on canal stones.
3) A. gracile Linstow 1900: Fauna Arctica I, p. 128, Table 7, Figures 42, 43. Spitsbergen. A doubtful species, probably from another genus.

70

1 (2). Tail pointed. . . . . . . . . . . . . . . . . . . . . . . **A. gracile** Linstow
2 (1). Tail rounded at end.
3 (4). Width at base $4^1/_2$ times greater than length, $1^1/_4 - 1^1/_2$ mm, oviparous . . . . . . . . . . . . . . . . . . . . . . **A. blanchardi** de Man
4 (3). Six times longer, about 2 mm, viviparous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **A. viviparum** (Bastian)

### 7. **Anoplostoma viviparum** (Bastian 1865)
(Table 2, Figure 7)

Symplocostoma v. Bastian 1865: Tr. Linn. Soc. 25, p. 133, Table 11, Figures 123 – 125.
An. v. Bütschli 1874: Abh. Senck. Ges. 9, p. 37, Table 5, b – Figure 21a.
G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 38, c – Figure 17a.
de Man 1907: Tijd. Nederl. Dierk. Ver. (2) 10, p. 233.
de Man 1908: Mém. Soc. Zool. France 20, p. 50, Table 1, Figure 9.

$$\text{♀}\ \frac{1.3}{0.6}\ \frac{9.7}{2.6}\ \frac{17.9}{3.1}\ \frac{?\ 46.4}{4.6}\ \frac{?\ 87.7}{1.8}\ 1250$$

$$\alpha = 23;\ \beta = 6;\ \gamma = 8.$$

| Young ♀ | Cephalic bristles | End of oral cavity | Cervical bristles | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length . . . . . . . . . . . . | 4 | 11 | 22 | 105 | 195 |
| Width . . . . . . . . . . . . | $6\frac{1}{2}$ | 10 | 13 | 27 | 33 |

The body greatly tapers (fivefold) from the end of the esophagus anteriorly and $2^1/_2$ times to the anus. The cuticle is smooth and thin. The lateral organs lie two lengths of the oral cavity from the anterior end. The tail is 7 times longer than its width at the base, which is $5^1/_2$ times narrower at the end. For other details I refer the reader to de Man's description cited above.

There was only one young female, which unfortunately was crushed when being examined: deep Cystoseira 6.12.

A. viviparum is widespread in the northern seas of Europe. English Channel: Falmouth, mud (Bastian, de Man), Normandy (de Man); North Sea: Dutch coast, very common (de Man); Baltic Sea: Kiel, fine sand on the shore (Bütschli); mud in the Tvärminne Bay on the Gulf of Finland (G. Schneider); Arctic Ocean – Kola Gulf, Lake Mogil'noe at Kildin (Savel'ev).

71

## 3. Subfamily **Oxystomini**

This small subfamily is characterized by the great extension of the anterior part of the body, which usually tapers also; because of this the cephalic part is very long. The cuticle is smooth; lips are absent. The cephalic bristles are (? always) disposed in two rows with six in the anterior row and four in the posterior. The lateral organ is usually large, cyathiform, lying far from the anterior end. The esophagus is attached anteriorly to the cuticle. The oral cavity is entirely absent or extremely small. The spicules are short. The female genital apparatus usually has only the posterior branch. The following genera belong to this subfamily:

1) Oxystoma Bütschli 1874, see below.
2) Halalaimus de Man 1888: Mém. Soc. Zool. France 1, p. 2.*
3) Thalassoalaimus de Man 1893: Mém. Soc. Zool. France 6, p. 81.** May be a freshwater and terrestrial genus also.
4) Alaimus de Man 1880: Tijd. Nederl. Dierk. Vereen. 5, p. 2; 1884 Nem. Niederl. Fauna, p. 29; Hofmänner 1913 Revue Suisse Zool. 21, p. 604. Six species.

1 (2). Bristles on anterior end of body absent, gubernaculum also. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Alaimus** de Man
2 (1). Bristles on anterior end of body present, gubernaculum also
3 (4). Lateral organ small, shifted anteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Thalassolaimus** de Man 1893
4 (3). Lateral organ lies far posterior to cephalic bristles.
5 (6). Lateral organ comparatively short, its enclosed part somewhat smaller than its aperture . . . . . . . . . . . **Oxystoma** Bütschli 1874
6 (5). Lateral organ in form of very long longitudinal slit, 6 – 8 times longer than width of head, enclosed part only a small pocket compared with overall length . . . . . . . . **Halalaimus** de Man 1888

---

* One species: H. gracilis de Man 1888, loc. cit., p. 3, Table 1, Figure 1. Walcheren, Holland, mud on stones.

** One species: Th. tardus de Man 1893, Loc. cit., p. 82, Table 5, Figure 1; de Man 1907: Mém. Soc. Zool. France 20, p. 34, Table 1, Figure 1; Jerseke, Falmouth, on rocks among algae.

## Genus OXYSTOMA **Bütschli 1874**

Abh. Senck. Ges. 9, p. 34.

Type species: O. elongatum Bütschli 1874

72 These are worms with a very elongated and pointed anterior end (hence the name). In many forms the body is also extremely extended and slender. The cuticle is smooth, relatively thick, almost free of bristles. Lips and oral cavity are absent. The cephalic bristles lie in two circlets, the anterior forward with six bristles, the posterior on the neck with four bristles. The lateral organ is quite large, cyathiform with a large aperture, shifted far from the anterior end. There is a pyriform cervical gland. The esophagus is very slender anteriorly, widens only posteriorly, not forming, however, a bulb. The female genital apparatus is unpaired, only its posterior part being preserved. The gonopore lies far anterior to midbody. The spicules are short and slender, curved, with a velum. A gubernaculum is present. The tail is long, of various shapes depending on the species.

The following species have so far been described:

1) Ox. elongatum Bütschli 1874: Abh. Senck. Ges. 9, p. 34, Table 4, d – Figure 18a. de Man 1907: Tijd. Nederl. Dierk. Ver. (2) 10, p. 231; Mém. Soc. Zool. France 20, p. 43, Table 1, Figure 6 – Falmouth, English Channel; Jerseke, Holland, frequently (de Man); oyster banks of Sylt (Bütschli); Kola Gulf (Savel'ev).
2) Ox. pellucidum Cobb 1898: Proc. Linn. Soc. NSW 23, p. 395 (mud below tidemark – Port Jackson NSW); species very similar to the foregoing, possibly not different from it.
3) Ox. clavicauda n. sp. see p. 50.
4) Ox. filiforme n. sp. see p. 51.
5) Ox. obtusum (Villot 1876); Anticoma o.: Arch. Zool. Exp. (1) 4, p. 463, Table 11, b – Figure 9a (after de Man 1878 p. 99); requires redescription

Stenolaimus macrosoma Marion 1870 is obviously not Oxystoma (de Man 1878 p. 99) but Leptosomatum.

1 (6). Narrow end of tail thickened, clublike. Aperture of lateral organ oblong.
2 (5). Distance from anterior end to lateral organ 5 – 6 times greater than width of head.
3 (4). Club of tail conspicuous – about half body width at anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. elongatum** Bütschli
4 (3). Club of tail inconspicuous – about $^1/_4$ body width at anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. pellucidum** Cobb
73 5 (2). Distance from anterior end to lateral organ is 12 – 14 times greater than width of head . . . . . . . . . . . . **O. clavicauda** n. sp.
6 (1). Tail fairly thick, truncated at end.
7 (8). Aperture of lateral organ round; length more than 100 times exceeding width. Esophagus very slender. . . **O. filiforme** n. sp.
8 (7). Body not so long (?) . . . . . . . . . . . . . . . . . . **O. obtusum** Villot

### 8. **Oxystoma clavicauda** n.sp.
(Table 2, Figure 8).

$$\text{♀}\;\begin{array}{ccccccc} & 10.5 & 24.4 & 38.7 & 41.0 & 57.8 & 93.6 \\ \hline 0.4 & 1.2 & 1.5 & 1.7 & & & 1.2 \end{array}\;3000$$

$$\alpha=59;\ \beta=4;\ \gamma=16.$$

$$\text{♂}\;\begin{array}{ccccc} & ? & 16.7 & ? & 93.1 \\ \hline 0.3 & & 1.1 & 1.1 & 1.0 \end{array}\;3800$$

$$\alpha=90;\ \beta=6;\ \gamma=14.$$

| | Anterior bristles | Posterior bristles | Lateral organ | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 5 | 37 | 65 | 250 | 270 | 620 |
| Width | 11 | 11 | 15 | 31 | 32 | 38 |

The **body** tapers greatly anteriorly, narrowing almost fourfold from the end of the esophagus, whence it widens slightly to midbody; it tapers slightly posteriorly; at the anus it is $^3/_4$ of the maximum diameter. The male is narrower than the female, almost of even thickness from the end of the esophagus to the anus. The **cuticle** is 2 μ, relatively thick, and smooth. There are bristles only on the head and posterior end of the male.

The **head** is rounded, without lips, and a slightly tapering neck follows it (Figures 8a, b). I found no labial papillae. The cephalic bristles lie in two circlets; the anterior with six bristles 4 μ long at the extreme anterior end and the posterior with four bristles $3^1/_2$ μ long considerably more posteriorly. The lateral organ is in general cyathiform, the anterior aperture is very wide, while the posterior enclosed part is small. The walls of the open part are thickened laterally, and a small denticle is
74 present on the dorsal wall of the enclosed posterior part; the extreme posterior tip curves slightly dorsally. Its length in the male is 24 – 30 μ, its width 7 μ (half the width of the body), and the length of the open part is 14 μ. In the female it is far smaller, its overall length being 8 μ and its width not exceeding $^1/_3$ of the corresponding diameter of the body. The **oral cavity** is absent. The esophagus widens gradually posteriorly but does not form a bulb. At its origin the intestine is S-shaped, making a loop, as described by Bütschli (1874) for O. elongatum. However, this is undoubtedly a postmortem manifestation due to the contraction of the body. This loop was present in by no means all my specimens. De Man emphasizes its absence in his examination of O. elongatum. The long **cervical gland** terminates near the posterior end of the esophagus. The excretory pore lies anterior to the nerve ring.

All the **female genital apparatus** is shifted far anteriorly and there is only one posterior ovary of the reflexed type. Eggs were not yet present in the uterus.

There is one testis, recurved posteriorly. The **spicules** (Figures 8c, d) are curved and there apparently is a velum; they taper evenly to the end, while an uneven outline is observed at the base. They are 55 μ long. The gubernaculum is 22 μ long and lies laterally over the spicules in the form of two separate plates not joined in the midline (Figure 8d). A thickened region of cuticle anterior to the anus in the midline is beset with a pair of stout bristles (Figures 8c, d). The **tail** tapers evenly for half its length, then widens into a terminal club (Figure 8c). The tubular caudal glands extend anteriorly towards the anus by the length of the tail. Each gland has a separate cone in front of the caudal pore. The proportions in the tail are: narrowest part 0.2; terminal club 0.5 (0.6 in female); length 5.0 (7.0 in female); spicules 1.3; gubernaculum 0.5; distance from anus to bristles mentioned above 1.2.

This species is found in oxeas sand: Peschanaya Bay 7.12, one female; Georgievskii Monastery 9 sajenes and 18 sajenes 7.12, 13 males.

O. clavicauda n.sp. is a very close relation of O. elongatum
75 Bütschli and O. pellucidum Cobb, but is easily distinguished from them by the elongated anterior end. It is interesting that the small oral cavity (strictly the vestibule), which is mentioned by de Man, Bütschli, and Cobb, is apparently absent here.

### 9. **Oxystoma filiforme** n.sp.
(Table 2, Figure 9)

$$\text{♂}\;\begin{array}{cccccc} & 5.0 & 15.0 & 31.8 & 63.8^{*} & 98.4 \\ \hline 0.2 & 0.6 & 0.6 & & (0.8) & 0.6 \end{array}\;3820$$

$$\alpha=130;\ \beta=6^1/_2;\ \gamma=60.$$

$$\text{♀}\;\begin{array}{ccccccc} & 7.1 & 13.0 & 36.1 & 40.4 & 52.7 & 97.6 \\ \hline 0.2 & 0.6 & 0.8 & 0.9 & & & 0.5 \end{array}\;4080$$

$$\alpha=115;\ \beta=7^1/_2;\ \gamma=40.$$

| ♂ | Cephalic bristles | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 2 | 20 | 195 | 580 |
| Width | 5½ | 9 | 25 | 25 |

The extremely long **body** tapers greatly anteriorly twofold from the end of the esophagus, fourfold or somewhat more from midbody, and to $^2/_3$ at the anus. The tapering is so gradual as to be almost insensible. The **cuticle** is relatively thick – $1^1/_4$ μ; bristles are absent except at the front.

---

* Beginning of the vas deferens.

The **head** is slightly conically rounded (Figure 9a). It is surrounded by a circlet of six small cephalic bristles $1^{1}/_{2}\,\mu$ long. I could not locate the remaining four bristles. The lateral organ (Figure 9a) is $4^{1}/_{2}\,\mu$ long, $3^{1}/_{2}\,\mu$ wide, cyathiform, with a rather constricted anterior aperture. In females and males it is of uniform size.

Inside the head there are some stiffenings, which I could not examine because of the small size of the specimen. The **esophagus** is very narrow at the beginning, $3\,\mu$ at the level of the lateral organ ($^{1}/_{3}$ of the body width – 76 Figure 9a), and then gradually widens; at the nerve ring it is $5\,\mu$, $^{1}/_{5}$ of the body width), and near the end it is $16\,\mu$ (about $^{2}/_{3}$ of the body width). Some large cells lie around it in the body cavity displacing it laterally (cel – Figure 9a). These cells run for the entire length of the body.

The **cervical gland** lies at the level of the posterior region of the esophagus and is $9\,\mu$ wide; the excretory pore lies exactly at the level of the nerve ring.

The **female genital organs** consist of the following parts: a single posterior reflexed ovary, succeeded by a short oviduct, followed by the uterus, which in my specimen was full of sperm. The vagina has very thick walls, so that a square is formed when they are tightly squeezed together. Another short uterus runs anteriad from the vagina. This is a part of the reduced anterior half of the female genital apparatus.

The **testis** is long and expanded at the base. The sperm are comparatively very long, oval, $3\times4\,\mu$; two hardly fit in the vas deferens together. The **spicules** (Figure 9d) are shorter than in the forgoing species; the base is slightly swollen, the end is pointed and anterior to it there is a velum; they are $30\,\mu$ long. The gubernaculum covers the ends of the spicules and is about $14\,\mu$ long. The cuticle is somewhat swollen behind the anus. The **tail** tapers gradually to the end, where it is rounded. The proportions at the posterior end are: length of tail of the male 2.7, female 4.5; width at end 0.3; spicules 5.2; gubernaculum 0.6.

This species is found in oxeas sand: Peschanaya Bay 1.12, male, 5.12, female; Georgievskii Monastery 8.13, 2 males.

O. filiformis is easily differentiated from O. clavicauda by the narrower esophagus and far narrower body. Apparently, "Anticoma" obtusa Villot is a close relation of our species, but differs from it (according to the drawing) by the shorter body.

## 4. Subfamily **Enoplini**

77 I include here those genera of family Enoplidae in which a masticatory apparatus consisting of three movable jaws has developed. Furthermore, I incorporate genus Enoplolaimus de Man, which does not possess such jaws, but is closely associated with Enoplus through Enoploides and has immovable pieces resembling jaws. These pieces are enclosed in a chitinized ring, which is homologous with the cephalic capsule of Leptosomatini. All the nematodes here are of large or medium size, and most frequently are stout. There is a superficial cephalic capsule separated by a cephalic line, three lips, six labial papillae or bristles, and ten cephalic bristles. The lateral organ is cyathiform, oval, with an anterior semicircular aperture. (Only in Enoplolaimus are unusual proportions described, and these have yet to be confirmed.) The esophagus is thick, the ovaries reflexed.

This subfamily is closely linked to Leptosomatini through genus Triodontolaimus de Man.

I isolate in it the following genera:

1) Enoplus Dujardin 1845, see page 53.
2) Enoploides Saveljev 1912, see page 62.
3) Enoplolaimus de Man 1893, see page 71.
4) Triodontolaimus de Man 1893.*

1 (6). Three distinct movable jaws.
2 (5). Jaws long with two (or three) hooks at end.
3 (4). Jaws solid posteriorly. Lips short. Labial papillae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Enoplus** Dujardin
4 (3). Jaws posteriorly extended in two processes between which lies aperture of esophageal gland, sometimes set on a tooth. Lips usually very large. Labial bristles. . . . . . . **Enoploides** Saveljev
5 (2). Jaws short, provided with one point each. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Triodontolaimus** de Man
6 (1). Jaws absent, replaced by immovable bars with two lateral processes anteriorly and two processes posteriorly. Teeth present. Labial bristles . . . . . . . . . . . . . **Enoplolaimus** de Man

## 78 Genus ENOPLUS Dujardin 1845

Hist. Nat. des Helminthes p. 233.
Bastian 1865: Trans. Linn. Soc. 25, p. 147.
Bütschli 1874: Abh. Senck. Ges. 9, p. 40.
de Man 1886: Anatomische Untersuchungen p. 9.
Rauther 1909: Zool. Jahrb. Anat. 23, p. 717 (structure of esophagus).
Enoplus ex p. Eberth 1863: Untersuchungen über Nematoden p. 31.
Schneider 1866: Monographie der Nematoden p. 50.
Enoplostoma Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 22.

Type species: E. tridentatus Dujardin 1845

Enoplus is one of the best-studied genera and is common in all seas. I shall give only a short account here, since there is an exceptional description by de Man (1886).

The body is stout, usually tapering slightly anteriorly. The cuticle is smooth with a layer of crossing fibers anteriorly, as in the Leptosomatini.

---

* Mém. Soc. Zool. France 6, p. 114 with one species: Tr. acutus (Villot 1875) Enoplus ac. Villot: Arch. Zool. Exp. 4, p. 460, Table 11, Figure 6; de Man loc. cit. p. 115, Table 7, Figure 12. In algae on rocks at Falmouth, Roscoff in the English Channel.

The head is provided with three lips, each of which is beset with two labial papillae. There are ten cephalic bristles. The small cyathiform lateral organ has a special slit in front of it. Behind its aperture is a discernable cephalic line. The inner layer of cuticle anterior to it is compacted into the superficial cephalic capsule. In the oral cavity there are three movable jaws, one dorsal and two subventral. Each has two points at the end, enlarges in the middle, and has a rounded base. The esophageal glands open in the oral cavity under the jaws (Rauther). The jaws are enclosed in the narrow but tight ring of the cephalic capsule. The esophagus is stout over its entire extent and partly pigmented. Anteriorly there are (not always) two eyes without lens. The female genital organs are paired, the ovaries reflexed; the testes are paired. The spicules are short and arched, a gubernaculum is present, and these structures are often of very complex form. An accurate definition of the species is usually possible only from the male genital organs. There is
79 a large preanal tubular accessory organ. The tail is long and conical.

There are two species from the Black Sea, and I described the third from the Sea of Azov.

This genus has not altered in scope since Bastian (1865). An historical survey is given by de Man (1886); so far only Rauther (1909) has made any significant additions to the anatomy.

The known authentic species of Enoplus are as follows:

Section α — species with pointed tail and notched spicules.

1) E. crassus Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 95, Table 5, Figure 8. — Murmansk — Vardö, Teriberka coastal zone.
2) E. alatus Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 109. Murmansk: Ekaterininskaya Harbor, Pala Inlet, muddy sand.
3) E. michaelseni Linstow 1896: Ergebn. Hamburger Magalhaenischen Sammelreise 1 No. 7, p. 14; de Man 1904 Rés. voy. Belgica; Nématodes libres p. 19, Tables 4—6, Figure 7; syn.: E. atratus Linstow 1896 loc. cit. p. 10. South America: Navarino Island, Ushuaia, Boie de Torrent, Londonderry Island, Canal Français.
4) E. communis Bastian 1865: Trans. Linn. Soc. 25, p. 148, Table 12, Figures 164—166; Bütschli 1874: Abh. Senck. Ges. 9, p. 40, Table 8, Figure 35; de Man 1886: Anatomische Unters. über freil. Nordsee-Nematoden p. 14, Tables 1—3; ? Villot 1875: Arch. Z. Ex. 4, p. 459, Table 11, Figures 4, 5; ? Rauther 1907: Zool. Jahrb. Anat. 23 pp. 704, 717 (structure of esophagus). Syn.: E. cochleatus Schneider 1866: Monogr. d. Nematoden p. 57, Table 4, Figures 9—13; ? E. dujardini Bastian 1865: loc. cit. p. 149, Table 12, Figures 168—170. Distributed in all the northern seas of Europe: Falmouth (Bastian), Roscoff (Villot), Walcheren (de Man), Kiel (Bütschli), Heligoland (Schneider, Rauther), Kola Gulf (Savel'ev), vegetation off the coast of Denmark (Ditlevsen), Spitsbergen (Linstow).
5) E. pigmentosus Bastian loc. cit. p. 149, Table 12, Figures 171, 172 (also possibly a synonym of communis).
6) E. euxinus n.sp. see p. 82.
7) E. tridentatus Dujardin 1845: Histoire naturelle des Helminthes p. 233; Bastian 1865 loc. cit. p. 151 (an exact repetition of the description of the forgoing species). "Entre les algues marines à Toulon, et a Sète dans l'étang de Thau" (Dujardin) Sète — canal de Bourdigues (Rouville) indications: "St. Malo dans l'océan" (Dujardin) in de Man's opinion the result of an error. The species is insufficiently clear.
8) E. hirtus (Marion 1870) Enoplostoma H.: Ann. Sci. Nat. Zool. (5) 13 Art. 14, p. 22, Table F, not a synonym of communis, as Marion thought (Cr. Ac. Sci. 80, p. 499). Common over the entire year around Marseilles).
9) E. macrophthalmus Eberth 1863: Unters. üb. Nematoden p. 35, Table 2, Figures 23, 24; Table 3, Figure 6. Nice. It will be possible to elaborate this species only when the male is described.

80 Section β — species with pointed tails and smooth spicules.

10) E. behringicus Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 98, Table 5, Figure 9. Bering Sea.
11) E. brevis Bastian 1865: Trans. Linn. Soc. 25, p. 150, Table 12, Figures 176, 177; de Man 1886 Anatom. Unters. über freilebende Nordsee-Nematoden p. 27, Tables 4, 5; Falmouth (Bastian); Walcheren (de Man); Kola Gulf (Savel'ev).
12) E. littoralis n.sp., see p. 60.
13) E. auriculatus Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43 livr. 1, p. 109. Murmansk: Pala Inlet, Lithothamnium.
14) E. maeoticus Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 101, Table 5, Figure 10. Sea of Azov: Arabat Tongue, among algae.
15) E. minor (Marion 1870) Enoplostoma minus: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 23, Table G, Figure 1. Around Marseilles, possibly a synonym for the following:
16) E. striatus Eberth 1863: Unters. über Nematoden, p. 36, Table 3, Figures 9—12. Nice.

Section γ — species with blunt tails.

17) E. obtusicaudatus Eberth 1863 loc. cit. p. 36, Table 3, Figures 7, 8. Nice.
18) E. brevicaudatus (Marion 1870) Enoplostoma br.: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 24, Table G, Figure 2. Among Chaetomorpha, in the winter around Marseilles.

Section δ — aberrant species with short jaws (probably not Enoplus).

19) E. inermis Bastian 1865: Trans. Linn. Soc. 25, p. 150, Table 12, Figures 173—175; in cortical sponges from rocks, Falmouth.

Unfortunately, I was unable to obtain descriptions of the following two species:

20) E. bisetosus Linstow 1908: Denkschr. med. naturwiss. Ges. Jena 13, p. 27.
21) E. macrolaimus Linstow 1908: ibid. p. 27. Both from the Atlantic coast of South Africa.

This list contains all the members of Enoplus established after 1865. It does not include a whole range of species that were described in insufficient detail by earlier authors.

1 (2). Jaws very short, with process in anterior part perpendicular to axis of jaw. Tail pointed . . . . . . . . . . . . **E. inermis** Bastian
2 (1). Jaws longer, without process.
3 (6). Tail blunt (following two species may be synonyms).
4 (5). Body same width at anus as for a great extent anteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. brevicaudatus** (Marion)
5 (4). Body tapers quite sharply to anus . . . . **E. obtusicaudatus** Eberth
6 (3). Tail pointed.
7 (10). Only female known.
81 8 (9). Very large jaws and eyes, tail with filiform part at end, six times longer than width at base . . . . . **E. macrophthalmus** Eberth
9 (8). Jaws regular. Eyes indistinct, esophagus greatly pigmented. Similar to E. communis, but jaws larger . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. pigmentosus** Bastian
10 (7). Males. Features do not accord with items 8 and 9.
11 (24). Spicules with special plates that create impression of indentations on trunk of spicule.
12 (13). Indentations exactly at middle of spicule. . . . **E. hirtus** (Marion)
13 (12). Indentations located nearer to end of spicule.
14 (17). Spicules twice shorter than tail.
15 (16). Jaws of length equal to half head width, widest at middle . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. euxinus** n. sp.
16 (15). Jaws of length equal to $^3/_4$ head length, widest anteriorly, of constant width anteriorly . . . . . . . . . . . . **E. tridentatus** Dujardin
17 (14). Spicules of same length as tail or only slightly shorter. Jaws of length equal to half head width. Lateral organ lies anterior to cephalic line.
18 (19). 10—12 mm; $\alpha = 45-55$; very similar to E. communis, spicules broader, with strongly developed internal plates. Gubernaculum of other form . . . . . . . . . . . . . **E. alatus** Saveljev
19 (18). Other features.
20 (21). Special mound on spicule posterior to indentations; manubrium absent. Lateral organ $^1/_{12}$ head width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. communis** Bastian
21 (20). Mound absent; manubrium present, sometimes hardly noticeable.
22 (23). $\alpha = 40-45$; lateral organ $^1/_{11}$ head width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. michaelseni** Linstow
23 (22). $\alpha = 25-30$; lateral organ $^1/_{16}$ head width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. crassus** Filipjev
24 (11). Spicules smooth without indentations.
25 (26). Two low mounds on spicules. Gubernaculum hollow, round, attached to spicules dorsally. Accessory organ long, tubular . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. behringicus** Filipjev
26 (25). Mounds on spicules absent. Gubernaculum envelops their ends. Accessory organ with funnel, short.
27 (30). Spicules with distinct manubrium. Following two species may be synonyms: differences are merely:
28 (29). Tail thickened at end. Accessory organ with internal partition . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. minor** (Marion)
29 (28). Tail not thickened at end. Partition absent. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. striatus** Eberth
30 (27). Manubrium absent.
31 (32). Esophagus has wavy outline and plasmatic substances interstratified with muscles (as in Enoploides). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. maeoticus** Filipjev
32 (31). Esophagus compact as usual.
33 (34). Gubernaculum of complex structure, divided into three . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. auriculatus** Saveljev
82 34 (33). Gubernaculum not divided into three. Spicules slightly curved.
35 (36). Lateral organ lies wholly anterior to cephalic line. Length of jaws almost equal to half diameter of head. Tail of male more than twice longer than wide, of female almost three times longer . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. brevis** Bastian
36 (35). Cephalic line intersects lateral organ. Length of jaws considerably less than half diameter of head. Tail of male shorter than twice diameter at anus, of female $2^1/_2$ times diameter at anus . . . . . . . . . . . . . . . . . . . **E. littoralis** n. sp.

### 10. Enoplus euxinus n. sp.
(Table 2, Figure 10)

$$\text{♂}\ \frac{1.1^{*}\quad 10.4\quad 17.1\quad 35.7\quad 55.4\quad 64.3\quad 93.9}{1.4\quad 2.4\quad 2.6\qquad (2.8)\qquad 2.4}\ 4200$$

$$\alpha=35,\ \beta=6,\ \gamma=14.$$

$$\text{♀}\ \frac{1.0^{*}\quad 8.7\quad 16.0\quad 34.7\quad 46.7\quad 55.7\quad 67.3\quad 78.3\quad 94.1}{1.5\quad 2.7\quad 2.7\qquad 3.3\qquad 1.8}\ 4600$$

$$\alpha=30,\ \beta=6,\ \gamma=17.$$

These dimensions are taken from summer specimens; following are formulas of larger females, with the dimensions of the genital tract omitted:

$$\text{Mussels 1.12: ♀}\ \frac{—\quad 9.7\quad 15.1\quad 60.0\quad 94.2}{1.5\quad 3.0\quad 3.0\quad 3.7\quad 2.0}\ 4950;\quad \text{♀}\ \frac{—\quad 7.1\quad 13.4\quad 54.9\quad 94.9}{1.3\quad 2.6\quad 3.1\quad 3.7\quad 1.8}\ 5250;$$

$$\text{♀}\ \frac{—\quad 7.1\quad 12.8\quad 51.3\quad 94.6}{1.3\quad 2.4\quad 2.8\quad 2.8\quad 1.8}\ 5700;\quad \frac{—\quad ?\quad 13.6\quad 53.3\quad 95.4}{1.4\quad ?\quad 2.6\quad 2.8\quad 1.8}\ 5850\ \text{(old female with eggs deposited)}$$

$$\text{Oxeas sand at Georgievskii Monastery}\quad \text{♀}\ \frac{6.0\quad 15.2\quad 33.1\quad 52.0\quad 71.5\quad 34.3}{1.4\quad 2.1\quad 2.5\qquad 2.8\qquad 1.6}\ 6525$$

The size varies greatly, as is seen from the formulas; particularly large specimens were encountered in deep parts. In winter they are also larger.

---

* End of jaws.

| Dimensions ♂ | Cephalic bristles | End of jaws | Eye | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 25 | 45 | 70 | 270 | 400 | 740 |
| Width | 60 | 65 | — | — | 95 | 105 |
| ♀ | | | | | | |
| Length | 25 | 45 | 75 | 320 | 470 | 820 |
| Width | 70 | 80 | — | — | 120 | 130 |

83 The body tapers very little anteriorly, narrowing less than twofold from the end of the esophagus to the front, so that it seems very stout and truncated. The middle of the body is quite swollen, more so in the female. The body tapers to the anus in the male very slightly, and almost twofold in the female. The thickness increases somewhat with growth, so that the longer specimens are relatively stouter (cf. formulas). The **cuticle** is $5-6\,\mu$ thick, smooth; layers of crossing fibers are observed only anteriorly. Several layers of cuticle are noted, the outer being about $^1/_4$ of the overall thickness and more compact. The inner layer divides further into secondary layers. The body is beset all over by numerous long thick bristles.

The **structure of the head** is very similar to that of E. communis Bastian as described by de Man (1886). Although for the most part I need only reproduce the data from this excellent description, I nevertheless shall give a more detailed account of my own species, so that when dealing with the structure of Enoploides and Enoplaimus it will not be necessary to refer to an extraneous source. Three large lips are observed anteriorly to the head enclosing the oral aperture (lab. — Figure 10a). Each lip consists of thicker lateral parts and a thinner median part, is stouter at the base and narrower at the end. A circlet of six labial papillae lies posterior to the lips. The papillae are well developed and project as mounds over the surface of the head (p. lab. — Figure 10a). There are ten cephalic bristles, six $24\,\mu$ long, and four shorter submedian bristles $19\,\mu$ long. The lateral organ is very small lying somewhat ventrally to the lateral bristles. It is oval, cyathiform, with an anterior aperture. Its length is about $9\,\mu$, width $5\,\mu$, equalling $^1/_{12}$ to $^1/_{14}$ of the corresponding diameter of the body. There is an additional special organ — a slit lying ventrally to the lateral bristles [cephalic slit] (fis. ceph. — Figure 10a). The lips seal the entrance to
84 a small vestibule, which passes to a fairly large funnel-shaped oral cavity circumscribed laterally by three jaws. Each jaw (gn. — Figure 10a) is a curved formation with two points at the end. Only the margins of the jaw are of homogeneous structure; a cross-hatching caused by small canals that pass through the jaws is observed. The length of the jaws is $33-34\,\mu$. The true cephalic capsule (c. ceph. — Figure 10a) is homologous with the cephalic capsule of Thoracostoma and Deontostoma, and is a chitinized ring bending around the pharynx at the level of the anterior end of the jaws. This ring sends off processes — thickenings on the internal lining of the esophagus — directed to the base of the jaws. Another, external, cephalic capsule is homologous with the striated capsule of Phanoderma and extends posteriorly as far as the cephalic line (l. ceph. — Figure 10a) and is simply a modification of the lower layer of cuticle. The structure of the **esophagus** has been described in detail by Rauther (1907). Along the esophagus parallel to the angles of its lumen run pigmented chords of plasma which are the result of the fusion of the ectodermal cells of the esophagus. Processes extend from these chords along the surface of the esophagus to the middle of its sectors. The most anterior process of the dorsal half of the subventral, laterally-disposed sectors is particularly well developed and constant (oc. — Figure 10a). It has an extended transverse form with some irregular thickenings and curves. This is the **eye**, which here is of extremely simple structure — a pigment cup with no lens. Its width is $16-20\,\mu$, length $8-11\,\mu$, depending on the individual. The distance from the eye to the anterior end is equal to the head width. The esophageal glands open under the jaws, half way along them, as Rauther observed (1907). The **nerve ring** is very narrow and hardly noticeable. The **cervical gland** is quite large, pyriform, and located at the level of the posterior part of the esophagus. The **excretory pore** lies three-quarters of the distance from the anterior end to the nerve ring. The **intestine** is in adults sometimes highly pigmented; in young it is usually clear. One young specimen found in mellina ooze from the Chernaya River had a completely black intestine and esophagus due to the accumulated pigment.

The **ovary** is long, straight, and the deposition of the vitelline granules
85 occurs in several eggs simultaneously. The oviduct has fairly thick walls consisting of a few large cells. The uteri of both sides are fused into one, with a thick wall. The eggs are $120\times130\,\mu$, the shell attains $4\,\mu$. The vagina is short, about $^1/_5-^1/_6$ of the body width. Its walls around the gonopore have chitinized stiffenings.

The internal male organs do not differ from E. communis Bastian.

The **spicules** (Figures 10d, e) are of the ribbed type, $145\,\mu$ long. They curve uniformly and gradually in a very characteristic arch, and are pointed at the end. There is a small manubrium at the base; a lateral chitinized fold begins in its posterior quarter running obliquely posteriorly. Between the middle and posterior third of the spicules 4—5 ribs are located. On closer investigation these ribs prove to be thin plates that cover the entire lower half of the spicule or some part of it (Figures 10d, e). The **gubernaculum** has a very characteristic shape, consisting of two lateral parts (a — Figures 10d, e) and a median unpaired part (b — Figures 10d, e). Its overall length is $60\,\mu$. The lateral parts consist of thick rolls of irregular form. On the upper end there are two processes, one running upwards and the other downwards from the spicules (c, c — Figure 10d). These lateral parts are constructed of thick chitin. The middle part consists of thin chitin and is irregularly saddle-shaped, connecting the two lateral parts (b — Figures 10d, e). The form of the gubernaculum is very characteristic and distinguishes E. euxinus from the other species studied. The **accessory organ** lies in front of the anus at a distance from it hardly exceeding the length of the tail. It is tubular with a funnel inside and an aperture at the end, is directed posteriad, and is $60\,\mu$ long. The ventral (anterior) wall covers a larger part of its gland than does the dorsal (posterior) wall. The supplementary bristle armature
86 comprises two long slender bristles immediately behind the anus ($s_1$ — Figure 10c), followed by some preanal elevations of cuticle furnished with sensory papillae (p. — Figure 10c), and finally a row of 10—12 long,

slender bristles running subventrally from a point not far behind the anus to the accessory organ ($s_2$ — Figure 10c).

The **tail** of the male and the female is approximately of the same form: it tapers conically to the end, sharply in the basal half and gradually in the terminal half. In the male the end is more slender than in the female and the tail is shorter. In the female the tail appears longer because the body narrows greatly around the anal pore. The caudal glands are small, pyriform, and located within the tail. The caudal pore pierces the cuticle as a cone, and the cuticle is somewhat thickened at the end of the tail.

The proportions at the posterior end are: length of tail of male 2.4, of female 3.0; width of tail at end of male 0.12, of female 0.16; length of spicule 1.4; gubernaculum 0.6; distance from anus to accessory organ 2.5.

E. euxinus is one of the most common nematodes of the Black Sea, being distributed over all its facies where there are merely algae, upon which they feed. I found adult E. euxinus in superficial facies only in winter; in the summer there were only young. In phaseolin mud and in deeper oxeas sand of the Georgievskii Monastery adults were found in the summer also, apparently owing to the lower temperature that predominates constantly there.

**Rock facies**: Mussels from rocks under the station 6.12, juveniles ∞; mussels from piles 1.12, adults ∞; Cystoseira 5, 7.12, many in all samples from various depths; stone algae 7.12, juveniles ∞; clay with incursions of Barnea, from the cordon on the North Side 7.13 juveniles ∞.

**Sandy facies**: Peschanaya Bay 1.12, 6.12, 7.12, 8.13 juveniles, few, coastal sand at the same place 6.12, 1 young. Sand, 9 sajenes, Georgievskii Monastery, juveniles. Dirty sand from under wharves of R.O.P. and T.* 1.12 adult male; Oxeas sand, 18 sajenes, Georgievskii Monastery 7.12, adult male and female.

87 **Coquina**: Georgievskii Monastery 7.12, some adults; oysters 6.12, young.

**Seaweed facies**: Ulva New Holland 6.12, young. Zostera 5.12, young. Phyllophores 6.12, very many young.

**Muddy facies**: sediment washed from Nassarius from mud of Artilleriiskaya Bay 1.12, young; mellina ooze from Chernaya River 6.12, young. Phaseolin mud from Georgievskii Monastery 7.13, young and semi-adult males.

E. euxinus n.sp. belongs to the group of Enoplus with indented spicules and is differentiated from the majority of them by the longer tail. In E. tridentus Dujardin the jaws are far shorter, judging from the description. However, it is possible that this feature will prove to be incorrect and the two species will be recognized as identical.

### 11. **Enoplus littoralis** n.sp.

(Table 2, Figure 11)

♂ (young) $\dfrac{-\quad 5.8\quad 10.8\quad ?\quad 95.4}{1.4\quad 2.5\quad 2.6\quad (3.0)\quad 2.7}\ 2240$

$$\alpha=33;\ \beta=9^1/_2;\ \gamma=19.$$

♀ (semi-adult) $\dfrac{-\quad 5.9\quad 16.8\quad 20\quad 31\quad 35\quad 51\quad 63.5\quad 94.3}{1.5\quad 2.8\quad 2.9\qquad\qquad\qquad 3.2\qquad\qquad\qquad 2.5}\ 2600$

$$\alpha=30;\ \beta=6;\ \gamma=17^1/_2.$$

---

* [A former steamship company.]

| ♀<br>2,600 $\mu$ | Labial bristles | Cephalic bristles | End of jaws | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | — | 12 | 17 | 125 | 210 |
| Width | 16 | 30 | 32 | 58 | 61 |

This species in the adult state is probably no more than $3^1/_2$ mm long, thus considerably shorter than E. euxinus. The **body** hardly tapers anteriorly and posteriorly, especially in the male, in which it is almost of uniform diameter from the nerve ring to the anus. In the female it swells somewhat in the middle and tapers to the tail. The width of the head is
88 almost twice greater than the body width at the nerve ring. The **cuticle** is 3 $\mu$ thick, and consists of two layers; the inner layer is thicker and indistinct signs of annulation are seen at its border with the outer. A few bristles are observed over the body.

The **head** is considerably shorter than in E. euxinus and the like, is reminiscent of E. brevis Bastian (de Man, 1886) in the position of the cephalic line, but still shorter than the latter. The elevations upon it are less pronounced than in E. euxinus, and because of this it appears more regularly rounded. It is separated from the trunk by the somewhat wavy cephalic line, which corresponds to an annular depression (l. ceph. — Figure 11a). The lips are considerably shorter, do not break the overall roundness of the head, and are in general constructed as in the foregoing species; the anterior plate is extremely thin and transparent. The labial papillae (p. lab. — Figure 11a) are six in number and protrude less than in E. euxinus. There are ten cephalic bristles, the length of the six larger ones is 9 $\mu$ and of the four smaller sublaterals $7^1/_2\mu$. The lateral organ is cyathiform, its length is 6 $\mu$, width 5 $\mu$ ($^1/_7$ of the width of the head), its anterior aperture $2^1/_2\mu$. It is intersected by the cephalic line. The internal structure of the head is as in the other members of Enoplus.

The **jaws** in this species are very small, only 14 $\mu$ long, which is less than half the width of the head at the level of the cephalic bristles. Owing to this the length of the oral aperture and the size of the cephalic capsule are very small. The subcuticular capsule is also shortened owing to the short head.

**Eyes** are absent and the esophagus is unpigmented. The **esophagus** is regularly cylindrical, expanding slightly posteriorly, and is not so well developed as in most forms of Enoplus; sufficient space is left for the organs of the esophageal part, which are not displaced to the cuticle. In respect of this the nerve ring also is here relatively thicker than in
89 other forms of Enoplus. The **cervical gland** lies normally, in the posterior part of the esophagus; the excretory pore is located anterior to the nerve ring. The **intestine** consists of numerous cells and is unpigmented.

I do not describe the structure of the female and male internal genital organs since there were only immature specimens at my disposal.

The **spicules** are of the smooth type (Figure 11d), of length (in a male 2,600 $\mu$ long) 73 $\mu$, curving gradually. The base is expanded, the following part is narrow; then there is a slight widening once more, and finally a pointed end. The **gubernaculum** (Figures 11d, e), as in E. euxinus, has lateral and median parts. Its overall length is 32 $\mu$. The lateral parts are more exposed than in E. euxinus, being not tubular but in the form of irregular plates that do not completely cover the ends of the spicules. At the end of these pieces the same spirals are observed as in E. euxinus. A thickening occurs on the median parts that join under the spicules (a—Figure 11e). The accessory organ in the male is 24 $\mu$ long and has the form of a short tube with thickened borders at the base (Figure 11f). Four large, stout supplementary bristles are present posterior to the anus in addition to the usual rows of 10—15 bristles lying subventrally between the anus and the accessory organ. Some bristles are found on the tail, mainly laterally.

The **tail** is far shorter than in E. euxinus. Its base is far narrower in the female, while the end of the tail is narrower in the male. The proportions at the posterior end are: tail length of male 1.8, of female 2.5; width at end of tail of male 0.2, of female 0.25; length of spicules 1.2; gubernaculum 0.6; accessory organ 0.4; distance from anus to accessory organ 1.2.

This species is very common in Peschanaya Bay in coastal dead seaweed and in the sand under it, along the high water mark where other species are not located. I did not come across 6 and 7.12 adult specimens, since they probably mature in the winter.

90 E. littoralis n.sp. is a close relative of E. brevis Bastian, but is distinguished from it by several minor features (see key).

## Genus ENOPLOIDES Saveljev 1912

Tr. Soc. Imp. Nat. St. Pétersbourg 43 livr. 1, p. 113.
Enoplus ex p. Bütschli 1874, Abh. Senck. Ges. 9, p. 40.

Type species: E. murmanicus Saveljev 1912

The members of this genus are medium-sized and small nematodes, often quite stout. The cuticle is usually finely annulated. The three lips are strongly developed such that a very broad oral aperture is obtained with angles reaching far posteriorly. At the sides of each lip there is a transversely striated plate (like a row of bristles fused together) which tightly seals the mouth when the lips are closed. The labial bristles, which here replace the labial papillae, are set in pairs on each lip. There are ten cephalic bristles. The lateral organ is very small, cyathiform, lying immediately behind the lateral cephalic bristles. The oral cavity is wide, bordered by three movable jaws furnished with two (rarely three) points at their ends and split deeply at their base. In the fork thus formed there lies a tooth homologous with the tooth in Oncholaimini, on which the duct of the esophageal gland opens. Sometimes it is highly developed, and sometimes there are only insignificant traces of it. Special chitinized plates lie in the space between the jaws. The entire oral armature is surrounded by the narrow chitinized ring of the cephalic capsule. The esophagus has a wavy outline and a characteristic structure: plasmatic parts are interstratified with bundles of muscle fibers. The ovaries are reflexed; there are two testes. The spicules in some species are very long, in others they are short, in all cases ornamented on the surface. The gubernaculum is insignificant. There is a preanal tubular accessory organ, as in Enoplus, but less developed.

91 This species, as Savel'ev notes, is an intermediary between Enoplus and Enoplolaimus. It is similar to the former in the presence in it of true movable jaws with hooks at their ends, which in Enoplolaimus are converted into special immovable bars. Two processes extend from the posterior end of these bars as from the jaws of Enoploides; a tooth lies between the processes. The strong development of the cephalic bristles is similar to that in Enoplolaimus. The structure of the lips is unique.

The first species of this genus was described as Enoplus labiatus Bütschli 1874. Savel'ev (1922) characterized this genus accurately and described four new species from Murmansk. I add here four Black Sea species.

Thus, the following nine species are known:

1) E. typicus Saveljev 1912: Tr. Soc. Imp. Nat. St. Pétersbourg 43, No. 1, p. 115. Mud from the Kola Gulf. 70—80 m.
2) E. amphioxi n.sp., see p. 64.
3) E. hirsutus n.sp., see p. 67.
4) E. brevis n.sp., see p. 69.
5) E. labiatus Bütschli 1874; Enoplus L.: Abh. Senck. Ges. 9, p. 41, Table 9, b—Figure 36a. Oyster banks at Sylt (Skaggerak).
6) E. tridentatus Saveljev 1912 loc. cit. p. 114. Kola Gulf.
7) E. murmanicus Saveljev 1912 loc. cit. p. 115. In muddy sand with stones at some meters in Ekaterininskaya Harbor.
8) E. pellucidus Saveljev 1912 loc. cit. p. 115. Kola Gulf. Mud at 70—80 m.
9) E. cirrhatus n.sp., see p. 70.

It is possible that the first six species, provided with long spicules, should constitute a new genus. It is also possible that a separate genus should serve for E. tridentatus Saveljev. The toothless E. amphioxi n.sp. may also constitute a special genus. I shall not make these changes until the problem is conclusively clarified.

1 (2). Three points on each jaw. Body tapers twofold from midbody to cephalic bristles and to anus. Cephalic bristles $^1/_5$ of width of head. Distance between points of jaws $1^1/_2$ times greater than their maximum width. . . . . **E. tridentatus** Saveljev
2 (1). Two points on each jaw.
3 (4). Cephalic bristles twice shorter than width of head. Distance between points of jaws twice greater than their maximum width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. brevis** n. sp. 92
4 (3). Cephalic bristles very much smaller than half width of head.
5 (8). Tail thickened at end into form of club.

6 (7). $2\frac{1}{2}$ mm. Cephalic bristles at beginning very thick, then narrow sharply, longer than width of head. Spicules $1\frac{1}{2}$ times longer than tail . . . . . . . . . . . . . . . . . . . . . . . . . **E. typicus** Saveljev
7 (6). $5\frac{1}{2}$ mm. Cephalic bristles evenly pointed, shorter than width of head. Spicules twice longer than tail. **E. amphioxi** n. sp.
8 (5). Tail not thickened at end.
9 (12). Cephalic bristles equal or almost equal to width of head, labial bristles about half. Jaws widely divergent posteriorly.
10 (11). Lips very greatly extended anteriorly. Cephalic bristles somewhat shorter than width of head. Circlet of supplementary bristles not very dense and bend far posteriorly. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. labiatus** (Bütschli)
11 (10). Lips not very greatly extended. Cephalic bristles somewhat longer than width of head. Circlet of supplementary bristles very abundant and lies immediately behind main circlet . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. cirrhatus** n. sp.
12 (9). Cephalic bristles half width of head, labial bristles far shorter. Jaws not greatly divergent posteriorly. Numerous bristles on body.
13 (14). Body of uniform diameter for almost entire extent. End of tail $\frac{1}{4}$ of width at anus. Distance between points of jaws twice their width. Spicules $\frac{1}{5}$ of tail . . . . **E. murmanicus** Saveljev
14 (13). Body narrows sensibly to end.
15 (16). Cuticle very thin. Tail at end $\frac{1}{3}$ of width at anus. Hooks extend for 3 times width of jaws. . . . . . . . . **E. pellucidus** Saveljev
16 (15). Cuticle not very thin. Tail at end $\frac{1}{6}$ of width at anus. Hooks extend hardly twice width of jaws. Spicules $2\frac{1}{2}$ times longer than tail . . . . . . . . . . . . . . . . . . . . . . . . **E. hirsutus** n. sp.

### 12. **Enoploides amphioxi** n. sp.

(Tables 2, 3, Figure 12)

$$\text{♂}\ \frac{—\quad 5.6\quad 18.0\quad 32\qquad 42\quad 55\quad 96.1}{1.4\quad 1.9\quad 1.9\qquad (1.9)\qquad 0.9}\ 5400$$

$$\alpha=51.\ \beta=5\tfrac{1}{2},\ \gamma=26.$$

$$\text{♀}\ \frac{—\quad 8.0\quad 17.5\quad 37.5\quad 47.5\quad 53.5\quad 59.5\quad 71.5\quad 94.3}{1.7\quad 2.3\quad 2.7\qquad 2.9\qquad 1.3}\ 5250\ \ (4800—5600)$$

$$\alpha=35,\ \beta=5\tfrac{1}{2},\ \gamma=17\tfrac{1}{2}.$$

| Dimensions ♀ | Labial bristles | Cephalic bristles | End of jaws | End of anterior thickening of esophagus | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | – | 40 | 75 | 120 | 660 | 990 |
| Width | 60 | 90 | 115 | 120 | 115 | 145 |

93 The **body** is fairly stout, narrows anteriorly less than twofold, so that the head is very wide. The narrowing occurs entirely in the esophageal region. The body narrows more than twofold to the anus and thus appears to be generally of even thickness. Males are thinner, and of uniform width from the nerve ring to midbody; the body narrows twofold to the anus. The **cuticle** is relatively thin ($4\frac{1}{2}\mu$) and double-layered. The outer layer is thin, the inner thick. In profile, indentations are seen along the boundary with the subcuticle, indicating a very fine annulation. Long slender bristles are observed over the entire body in fairly large numbers.

The **head**, as already stated, is very wide and separated from the neck by the cephalic line. Owing to the strong development of the musculature it seems more expanded than the neck. Anteriorly, the lips and the labial bristles project from it and create a complex outline, which at first is understood with difficulty. The lips (lab. — Figures 12a, b) are very complex. Their overall height from the end of the jaw to the anterior end is 22μ, and from the oral angles 46μ. The anterior part of the lips is compressed (lab. — Figure 12a) into a thin plate furnished with ornamented thickenings; the lateral parts (lab. — Figure 12b) are thin, transversely striated plates which appear to be composed of rows of bristles stuck together. When the lips are closed, these plates tightly seal the entrance to the oral cavity; they extend almost from the anterior tip of the lip to the angles of the broad oral aperture. The labial bristles (s l — Figure 12a) are set in pairs on each lip anterior to the angles of the mouth and replace the labial papillae of the majority of nematodes. These bristles are thick, 24μ long, and evenly pointed to the end. They are provided with longitudinal ridges and depressions that impart an irregular form to them in cross section.

94 The ten cephalic bristles lie more posteriorly; the six longer are 50μ long and the four shorter sublaterals are 24μ long. The tiny lateral organ measures $7\frac{1}{2}\times 6\,\mu$ (Figure 12c) and is disposed somewhat ventrally and posteriorly to the lateral bristles. It is constructed as in Enoplus: cyathiform, with an internal cavity and a small oval orifice anteriorly, and encircled by a rim of specially converted cuticle, also as in Enoplus.

The **oral armature** is very complex. It consists mainly of three jaws similar to those of Enoplus and supporting, also as in Enoplus, the three sectors of the esophagus (mand. — Figures 12a, b, e, f). The length of each jaw in fully adult specimens is 55—60μ. At its end each jaw bears two hooks that curve inwards (a — Figure 12e). Two pairs of processes are observed in the middle, the anterior pair shorter but more highly chitinized (p. a. — Figure 12e) than the posterior pair (p. p. — Figure 12e). In the middle of the posterior two-thirds of the jaw there is a depression with highly chitinized edges. At the anterior tip, in place of and homologous with the tooth which is present in other species, there is only a small chitinized tube that opens internally (d — Figure 12e). Within the posterior part of the tooth there are hollow spaces and the structure of the entire internal part is fibrous. At the base of the jaw I observed a chitinized structure (a — Figure 12a), probably belonging to the inner lining of the esophagus.

The **cephalic capsule** rings the skeleton of the jaws, as in Enoplus, but it is more powerfully developed than in the latter and of complex structure. It is a thick chitinized ring with a scalloped outline

(c. ceph. — Figures 12a, b) that narrows opposite the jaws and over the angles of the mouth and widens between these points. Its posterior margin (b — Figure 12a) bears an enlargement, which at first seems to be a completely separate
95 narrow ring. The anterior broad part (c. ceph. — Figure 12a) sometimes has an internal structure composed of separate granules interspersed in a less compact substance. A pointed tongue of this structure extends in the internal layer of the cuticle and posteriorly. Pieces such as this are also present opposite the jaws in the superficial cephalic capsule. At the narrowest points, opposite the jaws (c — Figure 12a), there is a small expansion. Processes from the central parts of the jaws are attached to the capsule (d — Figure 12b). Another chitinized structure is present in the spaces between the jaws. It is attached by one of its sides to the capsule and to the oral musculature by the other (e — Figure 12b). Apart from these structures there is a row of chitinized shields of various shapes on the esophagus at the level of the jaws and posterior to them.

The **esophagus** is highly muscular and occupies almost all the body cavity anteriorly. Special muscles that move the oral armature give rise to an expansion on the esophagus in that region; the outline is straight. More posteriorly, the structure of the esophagus changes completely: its outline becomes sinuous and plasmatic chords become strongly developed. These chords lie at the boundary of the sectors of the esophagus and run in the form of twisting lines, sending off processes to both sides. They probably mark the boundary of the muscle cells that compose the esophagus, as Bütschli thought as early as 1874, on the basis of his observations of E. labiatus. The esophageal glands are contained in the esophageal wall. Anteriorly, there are special reservoirs for them (gl. oes. — Figure 12b) from which a narrow duct (not drawn in the figure) runs forward and discharges into the hollows of the jaws. The nerve ring is thin because of the great development of the esophagus. I am unable to describe the **excretory gland** in detail, but it apparently lies opposite the posterior part of the esophagus, as in Enoplus. The **intestine** consists of numerous cylindrical cells.

96 The **ovaries** are paired and reflexed. In the extreme terminal parts the oocytes are packed like coins, perpendicular to the longitudinal axis of the animal. Longer oocytes disposed further from the central part of the genital tract stand obliquely to it. Their ventral edge remains attached to the wall, while the dorsal edge becomes detached and is drawn out into the free chamber of the ovary. The long, curved egg so formed separates entirely after ripening, takes on a round form, and passes into the uterus. The oviduct has thick walls. A special hollow organ lies anterior to the uterus: it is small and oviform, and its walls consist of densely packed crescent cells arranged in two rows; this is a modified section of the oviduct. In young individuals the gradual thickening and transformation of the oviduct into this organ are noted, while in old specimens the thickening is more pronounced. The function of the organ may be to form the shell of the eggs. The uterus is thin-walled; the eggs measure 300×100 μ, with a thick shell. At the end of each uterus there is a piece of thickened cuticle to which the very thick-walled and muscular vagina is attached; the latter organ traverses $^2/_5$ of the body width.

The testes are paired, straight, and long, and the sperm are about 5 μ in diameter. The spicules are very long — 500 μ and longer — i.e., an average of about 10% of the total body length. Figure 12d illustrates the three different parts of the spicule in uniform enlargement. At the base there is a slightly developed knob (a — Figure 12d) lying laterally, approximately at midbody. The spicule then curves upwards and its structure changes: it becomes indented with small transverse notches on its surface, giving the impression of spines in profile (b — Figure 12d). More posteriorly, the spicule once more becomes smooth and an extremely characteristic hook is observed at the tip (c — Figure 12d). The **gubernaculum** (gub. — Figure 12d) is a paired organ consisting of two characteristic tubular bodies on each side of the anal aperture. Its length is 65 μ. Each of the bodies is S-shaped, has an irregular internal cavity, and is thrust out of the orifice of the cloaca together with the spicules
97 during copulation. The accessory organ is 35×8 μ long and not always uniform: it is generally a tube directed slightly anteriorly from the aperture. In the supplementary bristle armature of the male the first organs that are evident are two claws behind the anus which are capable of bending anteriorly (d — Figure 12d). Subventrally and posterior to them are some ordinary bristles, but not in a continuous row as in Enoplus. Such bristles are also present preanally. In addition, bristles are present at the end of the tail in both sexes. The proportions at the posterior end are: length of tail 4.2; width at end 0.4; length of spicules 12.5; gubernaculum 1.0; accessory organ 0.7; distance from latter to anus 3.5; from anus to claws 0.7.

The tail in the male and female is uniform: it tapers sharply from the base to the middle, then widens gradually once more to the end. The caudal glands are bulb-shaped and do not extend beyond the tail. The caudal pore is short since the cuticle at the end of the tail is thin; there is a small cone in front of it (see Figure 12d) which is sometimes lost. In this case an artificial empty space appears on the end of the tail.

E. amphioxi is one of the most common nematodes, particularly frequently encountered in oxeas sand. In life it is very mobile, continually curling and straightening its body. It is quite transparent and only ripe or ripening eggs are visible as white spots. It reaches sexual maturity apparently in the summer. The nematodes were found only in oxeas sand, except for one chance specimen in Cystoseira from Shmit Bay 6.12. Peschanaya Bay 5.12, adult and young; 6.12 also; 7.13 also; 1.12, young. Georgievskii Monastery: sand at 9 sajenes 7.12, numerous; sand at 18 sajenes 7.12, numerous; sand at 12 sajenes 7.12, 13, numerous.

### 13. **Enoploides hirsutus** n.sp.

(Table 3, Figure 13)

$$\male\ \frac{-\quad 9.5\quad 26.3\quad ?\quad 94.2}{1.6\quad 3.2\quad 4.0\quad 4.2\quad 1.8}\ 2850$$

$$\alpha = 24;\ \beta = 3.8;\ \gamma = 19.$$

98

| Dimensions ♂ | Labial bristles | Cephalic bristles | Cephalic line | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | – | 22 | 55 | 70 | 265 | 765 |
| Width | 30 | 51 | 65 | 70 | 95 | 115 |

The **body** widens slightly from the nerve ring to midbody; it narrows anteriorly more than twofold and posteriorly very gradually, $2^1/_2$ times to the anus. The **cuticle** is thin ($4\mu$), double-layered, both layers being quite smooth. Numerous bristles cover the entire body; they are uniformly slender, reach $6\mu$ in length and less than $1\mu$ in thickness.

The **head** appears generally pointed if the upright bristles are disregarded. The lips are quite high and thicker than in E. amphioxi (lab.—Figure 13a). As in that species, the angles of the mouth cut further back and the margins of the lips form thin, transversely striated plates that seal the oral aperture. The labial bristles are thick and coniform, much shorter than in E. amphioxi, only $8\mu$. The cephalic bristles are disposed somewhat differently: both the laterals are thicker and shifted anteriorly, and are $27\mu$ long. The four sublaterals are $23\mu$ long and lie posterior to the four longer submedials. The lateral organ is very small, as in E. amphioxi, elongate, measuring only $4 \times 3^1/_2\mu$, which is about $^1/_5$ of the corresponding diameter of the body. Anteriorly, there is a small orifice and a fairly long chitinized tube containing its nerves joins its posterior edge.

The **oral cavity** extends behind the end of the jaws. It is $70\mu$ long, as measured from the end of the lips, and $37\mu$ wide. The three large jaws ($34\mu$ long) have two hooks at their anterior ends, while on the posterior end there are deep incisions through which three small teeth project into the oral cavity. The right subventral tooth is larger than the other two (d. subv.—Figure 13a). The internal cephalic capsule consists of a ring which encircles the jaws approximately half-way along them (c. ceph.—Figure 13a). Apart from this, broken but thicker rings of stiffenings
99 lie opposite the angles of the mouth, but they are of a different form than in E. amphioxi. In that species they are closely adjacent to the posterior end of the cephalic capsule, while here they are more or less free. Almost the entire thickness of the cuticle in front of the cephalic line is chitinized and converted into a superficial cephalic capsule. To this are attached the circular muscles that move the esophagus (x—Figure 13a). Anteriorly, processes of the internal cephalic capsule are attached between these muscles. A circlet of bristles lies along the posterior margin of the capsule.

The **esophagus** is more weakly developed than in E. amphioxi. I can say nothing about the cervical gland. The female is unknown.

The **spicules** are long and stout (Figure 13b), $425\mu$ long. They are thickest at the base where they widen into a knob. They then narrow gradually and are pointed at the end (Figure 13c). Their wall at the base is thin, but it thickens so much to the end as to almost occlude the internal canal. The entire surface of the spicules is rough. The **gubernaculum** is $43\mu$ long, unpaired, flat, and covers the ends of the spicules above and below. A thick plate lies above, triangular in outline, running as far as the anus; below, the plate is thinner (Figure 13c). The accessory organ is small, in the form of an irregular tube, with an aperture at the posterior end. It is $43\mu$ long (org. acc.—Figure 13b); its gland is small. The supplementary bristles are two large postanals on the anterior quarter of the tail, corresponding to the claws of E. amphioxi. Two smaller bristles are set in front of them (s.—Figure 13b). In addition, the entire tail is covered with small hairs (cf. Figure 13d, the drawing of the end of the tail).

The tail tapers evenly and greatly to the last quarter, after which there is a portion of uniform diameter, while at the extreme tip the tail becomes pointed and the cuticle very thin. No cone projects into the cuticle.

The proportions at the posterior end are: length of tail 3.2; width at end 0.12; distance from anus to claws 0.6; anus to accessory organ 3.0;
100 length of spicules 8.3; gubernaculum 0.8; accessory organ 0.8.

There was only one male; it had developed genital organs but was apparently still not fully mature. Phaseolin mud of Georgievskii Monastery 7.13.

## 14. **Enoploides brevis** n.sp.

(Table 3, Figure 14)

$$\text{♀ (immature)}\ \frac{— \quad ? \quad 27 \quad 41 \quad 56 \quad 76 \quad 95.3}{3.3 \quad ? \quad 6.0 \qquad 6.0 \qquad 2.7}\ 2270$$

$$\alpha = 17;\ \beta = 3.7;\ \gamma = 21.$$

| | Cephalic bristles | Cephalic line | End of jaws | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 25 | 45 | 70 | 330 ? | 515 |
| Width | 70 | 87 | 100 | 120 | 120 |

The width in the formula and table is quite large as the specimen was compressed.

The **body** of this species is short and stout, tapering almost twofold anteriorly and to the anus, greatly to the latter.

The **cuticle** is $3-4\mu$ thick with a slight annulation on the boundary of the internal layer and the epidermis, the intervals between the annules being $1^1/_2\mu$; the outer layer is the thinner. The bristles are short and slender, and are observed in small numbers all over the body.

The **head** is on the whole conically pointed, as in the other members of Enoploides, but the lips break its regularity. They are more weakly developed than in the two preceding species. The labial bristles here are $8\mu$ long, which is shorter than in the forgoing species. The cephalic bristles are also shorter, the sublaterals more than twice shorter than the rest (26 and $12\mu$); they are considerably more slender. The lateral organ is located immediately behind the lateral bristles; it is small, round, $5\mu$ in diameter. A fairly voluminous conical **oral cavity** is $70\mu$ deep, as measured from the end of the lips. There are three jaws in it which are even less developed than in E. hirsutus m. They bifurcate at the posterior end; their length is $56\mu$. There are probably also three teeth,
101 projecting through the fork of the jaws. Three plates, wider anteriorly and narrow posteriorly, are located between the jaws

(a—Figure 14a). Anteriorly, each of them bears two small processes directed to the lips. The jaws and plates are encircled by the thin ring of the cephalic capsule; against the plates it curves posteriad and forms thickenings. Powerful muscle bundles are attached to the ring. The bristles at the end of the cephalic capsule are present here also, and are very slender and short.

The esophagus is stout and of the same structure as in the other forms of Enoploides, but there is no specialized part anteriorly that moves the jaws; it does not expand posteriorly.

The ovary is short.

The **tail** is short compared with the body length, and conical (Figure 14b); the terminal filiform part was broken off. The length of the conical part is twice greater than the width, while the width at the end is $^{1}/_{7}$ of the width at the base. The caudal pore is provided with thick bristles along the sides.

I had only one female with developed genital tract but without eggs: mussel mud, Kacha River 8. 13.

### 15. **Enoploides cirrhatus** n.sp.

(Table 3, Figure 15)

$$♂\ \frac{4.1 \quad 19.0 \quad ? \quad 93.8}{1.0 \quad 1.6 \quad 2.0 \quad 2.4 \quad 1.4}\ 4350$$

$$\alpha=26;\ \beta=5^{1}/_{4};\ \gamma=16.$$

| | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 26 | 36 | 185 | 740 |
| Width | 44 | 51 | 68 | 86 |

The **body** tapers slightly to the end of the esophagus, twofold to the head from the end of the esophagus, less than twofold to the anus. There are numerous long bristles.

The **head** appears pointed owing to the prominent lips, as in the other
102 forms of Enoploides (Figure 15a). The lips are as in the other Enoploides, i.e., fairly thick, with small transversely striated areas in the angles of the mouth only and thicker areas elsewhere along the margins of the mouth. The labial bristles are long (13 μ) and pointed. The ten cephalic bristles are very long, reaching 40 μ, which is almost the diameter of the head. They are followed by a circlet of at least 20 bristles, some of them as long as the cephalic bristles. I could not distinguish the lateral organ.

Inside the voluminous **oral cavity** (36 × 18 μ) there are three jaws, which are weakly developed in this species (Figure 15b). They are 21 μ long. The posterior processes bifurcate; the anterior points are slightly separated, the space between them being twice greater than the width of the jaw. Three teeth project through the forks of the jaws; the left subventral is the longest and stands 17 μ from the bottom of the oral cavity; the other two are shorter, rising 14 μ from the bottom.

The entire oral cavity is encircled by a chitinized ring, which is wider opposite the angles of the mouth and narrower opposite the jaws. I was unable to distinguish other chitinized parts. The outline of the esophagus is wavy, as in the other species, but here the organ is very narrow, occupying posteriorly less than half the thickness of the body. Its glands are well developed, and their junction with the teeth of the oral cavity is clearly discernible. At the end of the chitinized part of the tooth they expand (gl. oes.—Figure 15a). The **nerve ring** is shifted far anteriad, encircling the esophagus over its anterior quarter or fifth.

The **spicules** are 60 μ long. There is a funnel-shaped opening at the base and the walls are thinner at that part; they are thickest at the end, where the lumen narrows down to a slender canal. At the end of the spicule four cylindrical annular thickenings encircle it. The **gubernaculum** is very small (only 15 μ) and is adjacent to the spicule on the dorsal side; its upper edge is curved. Seven or eight papillae are located preanally in the midline. The posterior of these lies 14 μ from the anus, the distance between this and the following one is 25 μ, while the most anterior papilla is 60 μ from the penultimate.

103 The **tail** (Figure 15c) tapers evenly to the posterior third to $^{1}/_{4}$ of its width at the anus, and thence to the end it tapers twofold to $^{1}/_{7}$ of the width at the anus. The proportions at the posterior end are: length of tail 4.5; length of spicules 1.0; gubernaculum 0.27; distance from anterior papilla to anus 4.0.

This species was found in saccocirrous sand in Shmit Bay 7.12, three males.

This species is a close relative of E. murmanicus Saveljev and E. pellucidus Saveljev, but is easily distinguished from them by the pointed tail, the longer cephalic bristles, the preanal papillae in the male, and the small gubernaculum.

## Genus ENOPLOLAIMUS de Man 1893

Mém. Soc. Zool. France 6, p. 118.
Saveljev 1912: Tr. Soc. Imp. Nat. St. Pétersbourg 43, livr. 1, p. 110.

Type species: E. vulgaris de Man 1893

These are medium-sized worms, usually narrowing markedly anteriorly and to the anal aperture. The inner layer of the cuticle is slightly annulated: this may depend on the corresponding disposition of the punctations observed there. Three well developed lips are observed on the head, as in Enoploides, with the pair of labial bristles on each lip converted in this species to labial papillae. The ten cephalic bristles are always well developed. A cephalic line is present. Some bristles are set behind it, usually the same number in male and female. I was unable to detect the lateral organs in either of the species that I examined, but I think that the structures described by de Man as lateral organs in E. vulgaris de Man and E. australis de Man can hardly be considered as such. These organs consistently lie **behind** the lateral bristles, whereas here they are **in front** of them. By analogy with Enoploides, I think that the lateral organs here also are set immediately **behind** the lateral bristles, are very small, and their structure is as in Enoplus.

104 The structure of the mouth, which was described correctly for the first time by Savel'ev, is a distinctive generic feature. There are three bars, homologous with the jaws in Enoplus. Anteriorly, these give rise to two points projecting laterally, and posteriorly to two parallel processes projecting backwards. Between these processes there are three teeth of various or uniform size. The esophageal glands open on these teeth, as in Oncholaimini and Enoploides. All these structures are encircled by the ring of the cephalic capsule, which is narrower opposite the teeth but forms thickenings of various shapes opposite the angles of the mouth. The inner layers of the cuticle of the cephalic part are usually thickened, forming a superficial cephalic capsule, which is separated from the cervical region by the cephalic line. Eyes are lacking. The esophagus, as in Enoploides, has a strongly developed plasmatic part interstriated with muscles, owing to which the outline of the esophagus is wavy. The ovaries are paired and reflexed, the spicules short and curved. There is an accessory organ (which I could not find in E. conicus n.sp.). In E. conicus n.sp. a row of median preanal papillae is observed.

Genus Enoplolaimus is the most advanced member of subfamily Enoplini. The powerful development of the lips and disappearance of separate jaws are progressive features, while the structure of the esophagus is primitive. Savel'ev suggests the opposite direction of development, but it is difficult to envisage how the jaws could have developed from the bars, while the reverse is easily comprehended as the outcome of the powerful development of the terminal ducts of the esophageal glands.

This genus was established by de Man from one rather inaccurately described species from the North Sea. Savel'ev characterized the genus more accurately and described two new species. Two more species are added now.

Thus, the following six species are now known:

1) E. vulgaris de Man 1893: Mém. Soc. Zool. France 6, p. 119, Table 7, Figure 13; Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 104, Table 5, Figure 11—very common in the sand at Falmouth, Walcheren (de Man); Kola Gulf, Lake Mogil'noe (Savel'ev). I found some aberrant specimens in material from Vardö.

105 2) E. tenuicaudatus Saveljev 1912: Tr. Soc. Imp. Nat. St. Pétersbourg 43, livr. 1, p. 111—Kola Gulf, mud at 50—60 m.

3) E. dubius n.sp., see p. 74.

4) E. australis de Man 1904: Rés. voy. Belgica: Nématodes libres p. 17, Table 4, Figure 6.—On a crab: Orange Bay.

5) E. acantholaimus Saveljev 1912: Tr. Soc. Imp. Nat. St. Pétersbourg 43, livr. 1, p. 112—Kola Gulf, Ekaterininskaya Harbor, Olen'ya Bay—copepods with yellow mud, several meters.

6) E. conicus n.sp., see p. 73.

1 (4). All three teeth in oral cavity uniform.
2 (3). Tail narrows only twofold to end, not very long. Spicules short, gubernaculum flat, with upper edge curving posteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. vulgaris** de Man
3 (2). Tail very long, its posterior $^5/_6$ filiform, end slightly swollen. Spicules long, as long as tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. tenuicaudatus** Saveljev
4 (1). One of the teeth larger than the others.
5 (6). Cephalic bristles stout, almost as long as width of head. Tail very long, 10 times longer than width at anus, its posterior half filiform, $^1/_{4-5}$ width at anus . . . . . . . . . . . **E. dubius** n. sp.
6 (5). Bristles not longer than half width of head, comparatively slender.
7 (10). Bristles about half width of head.
8 (9). Only a few spines run into oral cavity from level of ring posteriorly. Bristles slightly longer than width of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. australis** de Man
9 (8). These spines numerous (14—15). Bristles somewhat shorter than half head width . . . . . . . . . . . . . **E. acantholaimus** Saveljev
10 (7). Bristles about three times width of head . . . . . **E. conicus** n. sp.

### 16. **Enoplolaimus conicus** n.sp.

(Table 3, Figure 16)

$$\text{♀}\ \begin{array}{ccccccccc} & 6.4 & 19.2 & 43 & 47 & 53 & 58.5 & 64 & 92.8 \\ \hline 0.8 & 2.0 & 3.2 & & & 3.6 & & & 1.6 \end{array}\ 3780$$

$$\alpha = 28,\ \beta = 5,\ \gamma = 14.$$

| | Cephalic bristles | Cephalic line | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 12 | 30 | 40 | 225 | 700 |
| Width | 30 | 45 | 50 | 80 | 120 |

The **body** narrows uniformly and conically anteriorly and posteriorly, its maximum narrowing in the region of the esophagus—fourfold from the end of the esophagus to the cephalic bristles. The tail is more than twice narrower at the base than the body at midbody. The **cuticle** is very thin

106 $(1^{1}/_{2}\mu)$, completely smooth, thickening somewhat anteriorly, where its double contour becomes noticeable. Very short bristles are observed over the entire body. The **musculature** is very powerful.

The **head** has a generally irregularly pointed form. There are three low lips. Two labial bristles $7^{1}/_{2}\mu$ long are present on each lip. There is the usual number of cephalic bristles, $11\mu$ long, which is relatively short; the sublaterals are only $7^{1}/_{2}\mu$ long. I was unable to detect the lateral organ.

The **oral cavity** is voluminous, $40\mu$ long, as measured from the end of the lips, $20\mu$ at its maximum width. Three teeth serving as ducts of the esophageal glands occur in it (d—Figure 16a). The dorsal tooth is smaller than the other two, standing $27\mu$ from the bottom of the cavity, while both subventral teeth are more prominent and shifted further anteriorly, standing $29\mu$ from the bottom, but not pointed or converging, as in E. acantholaimus Savel'ev and E. australis de Man. The wall of the oral cavity is composed of several chitinized pieces, mainly three elevations supporting the lips; these are homologous with the teeth of Enoplus and Enoploides (a—Figure 16a). Each elevation has two processes posteriorly, directed backwards. The anterior ends of these processes are joined in a semicircle and send off laterally two curved appendages in the form of tubercles that are directed externally. The ring of the cephalic capsule covers this specialized armature. Lobular posterior enlargements of the ring are noted opposite the angles of the mouth, while the ring narrows to a thin cross-piece opposite the teeth (c. ceph. —Figure 16a). The cephalic capsule is united with the superficial capsule, which here is very well developed as the entire cuticle in the cephalic region is chitinized. Posteriorly, the cephalic region is demarcated by a distinct cephalic line.

The esophagus is narrow, 0.4 of the body width anteriorly, widening posteriorly $1^{1}/_{2}$ times. The intestine also is very narrow relative to the body.

107 The ovaries are short and reflexed. The eggs measure $210\times120\mu$, with a thin shell. The vagina is very thick-walled, traversing half the width of the body. There are no special bristles around the vulva.

The **tail** tapers very gradually posteriorly; its length is $4^{1}/_{2}$ times greater than its width, and the width at the end is $^{1}/_{6}$ that at the base. The narrow portion of uniform diameter at the end is very short. Two slender bristles are present at the end of the dorsal surface.

On fixation this species becomes elongated, like Enoplus. It was found in plankton Zostera from the North Side; 5.12, 6.12; Peschanaya Bay, adult female 1.12.

### 17. **Enoplolaimus dubius** n. sp.

(Table 3, Figure 17)

$$♀\ \frac{6.0\quad 22.0\quad 48.6\quad 60\quad 67\quad 76\quad 87.6}{1.0\quad 1.5\quad 1.9\qquad 2.3\qquad 1.3}\ 3375$$

$$\alpha=42,\ \beta=4^{1}/_{2},\ \gamma=8.$$

| Dimensions ♀ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 24 | 205 | 720 |
| Width | 30 | 50 | 65 |

The **body** tapers almost twofold from the end of the esophagus anteriorly, from the middle to the esophagus by $^{1}/_{6}$, to the anus less than twofold. The body is slender and extended. The **cuticle** is $1^{1}/_{2}\mu$ thick, and smooth. I observed bristles only anteriorly.

The **head** appears pointed, as in the other forms of Enoploides and Enoplolaimus. The lips are $7\mu$ long from the end of the jaws to the anterior end, constructed as in the other species. The labial bristles are quite long $(9\mu)$, extending anteriorly beyond the lips. The cephalic bristles are very stout and long $(28\mu)$, set far back, as in E. vulgaris de Man, and are one of the most distinctive features of E. dubius. The submedian bristles are thinner and shorter. All the parts characteristic for Enoplolaimus are present inside the oral cavity: elevations
108 homologous with the jaws of Enoplus and three teeth—two large subventrals and a small dorsal. The ring of the cephalic capsule is most curved opposite the angles of the mouth, forming here broad posterior tonguelike processes. Opposite the teeth it forms anterior arches. The esophagus is long with plasmatic parts, as in the other members of Enoplolaimus.

The ovaries are quite long and oblique oocytes are observed in them, as in Enoploides. The eggs are $65\times200\mu$, with a thick shell of $4\mu$, in places reaching $7\mu$, with pores in it. The tail is long, tapering gradually and conically to the middle, its posterior half being of even width. The proportions of the posterior end are: length of tail 10, width at end 0.23.

Two specimens of this species were found in oxeas sand of the Georgievskii Monastery at 9 sajenes 7.12.

## 5. Subfamily **Oncholaimini**

These are elongated nematodes, always expanding to midbody, with a thin, smooth cuticle. The head is more or less truncated. The oral aperture is **covered by six thin movable lips**; a labial papilla lies at the base of each of them. There are ten cephalic bristles, sometimes also converted into papillae. The lateral organ is cyathiform with an anterior orifice, usually quite large (especially in Viscosia), although it may also be small (Paroncholaimus). It is commonly extended transversely, although it may be perfectly round and even extended longitudinally (Paroncholaimus). Its closed part (pouch) occupies not more than half its length, sometimes less. The two layers of the cuticle part somewhat anteriorly and form an **annular space under the anterior surface of the head,** filled with a granular mass. The anterior end of the head is occupied by a **thick-walled oral capsule** usually containing three immovable teeth, on which the ducts of the esophageal glands open. The dorsal tooth is always smaller than the other two. The two subventrals are rarely equal (Paroncholaimus); more frequently one of them is

109 far larger than the other, which is the same size as or just longer than the dorsal. Rarely, the teeth are lacking (Pelagonema). The esophagus is straight, gradually widening posteriorly. The male and female genital organs are variable and I suggest dividing the old genus Oncholaimus into several more accurately defined genera on the basis of their structure. The synoptical table that follows will be more convenient for differentiating the genera of Oncholaimini than a simple analytical table (see p. 77).

## Genus PARONCHOLAIMUS Filipjev 1916

Ann. Mus. Zool. Petrograd 21, p. 105.
Oncholaimus ex p. Bastian et auct.

Type species: P. vulgaris (Bastian 1865)

These are large worms, tapering quite markedly anteriorly, more slightly posteriorly to the anus. The cuticle is thick and smooth; there are many bristles all over the body. There are six scaly lips, the same number of labial papillae, ten short cephalic bristles. The lateral organ is cyathiform, **small, elongated,** with a semicircular anterior orifice. In the oral cavity there are **two ventral teeth of uniform length** and a smaller dorsal tooth. The esophagus expands gradually posteriorly. The glands are tubular. The **ovaries are paired,** reflexed, with a well-developed ovejector. The **tubular organ is lacking,** but in its place there is a special "gonenteric duct" connecting the uterus to the intestine (described by Stewart, 1906). The testes are paired. The **spicules are greatly curved and there is a well-developed gubernaculum.** Typically, there is a small accessory organ. In P. papilliferus Filipjev 1916 there are some median preanal papillae. The **tail is short and rounded.** The histological preparations of this genus are characteristically large and sturdy and are well preserved in any preservative.

The first species of the genus was described by Bastian (1865) as a species of genus Oncholaimus, and entered the literature as such, being redescribed several times. 112

A new Black Sea species is described here which is very similar to P. vulgaris Bastian, but nevertheless different. Thus, the following three species are known at present:

1) P. vularis (Bastian 1865); Oncholaimus v. auct: Bastian: Trans. Linn. Soc. 25, p. 135, Table 11, Figures 126–128; Bütschli 1874: Abh. Senck. Ges. 9, p. 38, Table 9, b–Figure 37a; Stewart 1906: Quart. Journ. Micr. Sci. 50, p. 102, Tables 7, 8 (anatomy); Rauther 1907: Zool. Jahrb. Anat. 23, pp. 704, 712 (structure of esophagus and oral cavity); Par. v.: Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 106, Figures A–C; Table 5, Figure 12; nec. Golowin 1901–1902, nec. Filipjev 1912. P. vulgaris is very widely distributed in the northern seas of Europe: Arctic Ocean: Kola Gulf (Savel'ev, also found by me on algae at low tide); Vardö–Gertsenshtein's collection of 1886 (Linstow, Filipjev); in

(110-111)

| Name of genus (type species) | Lateral organ | Longest tooth | Female genital tract | Tubular organ | Spicules | Gubernaculum | Tail | Remarks |
|---|---|---|---|---|---|---|---|---|
| Pelagonema Cobb p.83.<br>(P. simplex Cobb) | small round | teeth lacking | paired | ? | ? | ? | of variable length | |
| Paroncholaimus m. p.76.<br>(P. vulgaris (Bastian)) | small elongate | both subventrals | | lacking | short curved | well developed | short | |
| Viscosia de Man p.85.<br>(V. viscosa (Bastian)) | large round | one of the subventrals | | | short straight | lacking | long | oral cavity long |
| Oncholaimus Dujardin p.89.<br>(O. attenuatus (Dujardin)) | medium-size transverse | | unpaired | without terminal duct | | | of various length | |
| Adoncholaimus n.gen.<br>(A. fuscus (Bastian))* | | | paired | | medium-length curved | small | long, with filiform part | |
| Metoncholaimus n.gen. p.98.<br>(M. demani (Zur Strassen)) | | | unpaired | with long terminal duct | very long slender | small or lacking | long | |
| Oncholaimellus de Man.<br>(O. calvadosicus de Man)** | ? | | paired | lacking | likewise, of different length | small | | oral cavity very narrow, teeth fill it almost entirely. Bursa present |

---

* The following species belong here: O. fuscus Bastian 1865; Trans. Linn. Soc. 25, p. 136, Table 11, Figures 139, 140; Bütschli 1874: Abh. Senck. Ges. 9, p. 39; de Man 1886: Anat. Unters. p. 39, Tables 6–8: North Sea, coast of France (Villot), England, Kiel, Indicated by Golovin for Sevastopol (oxeas sand), but not found by me—O. lepidus de Man 1889: Tijd. Nederl. Dierk. Vereen. (2) 2, p. 165, Table 6, f-Figure 2a, G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 33, Figure 15. On land with brackish water—Holland (de Man); Tvärminne—(Gulf of Finland) in mud (Schneider); — O. thalassopygus de Man 1876: Tijd. Nederl. Dierk. Vereen. 2, p. 181, Tables 12, 13, Figure 48; 1880: ibid. 5, p. 25; 1884: Nem. Niederl. Fauna, p. 68, Table 10, Figure 39; 1889: Tijd. Nederl. Dierk. Vereen. (2) 2, p. 162, Table 6, Figure 1. On marshes with brackish water—Holland (de Man), in freshwater ponds: on the roots of Scirpus, among algae—Denmark (Ditlevsen)—O. indicus Linstow 1907: Rec. Indian Mus. Calcutta, p. 45, Figures 1, 2: among algae in brackish water, Port Cunning, Lower Bengal.—O. derjugini Savel'ev 1912: Trav. Soc. Nat. St. Pétersbourg 43, Livr. 1, p. 116—salt Lake Mogil'noe on Kil'din Island—O. angustatus Cobb 1891 (possibly Viscosia?) Proc. Linn. Soc. NSW 5, p. 461; in sand on the coasts of Arabia.

** 1890. Mém. Soc. Zool. France 3, p. 183, Table 5, Figure 10: very common in the English Channel among algae, sole species of the genus.

a sponge from Western Greenland (Bütschli); **North Sea:** Heligoland (Rauther); **Baltic Sea:** Kiel Firth, very common in mud, some sajenes deep, mostly among mussels (Bütschli). Later caught in masses at the same place by a dragnet with rotting mussels as bait (Buerkel). Indicated for Revel [Tallinn] (Braun) and Libava [Liepaja], sands (Grimm). **Atlantic Ocean:** among sand and stones and in algae at low tide, Falmouth (Bastian). 20–30 specimens under one stone at low tide at St. Andrews (Stewart); Roscoff (Villot).

2) P. zernovi n.sp., see below.

3) P. papilliferus Filipjev 1916: Ann. Mus. Zool. Petrograd 21, p. 109, Table 5, b – Figure 13a. Bering Sea.

1 (2). Dorsal tooth in posterior half of oral cavity. Row of median preanal papillae in male . . . . . . . . . . . . **P. papilliferus** Filipjev

2 (1). Dorsal tooth only slightly shorter than two ventrals, lying in anterior half of oral cavity. Preanal papillae absent.

3 (4). Adult specimens very large, up to 20 mm. Preanal bristles divided into two groups, an anterior of four and a posterior of six. Spicules slender, gubernaculum thick. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. vulgaris** Bastian

4 (3). Adult specimens not greater than 12 mm. Preanal bristles in one group of ten. Spicules broad. Gubernaculum thin, in parts scaly . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. zernovi** n. sp.

### 18. **Paroncholaimus zernovi** n.sp.

(Table 3, Figure 18)

Oncholaimus vulgaris (nec Bastian 1865) Golovin 1901: Observations on Nematodes I, p. 36, Table 2, Figures 2, 3, 5, 7–10 (phagocytic cells).
Golovin 1902: ibid. II, p. 68, Figure 19, Table 4, Figures 80, 87, 91 (excretory glands).
Filipjev 1912: Tr. Soc. Imp. Nat. St. Pétersbourg 43, livr. 1, pp. 205, 216, Figure 7 (nervous system).

113

$$\text{♂}\ \frac{0.8\quad 4.3\quad 10.7\quad 36\quad 51\quad 98.9}{0.6\quad 1.1\quad 1.1\quad 1.2\quad 1.0}\ 10680-11460.$$

$$\alpha=84;\ \beta=9^1/_2;\ \gamma=91.$$

$$\text{♀}\ \frac{0.7\quad 3.9\quad 9.8\quad 31\quad 36\quad 54\quad 57\quad 60\quad 75\quad 80\quad 98.9}{0.55\quad 0.9\quad 1.0\qquad 1.2\qquad 0.7}\ 12450$$

$$\alpha=84;\ \beta=10;\ \gamma=91.$$

$$\text{♀}\ \frac{0.6\quad 3.3\quad 8.8\quad 29\quad 35\quad 52\quad 55\quad 58\quad 71\quad 78\quad 98.9}{0.5\quad 0.8\quad 0.9\qquad 1.2\qquad 0.8}\ 13500$$

$$\alpha=82;\ \beta=11^1/_2;\ \gamma=90.$$

$$\text{♀}\ \frac{0.7\quad 3.9\quad 9.5\quad 29\quad 35\quad 52\quad 54\quad 56\quad 75\quad 80\quad 99.0}{0.54\quad 1.0\quad 1.1\qquad 1.4\qquad 0.8}\ 12300$$

$$\alpha=70;\ \beta=10^1/_2;\ \gamma=100$$

Dimensions of anterior end

| ♀ 12,000 | Cephalic bristles | Lateral organ | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length . . . . . . . . . . . . | 19 | 24 | 90 | 410 | 560 | 1,220 |
| Width . . . . . . . . . . . . | 68 | 70 | 89 | — | 115 | 125 |
| ♀ 11,000 | | | | | | |
| Length . . . . . . . . . . . . | 19 | 22 | 84 | 315 | 450 | 1,125 |
| Width . . . . . . . . . . . . | 68 | 70 | 89 | — | 115 | 125 |
| ♂ 11,000 | | | | | | |
| Length . . . . . . . . . . . . | 16 | 20 | 84 | 300 | 460 | 1,140 |
| Width . . . . . . . . . . . . | 65 | 68 | 86 | — | 113 | 124 |

The **body** tapers so slightly to the ends that the width appears uniform. The anterior narrowing of the body, which is somewhat less than twofold, is limited to the region anterior to the nerve ring, while the narrowing to the anus is more even. In the female the body width at the anus is about half the maximum width and in the male it is about $^2/_3$. The body narrows very little to the end of the esophagus. Males are generally narrower but have a stouter tail. The **cuticle** is fairly thick, about $4\mu$, thickening anteriorly and on the ventral side posteriorly to $5^1/_2\mu$; the two layers are distinct: the outer is the thinner, about $^1/_4$ of the overall thickness. The bristles are numerous, mainly concentrated along the longitudinal lines, although they are present also opposite the muscle fields. They are located mostly anterior to the nerve ring, in the vulvar region of females and the anal region of males.

114

The **head** (Figure 18a) is truncated with rounded margins. The cephalic region is clearly distinguished by the presence between the outer and inner layers of the cuticle of a special pocket filled with a granular mass; this was noted by Stewart (a – Figure 18a). This pocket always corresponds exactly to a region of ten anterior epidermal cells; the six in the first row form lips, on which lie labial papillae and a submedian pair of cephalic bristles, and the four in the second row give rise to two lateral bristles and the lateral organs. The inner layer of the cuticle, which is homologous with the superficial cephalic capsule, is attached to the oral capsule. Anteriorly, the oral aperture is closed by six lips (lab. – Figures 18a, b). Each lip consists of a thin plate which is wider at the base and tapers to the apex. The wide basal part is far thicker than the narrow terminal part (lab. – Figure 18b). Only this latter part is movable. A labial papilla is set against each lip. The external elevation around the papilla is very small. Internally, a narrow canal traverses the cephalic capsule and passes to the sensory bulb of the papilla, over which the cephalic capsule forms a small chitinized vault with an aperture in the center and the sides passing gradually into the softer surrounding mass of the capsule. A circlet of cephalic bristles follows posteriorly. These are relatively stout and short ($8-10\mu$), or $^1/_7-^1/_8$ of the width of the head. Each is pierced by a canal along the longitudinal axis (s. c. – Figure 18c) and each has a corresponding sensory organ (o.s.c. – Figures 18b, c). There are the usual ten bristles. The lateral organ lies immediately posterior to the

lateral bristles (Figure 18c). It is of the usual cyathiform type with an anterior orifice, small and elongate, measuring $11\times 8\,\mu$, which is $^1/_9-^1/_{10}$ of the width of the head; the anterior orifice is $5^1/_2\,\mu$. Within the cavity a deeper pit is excavated half way along and a crease lies in its bottom. A chitinized papilla, in which the nerve fibers of the long pyriform nervous
115 apparatus terminate, enters the cavity posteriorly (a. o. l. — Figure 18c).

The voluminous thick-walled **oral cavity** is $84-90\,\mu$ long and $50-59\,\mu$ wide. It contains three teeth disposed symmetrically: two large subventrals and one smaller dorsal. The subventrals stand $62\,\mu$ from the bottom of the cavity and the dorsal $50\,\mu$ from it. Each of the teeth contains a terminal duct of the esophageal glands. Before opening in the apex of the tooth, each gland forms an enlargement (gl. oes. — Figure 18a). The walls of the oral cavity are thinner anteriorly ($2^1/_2\,\mu$), while posteriorly they are $4-7\,\mu$ thick. The esophagus is smooth, hardly swelling posteriorly. Anteriorly, it is about $45\,\mu$ thick (45 % of the width of the body); at the nerve ring it is $60\,\mu$ (50 %), while posteriorly it widens to $90\,\mu$ (60 — 65 %). Its muscular part is directly adjacent to the bottom of the oral cavity, embracing its posterior part. Pigment strips run along it. Its detailed structure is described by Rauther. The nerve ring encircles the esophagus at 0.4 of its length from the anterior end.

The **ventral gland** is very long, tubular, extending far behind the end of the esophagus and discharging in front of the nerve ring. Anterior to the ring it forms a characteristic expansion to which special chitinized ducts $30\,\mu$ long are joined.[*] The **intestine** in life is packed with small yellow-brown spheres. Along the entire body, mainly following the sublateral lines, there are large **phagocytic cells.**[**] In the northern form P. vulgaris they are considerably more numerous.

The female genital tract is paired and very long, each of its branches occupying 25 % of the body length. The free ends of fully developed ovaries in younger individuals take up a far greater part of the genital tract (up to 45 — 50 %) than in the older specimens (20 — 30 %). However,
116 the absolute length increases with age, i.e., the growth of the ovaries proceeds more slowly than the growth of the uterus. At the end of the ovaries the accumulation of vitelline granules occurs simultaneously in 5 — 6 oocytes. The basal part of the ovary is very long and extends alongside the uterus up to the middle of the latter; this is shorter than the extent Stewart found in P. vulgaris (Bastian). At the beginning of the uterus the separate oocytes already take on an elongated form. A fairly wide oviduct originates at the distal end of the ovary. Its first part is thin-walled and is a direct continuation of the walls of the ovary. The second part is barrel-shaped and is sharply demarcated from the adjacent parts. Its walls are constructed of a large number of muscle cells lying obliquely.

The uterus is thin-walled. Its epithelium in the part still free of eggs is cylindrical, but it becomes flattened against the eggs, of which there are up to 20 in the uterus. In fully mature females the uterus accounts for 57 — 72 % of the length of the genital tract. The eggs are relatively of small dimensions. When lying packed together in the uterus they are irregularly shaped, but when isolated they are elongated, measuring $140-150\times 120\,\mu$; the shell is thin. In the mature female eggs occupy almost the entire body width, while in P. vulgaris Bastian they take up no more than half. A considerable length of the terminal part of the uterus is converted into a muscular ovejector, which accounts for 9 — 13 % of the total length of the genital tract ($215-300\,\mu$). The short, straight vagina that traverses $^1/_4-^1/_5$ of the body width leads directly into the lumen of the ovejector. Its walls are thin. The vulva is located somewhat posterior to midbody. It is a small transverse slit with thick walls. Radial muscles are attached all around it and are capable of enlarging its aperture (Figure 18d). Numerous small bristles are set around the vulva with no particular regularity. The tubular organ is lacking. Stewart described in P. vulgaris Bastian a "gonenteric canal," connecting the uterus with the intestine, which probably serves for the elimination of superfluous sperm. I could not find it in the Black Sea species in whole
117 mount.

There are two **testes**, the anterior directed forward and the posterior backward. A long vas deferens follows, its posterior part encircled by musculature and serving as the ejaculatory duct. The sperm are very large — $11\,\mu$. The **spicules** are $160-165\,\mu$ long (Figures 18f, h, i, k, l). They are markedly curved and have a knob at the base whose internal lumen is enlarged and whose walls are thin. The form of the knob varies, and sometimes the walls are not thinner than over the remainder of the spicule (see Figure 18h). The walls are thickest in the middle, once more thinning to the end, and a plate is present on the internal margin of the spicule (v. — Figure 18k). It originates from the posterior third of the body of the spicule as two thicker folds and continues as a thin blade to the end. The **gubernaculum** (Figures 18h, i) is well developed and of complex form; it is $40\,\mu$ long. The terminal part may protrude from the anal aperture together with the spicules (Figure 18h). It is paired and has a basal knob directed posteriorly (a — Figure 18i). This is followed more internally by a spoon-shaped part that encloses each spicule separately (b — Figures 18h, i). The two lateral parts are joined by a thin chitinized cross-piece, which has at its center a chitinized capitate thickening (c — Figure 18i). Finally, thin chitinized processes run far anteriad along the spicules (d — Figures 18h, i).

Supplementary bristles, apart from those on the tail in both sexes, are present in the male in two groups. One group lies a short distance (about $25\,\mu$) anterior to the anus ($s_1$ — Figures 18f, m), consisting of 10 short ($4^1/_2\,\mu$) bristles. They are set along the margins of a fairly sharply demarcated hatched plate and are disposed completely symmetrically. Each bristle is provided with a pronounced sensory organ, while subsidiary terminations of the nerve fibrils are set directly in the plate itself. The second group lies more anteriorly, $160\,\mu$ from the anus (a spicule length).
118 It consists of 6 smaller ($3^1/_2\,\mu$) bristles ($s_2$ — Figures 18f, n); the accessory organ opens among this group. These bristles are also set on a raised plate, but this plate is far less sharply demarcated from the surrounding cuticle.

The presence of a small accessory organ is very interesting. This, as usual, is the chitinized tube of a special gland, here in the form of a hook. It is very small, like the gland itself.

---

[*] See also Golovin 1902, loc. cit., p. 62.

[**] See Golovin 1901, loc. cit., p. 36.

The **tail** in the male is rather more elongated than in P. vulgaris, tapering somewhat to the end (Figure 18f). In the female it is more rounded at the end, exactly as in the northern form (Figure 18e). The caudal glands have already been described and drawn by Golovin (1902). They are of the tubular type and terminate a short distance in front of the anus.

The caudal pore (Figure 18g) is reinforced by two chitinized rings (a—Figure 18g). There is a small cavity at the end (c—Figure 18g). The space between the rings is taken up by a chitinized cone to which the caudal glands are attached (b—Figure 18g). The cone is striated along its length and appears to be pierced by pores. Slits are present in its sides. Golovin considers these to be the ducts of the caudal glands, but I cannot vouch for the accuracy of this interpretation (see general part).

The proportions at the posterior end are: length of tail: male 1.1, female 1.1—1.3, length of spicules 1.65, gubernaculum 1.0, distance from anus to first group of bristles 0.3; to second group of bristles (accessory organ) 1.65. These proportions are very constant.

P. zernovi is the largest and one of the most common Black Sea nematodes, inhabiting oxeas sand almost exclusively. Nearer Sevastopol it is encountered only rarely, but it is very abundant in Peschanaya Bay and Georgievskii Monastery. It matures in winter, so that in summer only immature forms are encountered, although frequently they have reached full size. Their color in life, corresponding to the color of the intestine,
119 is yellow-brown, somewhat darker in specimens from Georgievskii Monastery. When laid the eggs appear white. Males can easily be distinguished, even when immature, by the form of the tail.

Peschanaya Bay 12.11, 1.12, 12.13, adults; in summer 12.13, immature worms. Sand of Georgievskii Monastery 7.12, 7.13, many immature worms. Saccocirrous sand of Shmit Bay 7.12, one female; oyster bank 6.12, 1 specimen; shells of Georgievskii Monastery 7.12, 3 semi-adults, many juveniles; 7.13, many juveniles; dirty saccocirrous sand from the road 7.12, 3 specimens; dirty sand from the wharf of R.O.P. and T. 1.12, few. They were found for the first time in the Black Sea by Golovin, who took them for P. vulgaris Bastian (as I did at first in my note on the nervous system of nematodes).

P. zernovi is distinguished from the latter species by its smaller size, somewhat longer tail (particularly in males), and especially the form of the spicules, which are considerably longer and wider than in P. vulgaris. Furthermore, the accessory organ of the male in P. vulgaris lies further from the anus than in P. zernovi. The question now arises as to whether different species are described under the single name Oncholaimus vulgaris by Bastian on the one hand and by Bütschli and Stewart on the other. The northern species that I saw at Murmansk and which I have often mentioned above is identical with O. vulgaris of Bütschli and Stewart.

## Genus PELAGONEMA Cobb 1893

Proc. Linn. Soc. NSW 8, p. 391

Type species: P. simplex Cobb 1893

Oncholaimini lacking teeth are related to this genus. I believe that these Oncholaimini include several species similar to the three-toothed forms, and that also we shall eventually have to distinguish among them a whole range of genera. The material now available is insufficient to establish this conclusively.

The body widens greatly in the middle and tapers to the ends. The
120 cuticle is smooth. The six lips are disposed as in the other Oncholaimini. There are six labial papillae and ten cephalic bristles or papillae. The lateral organs are small; in the species that I studied they are circular with a small pouch. The voluminous thick-walled oral cavity is devoid of any sign of teeth, and the tooth drawn by Cobb at the bottom of the oral cavity is in fact a fold of cuticle (see Figure 19a, Table 3, and the corresponding description on p. 84). The esophageal glands apparently discharge half way up the oral cavity. The esophagus widens gradually posteriorly. The cervical gland was very large in the species I studied (in Cobb's species it is small). The ovaries are paired and reflexed. The tubular organ is absent. Males are unknown.

Two species are known:

1) P. simplex Cobb 1893: Proc. Linn. Soc. NSW 8, p. 391, Figure 4. Among algae in Ceylon, March, 1889.
2) P. obtusicauda n. sp., see below.
   Enoplus coerulens Eberth 1863 (Unters. über Nematoden, p. 39, Table 4, Figures 6—12; Table 5, Figure 3) from Nice, very similar, but probably related to a new, similar genus.

1 (2). Tail five times longer than diameter at anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. simplex** Cobb
2 (1). Tail $1^1/_2$—2 times longer than diameter at anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. obtusicauda** n. sp.

## 19. **Pelagonema obtusicaudata** n. sp.

(Table 3, 4, Figure 19)

$$\text{♀}\ \frac{0.9 \quad 6.9 \quad 15.7 \quad 41 \quad 50 \quad 60 \quad 62 \quad 71 \quad 97.7}{0.6 \quad 1.4 \quad 1.4 \qquad\qquad 2.7 \qquad\qquad 1.2}\ 4030$$

$$\alpha=37,\ \beta=6^1/_2,\ \gamma=43.$$

| Dimensions<br>♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 5 | 32 | 60 | 260 | 590 |
| Width | 22 | 35 | | 49 | 51 |

The **body** is greatly expanded in the middle, so that to the end of the 121 esophagus it narrows almost twofold and to the anus more than twofold. The esophageal part is thus disproportionately slender. The body tapers from the end of the esophagus to the head even more than twofold; all the tapering is limited to the region anterior to the nerve ring and is especially pronounced opposite the oral cavity (see Figure 19a). The **cuticle** is thin ($1^1/_2\mu$) and smooth. The short bristles are fairly numerous.

The **head** is rounded and truncated; the tapering in the region of the oral cavity is very pronounced; the angles of the head are rounded. There are six lips, as in all Oncholaimini, their incisions cutting fairly deep. A hardly noticeable labial papilla lies at the base of each lip. There are ten cephalic bristles disposed as usual; they are 6 $\mu$ long or about $^1/_4$ of the head width. The lateral organ is circular with an anterior oval orifice. Its width is 6 $\mu$, or $^1/_5$ of the corresponding body width, and it lies somewhat posteriorly and ventrally to the lateral bristles.

The **oral cavity** has thin walls, anteriorly about 1 $\mu$, and posteriorly not more than 2 $\mu$. Its dimensions are length 32, width 15 $\mu$. There is no sign of the teeth that are characteristic for the other Oncholaimini. A fold lies deep in each sector of the esophagus; one of these is drawn by Cobb in the figure of P. simplex. There it seems to occur independently, but this is due to the obliquity of the section. These folds do not correspond to the teeth of the other Oncholaimini, but in all the forms of this subfamily are present at the bottom of the oral cavity, developed to a greater or lesser degree. The esophageal glands open in the middle of the oral cavity. Here, as in all forms of Oncholaimini, the inner layer of the cuticle is separate from the outer and attached separately to the oral capsule. Between the layers under the anterior surface of the head there is an annular cavity filled with a granular substance.

The **esophagus** is greatly thickened posteriorly, but a bulb is not formed. The **cervical gland** is very large ($270\times45\mu$), lying behind the end of the esophagus and occupying a large part of the body cavity, displacing the 122 intestine to the side. It is widest in the middle and tapers to both ends; its nucleus is very large. In front of the ring its duct forms a pronounced expansion to which the short, chitinized excretory canal, about 10 $\mu$ long, is joined. The pore lies near the oral cavity. The intestine consists of large elongate cells of irregular form, with well-marked nuclei. Phagocytic cells similar to those in Paroncholaimus are few.

The ovaries are very short, containing not more than 3–4 large oocytes; they are paired and reflexed. The uterus does not divide into two parts with a continuous lumen. The eggs measure $140\times90\mu$. The vagina with thin walls internally traverses $^2/_7$ of the diameter of the body. The tubular organ is absent.

The tail is short, bluntly pointed at the end, and twice longer than wide. The caudal glands are tubular, extending somewhat beyond the anus, but I could not determine how far. The cuticle is thin at the end of the tail, so that the caudal pore is short. There is no cone.

Some young and adult females were found in the sand at Peschanaya Bay, 1.12. All specimens rolled into a ball on fixation.

## Genus VISCOSIA de Man 1890

Oncholaimus ex. p. Bastian 1865, Bütschli 1874, Cobb 1898.
Oncholaimus subg. Viscosia de Man 1890: Mém. Soc. Zool. France 3, p. 184.

Type species: V. viscosa (Bastian 1865)

The body is slender, tapering greatly anteriorly. The cuticle is smooth and in some species viscous, so that various foreign particles adhere to it, and worms that have chanced onto the surface of water are unable to leave it, and swim upon it. The oral cavity is greatly extended in length and provided with three teeth. Its structure is asymmetrical and **one of the subventral teeth is considerably larger than the other two.** The chitinized lining of the esophagus forms on passing to the bottom of the oral cavity a valve that is seen well only on a live specimen. The 123 lateral organs are circular, large, and considerably larger in the male (? always). The glands are pyriform, the cervical gland lying behind the esophagus, the caudal glands within the tail. The **female genital organs are paired and a tubular organ is absent. The spicules are short, almost straight; a gubernaculum is absent.** There are only a few supplementary bristles around the anus in the male. The tail is long, but usually (not always) very slightly tapering to the end, sometimes swollen at the tip.

This genus differs from the other genera of Oncholaimini by the features that have been emphasized. The absence of a tubular organ assimilates it to Paroncholaimus, while the structure of the spicules assimilates it to Oncholaimus s. str., from which it is easily distinguished by the length of the tail and the absence of a tubular organ.

At present genus Viscosia consists of the following seven species:

1) V. viscosa (Bastian 1865)—Oncholaimus v. Bastian 1865: Tr. Linn. Soc. 25, p. 136, Table 11, Figures 131–133; Bütschli 1874: Abh. Senck. Ges. 9, p. 39, Table 9, Figure 38; Oncholaimus (Viscosia) v. de Man 1890: Mém. Soc. Zool. France 3, p. 184, Table 4, Figure 7. Holland, France (de Man), Falmouth, mud from the harbor (Bastian), Kiel Firth, oyster bank at Sylt—Norway (Bütschli).
2) V. minor n. sp., see p. 88.
3) V. cobbi n. sp., see p. 86.
4) V. langrunensis (de Man 1890); Oncholaimus (V.) l. de Man: Mém. Soc. Zool. 3, p. 186, Table 4, Figure 8.
5) V. glabra (Bastian 1865), see p. 127.
6) V. linstowi (de Man 1904); Oncholaimus (V.) l. Rés. voy. Belgica. Nématodes libres p. 15, Table 3, Figure 5. On shell of crab: Orange Bay, Tierra del Fuego.
7) V. pellucida (Cobb 1898); Oncholaimus p. Cobb: Proc. Linn. Soc. NSW 23, p. 39. Sand near tidemark. Port Jackson NSW.

1 (8). Cephalic bristles well developed. Right subventral tooth larger than the others.

2 (5). Two small teeth that do not reach midway along oral cavity.
3 (4). Body about 2.6—2.8 mm long, tapering anteriorly (from end of esophagus) less than $1^1/_2$ times. . . . . . . . . **V. viscosa** Bastian
4 (3). Body 1.9 mm, anteriorly tapering more than twofold. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **V. minor** n. sp.
5 (2). Two small teeth reach midway along oral cavity.
6 (7). Oral cavity less than twice head width, lateral organ $^1/_{3\cdot5}$ head width. . . . . . . . . . . . . . . . . . . . . . . . **V. langrunensis** de Man
7 (6). Oral cavity somewhat longer than twice head width, lateral organ of male half head width, of female $^1/_3$ head width . . . . . . .
124 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **V. cobbi** n. sp.
8 (1). All body bristles converted into papillae.
9 (10). Left subventral tooth greater than the others, tail at end $^1/_5$ of the width at base . . . . . . . . . . . . . . . . . . . . . **V. pellucida** Cobb
10 (9). Right subventral tooth greater than the others, tail thicker at end. . . . . . . . . . . . . . . . . . . . . . . . . . . . . **V. glabra** Bastian

Also belonging here is V. linstowi de Man, which is distinguished by the different form of the dorsal tooth and the smaller lateral organ. The description is incomplete.

## 20. **Viscosia cobbi** n. sp.

(Table 4, Figure 20)

$$\text{♂}\ \frac{0.9 \quad 6.8 \quad 12.9 \quad 26.4 \quad 30^{*} \quad 94.5}{0.5 \quad 1.2 \quad 1.2 \quad (1.3) \qquad\quad 0.6}\ 4650$$

$$\alpha=77,\ \beta=7^2/_3,\ \gamma=18.$$

$$\text{♀}\ \frac{0.8 \quad 5.2 \quad 10.3 \quad 45^{**} \quad 54 \quad 62^{**} \quad 93.2}{0.5 \quad 1.0 \quad 1.1 \qquad\quad 1.2 \qquad\quad 0.6}\ 4650$$

$$\alpha=77,\ \beta=9,\ \gamma=15.$$

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 8 | 37 | 295 | 560 |
| Width | 24 | 34 | 53 | 54 |

Note. The dimensions of ♀ are not given as there were very few good specimens.

---

* End of testis.

** Only the overall length of the tracts is given

The **body** tapers anteriorly (from the end of the esophagus) and to the anus almost twofold. It is of almost uniform diameter from the nerve ring to the posterior third. The tapering to the anus is very gradual. The **cuticle** is smooth, 2 μ. I have never observed its reputed viscosity. There are a few slender bristles.

The **head** is truncated, as is usual in Oncholaimini, with rounded margins. The six lips here are very long, so that the incisions between them cut deeply posteriorly (lab. —Figure 20a). Each lip is beset with one well-marked labial papilla. The cephalic bristles are fairly short and 125 slender—6 μ, or $^1/_4$ of the head width. The cephalic line here is hardly marked and passes directly behind the cephalic bristles. The lateral organ in the male is very large (13 μ), taking up half the head width. In the female it is only 6 μ, about $1:3\frac{1}{2}$ of the head width. It is of course cyathiform, the pouch occupying only the posterior third (4 μ). The cuticle lining the pouch is quite thick. Posteriorly, its well-developed sensory organ is connected with the cavity by means of a short tube (o. o. l.—Figure 20a). A lingula is present anteriorly on the posterior dissepiment.

The **oral cavity** is elongate, the length exceeding the width more than twice—37×17 μ. The wall in the anterior part is very thin, only 1 μ, while more posteriorly it thickens to 2 μ. The boundary between these two parts is marked by the teeth, of which there are three in the oral cavity; the right subventral is the largest, reaching almost as far as the lips, 33 μ from the bottom of the oral cavity. The left subventral is smaller—25 μ, and the dorsal is smaller still—22 μ from the bottom.

The **esophagus** is straight, expanding slightly posteriorly, always somewhat more than half the width of the body. The **nerve ring** encircles the esophagus at the boundary of the posterior third. The pyriform **cervical gland** is located directly behind the end of the esophagus; its dimensions are 45×20 μ; a narrow duct runs anteriad, but I could not determine where it discharges.

The **ovaries** are fairly long, 5—6 large eggs with vitelline granules lying at their end. The two uterine branches join in a single common cavity. The ripe eggs are very long, 140×35 μ. The vagina internally traverses $^1/_3$ of the width of the body.

There is apparently one **testis**. The **spicules** are short and almost completely straight, 40 μ long (Figure 20d). There is a weakly developed manubrium at the base, and in addition a slight swelling anterior to the end. The gubernaculum is absent. There is a pronounced abductor muscle of the spicules and a bursal musculature. All the bristles are paired, two pairs set in front of the anus ($s_1$—Figure 20d), one closer to the midline, the other more lateral; there is one pair at each side of the 126 anus and two postanal pairs.

The **tail** (Figures 20b, c) in the male is slightly longer than in the female, but the body is stouter around the anus, so that the proportions remain the same in both sexes. The tail tapers more sharply in the anterior third, whence to the end it is of uniform diameter, in the male about 0.4 of the diameter at the anus. The proportions at the posterior end are: length of tail $7^1/_2$—8; spicules 1.25; distance from anus to anterior and posterior groups of bristles 0.5. The caudal glands lie within the tail; the cuticle is thin at the end so that the caudal pore is short; there is a clearly visible cone.

Three males, two young females—oxeas sand of the Georgievskii Monastery 7.12; mature males—Peschanaya Bay 1.12, 5.12; 6.12, some juveniles.

The extensive oral cavity and the large lateral organ of the male differentiate this species clearly from the other known forms of Viscosia.

21. **Viscosia minor** n. sp.
(Table 4, Figure 21)

$$\text{♀}\ \frac{1.0 \quad 5.0 \quad 15.0 \quad 38 \quad 42.5 \quad 49.5 \quad 51 \quad 58.5 \quad 92.6}{0.6 \quad 1.4 \quad 1.6 \qquad\qquad 1.9 \qquad\qquad 1.0}\ 1900$$

$$\alpha=53,\ \beta=7,\ \gamma=14.$$

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 5 | 19 | 87 | 270 |
| Width | 12 | 16 | 25 | 30 |

The **body** is greatly elongated, tapering anteriorly from the end of the esophagus more than twofold, almost all the tapering confined to the preneural part, with hardly any expansion to midbody. The body tapers almost twofold from the middle to the anus. The **cuticle** is thin, about $1^1/_4\mu$; I saw no evidence of viscosity. There are few bristles.

The head is more rounded than is usual in Oncholaimini, hardly truncated. The incisions along the angles of the mouth are considerably
127 less developed than in V. cobbi m., but nevertheless are quite pronounced. I could not distinguish labial papillae. The cephalic bristles are about $2^1/_2\mu$ long, or $^1/_5$ of the diameter of the head. The lateral organ is large and circular; the anterior orifice is oval. The diameter of the lateral organ is $5\mu$, or $^1/_3$ of the corresponding width of the body.

The **oral capsule** is twice longer than wide ($9\times19\mu$), and its wall is thinner anteriorly. The right subventral tooth is the largest, rising through the oral cavity for more than $^3/_4$ of its length ($15\mu$). The other two teeth, which appear as very small elevations, fall far short of midlength of the cavity ($6\mu$ from the bottom). The **esophagus** is constructed as in the other forms of Viscosia. At the nerve ring an apparent constriction of the esophagus is observed; the nerve ring encircles the latter at its anterior third. I could not discern the cervical gland.

The **ovaries** are short, reflexed, and paired; only 1—2 oocytes in it are furnished with vitelline granules. The oviduct originates at their end and forms an expansion—the prouterus. The uterus is thin-walled, the cavities of the two sides uniting to form a common cavity. The eggs measure $80\times50\mu$ and are elongate. The vagina is very short, internally traversing only $^1/_9$ of the body width.

The **tail** (Figure 21b) tapers conically for 0.6 of its length, after which there is a portion of even width, namely, 0.2 of the width at the base that extends for 0.2 of the length of the tail; the most posterior part widens once more to 0.4 of the width at the base. The pyriform caudal glands are accommodated within the tail. The cuticle thickens somewhat at the extreme tip of the tail. The length of the tail is $7^1/_2$ times greater than its width at the base.

Only one female with eggs was found in oyster bank 6.12.

V. minor s.sp. is the most similar to V. viscosa (Bastian) among the other species, differentiated from it by its smaller size and pronounced tapering of the body anteriorly.

22. **Viscosia glabra** (Bastian 1865)

Oncholaimus glaber Bastian 1865: Trans. Linn. Soc. 25, p. 136, Table 11, Figures 129, 130.
O. (Viscosia) g. de Man 1890: Mém. Soc. Zool. France 3, p. 188, Table 5, Figure 9.

128 I encountered only one immature female of this species; this so closely conformed to de Man's description that there is no need for me to describe it, especially as my material was quite inadequate. Its formula is:

$$\text{♀}\ \frac{1.4 \quad ? \quad 18.7 \quad 43 \quad 51.5 \quad 67.5 \quad 90.6}{1.3 \quad ? \quad 2.5 \qquad\quad 2.6 \qquad\quad 1.4}\ 1850$$

It was found in oyster bank 6.12.

So far it has been found only in the English Channel: mud at low tide at Falmouth (Bastian), Penzance, rare (de Man), Roscoff—(Villot).

## Genus ONCHOLAIMUS Dujardin 1845

Oncholaimus ex p. auct.: Dujardin 1845 Hist. Nat. des Helminthes, p. 235.
Eberth 1863: Unters. über Nematoden, p. 24.
Bastian 1865: Trans. Linn. Soc. 25, p.134.
Bütschli 1874: Abh. Senck Ges. 9, p. 37.
de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 92.
de Man 1886: Anat. Untersuch., p. 34.

Type species: O. attenuatus Dujardin 1845

The body is usually greatly elongated, tapering slightly anteriorly. The cuticle is smooth. The oral cavity, as in all Oncholaimini, is closed by six thin movable lips, whose bases are beset with six labial papillae. Ten short cephalic bristles are set some distance posterior to them. The **lateral organ** is cyathiform, of medium size, **extended transversely.** Under the anterior surface of the head there is an annular pocket created by the separation here of the two layers of cuticle. **The oral capsule is usually short,** and contains three teeth that serve as the ducts of the esophageal glands. **One of the subventral teeth is larger than the other subventral and the dorsal,** and these last may be unequal in size. The esophagus is 129 straight, expanding gradually posteriorly. The nerve ring encircles it at its middle. The excretory pore is shifted far anteriorly. The pyriform cervical gland ordinarily lies at the beginning of the intestine. **The female genital tract is unpaired,** having only a single anterior branch. The ovejector is absent. The tubular organ is of the same type as in O. fuscus Bastian,* i.e., **does not have a rosette** as in genus Metoncholaimus m., **and the posterior pair of ducts is not developed.** The testes are paired (? always). **The spicules are short, straight** or almost straight (as in Viscosia). The gubernaculum is absent. The bristles around the anus in the male are variously disposed, sometimes in a perianal subventral row, sometimes irregularly. The tail is constructed variously: it may be long, as in Viscosia or Metoncholaimus (O. campylocercus de Man), or quite short (O. brachycercus de Man, O. brevicaudatus n.sp.).

This genus differs from Viscosia by the short oral cavity, the unpaired female genital tract, and the presence of a tubular organ. The form of the spicules, the absence of the gubernaculum, and the tubular organ differentiate it from Paroncholaimus, the form of the spicules and the tubular organ from Metoncholaimus.

The genus was first described by Dujardin (1845), who included in addition to the type species O. attenuatus two more species, which Bastian (1865) isolated in genus Mononchus. The genus has maintained the same scope from then until now. Only de Man (1890) removed several species from it and isolated them in the new subgenus Viscosia, which here I raise to the rank of genus. In this study I make a further division of the genus, as given in detail above (p. 77).

The species belonging to this genus now follow. They may easily be divided into three groups according the genital armature in the male.

First group: the tail of the male tapers immediately posterior to the anus; the supplementary bristles of the male, which are long and short, do 130 not form unbroken perianal rows. The tail of the female is short, conical, and usually curving ventrally. The group includes:

1) O. attenuatus Dujardin 1845: Hist. Nat. des Helminthes, p. 236; Bastian 1865: Trans. Linn. Soc. 25, p. 137, Table 11, Figures 134—136. On marine algae in the English Channel: Falmouth (Bastian), Lorient (Dujardin).
2) O. dujardini de Man 1878, see p. 94.
3) O. armatus Daday 1901: Termész. Füzetek 24, p. 440, Table 21, Figures 11—15: Fiume, on algae on the jetty.
The following species also probably belongs to this group:
4) O. viridis Bastian 1865: Trans. Linn. Soc. 25, p. 137, Table 11, Figures 137, 138; Ditlevsen 1911: Vidensk. Medd. naturh. Fören. Kjöbenhavn 63, p. 229, on algae at low tide, Falmouth (Bastian); Denmark, in decaying seaweed (Ditlevsen). Only the female known. Ditlevsen's species probably does not correspond to Bastian's. I do not include it in the key as the description is insufficient.

1 (2). On cuticle are large clawlike and spinelike appendages. 1.9—2.2 mm. Large tooth 0.8 length of oral cavity, two small teeth 0.5 of length of oral cavity. Spicules longer than tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. armatus** Daday
2 (1). Such spines absent.
3 (4). Excretory pore located at a distance shorter than length of oral cavity from its bottom. Pigment spots on esophagus red. Tail of male may be of regular form . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. attenuatus** Dujardin
4 (3). Excretory pore located at distance almost equal to length of oral cavity posterior to its bottom. Pigment of esophagus black. Tail of male of irregular form . . . . . . . . . **O. dujardini** de Man

Second group: the tail is short, sometimes rounded. At the sides of the anus in the male there is a row of bristles. The tail of the female is hardly different in form from the male. The following three species belong to this group:

5) O. oxyuris Ditlevsen 1911: Vidensk. Medd. naturhist. Fören. Kjöbenhavn 63, p. 230, Table 2, Figures 8, 9, 12, 13. On the coasts of Denmark.
6) O. brachycercus de Man 1889: Mém. Soc. Zool. France 2, p. 211, Table 8, Figure 12. Rocks in English Channel (Penzance, St. Vaast), Scheldt River estuary. Kola Gulf (Savel'ev).
7) O. brevicaudatus n.sp., see p. 92.

1 (2, 3). Tail pointed. In male a tooth observed not far from end . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. oxyuris** Ditlevsen
2 (1, 3). Tail at base stout and tapering sharply to end . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. brachycercus** de Man
3 (1, 2). Tail tapering directly from base conically to end, very short, shorter than its width . . . . . . . . . . . . . **O. brevicaudatus** n. sp. 131

Third group: The tail is fairly long, as in the other related genera; in the male there is a perianal row of bristles. Here belong:

8) O. campylocercus de Man 1878, see p. 95.

In addition, the following species are tentatively placed in this group:

9) O. orientalis Cobb 1891: Proc. Linn. Soc. NSW 5, p. 458. Arabia, Ceylon, in sand and on algae.
10) O. exilis Cobb 1891: ibid., p. 462. Aden, in sand.
11) O. papillosus Eberth 1863: Unters. über. Nematoden p. 26, Table 1, Figures 13—17. Nice.

---

* See de Man, Anatomische Untersuchungen, p. 39 ff.

To judge from Eberth's drawing, O. papillosus is very similar to O. campylocercus. Cobb's observation that in his O. orientalis the ovary "extends... backwards, past the vulva, apparently to near the anus," is interesting. He is surely referring to the tubular organ.

1 (4). Tail tapering evenly to end.
2 (3). Diameter of tail at end $^1/_2 - ^1/_3$ of diameter at anus; in male there is a swelling before the end and pyriform organ in front of anus . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. campylocercus** de Man
3 (2). Diameter of tail at end is not more than $^1/_4$ of diameter at anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. exilis** Cobb
4 (1). Tail of uniform diameter in posterior half (about $^1/_5$ of anal diameter).
5 (6). Clearly visible knob present on spicules . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **O. papillosus** Eberth
6 (5). Knob hardly marked . . . . . . . . . . . . . . . . . . . **O. orientalis** Cobb

It is probable that the following also belong to this genus:

12) O. albidus Bütschli 1874 (nec Bastian 1865): Abh. Senck. Ges. 9, p. 39, Table 9, Figure 39. Kiel Firth; de Man identifies it with his own O. brachycercus, but Zur Strassen (1894, p. 460) indicates that this is not so: in brachycercus the large subventral tooth lies on the left, while in the species described by Bütschli it is on the right.

13) O. spiralis Linstow 1908: Denkschr. med. naturwiss. Ges. Jena 13, p. 27; Atlantic coast of South Africa; unknown to me.

### 23. **Oncholaimus brevicaudatus** n. sp.

(Table 4, Figure 23)

$$\male\ \frac{?\quad ?\quad 12.0\quad ?\quad 99.0}{?\quad ?\quad 1.5\quad 1.7\quad 1.3}\ 3500$$

$$\alpha = 60,\ \beta = 7^1/_2,\ \gamma = 100.$$

132

$$\female\ \begin{array}{ccccccc} 1.0 & 5.7 & 12.4 & 50 & 60 & 72 & 98.9 \\ \hline 0.9 & 1.6 & 1.6 & & & 1.9 & 1.4 \end{array}\ 3845$$

$$\alpha = 52,\ \beta = 8,\ \gamma = 90.$$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 9 | 40 | 207 | 450 |
| Width | 37 | 47 | 60 | 60 |

The **body** is of even thickness throughout, only slightly expanding in the middle; in the male it expands more to the posterior end. It tapers less than twofold from the end of the esophagus to the cephalic bristles. The **cuticle** is smooth, about 3 $\mu$ thick, double-layered; its outer layer is about $^1/_4$ of the overall thickness. A few short, slender bristles are present.

The **head** appears rounded. Six thin lips close the oral aperture. The six labial papillae are well defined and encircled by distinct chitinized thickenings of the cephalic capsule. The cephalic bristles are 6 $\mu$ long, or $^1/_6$ of the head width. The cell borders are clearly marked over the entire cephalic end. The lateral organ is quite large, extended transversely, and measures $8 \times 6\,\mu$, or $^1/_5$ of the corresponding width of the body; the pouch takes up the posterior $^2/_3$.

The **oral cavity** is thick-walled in the main, up to 3 $\mu$ posteriorly and about 1 $\mu$ anteriorly, 38 $\mu$ long and 27 $\mu$ wide. The large right subventral tooth stands 33 $\mu$ from the bottom of the oral cavity; the other two teeth stand 26 $\mu$. The **esophagus** is straight, expands slightly posteriorly; at the middle its width is about half the body width and at the posterior end it increases to three-quarters. The nerve ring encircles the esophagus just anterior to its middle.

Only the anterior ovary is present; it is long and of the same structure as in O. campylocercus de Man.* The vitellus begins to accumulate 133 as early as the flat oogonia stage.

Five eggs measuring $50 \times 100\,\mu$ are located in the uterus. The vagina runs slightly anteriorly, almost straight, traversing $^1/_5$ of the body width. The tubular organ is of the type in Adoncholaimus fuscus (Bastian).** Anteriorly, it opens in the intestine; there follows a nucleated capsule homologous to the rosette in Metoncholaimus;† after this there is an unpaired sac that opens by two apertures **under** the lateral line, 40 $\mu$ anterior to the anus. The sac continues for a short distance posteriad beyond the aperture. The overall length of the organ is about 70 $\mu$, the nucleated capsule lying in the anterior third.

I could not detect the internal male genital organs. The **spicules** are short (46 $\mu$) and slightly curved. The basal half is somewhat narrower than the terminal half. The end comes to a blunt point on which a short longitudinal streak is observed. The gubernaculum is absent. Bristles lie around the anus in a semicircle which is open postanally. The semicircle is made up of a straight row of five bristles 11 $\mu$ long, lying subventrally adjacent to the anus; the two anterior are preanal and the three posterior are postanal ($s_1$—Figure 23c is the central bristle of the five in this row). A row of four bristles of the same length curving ventrally follows ($s_2$—Figure 23c). Finally, the semicircle is closed anteriorly by two pairs of bristles 7 $\mu$ long set directly against the ventral line. These are probably homologous with the group of bristles around the accessory organ in Paroncholaimus. A group of slender bristles 6 $\mu$ long lies immediately anterior to the anus ($s_4$—Figure 23c), and slightly anterior to these there are a few conical bristles 2 $\mu$ long.

The **tail** in this species is very short: its length in both sexes is rather less than its width (Figures 23b, c). The tubular caudal glands extend

---

* See p. 95.

** de Man 1886: Anat. Untersuchungen, p. 47.

† See p. 101.

slightly anterior to the anus. The chitinized wings, which in
134 Paroncholaimus zernovi lie closely adjacent to the cuticle (cf. Table 3, Figure 18g), are here shifted interiad and cover the cone more loosely. Some short bristles are observed along the tail in both sexes. Bristles are also present around the caudal pore (s. caud. — Figure 23e). The proportions at the posterior end are: length of tail of male 0.8, of female 0.7; length of spicules 0.85, distance from anus to anterior supplementary bristles ($s_3$ — Figure 23c) 0.44.

Male and female of this species were found in saccocirrous sand from the road 1.12.

This species belongs to the same group as O. brachycercus de Man and O. oxyuris Ditlevsen, but is easily differentiated from them by the even shorter tail. This form has the shortest tail of the members of Oncholaimini so far known.

### 24. **Oncholaimus dujardini** de Man 1878
(Table 4, Figure 24)

$$\text{♀}\ \frac{\begin{array}{ccccccc}1.0 & 5.3 & 14.3 & 32 & 50 & 67 & 97.0\end{array}}{\begin{array}{ccccccc}0.8 & 1.8 & 1.8 & & & 2.2^{*} & 1.0\end{array}}\ 2850$$

$$\alpha=45,\ \beta=7\text{—}8,\ \gamma=34\text{—}47.$$

Esophagus up to 12$\mu$, tail up to 97.9$\mu$, overall length up to 3,600$\mu$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 7 | 30 | 55 | 170 | 365 |
| Width | 24 | 33 | — | 60 | 60 |

The **body** tapers markedly anteriorly, more than twofold from the maximum width to the cephalic bristles. It tapers by $^1/_5$ to the end of the esophagus and more than twofold to the anus. The **cuticle** is very thin, not thicker than $1^1/_2\mu$, and is entirely smooth. There are few bristles on the body.

The **head** is rounded and truncated. The oral aperture is narrow, the angles of the mouth are confined to the anterior surface of the head. The
135 length of the lips is $2^1/_2\mu$. The labial papillae are small, but well marked. The cephalic bristles are 4$\mu$ long, or $^1/_6$ of the head width. The lateral organ is slightly extended transversely, its posterior half forms a pouch; its dimensions are 5×6$\mu$. The oral cavity is more elongated than in the forgoing species: it is 30$\mu$ long and 17$\mu$ wide. The left subventral tooth is the largest, standing 22$\mu$ from the bottom of the cavity; the right subventral stands 17$\mu$ from the bottom, and the dorsal, which is the smallest, 15$\mu$. The **esophagus** in some specimens was highly pigmented, almost black. The pigmentation begins slightly posterior to the oral cavity. The black particles of pigment are contained throughout the esophagus and are especially dense anteriorly. The same pigmentation is present in the intestine also. The width of the esophagus increases from 25$\mu$ anteriorly (70% of the body width) to 30$\mu$ (50%) at the nerve ring to 45$\mu$ (75%) at the end. The excretory pore opens near the anterior end (see dimensions).

In the female only the anterior genital tract is present. The **ovary** is long, but only 1—2 eggs are provided with vitelline granules. The uterus is thin-walled and contains up to 6 eggs measuring 80×55$\mu$. The vagina runs obliquely. I did not observe a tubular organ.

The tail curves characteristically ventrally, and the caudal glands are accommodated within it. The cuticle thickens considerably on the tail, particularly at the end, so that the caudal pore is long. The cone is short. At the end the width of the tail is $^1/_3$ of its width at the base and its length is 2.2 of that width.

This species was found in deep sand from Peschanaya Bay 1.12, adult female; Georgievskii Monastery at 18 sajenes 7.12, adult female; phyllophores 6.12, 2 adult females.

In addition, some immature specimens that were very similar to this species, but larger, were found in saccocirrous sand from the road 1.12; rocks at Spasenie, Georgievskii Monastery, Cystoseira 7.12. I have decided not to describe these specimens separately as they were
136 immature and very poorly preserved.

The species was described from Naples by de Man. Rouville establishes it for Sète in dirty sand with Notomastus and Polydora.

This definition can be confirmed only when the male is found.

---

* Maximum width, width at vulva somewhat less

### 25. **Oncholaimus campylocercus** de Man 1878
(Table 4, Figure 25)

Tijd. Nederl. Dierk. Vereen. 3, p. 35, Table 7, b — Figure 3a.

$$\text{♂}\ \frac{\begin{array}{cccccc}1.0 & 6.3 & 12.4 & 28 & 66^{*} & 98.0\end{array}}{\begin{array}{cccccc}0.8 & 1.3 & 1.3 & & 1.4 & 0.8\end{array}}\ 3920$$

$$\alpha=70,\ \beta=8,\ \gamma=50.$$

$$\text{♀}\ \frac{\begin{array}{ccccccc}1.1 & 5.6 & 11.5 & 34 & 49 & 66 & 97.5\end{array}}{\begin{array}{ccccccc}0.7 & 1.2 & 1.3 & & & 1.7 & 0.8\end{array}}\ 4200$$

$$\alpha=60,\ \beta=8^1/_2,\ \gamma=42\text{—}45.$$

---

* Posterior end of posterior testis.

| Dimensions<br>♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 8 | 35 | 77 | 235 | 485 |
| Width | 27 | 38 | 43 | 51 | 54 |
| ♂ | | | | | |
| Length | 8 | 35 | 97 | 255 | 510 |
| Width | 27 | 35 | 44 | 52 | 52 |

The **body** in the female is thickest at the level of the end of the ovaries, gradually narrows anteriorly and posteriorly; the esophageal region tapers slightly also, by only $^1/_4$ from the end of the esophagus to the head. Posteriorly, there is a pronounced tapering between the end of the tubular organ and the anus, so that the base of the tail is narrow. In the male the anal region is somewhat thicker than in the female, but the body itself is very slender, hardly tapering to the end of the esophagus. The **cuticle** is thin ($2^1/_2\,\mu$), smooth, with two distinct layers. Many slender and fairly long bristles are observed over the entire body, particularly anteriorly
137 and posteriorly.

The **head** is rounded and indistinctly truncated. The lips ($2^1/_2\,\mu$) and oral aperture ($5\,\mu$) are small, as are the labial papillae. The cephalic bristles are $5\,\mu$ long, which is about $^1/_5$ of the width of the head. The lateral organ measures $6 \times 5\,\mu$, or $^1/_5$ of the head width, and is somewhat extended transversely. It is cyathiform and the wall enclosing the pouch has a small anterior bulge. The organ lies some distance posterior to the lateral cephalic bristles (see Figure 25a).

The **oral cavity** is $42\,\mu$ long, $22\,\mu$ wide. The left subventral tooth is the longest ($30\,\mu$), while the other two are only $26\,\mu$ long. The form of all three teeth is fairly characteristic: they are cut down at the base, and therefore their ends project sharply into the oral cavity (see d.d. — Figure 25a).

The **esophagus** is straight, widening posteriorly $1^1/_2 - 1^3/_4$ times. Its width is 40 — 50% of the body width anteriorly and 60 — 80% posteriorly. In males it is narrow. The **nerve ring** encircles it exactly at its middle. The **intestine** is lined with large cylindrical cells that are sometimes of irregular form superficially. The excretory pore is located a short distance behind the oral cavity (see dimensions); its chitinized tube is $12\,\mu$ long.

Only the anterior portion of the female genital apparatus is developed. The **ovary** is very long, reflexed; at least 50 eggs can be seen in it; the posterior oogonia lie in two rows, while the anterior ones lie in one row; and the 5 — 6 most anterior eggs are provided with vitelline granules. Five to six eggs lie in the uterus. They are almost round — $55 \times 60\,\mu$. The vagina is short and runs obliquely. The tubular organ is short ($360\,\mu$), beginning as a funnel originating from the intestine. This is followed by a thin-walled tube ($215\,\mu$) and then a round nucleated capsule homologous with the rosette in Metoncholaimus ($40\,\mu$). Posterior to this there is an unpaired sac to which the terminal tubes of the organ are joined. The sac extends for a short distance posteriorly to them. The tubular organ is distinguished
138 only in adult females after the last molt.

The **testes** are paired, short, and the portion of the vas deferens between them is so long that the posterior testis seems to be a small posteriorly-directed appendage of it.

The **spicules** are straight, pointed at the end, and thickened slightly at the middle and at the base; they are $32\,\mu$ long. The gubernaculum is absent. In the male a small bulb containing a sensory apparatus is observed in the midline anterior to the anus; the terminations of the apparatus are concentrated outside the bulb as small papillae (a — Figure 25c). In front of this there is an additional small papilla (b — Figure 25c). The bristles mainly form a lateral perianal row of about six long and three shorter bristles ($s_2$ — Figure 25c); an additional group of bristles is located anterior to the anus ($s_1$ — Figure 25c). The whole tail in both sexes is beset with bristles. In the male there is a fold of cuticle parallel to the slit of the anal aperture; this fold also probably has some sensory function (d — Figure 25c).

The **tail** in the male is thicker at the base and tapers more sharply than in the female (see Figures 25b, c). In addition, it always curves ventrally and expands markedly at its middle (c — Figure 25c), where there are several small bristles. The caudal glands are accommodated within the tail. The cone in front of the caudal pore is small.

The proportions in the tail are: spicules 1.0; to the pyriform organ of male 0.6; length of tail in male 1.7, in female 3.2; width at end in male 0.3, in female 0.4; narrowest part in the female 0.3; distance from anus to tubular organ 1.8.

O. campylocercus is found in many facies and matures all the year round: dirty saccocirrous sand from the road 1.12, adult male and female, fairly numerous; clean saccocirrous sand — Shmit Bay 7.12, adult female; dirty sand from the wharf of R. O. P. and T. 1.12, adult females; oxeas sand, Peschanaya Bay, 1.12, adult female, algae on them 6.12, adult male and female. Ulva from New Holland 6.12,
139 adult female. Nassarius from mud of Artilleriiskaya Bay 7.12, adult male and female. The entire tail in these specimens was covered with some kind of bulblike appendages, probably algae or fungi. Mussel mud of Kacha 8.13, adult female; phaseolin mud of Georgievskii Monastery 7.13, juveniles and adult female; mussels on rocks under the station 6.12, adult male, female, many juveniles; clay from the North Side 7.12, very many males, females, and juveniles.

De Man described this species from Naples.

This species is apparently a close relative of O. exilis Cobb, O. orientalis Cobb, and O. papillosus Eberth; the differences between them are shown in the table. The length of the tail easily differentiates this group from the other members of Oncholaimus.

## Genus METONCHOLAIMUS n.g.

Oncholaimus exp. Bastian 1865; de Man 1878, 1893; Zur Strassen 1894.

Type species: M. demani Zur Strassen 1894

These worms are mainly of medium size or fairly long. As in the other forms of Oncholaimini, the oral aperture is provided with six lips, and there are ten bristles on the head. The lateral organ is not very large; its posterior wall is usually thickened. The female genital tract is unpaired, there being a single anterior tube, as in Oncholaimus. The ovary is very long. The tubular organ consists of an unpaired part to which are attached the rosette and two paired ducts invested by a row of characteristic cells lying packed like coins; these ducts open on the ventral side, a short distance anterior to the anus. **The spicules are slender and very long.** The gubernaculum is not well developed if present. Supplementary bristles are present immediately in front of the anus and as a subventral row on the tail; the latter bristles are sometimes converted into triangular papillae. The tail is long, usually thickened at the end. Two species were found in the Black Sea, although M. eberthi n.sp. may belong to another genus.

This genus is most similar to Oncholaimus s.str., but is also 140 distinct from it; the males are distinguished by the long spicules and the females by the different structure of the tubular organ.

The first species of this genus—M. albidus—was described by Bastian (1865) and subsequently redescribed by de Man (1893). Zur Strassen (1894) provided a detailed description of the tubular organ of two new species, having made use of the method of sections.

First group: true forms of Metoncholaimus. The tail gradually tapers to the end, and is usually quite stout. The spicules are very slender, longer than the tail; the tubular organ is developed characteristically (see description of M. demani Zur Strassen). The following species are related to this group:

1) M. antarcticus Linstow 1896: Erg. Hamburger Magalhaenischen Sammelreise 1, No. 7, p. 9, Figures 10, 11. Ushuaia — South America.
2) M. demani Zur Strassen 1894, see p. 99.
3) M. pristiurus Zur Strassen 1894: Zeit. Wiss. Zool. 58, p. 461, Table 29, Figures 1, 3. In dirty sand—Naples; known to me from Villefranche.
4) M. albidus Bastian 1865: Tr. Linn. Soc. 25, p. 137, Table 11, Figures 141, 142; de Man 1893: Mém. Soc. Zool. France 6, p. 32, Table 7, Figure 11; nec Bütschli 1874; nec de Man 1878. Very common under stones at Penzance, Falmouth—English Channel.

1 (2). Spicules $3^{1}/_{2}$ times longer than tail, triangular papillae on tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. antarcticus** Linstow
2 (1). Spicules shorter.
3 (6). Spicules twice as long as tail.
4 (5). Paired terminal ducts of tubular organ more than $1^{1}/_{2}$ times longer than tail. Eggs in uterus located in single row. In male only anterior subventral row of short bristles on tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. demani** Zur Strassen
5 (4). Paired terminal ducts of tubular organ hardly longer than tail. Eggs in mature uterus located in several rows. Row of triangular papillae posterior to anterior row of bristles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. pristiurus** Zur Strassen
6 (3). Spicules slightly longer than tail; only small bristles on tail of male. Terminal tube of tubular organ shorter than tail. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. albidus** Bastian

Second group: doubtful Metoncholaimus. The tail narrows sharply a short distance behind anus, after which follows a portion of uniform diameter. The spicules may be long, usually stout. **The genital tract in the female is unpaired** (which is why I include the species here). There 141 are no data on the tubular organ. Here belong:

1) M. eberthi n.sp., see below, p. 102.
2) Oncholaimus megastoma Eberth 1863: Unters. über Nematoden, p. 26, Table 1, Figures 18—20. Villefranche.
3) Oncholaimus anthophorus Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 116. Kola Gulf, Olen'ya Inlet; sand 20—30 m.

1 (4). Cells of lateral fields very strongly developed, particularly posteriorly, projecting deeply internally.
2 (3). Spicules shorter than tail; tail swollen at end, $^{1}/_{4}$ of base diameter . . . . . . . . . . . . . . . . . . . . . . . . . **O. megastoma** Eberth
3 (2). Spicules longer than tail. Tail not swollen at end—$^{2}/_{5}$ of base diameter in male, $^{1}/_{4}$ in female . . . . . . . . . . **M. eberthi** n. sp.
4 (1). Cells of lateral fields normal. Spicules half length of tail. Complex supplementary armature composed of papillae in male. Large cephalic bristles ($^{1}/_{4}$ of head). . . **O. anthophorus** Saveljev

### 26. **Metoncholaimus demani** (Zur Strassen 1894)

(Table 4, Figure 26)

Oncholaimus albidus de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 93, Table 7, c—Figure 2a.
O. demani Zur Strassen 1894: Zeit. Wiss. Zool. 58, p. 46, Table 29 Figure 2.

$$♂\ \frac{0.6\quad 4.4\quad 9.1\quad 17^{*}\quad 97.2}{0.6\quad 1.1\quad 1.2\quad (1.4)\quad 0.7}\ 6700$$

$$\alpha=70,\ \beta=11,\ \gamma=35.$$

$$♀\ \frac{0.6\quad 4.3\quad 9.0\quad 28.5\quad 42\quad 63.5\quad 97.9}{0.6\quad 1.1\quad 1.2\qquad\qquad\qquad\qquad 1.6\quad 0.7}\ 6700$$

$$\alpha=63,\ \beta=11,\ \gamma=48.$$

---

* Anterior testis.

| Dimensions ♂ 6,500μ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 10 | 40 | 110 | 265 | 585 |
| Width | 32 | 40 | — | 60 | 65 |
| ♀ 6,000μ | | | | | |
| Length | 10 | 40 | 110 | 265 | 540 |
| Width | 30 | 40 | — | 62 | 68 |

The **body** narrows discernably to the esophagus (by $^1/_4$ in the female, less in the male), approximately twofold to the anus. It tapers from the
142 beginning of the esophagus to the cephalic bristles twofold or even more, mainly in the preneural part and especially in the region of the oral cavity. The cuticle is thin ($1 - 1^1/_2\mu$) and completely smooth. The bristle armature, as correctly observed by Zur Strassen, is very weak: apart from the anterior and posterior bristles in the male there are hardly any.

The **head** is sharply truncated anteriorly. The oral aperture is about 8μ in diameter. The lips are well developed (4μ) and the incisions of the angles of the mouth cut far backwards, almost to the cephalic bristles (lab. —Figure 26a). Each lip is beset with a very small labial papilla. The usual ten cephalic bristles are present; they are 8μ long ($^1/_4$ of the head width) and very slender. The lateral organ lies 4μ posterior to the lateral bristle (o.l. —Figure 26a). It is 9μ long, 5μ wide, somewhat extended longitudinally, with a round anterior orifice. A space lies around the head under the anterior margin (a—Figure 26a) only anterior to the cephalic bristles; more posteriorly the cuticle is separated into two distinct layers, but without the formation of a space, approximately as far back as the posterior end of the lateral organs (see Figure 26a).

The **oral cavity** is elongate, twice longer than wide; its wall is thickest posteriorly and thinner anteriorly, gradually becoming even thinner to the extreme anterior margin. In the posterior part the thick oral wall extends to the middle of the oral cavity opposite the sectors of the esophagus (b—Figure 26a), while laterally between the sectors there is only a thin veneer (c—Figure 26a); the thick parts of the wall send off processes into the tissue of the esophagus (d—Figure 26a). Three teeth project into the oral cavity. The **left** subventral is the longest and reaches $^3/_4$ of the height of the oral cavity, while the other two only slightly exceed its middle. The dorsal tooth is just shorter than the right subventral. The apertures of the esophageal glands are located somewhat posterior to the apices of the teeth. The dimensions of the oral cavity are: length 40μ, width 20μ; left subventral tooth 32μ high, the right subventral
143 26μ high, the dorsal 25μ high.

The **esophagus** gradually expands posteriad from 25μ behind the oral cavity (65% of the body width) to 30μ in the middle (50%) and to 45μ posteriorly (70%). The nerve ring is located slightly behind the middle of the esophagus. The cardia is weakly developed and rectangular. The **cervical gland** is large, pyriform, and lies posterior to the esophagus; its duct opens anteriorly somewhat in front of the nerve ring. The walls of the **intestine** are thick, $^1/_4$ of the overall thickness of the body. Its individual cells are almost as high as they are wide. The **lateral fields** are clearly seen to be constructed of very narrow cells. There are many **phagocytic cells**, particularly in the testicular region in the male. Their structure is similar to that of the cells of Paroncholaimus.

Only the anterior part of the female genital tract is present. The eggs increase in size gradually to the anterior end of the ovary; at first they lie in two rows, then are packed like coins in a single row. The uterus in the oldest females contains about 26 eggs and is greatly distended, but, as Zur Strassen has already noted, the eggs always lie in one row. Their diameter is about 70μ, and they are flattened anteriorly and posteriorly. An ovejector is absent, the uterus being joined to the vagina directly and extending somewhat posterior to it. The vagina is short and thick-walled. The vulva is a narrow transverse slit 24μ wide. The

organe de
de Man

tubular organ has been described in detail by Zur Strassen. Initially, an anterior tube runs to the intestine, where it opens (240)μ); the rosette is adjacent to the tube (50μ, b—Figure 26b); the unpaired part terminates just posterior to the rosette (c—Figure 26b), and two paired canals proceed ventrally from it (d—Figure 26b; their beginning lies 35μ from the rosette) and open by an aperture in the ventral wall 95μ from the anus (e—Figure 26b). The total length of these canals is about 100μ. Their structure is quite interesting: along their internal surface lies a slender canal with
144 chitinized walls. A row of cells from the external wall is adjacent to this canal; these cells lie like a pile of coins. At its end can be observed the nucleus of the cells forming the inner wall of the canal (cel. —Figure 26~~g~~c).

In younger females the paired canals are shorter, so that the organ is entirely similar to M. pristiurus Zur Strassen. I have a few observations as to the function of these formations. While studying the belts seen and drawn by de Man in M. albidus Bastian (1893 p. 414, Table 7, Figure 11e) that encircled the body of the nematodes at the aperture of the tubular organ it became clear to me that the substance of these belts was produced by the tubular organ. I suggest that on swelling this substance produces a mucus which covers the eggs of the species; however, there are no direct observations to support this. Furthermore, the significance of the junction with the intestine is not understood.

The **testes** are paired, originating very close to the anterior end. The testis itself is very short. The seminal duct consists of two rows of large cells with their upper ends inclined anteriorly. The spicules are slender, only 3μ wide, but extremely long, reaching up to 400μ, or more than twice the length of the tail (Figure 26c). The walls, particularly at the beginning, are very thin, becoming thicker to the end; the end of the spicule is truncated obliquely (Figure 26e). There is no knob at the basal end.

The small, lobate gubernaculum is 35μ long, its dorsal wall adjacent to the spicules. The **supplementary bristle armature in the male** consists of a preanal group: immediately in front of the anus there is a mound like a half lemon on which several (4—6) papillae are set (a—Figures 26d, e, f). On each side of it are three fairly large bristles ($s_1$—Figures 26d, e, f), the central one set more to the midline. Finally, anterior to them at the same level from the center, there are two more pairs of shorter bristles; these are not always present ($s_2$—Figures 26d, e). A row

145 of 12 bristles lying more laterally ($s_3$ – Figures 26d, e) begins somewhat in front of the anus and extends posteriorly half way down the tail. Apart from these, two small papillae may be present in the male on the ventral side behind the anus (p – Figure 26d).

The tail in the female is straight, elongate, and quite stout at the end (Figure 26b). The tail in the male is slightly longer, usually curves ventrally, and is only rarely elongate (Figure 26c). There is a group of bristles at the end of the tail in both sexes. The caudal pore is long and the cone of the caudal glands is inserted into it. The glands themselves are pyriform and accommodated within the tail. The proportions at the posterior end are: length of tail in female 4, in male 4.5; width at end 0.4; length of spicules 9.6; gubernaculum 0.8.

This is a common species, encountered primarily in sand, and matures all the year round. They were especially frequent 1.12, in dirty sand from the wharf of R. O. P. and T. If such sand is kept in a vessel, the worms crawl to its walls and collect in their hundreds in light orange piles together with Capitella capitata. Zernov (1914) mentions this also. Utilizing this phenomenon, I collected them together with M. pristiurus Zur Strassen in Villefranche in May, 1911. In addition, they were found in sand in Kruglaya Bay 6.12, few; in algae of the same place, many males and females; mussels from under the station 6.12, few; mud of Artilleriiskaya Bay 7.12, one female; a patch on Potamogeton of Streletskaya Bay 3.10 by Zernov, many young and adult. In the latter the head was rather narrower than in the other specimens, but I decided not to describe them separately as the preservation was very bad, and the posterior end was completely normal.

They are known from Naples as well as Sevastopol (de Man, Zur Strassen) and from Villefranche (personal observations); also in dirty sand from the municipal sewage system.

The species is easily distinguished from the similar M. albidus Bastian by the longer spicules, and from M. pristiuris Zur Strassen 146 and M. antarcticus Linstow by the short and few bristles on the tail in the male.

## 27. **Metoncholaimus eberthi** n.sp.

(Table 4, Figure 27)

$$♂\ \frac{0.9 \quad 6.3 \quad 12.8 \quad ? \quad 97.5}{0.9 \quad 1.8 \quad 2.0 \quad 2.3 \quad 0.6}\ 3750$$

$$\alpha=43,\ \beta=8,\ \gamma=40.$$

$$♀\ \frac{1.5 \quad 6.8 \quad 13.9 \quad 40 \quad 60 \quad 75 \quad 97.5}{1.1 \quad 2.3 \quad 2.5 \qquad\qquad\qquad 3.0 \quad 1.2}\ 3400$$

$$\alpha=33,\ \beta=7,\ \gamma=22.$$

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 10 | 46 | 215 | 450 |
| Width | 32 | 46 | 70 | 75 |
| ♀ | | | | |
| Length | 14 | 55 | 250 | 485 |
| Width | 34 | 45 | 68 | 76 |

The **body** tapers markedly anteriorly and to the anus, in the female less than in the male, which is generally considerably narrower. The body tapers a little more than twofold from the base of the esophagus anteriorly. The **cuticle** is $1^1/_2-2\mu$ thick, thicker anteriorly; a fine annulation is observed with intervals of $1^1/_2\mu$. There are few bristles. Lateral lines are observed consisting of large swollen cells which appear vesicular in preparations, especially at the posterior end (this may be a postmortem change). According to his drawings, Eberth observed this in his Oncholaimus megastoma.

The **head** is somewhat truncated; the mouth has a diameter of $10\mu$. The six lips are $4\mu$ long and do not cut deeply backwards. The labial papillae are inconspicuous. The cephalic bristles are $6\mu$ long, or about $^1/_5-^1/_6$ of the head diameter. The lateral organ is large, about $^1/_4$ of the head width – $8\mu$ long and $10\mu$ wide. Its posterior end is bordered by a 147 thick wall which gradually fades out anteriorly. The chitinized tube that projects into its cavity is well developed, and wall projecting anteriad half closes the cavity.

The **oral cavity** is comparatively thin-walled; anteriorly the wall is thicker and posteriorly considerably thinner. The length of the cavity in the female is $56\mu$, width $33\mu$; the left subventral tooth is markedly larger than the other two, standing $37\mu$ from the bottom of the oral cavity, while the other two stand $25\mu$ from it. The **esophagus** is about $25\mu$ wide anteriorly (45% of the body width at the nerve ring), and expands to $50\mu$ (70%) posteriorly. The **cervical gland** lies behind the esophagus. It is elongate, measuring $37 \times 12\mu$.

The **female genital tract** is unpaired, only the anterior branch being present. The ovary is very long and anteriorly contains many eggs with vitelline granules, of which even the most anterior ones are round. In the uterus there are six eggs which do not fill it measuring $55 \times 70\mu$. The vagina is oblique, opening directly into the uterus. A tubular organ is not observed.

The **spicules** are long ($120\mu$), i.e., longer than the tail (Figures 27c, d). They are located in a highly muscular sheath – the protractor of the spicules (pr. sp. – Figure 27c). Their base is greatly widened in the form of a tube (a – Figure 27c). Another widening is observed before the end (b – Figures 27c, d); the extreme tip is separated from this widening by a constriction (c – Figures 27c, d). The **gubernaculum** is fairly large, $45\mu$, or about $^2/_5$ of the spicules, and has the form of a plate over their terminal part (gub. – Figures 27c, d). A group of preanal bristles is present. Two pairs of smaller bristles lie nearer the midline, one pair directly anterior to the anus, the other somewhat more anterior. Two pairs of longer bristles lie at its sides (see Figure 27d). In front of this group a small papilla lies in the midline. This is possibly the remains of the accessory organ of Paroncholaimus and other subfamilies. The **tail** of the male is smooth and bristles are observed only at its end. The tail in the female is conical for $^{2}/_{5}$ of its length and in the male for 148 $^{1}/_{3}$ of its length; the posterior part is of uniform thickness. In the male the tail is very slender from the anus (Figure 27c). The proportions at the posterior end are: length of tail of female 3.5, of male 4.3; width at end of female 0.2, of male 0.33; length of spicules 5.0; gubernaculum 2.0. The caudal glands run far anterior to the anus. The caudal pore (Figure 27e) is of interest in that the cone of the caudal glands (con. – Figure 27e) is pressed into the cuticle, as is observed in Symplocostomini and Enchelidiini.

The species was found in small numbers in mussel mud from Kacha 8.13. The eggs were already in the uterus, although the female had not yet attained full growth.

The spicules and powerful development of the cells of the lateral lines assimilate this species most closely to Oncholaimus megastoma Eberth, but it is distinguished from the latter by the length of the spicules (in the latter species they are shorter than the tail) and by the shorter tail.

## 6. Subfamily **Enchelidiini**

This subfamily consists of one genus, Enchelidium Ehrenberg, in which I also include Lasiomitus Marion. Calyptronema paradoxum Marion is also a species of this genus.

At first the absence of an oral cavity and the presence of eyes seem to bring Enchelidium very close to Leptosomatini, but these forms have undergone an entirely different path of development and are not closely related. In Enchelidium the form of the lateral organs is quite different, as are the distinct cephalic line, the characteristic structure of the esophagus, and the row of unpaired papillae on the ventral surface of the male. These features not only distinguish Enchelidium from Leptosomatini, but they even cast some doubt upon the membership of the genus in Enoplidae altogether. The head structure – cephalic line and lateral organs, and also the lining – makes them most similar to Symplocostomini among the other subfamilies. The final answer must be delayed until a more detailed characterization of the internal organization is made.

The features of the subfamily conform with those of the sole genus:

149

### Genus ENCHELIDIUM Ehrenberg 1836

Die Akalephen des Rothen Meeres und die Organisation der Medusen, pp. 41, 57.
Eberth 1863: Unters. über Nematoden, p. 22.
De Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 27.
De Man 1888: Mém. Soc. Zool. France 1, p. 12.
Lasiomitus Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 10.
Calyptronema Marion 1870: ibid., p. 12.

Type species: E. marinum Ehrenberg 1836 (de Man 1888)

These are medium-sized worms, noticeably, and sometimes greatly, tapering anteriorly (except for L. exilis Marion). The cuticle is smooth. Lips are absent; six labial papillae are disposed around the oral aperture. Ten fairly long cephalic bristles are present, the sublaterals considerably shorter and sometimes disappearing entirely so that only six remain. A very distinct and characteristic cephalic line forms an annular cleft around the head behind the cephalic bristles. Laterally, it is adjacent to the lateral organ, which is transversely oval with a posterior pouch. The regularity of the orifice is broken by a tongue that projects from the posterior (see Figure 28b). The internal cephalic capsule forms an arch under the anterior surface of the head. There is no oral cavity: the esophageal tube is attached directly to the mouth. At first the esophagus is narrow, completely lacking muscle fibers, but then it expands slightly and forms eyes with two lenses directed obliquely laterally and anteriorly. The pigment of the two sides is usually fused into a single mass. A narrower part of the esophagus follows posteriorly as far as the nerve ring; this part has a weakly developed musculature, which becomes more powerful only in its posterior part. The cervical gland is located behind the esophagus, while its duct is shifted anteriorly. It is interesting to note that in all but one (L. bierstedti Marion) of the nine species described only males were found. The spicules are slender, curved, and fairly long. In front of the anus in the majority of species there are many 150 dense median papillae; in E. eberthi de Man there are few of these papillae, while in E. subrotundum Eberth and E. acuminatum Eberth they are not described at all, although this may be an error. The tail is pointed, of different form in different species. Apart from E. marinum Ehrenberg, all the species are known only from the Mediterranean Sea.

This genus was established by Ehrenberg for marine nematodes provided with eyes. It was characterized more accurately by Eberth, whose description was confirmed by de Man. Marion described his two species as representatives of a new genus Lasiomitus, while he took the molting Enchelidium for something entirely separate, which he described as Calyptronema paradoxum n.g., n.sp. The special chitinized bulges drawn in the mouth of his L. exilis are probably the incorrectly interpreted bulges of the cephalic capsule; thus, his Lasiomitus must be fully incorporated into Enchelidium.

The following species have been described so far:

1) E. marinum Ehrenberg 1836: Die Akalephen des Rothen Meeres und die Organisation der Medusen, pp. 41, 57.
Dujardin 1845: Hist. nat. des Helminthes, p. 238.
De Man 1888: Mém. Soc. Zool. France 1, p. 13, Table 2, Figure 8. Walcheren – seawater canal, mud on stones. Indications for the Baltic Sea (Eichwald) not confirmed.

2) E. longicolle n.sp., see next page.
3) E. paradoxum (Marion 1870) Calyptronema par: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 12, Table A, Figure 2 (Anse de la Fausse-Monnaie à Endoume près de Marseille au milieu des Bryopsis).
4) E. bierstedti (Marion 1870) Lasiomitus b. Marion: Ann. Sci. Nat. Zool. (5) 14, Art. 1, p. 8, Table L. Figure 2. (Very numerous August—September 1869 on the rocks of Lake Ratonneau and March 1870 "au Pharo a l'entrée du port de Marseille."
5) E. tenuicolle Eberth 1863: Unters. über Nematoden p. 23, Table 3, Figures 1—3 (Nice).
6) E. exile (Marion 1870) Lastiomitus exilis Marion: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 11, Table A, Figure 1 (quite rare around Marseilles. "Endoume, dans les environs de la Batterie" June 1868).
7) E. eberthi de Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 97, Table 7, c—Figure 6a (Naples).
8) E. subrotundum (Eberth 1863) Enoplus s. Eberth: Unters. über Nematoden p. 33, Table 2, Figures 11, 12. (Nice).
9) E. acuminatum Eberth 1863: Unters. über Nematoden p. 24, Table 3, Figures 4, 5 (Nice).
E. obtusum Grube 1861: Ein Ausflug nach Triest und dem Quarnero, p. 103, Table 1, Figure 4, —insufficiently described and hardly likely to be recognized anywhere again.
E. polare Steiner 1916 belongs to quite a different group (different disposition of the eyes, structure of the esophagus).

151

1 (12). Excretory pore lies far posterior to eyes; in male numerous dense median preanal papillae.
2 (11). Head width $^1/_3$—$^1/_4$ of body width at end of esophagus; spicules more than half of tail length.
3 (10). Esophageal region of body not very greatly extended (6—8 times longer than body width at end of esophagus). Spicules not longer than $^2/_3$ of tail. Papillae begin directly anterior to anus, small, and extend not far anteriad. No swellings opposite eyes.
4 (5). Spicules bend at an angle; cells of lateral fields vesicular . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. bierstedti** (Marion)
5 (4). Spicules bend gradually. Cells of lateral fields not vesicular.
6 (7). Tail conical to end, eyes separate. . . . . **E. paradoxum** (Marion)
7 (6). Tail at end has portion of uniform thickness.
8 (9). This portion only $^1/_5$ of tail length. Head $^1/_4$ body width at end of esophagus. Six cephalic bristles . . . . . . . . **E. longicolle** n. sp.
9 (8). This portion about $^1/_2$ length of tail. Ten cephalic bristles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. marinum** Ehrenberg
10 (3). Esophageal region of body very extended (14 times longer than body width at end of esophagus). Distinct swellings opposite eyes. Spicules almost as long as tail. Papillae in male very large, begin some distance from anus, and extend far anteriad . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. tenuicolle** Eberth
11 (2). Head width $^2/_3$ body width at end of esophagus. Tail conical. Spicules less than $^1/_2$ tail length . . . . . . . . . . **E. exile** (Marion)
12 (1). Excretory pore located opposite eyes. Few or no (?) preanal papillae.
13 (14). Spicules less than half tail length, 7 sparsely disposed preanal papillae . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. eberthi** de Man
14 (13). Spicules $^2/_3$ of tail length; papillae absent (?). These two species may be synonyms.
15 (16). Gubernaculum present; no chitinized pieces in mouth; lens located in front of eyes . . . . . . . . . . . . . . **E. acuminatum** Eberth
16 (15). Gubernaculum absent; chitinized pieces present in mouth; lens located in center of eyes . . . . . . . **E. subrotundum** (Eberth)

## 28. **Enchelidium longicolle** n. sp.

(Tables 4, 5, Figure 28)

$$\text{♂}\ \frac{\quad 15.2 \quad 20.8 \quad 52.8 \quad 56.4 \quad 94.4}{0.5 \quad 1.6 \qquad (1.7) \qquad 1.2}\ 3870$$

$$\alpha=60,\ \beta=6^1/_2,\ \gamma=18.$$

| Dimensions ♂ | Cephalic bristles | Cephalic line | Eyes | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 5 | 9½ | 16 | 70 | 220 | 500 |
| Width | 16 | 16 | 18 | 22 | 54 | 60 |

152 The **body** of the male tapers greatly anteriorly—almost fourfold to the cephalic bristles from the end of the esophagus; it is slightly wider at midbody, and tapers $1^1/_2$ times to the anus. The **cuticle** is completely smooth, fairly thick—$2^1/_2\mu$. Bristles are present in fairly large numbers over the entire body, particularly along the subventral lines; they are about $4\mu$ long.

The **head** is generally rounded, with labial papillae projecting somewhat anteriorly; these have the form of small cones around the margins of the mouth. The cephalic bristles are $11\mu$ long, or $^3/_4$ of the head width, and only number six. A distinct cephalic line lies behind them and forms a groove marking the head, particularly evident in Figure 28b. The cephalic line is adjacent to the lateral organ, which has an orifice of characteristic form. It is wide (Figure 28b), and a tongue with a flattened point projects into it from the posterior margin. Lateral examination shows that this tongue curves somewhat externally. The lateral organ is shifted far dorsally.

The **cephalic capsule** lies inside the head (c.ceph. —Figures 28a, b). It consists of an arch whose margins are set against the cephalic line and lateral organs, as is seen from Figures 28a, b. The tube of the **esophagus** is attached to it directly, so that there is no oral cavity. The beginning of the esophagus possesses no musculature (not clearly shown in the drawings); it then expands somewhat and is transformed into eyes. (The widening of the lumen in Figure 28a is apparently accidental). The **eyes** here are well developed and the two pigment cups combine (Figure 28a), but two separate lenses are maintained. The lenses are apparently cuticular and correspond to the cuticular bodies located behind the oral cavity in Symplocostoma, but they are by no means true lenses. Laterally, the pigment cup has a regular oval form (Figure 28b). The lens is about $3\mu$ wide, and the entire eye is about $12\mu$. The **nerve ring** encircles the esophagus somewhat anterior to its middle. The **cervical**
153 **gland** lies $300\mu$ behind the esophagus. It is round, slightly elongated, measuring $80 \times 55\mu$; a narrow duct runs anteriorly from it, terminating in the anterior third of the distance between the nerve ring and the anterior end of the body.

Behind the eyes the **esophagus** continues as a narrow tube $8\mu$ wide, with very weakly developed muscle fibers; esophageal glands are not observed here. The esophagus expands to $16\mu$ to the nerve ring without changing its structure. A short distance posterior to the nerve ring, i.e., at the beginning of the posterior half, the esophagus begins a wide expansion (up to $32\mu$ in the posterior part) and only in this region are well-developed musculature and glands observed. The intestine consists of very large cells.

Females were not found.

The anterior **testis** begins a short distance behind the end of the esophagus, and the posterior testis is reflexed posteriorly. The vas deferens consists of large epithelial cells disposed in two rows. In the ejaculatory duct these cells line a further row of oblique muscle cells. The **spicules** (Figures 28c, d) are long ($160-180\mu$), slender, and greatly curved in their terminal half. Their base is slightly expanded, and the end is pointed like a sharpened quill. The gubernaculum is small ($35\mu$), and lies next to the terminal part of the spicules. Individual bristles are observed around the anus in the male; a pair of thick preanal bristles near the midline is particularly constant (s—Figure 28c). A median row of 50—70 very small papillae lies preanally in the midline.

The **tail** gradually tapers conically to the end. Only at the extreme tip is there a short portion of uniform width. The tubular caudal glands terminate slightly anterior to the anus. The cuticle at the end of the tail is thickened, so that the caudal pore is quite long; a cone is inserted into it and covered by cuticle. Many bristles are observed over the entire tail. The proportions at the posterior end are: length of tail 4.5; its width at end 0.15; length of spicules 3.3; gubernaculum 0.7; distance from anus
154 to most anterior papilla 13—14.

This species was found in fairly large quantities: mussels in piles 1.12 ∞; Cystoseira on the coast 7.12, several; saccocirrous sand from the road 1.12, 1 specimen; oxeas sand of Georgievskii Monastery at 9 sajenes, 18 sajenes 7.12, several; Zostera 5.12; phyllophores 5.12, several. It is noteworthy that only males were encountered. Other authors who have studied Enchelidium also describe only males. Only in L. bierstedti Marion are females known. I cannot understand this phenomenon at all.

This species is most similar to the type species E. marinum Ehrenberg, whose general head structure is exactly alike The differences are that here there are only six cephalic bristles, and the head apparently tapers even more; furthermore, the tail of E. marinum has a longer filiform termination. E. tenuicolle Eberth, to which the Black Sea species at first seem similar, is differentiated by many essential features which make it unique among the other members of Enchelidium (see key).

## 7. Subfamily **Symplocostomini**

This subfamily is characterized by its oral cavity: its aperture is not closed by any lips, but is widely open. The cavity itself is fairly wide with thick walls, and a large tooth arises from its bottom; the tooth is protrusible in Symplocostoma and immovable in Eurystoma. In other respects the two genera are fairly well differentiated:

1 (2). Stout conical tooth in oral cavity. Lateral organ with transversely oval orifice. Spicules greatly curved. Two accessory organs of characteristic structure . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Eurystoma** Marion (p. 109)

2 (1). Slender movable spear in oral cavity. Lateral organs with large orifice and posterior pouch. Spicules long and slightly curved. Accessory organs absent. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Symplocostoma** Bastian (p. 114)

155 This subfamily displays a close relationship with Enchelidiini. The form of the lateral organs and cephalic lines is similar to Eurystoma and the cuticular bodies around the eyes and the structure of the spicules are as in Symplocostoma.

### Genus EURYSTOMA Marion 1870

Ann. des Sciences Natur. Zool. (5) 13, Art. 14, p. 20.
Villot 1875: Arch. Zool. Exp. 4, p. 460.
De Man 1888: Mém. Soc. Zool. France 1, p. 24.

Type species: Eurystoma spectabile Marion 1870

This is a completely natural and well differentiated genus. The worms that belong to it are very slender and greatly elongated; the body is of uniform width and appears filiform. The cuticle is smooth. The head is beset with six labial papillae and ten cephalic bristles; it is marked off by an annular groove —the cephalic line—which is adjacent to the lateral organs. These are large and formed of a transversely oval depression, into which a tongue from the posterior wall projects (in the species that I examined; it is possible that in E. terricola de Man 1907 the structure of the lateral organs is slightly different). At the cephalic line the outer and inner layers of the cuticle part and are attached separately to the cephalic capsule, leaving between them an annular canal as in Oncholaimini. The oral cavity is voluminous and divided by annular folds into several chambers: three teeth arise from its bottom — a large subventral, a small subventral, and a small dorsal tooth. Two eyes provided with lenses are present behind the oral cavity. The esophagus is straight. The cervical gland is present. The intestine consists of large cells. Phagocytic cells are present. The genital tract is paired, with short and reflexed ovaries and a thin-walled uterus. The vagina is highly developed. The testes are paired; the spicules are arched, and fairly slender. The gubernaculum is well developed and has a large appendage of irregular form directed posteriorly. There are two median 156 bell-shaped accessory organs provided with anterior and posterior processes. The anterior organ is always the larger. A cuticular thickening directly anterior to the anus is beset with bristles. The tail is conical, of medium length. Only one species in the Black Sea — Eurystoma assimile (de Man, 1878).

Max Schultze (1859) drew Eurystoma for the first time and designated it Enoplus sp.; Eberth (1863) described Enoplus ornatus n. sp., which also belongs here. Marion (1870) established genus Eurystoma with two species, one of which corresponds to that of Eberth. De Man made an obvious mistake (1878) when he described what is in my opinion a new species of Eurystoma as Oncholaimus assimilis n. sp. The mistake was repeated later by Daday (1901) and Golovin (1901—1902), who quite rightly identified O. assimilis de Man with the Black Sea species but failed to associate it with genus Eurystoma. De Man (1888) described the new species E. filiformis from the northern seas, but I feel that this species corresponds exactly to his E. (Oncholaimus) assimile. This mistake is explained by the fact that in 1878 de Man had available only young females of this species and later considered them identical with Enoplus ornatus Eberth = Eurystoma tenue Marion. However, the position of the eyes indicates that the latter species is different from E. assimile. On the basis of the large amount of material that I collected in the Black Sea it is possible to regard E. assimile and E. filiforme as identical.

Thus, the following five species are now considered as established:

1) Eur. spectabile Marion 1870: Ann. Sci. Nat. Zool. (5) 13, p. 20, Table E, Figure 1 — quite rare: Endoume, Fausse-Monnaie inlet near Marseilles.
2) Eur. ornatum (Eberth 1863) — Enoplus ornatus Eberth: Unters. über. Nematoden p. 40, Table 4, Figures 13—15; Table 5, Figures 5, 6; Eur. tenue Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 21, Table E, Figure 2; nec Oncholaimus ornatus Daday 1901 — Nice (Eberth); sur les débris de Posidonia... et dans la terre amassée auprès des algues encroûtées... dans les grands fonds — le long de l'île Pomègue — 30 m. (Marion; Sète, canal de Bourdigues (Rouville).
157 3) Eur. assimile (de Man 1878), see below.
4) Eur. lithothamnii Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 117. ? Eur. filiforme Steiner 1916: Z. Jahrb. Syst. 39, p. 602, Table 16, Figure 24a; Table 28, Figure 24b; Murmansk. — Pala Inlet, lithothamnium. Steiner probably had the same species from algae from the White Sea strait, see p. 114.
5) Eur. terricola de Man 1907: Tijd. Nederl. Dierk. Vereen. (2) 10, p. 242; 1908: Mém. Soc. Zool. France 20, p. 84, Table 4, Figure 17. — damp earth near gutters with brackish water — Walcheren Island, Holland (de Man); roots of Salicornia and Atriplex — Denmark (Ditlevsen).

Oncholaimus ornatus Daday 1901: Termész. Füz. 24, p. 442, Table 22, Figures 1—3. Fiume, patches of algae on the sea; apparently a new species, but poorly described and therefore not included in the key. Enoplus sp. M. Schultze 1857: Carus, Icones Zootomicae, Table 8, Figure 3, from Trieste, also belongs to this genus.

1 (8). Margins of mouth hardly cover it, so that it is widely open; cephalic line located at $^1/_3$ of height of oral cavity.
2 (5). Spicules $^1/_3$ of length of tail, fairly stout.
3 (4). Accessory organs massive, anterior almost same size as posterior . . . . . . . . . . . . . . . . . . . . . . . . **E. spectabile** Marion
4 (3). Accessory organs not so massive, anterior always larger than posterior . . . . . . . . . . . . . . . . . . . . . **E. ornatum** (Eberth)
5 (2). Spicules very slender with hooks at end, $^2/_3$ of length of tail or even more.
6 (7). Distance between two accessory organs less or only slightly more than length of spicules. . . . . . . . . . . . . **E. assimile** de Man
7 (6). This distance twice greater than length of spicules. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. lithothamnii** Saveljev
8 (1). Margins of mouth partially close it; cephalic line at anterior $^1/_4$ of height of oral cavity . . . . . . . . . . . . **E. terricola** de Man

## 29. **Eurystoma assimile** de Man 1878
(Table 5, Figure 29)

Oncholaimus assimilis de Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 95, Table 7, b — Figure 5a.
O. ass. Daday 1901: Termész. Füzetek 24, p. 439, Table 21, Figures 9, 10. Golovin 1901: Observations on Nematodes I, pp. 86, 95.
Eurystoma filiforme de Man 1888: Mém. Soc. Zool. France 1, p. 26, Table 3, Figure 13; nec Eur. tenue Marion = Eur. ornatum (Eberth), nec (?) Eur. filiforme Steiner 1916.

$$♂\ \frac{0.5 \quad 6.8 \quad 16.6 \quad 26.0 \quad 97.9}{0.5 \quad 1.0 \quad 1.0 \quad 1.0 \quad 1.1}\ 5100$$

$$\alpha=90;\ \beta=6;\ \gamma=45.$$

$$♀\ \frac{0.5 \quad 6.3 \quad 15.2 \quad 40 \quad 47.5 \quad 55.5 \quad 65.0 \quad 75.5 \quad 98.0}{0.5 \quad 0.8 \quad 0.9 \qquad\qquad 1.0 \qquad\qquad 0.6}\ 6200$$

$$\alpha=100;\ \beta=6^1/_2;\ \gamma=50.$$

158

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Eyes | Nerve ring | Excretory pore | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 6 | 20 | 30 | 250 | 300(?) | 620 |
| Width | 19 | 24 | 27 | 46 | – | 46 |
| ♀ | | | | | | |
| Length | 6 | 22 | 30 | 265 | – | 640 |
| Width | 19 | 24 | 27 | 42 | – | 46 |

The **body** tapers twofold from the middle of the esophagus to the anterior end, and tapers slightly in the female to the anus. All the remainder of the body is filiform, of uniform width, generally very slender. The **cuticle** is extremely thin (about $^1/_2\mu$) and smooth. There are very few bristles.

The head is generally rounded. Lips are absent and no structure closes the round oral aperture. Six small labial papillae are set around it. A circlet of ten long cephalic bristles lies around the level of the middle of the oral cavity. These bristles are $11\mu$ long, which is just greater than half the head width. The lateral organ is large with a transversely oval slit $11\mu$ wide, or more than half the head width. A tongue projects half way from the posterior margin so that the width of the slit seems to be more than $4\mu$. The lateral organ is shifted dorsally (Figure 29a).

The cuticle thickens at the level of the lateral organs as it approaches the head; then a thin layer proceeds to the anterior end (Figure 29a). The most anterior part is separated by a line on the cuticle (lin. —Figure 29a). The inner layer curves internally from the thickening, as in Oncholaimini, and is attached independently to the cephalic capsule (c—Figure 29a). The **oral cavity** is large, resembling that in Oncholaimini. Thickenings divide it into chambers: the first is separated by a thin chitinized band parallel with the mouth (a—Figure 29a), the second by a double row of longitudinal chitinized protuberances that ring the entire wall (b—Figure 29a); the third chamber extends to the bottom of the oral cavity. Three teeth arise from this part, one large—the right subventral (d.d. sv. —Figure 29a) and the other two very small (d.d.
159 dorsal tooth Figure 29a); the latter two seem to be merely the apertures of the esophageal glands in the cuticle. The length of the oral cavity is $19\mu$, width $12\mu$, and the point of the largest tooth is $15\mu$ from the bottom.

The **eye** has a fairly rectangular form with rounded margins, and a light lens is adjacent to it anteriorly. The distance from the eye to the mouth is always less than the length of the oral cavity. Its diameter is $6-8\mu$. The **esophagus** is very slender anteriorly—$11\mu$ (40% of the body width); at the nerve ring it is $16\mu$, and posteriorly it is $30\mu$ (66%). In the female it is slightly thicker, reaching $35\mu$ (75%) posteriorly. The esophageal glands are observed only in its posterior part, but their ducts open on the teeth. The cells of the **intestine** are very elongated, large, and of fairly irregular form. The **nerve ring** is round, thick, and encircles the esophagus behind its anterior third. The **cervical gland** is weakly developed, lying $^3/_4$ of the length of the esophagus behind its posterior end. The cervical pore lies behind the nerve ring half way along the esophagus. **Phagocytic cells** are present in the body cavity; their structure is similar to that in Paroncholaimus (Golovin).

The ovaries are paired, reflexed, and short; very young oogonia disposed in one row are already present. The terminal part of the oviduct forms an expansion consisting of small cells The uterus is thin-walled. The eggs in the uterus are very long, measuring $140\times50\mu$. The vaginae are thick-walled and diverge at an acute angle directly from the vulva.

There are two short testes. The seminal ducts consist of large cells. The **spicules** are slender, curved (Figure 29c), $65\mu$ long. Their base widens slightly, while some hooks that are very characteristic for this genus are observed at the end (Figure 29a). The **gubernaculum** has a very characteristic form. It is large and extends both anteriorly and posteriorly to the spicules. Only a slender process extends anteriorly, while the principal part is directed posteriad. This is a thick, irregularly-shaped process curved ventrally with a cavity inside (gub. —Figure 29c),
160 sometimes with a hook $30\mu$ long at the end. Two uniform accessory organs are located preanally. These are round capsules with an aperture above and below and two processes anteriorly and posteriorly ($ao_1$, $ao_2$—Figure 29c). Two large glands discharge through them. The anterior organ is always rather larger than the posterior. Their relative position varies somewhat, so that their ends are in some cases almost adjacent and in others are far apart. In the former case the tail is usually also shorter. When I first studied the material I took such males for another species. However, more careful inspection indicated that they were merely variant forms of the same species. An examination of several males gave the following relationships: length of tail 1.8—2.5; distance from anus to first accessory organ 1.5—2.1, possibly both slightly larger than the tail (exception) or smaller (rule); distance between first and second accessory organ 1.2—2, almost always less than the distance between the first accessory organ and the anus, rarely equal or slightly more; less than the length of the tail. Spicules (chorda) 1.3—1.6, always shorter than the tail, rarely almost equal. Absolute length $63-82\mu$. Gubernaculum 0.7—0.9, about half the length of the spicules. Absolute length $30-40\mu$. Posterior accessory organ 0.7—1.2, absolute length $33-53\mu$. Anterior accessory organ 1.1—1.4, absolute length $46-66\mu$, equalling 1.1—1.6 of the length of the posterior. No correspondence is observed between the size of the accessory organs and the distance between them. These relationships may vary.

The bristles in the male occur in the following places: (1) 2 pairs around the caudal pore (uniform in male and female: $s_1$ — Figure 29c); (2) 3 pairs of submedian bristles half way along the tail ($s_2$); (3) a preanal portion of thickened cuticle $14\mu$ long is beset with 2 pairs of long bristles at each end and two pairs of shorter bristles between them ($s_3$); (4) 5 median papillae between the anus and the posterior accessory organ ($p_4$); (5) 2 pairs of short bristles posterior to the last ($s_5$); (6) 1 median papilla halfway between the anterior and posterior accessory
161 organs ($p_6$).

The **tail** gradually tapers conically to the end and is of different length in different individuals. The caudal glands continue anteriorly far beyond the anus; the cone projects into the caudal pore.

This species was found in the following places: Cystoseira from a small area in the road 6.12, juveniles; Shmit Bay 7.12, adult male and female; deep Cystoseira 6.12, immature female; stone algae 7.12 ∞; mussels from rocks under the station 6.12, young and adult, ∞; Ulva from New Holland 6.12, young male; Zostera 5.12, several adults; Streletskaya Bay — layer washed from Potamogeton 3.10 by Zernov, ∞; seaweed on the coast of Peschanaya Bay 7.12, immature female; shingle of Georgievskii Monastery 7.12, juveniles; oxeas sand of the Georgievskii Monastery 7.12, ∞; Peschanaya Bay 1.12, ∞; 5.12 — 7.12, single specimens; algae on the sand at the same place 6.12, several; coquina of Georgievskii Monastery 7.12, juveniles. It was first noted for Sevastopol by Golovin as Oncholaimus assimilis de Man in large quantities in seaweed in the northern part of the bay.

This is a widespread species known from the coasts of Holland — a seawater canal on Walcheren Island (de Man). Mediterranean Sea: Naples (de Man); Adriatic Sea: Fiume, patches of algae on the pier (Daday). E. filiforme de Man, found by Steiner in the White Sea strait, is related to another species, judging from the position of the eyes; possibly E. lithothamnii Saveljev (this description was unknown to Steiner). The definition was made according to a single molting individual.

## Genus SYMPLOCOSTOMA Bastian 1865

Trans. Linn. Soc. 25, p. 132.

De Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 90.
De Man 1888: Mém. Soc. Zool. France 1, p. 78.
Amphistenus Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 14.

Type species: S. longicolle Bastian 1865

The species of this genus usually **taper greatly to both ends**, so that
162 the diameter at the end of the esophagus in extreme cases is 5 — 6 times greater than the diameter of the head, although there are species in which the head is wider. The cuticle is usually smooth and thin (in S. marioni n. sp. the outer layer is slightly annulated). Lips are absent; there are six labial papillae, and six, rarely ten, long cephalic bristles. The lateral organ is **cyathiform with a round anterior orifice** and usually with a fairly elongated pouch. The two layers of cuticle part at the level of the cephalic line and the inner is attached separately to the cephalic capsule. The mouth is not enclosed by lips and is constantly open. **The oral cavity is wide** and provided with thick chitinized walls. **On the wall annular thickenings are observed** which sometimes divide the cavity into several chambers. There are three teeth in the anterior part of the oral cavity; the largest of them is one of the subventrals, and adjacent to this tooth is a **spear that rises from the bottom of the oral cavity** and which may protrude and serve as a piercing organ. The remaining two teeth (the other subventral and the dorsal) in the anterior part of the cavity are far less developed and may even be absent. In some species there are three small teeth in the posterior part of the oral cavity corresponding to the teeth in Oncholaimini; the esophageal glands open on these.

Near the posterior end of the oral cavity two **shiny cuticular bodies** are located, and behind them pigment spots. The esophagus at first is narrow and completely lacking in muscle fibers, which are well developed only in its posterior part, where it expands greatly in the form of a bottle. The plasmatic part of the esophagus is well developed here and is interstratified with the muscles, which gives the esophagus a very characteristic shape. In one species there are six bulbs. The nerve ring is flat and wide. The cervical gland is located behind the esophagus and its pore is shifted anteriorly.

The ovaries are short and reflexed; they are paired in all but one species, where only the posterior ovary is present. The vagina is well developed. The spicules are slender, long, evenly curved, and the
163 gubernaculum is adjacent to them. Males are more rare than females. The tail is long and conoid. The cuticle at the end of the tail is thickened and a cone is inserted into the pore. Five species are found in the Black Sea, four of them new.

Although genus Symplocostoma contains diverse forms, it is nevertheless a fully natural grouping. It is most similar to Enchelidium among the other genera; the latter has similar cuticular bodies that play the part of lenses, and the genital system is also alike. The structure of the oral cavity, however, assimilates Symplocostoma to Eurystoma, but the genital systems of these two genera are considerably different.

The first species of this genus was described by Eberth (1863) as a species of genus Enoplus. Bastian (1865) established genus Symplocostoma and included in it, apart from Eberth's species Enoplus tenuicollis, several other species now related to Eurystoma, and finally S. vivipara, which was isolated by Bütschli (1874) in the special genus Anoplostoma. Marion (1870) described two forms of Symplocostoma as representatives of a new genus Amphistenus. De Man (1878) divided up all these diverse elements correctly, and since then genus Symplocostoma has maintained its present scope. A detailed description of the genus was provided by de Man (1888).

The following nine species are so far known:

1) S. longicolle Bastian 1865, see p. 117.
2) S. ponticum n. sp., see p. 119.

3) S. murmanicum Saveljev 1912: Trav. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 118 — Murmansk, Ekaterininskaya Harbor, muddy sand, some meters. Probably related here is the species mentioned by Steiner (Zool. Jahrb, Syst. 39, p. 603), S. longicolle, from the White Sea strait. Definition made according to one young specimen.

4) S. hexabulba n. sp., see p. 120.

5) S. tenuicolle (Eberth 1863) Enoplus t. Eberth: Untersuchungen über Nematoden, p. 41, Table 4, Figure 16; Table 5, Figures 1, 2; S. t. de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 90, Table 7, Figure 1; Amphistenus agilis Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 14, Table B, Figure 1, (nec. de Man 1878: loc. cit.; Marion 1875: C. R. Ac. Sci. 80, p. 499; Rouville 1904) — Nice, Naples; Sète, canal de Bourdigues; Marseilles — rocks and algae. Pharo, Endoume, vallon des Auffes, very common in winter months.

6) S. sabulicola n. sp., see p. 122.

7) S. pauli (Marion 1870) Amphistenus p. Marion: Ann. Sci. Nat. Zool. (5) 13, Art 14, p. 15, Table B, Figure 2. "Au milieu des Floridées qui recouvrent les maçonneries du quai au Pharo" around Marseilles.

164 8) S. antarcticum Linstow 1896: Erg. Hamburger Magalhaenischen Sammelreise 1, No. 7, p. 11, Figure 19; Ushuaia, 2 sajenes.

9) S. marioni n. sp., see p. 123.

It is impossible to decide, without re-examination, the position of Urolabes barbatus Carter 1859: Ann. Mag. Nat. Hist. (3) 4, p. 43. Table 3, Figure 32, which Bastian related to Symplocostoma. The freshwater S. lacustris Daday 1894 (Zool. Jahrb. Syst. 10, p. 120, Table 14, Figures 5 — 7) belongs, of course, to another, possibly new, genus; the anterior end, as far as can be judged from the poor drawing, is reminiscent of genus Bunonema Jägerskiöld.

1 (12). Oral cavity with many cuticular rings, six cephalic bristles.
2 (9). Body tapers at least fourfold from end of esophagus to head.
3 (8). No bulbs in esophagus.
4 (5). In male spicules shorter than tail; adult female $5^1/_2$ mm long; eggs short, about 90$\mu$, many present in uterus. Supplementary bristles absent in male. Anterior part of oral cavity $^1/_3$ of its overall length. . . . . . . . . . . . . . . . . . . . **S. longicolle** Bastian
5 (4). Spicules in male equal in length to tail (in S. ponticum n. sp. males unknown). Adult female $7 - 7^1/_2$ mm.
6 (7). Supplementary bristles present in male. Oral cavity as in S. longicolle . . . . . . . . . . . . . . . . . **S. murmanicum** Saveljev
7 (6). Oral cavity with shorter anterior part, $^1/_4$ of overall length. Cephalic bristles shorter and thicker than in S. longicolle. Eggs elongate, never many present in uterus. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **S. ponticum** n. sp.
8 (3). Six bulbs at end of esophagus . . . . . . . . . . **S. hexabulba** n. sp.
9 (2). Body does not taper more than twofold from end of esophagus anteriorly.
10 (11). Female genital tract paired . . . . . . . . . . . S. **tenuicolle** (Eberth)
11 (10). Only one posterior tract . . . . . . . . . . . . . . **S. sabulicola** n. sp.
12 (1). Oral cavity relatively short with one ring, ten thick cephalic bristles.
13 (14). Oral cavity with constriction at level of ring. True teeth at extreme bottom of oral cavity . . . . . . . . . . **S. marioni** n. sp.
14 (13). Oral cavity without constriction.
15 (16). Oral cavity widens anteriorly. Cephalic bristles thick. Teeth absent (?). . . . . . . . . . . . . . . . . . . . . . **S. antarcticum** Linstow
16 (15). Oral cavity almost cylindrical. Teeth in middle of posterior section of oral cavity . . . . . . . . . . . . . . . . . **S. pauli** (Marion)

## 30. Symplocostoma longicolle Bastian 1865
(Table 5, Figure 30)

Trans. Linn. Soc. 25, p. 133, Table 11, Figures 119 — 122.

De Man 1888: Mém. Soc. Zool. France 1, p. 30, Table 3, Figure 14. nec Golovin 1901: Observations on Nematodes 1, p. 97, Table 2,
165 Figures 1, 6.

$$\male\ \frac{0.4\quad 9.0\quad 20.5\quad 34.5\quad 94.5}{0.4\quad 1.5\quad 1.9\quad 2.4\quad 1.4}\ 4180$$

$\alpha=42;\ \beta=5;\ \gamma=18.$

$$\female\ \frac{0.4\quad 7.1\quad 20\quad 38\quad 41\quad 56\quad 71\quad 74\quad 94.5}{0.4\quad 1.5\quad 1.7\qquad\qquad\qquad 2.3\qquad\qquad\qquad 1.0}\ 5370$$

$\alpha=43,\ \beta=5,\ \gamma=19.$

| Dimensions<br>♂ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 3 | 16 | 95 | 385 | 805 |
| Width | 12 | 16 | – | 51 | 68 |
| ♀ | | | | | |
| Length | 4 | 19 | 73 | 300 (420*) | 840(1,020*) |
| Width | 15 | 18 | 24 | 65 | 84 |

The **body** narrows greatly anteriorly, becoming $5^1/_2 - 6$ times narrower at the cephalic bristles than at the end of the esophagus, whence the body widens by $^1/_3$ to the middle and then tapers to the anus more in the female ($2^1/_2$ times) than in the male ($1^1/_2$ times). The **cuticle** is thin (2$\mu$) and smooth; fairly numerous bristles 5$\mu$ long are observed over the entire body.

---

* The maximum dimensions are in parentheses; the other figures more or less agree

The narrow **head** is truncated anteriorly. The oral cavity is 7μ wide and lacks lips. Six small labial papillae and six very slender cephalic bristles 8μ long are present. The lateral organ is located posteriorly and dorsally to the lateral bristles. This is elongate, with a round anterior orifice 5μ wide ($^1/_3$ of the head). Anteriorly, the inner cuticular layer parts from the outer and is attached to the cephalic capsule.

The **oral cavity** is enclosed by thick walls on which transverse rings are observed; these are very characteristic for S. longicolle and similar species. Two grooves are located in the anterior chamber of the oral cavity, which is separated from the posterior at the level of the 166 anterior third by a third groove. A fourth groove lies in the posterior chamber. Two immovable teeth project into the cavity anterior to the groove that separates the two chambers (d. imm. — Figure 30a). These are simple hooks and are not homologous with the teeth of Oncholaimini in that the esophageal glands do not discharge upon them. A thin, spearlike tooth rises from the bottom of the cavity (d. mob. — Figure 30a), closely adjacent to the larger of the two immovable teeth — the right subventral. The spearlike tooth may be protruded to the outside and thus serve as a piercing organ. The dimensions of the oral cavity are length 20μ, width 12μ, length of tooth 16μ, width of mouth 6μ. A shiny cuticular body ("vésicule auditive" of Marion) lies behind the oral cavity. This corresponds to the lens in Enchelidium, but here it does not have a similar function as the eyes are shifted farther back. In the male the eyes and the cuticular body lie more posteriorly than in the female. The **esophagus** is very narrow anteriorly, corresponding to the narrowness of the body, only 8 — 10μ (50% of the body width); muscle fibers are not developed in it, and the internal chitinized tube is very thick. It widens more than twofold by the level of the nerve ring, reaching 24μ (35%), and continues to gradually widen posteriorly to 60μ (75%). In this region the musculature and glands are fully developed. The structure of the esophagus is very characteristic here: the plasmatic part is interstratified with the muscle fibers, which gives the esophagus a segmented appearance. I was unable to find the cervical gland. The cervical pore in the female lies $3^1/_2$ lengths of the oral cavity from the anterior end, 5 lengths in the male.

The **ovary** is very short, similar in structure to that of Eurystoma, with only its one terminal cell blackened by inclusions. The thin-walled uterus contains up to 20 — 25 eggs in the adult female. The eggs are either perfectly round (90×90μ) or slightly elongated when free of the pressure of the neighboring eggs (105×75μ). The vagina is well developed 167 and traverses internally half the body width. As distinct from Eurystoma, the vagina does not branch but has one direct right-angled connection with the short ovejector (oveject. — Figure 30b); this has a common longitudinal lumen, each of whose ends is transformed into the thin-walled uterus. The external end of the vagina is narrow, the internal widened, forming two semicircular swellings on the anterior and posterior margins, exactly as in S. ponticum (see Figure 31c).

The **testis** is apparently single. The vas deferens consists of two rows of very large cells. In the ejaculatory duct, which is a little longer than the spicules, these layers overlie an additional internal layer of oblique muscle cells. The bursal musculature is strongly developed. The spicules (Figures 30d, e) are quite long, about $^2/_3$ of the tail; a funnel is observed at the base, the end is blunt, and their length is 140μ. The gubernaculum is lamellar, its dorsal wall adjacent to the spicules and their ends; its length is 45μ (Figure 30e). As distinct from S. murmanicum Saveljev, there are no supplementary bristles in this species.

The tail gradually tapers conically to the end; in the female the base of the tail is narrower than in the male, which makes it appear wider at the end. The tubular caudal glands are confined to the tail, the part containing the nucleus being very inconspicuous. The cone of the caudal glands is very small and is slightly inserted into the cuticle, which is greatly thickened at the end of the tail, so that the pore is very long (see Figure 30b). The proportions in the tail are: length in male 4, in female 5; width at end in male and female 0.25; spicules 2.4; gubernaculum 0.7.

The indications of Golovin on S. longicolle relate to S. ponticum. I found them in the following places: Cystoseira on the water surface 5.12, juveniles; 7.12, adult males, females; Cystoseira, 6 sajenes 6.12, juveniles, adult females; stone algae 7.12, adult females; mussels 1.12, ∞ males, females, juveniles; 6.12, adult female; Zostera 5.12, juveniles and highly pigmented adult female; Nassarius from mud of Artilleriiskaya Bay 6.12, young females; phyllophores 6.12, adult female.

168 The live S. longicolle is a reddish color (the color of the intestine), swims rapidly and is capable of making serpentine movements of the head in all directions. Its geographical distribution is: coast of England — Falmouth, Brighton; at low tide on Cladophora and other algae where there are many diatoms (Bastian); Walcheren Island (de Man). Bastian's indications correspond with my findings that in the Black Sea this species lives in seaweed facies.

## 31. **Symplocostoma ponticum** n. sp.

(Table 5, Figure 31)

S. longicolle Bastian; Golovin 1901: Observations on Nematodes 1, p. 97, Table 2, Figures 1 — 6.

$$\text{♀}\ \frac{0.3 \quad 22.0 \quad 42 \quad 49 \quad 59 \quad 71 \quad 76 \quad 96.8}{0.25 \quad 1.3 \qquad\qquad\quad 2.0 \qquad\qquad 0.8}\ 7250$$

$$\alpha=50,\ \beta=4^1/_2,\ \gamma=27.$$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | – | 24 | 62 | 455 | 1,280 |
| Width | 16 | 21 | — | 75 | 85 |

The **body**, as in the preceding species, narrows greatly anteriorly, more than fivefold from the end of the esophagus; from here it widens $1^{1}/_{2}$ times to midbody, whence it tapers more than twofold to the tail. The **cuticle** is thin ($2\mu$) and smooth; there are few bristles on it.

The head structure is very similar to that of the foregoing species. The cephalic bristles are $6\mu$ long (less than $^{1}/_{3}$ of the head width). The orifice of the lateral organ is $4\mu$ in diameter ($^{1}/_{4}-^{1}/_{5}$ of the head width), its posterior pouch is very small.

The structure of the **oral cavity** (Figure 31a) is also very similar to that in S. longicolle: there are the same four grooves in its wall, but the **third** from the front, which is the largest, **is shifted less posteriorly than in S. longicolle**, so that the anterior chamber in this species is
169 $^{1}/_{4}$ of the total length of the oral cavity, while in S. longicolle Bastian it is $^{1}/_{3}$. The immovable teeth are better developed, and a small, distinct dorsal tooth is present (d.d. —Figure 31a). A movable tooth, the right subventral, is also well developed. Figure 31b illustrates it in its semi-protruded position. The cuticular body is considerably smaller. The length of the oral cavity is $24\mu$ and the tooth stands $16\mu$ from its bottom; its width is $15\mu$.

The **esophagus** is of the same proportions as in S. longicolle: its beginning is very slender and lacks muscle fibers, and its chitinized tube is very thick; the esophagus gradually widens greatly, and posteriorly possesses strongly developed musculature interstratified with plasmatic substance. Its thickness increases from $10\mu$ anteriorly to $54\mu$ posteriorly.

The genital tracts do not differ from S. longicolle. The uterus is somewhat longer, and contains not more than five eggs, which are larger, the eggs I measured fluctuating in size between 150 and $180\times90\mu$. Thus, the **eggs are clearly elongate and twice longer than** in the preceding species. The vagina is the same size, and traverses half the width of the body internally; its upper part forms two swellings on each side containing a fibrillary structure (Figure 31c).

The **tail** (Figure 31d) narrows gradually to the end so that its end is of uniform diameter. The proportions are: length of tail 5, width at end 0.3. The internal structure of the tail is as in S. longicolle.

This species is found exclusively in oxeas sand and in the coquina under it. Adult females were found in large quantities in Georgievskii Monastery 7.12, 13. Only a few not fully mature females were found in Peschanaya Bay 1,5.12; 8.13 and in coquina 7.13. Golovin described it for the first time for the Black Sea as S. longicolle Bastian. This species is so delicate that the nematodes were not taken alive from Georgievskii
170 Monastery. In life they swim rapidly and are a light brown color.

32. **Symplocostoma hexabulba** n.sp.
(Table 5, Figure 32)

$$\text{♀}\ \begin{array}{ccccccccc} 0.6 & 6.3 & 15.0 & 41 & 49 & 60 & 66 & 71 & 97.5 \\ \hline 0.3 & 1.1 & 1.2 & & & 1.7 & & & 0.8 \end{array}\ 5300$$

$\alpha=60,\ \beta=6{,}6;\ \gamma=40.$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 8 | 22 | 60 | 325 | 720 |
| Width | 15 | 21 | | 57 | 62 |

The **body** narrows greatly to the anterior end, being at the cephalic bristles $^{1}/_{4}$ of the width at the beginning of the esophagus. From this point it widens an additional $1^{1}/_{2}$ times to midbody and then narrows twofold to the anus. Anteriorly, most of the narrowing occurs in the preneural region (Figure 32a), while posteriorly it is quite gradual. The **cuticle** is smooth, not thick, about $1^{1}/_{2}\mu$. Bristles are present only on the head.

The **head** is rounded, and the extreme anterior end is somewhat truncated (Figure 32c). Lips are absent. The margins of the mouth are beset with six labial papillae which project slightly, and a small chitinized canal connected to the sensory organ runs posteriorly from them. Six cephalic bristles are present; they are fairly long—$10\mu$, or $^{2}/_{3}$ of the head width. The lateral organ is shifted somewhat posteriad; it is cyathiform, with a perfectly round orifice $3^{1}/_{2}\mu$ in diameter. Its posterior pouch is very shallow (o. l. —Figure 32c). At the level of the posterior $^{1}/_{3}$ of the oral cavity the inner layer of the cuticle parts from the outer and is attached separately to the cephalic capsule (cut.—Figure 32c). The mouth is widely open, $5\mu$ in diameter. The entire wall of the **oral cavity** is thick, more notably posteriorly than anteriorly. Anteriorly, three cuticular rings are noted: the anterior lies almost at the extreme front, the posterior approximately at $^{1}/_{5}$ of the length of the oral cavity; the central
171 ring is nearer the anterior. Three immovable teeth are set on the lateral walls of the oral cavity, the largest of them being the right subventral (d. subv. d. —Figure 32b); the other subventral is of almost equal size, and the dorsal (d.d. —Figure 32b) is smaller. The oral cavity narrows slightly at the level of the teeth. The movable spear that is characteristic for Symplocostoma (d. mob. —Figure 32b) rises from the bottom of the oral cavity adjacent to the large right subventral tooth. The bottom of the oral cavity is also provided with cuticular thickenings (a—Figure 32b). The overall length of the oral cavity is $26\mu$, maximum width is $16\mu$, and the movable tooth stands $20\mu$ from the bottom. The esophagus is attached to the bottom of the oral cavity as usual, and extends more anteriorly opposite the sectors than between them. A transversely oval cuticular body is located immediately behind the oral cavity (c. cut. —Figure 32b), and a pigment spot lies behind the body, but is shifted from it so that the cuticular body cannot be considered as the lens of an eye. The **esophagus** (Figure 32a) is narrow anteriorly, as in all Symplocostoma, and lacks muscle fibers; the thick chitinized tube only just fits into it (oes. —Figure 32b); more posteriorly, a weak development of the muscle fibers is noted first, and then a strong development. In the posterior part, however, there are **six distinct bulbs**, although they are not greatly developed (Figure 32a). Externally, their presence is indicated by annular depressions on the surface of the esophagus, while internally, the rays of the tube form hollows at the center of each bulb, thus producing a distinctly lenticular cavity (Figure 32a). The posterior bulbs are somewhat

longer than the anterior. The internal structure of the esophagus within the bulbs is the same as in the other forms of Symplocostoma; the interstratification of the granular tissue with the muscle fibers is also the same. Anteriorly, the esophagus is 12$\mu$ thick (48% of the body width); at the nerve ring it is 20$\mu$ (38%), and posteriorly it is 55$\mu$ (73%). The esophageal glands discharge through special elevations at the beginning of the oral cavity (gl. oes. — Figure 32b). The preneural region accounts for 45% of the length of the esophagus, the portion from the nerve ring to the 172 bulbs accounts for 20%, and the six bulbs take up the remaining 35%.

The **intestine** consists of large cells which narrow its lumen and make it irregular. There are numerous fat droplets in the cells. The **nerve ring** is very flat and wide. The elongate, pyriform **cervical gland** (80×25$\mu$) is located some distance behind the end of the esophagus. The excretory pore is shifted greatly anteriorly (see dimensions). The **ovaries** are paired, reflexed, and short. The uterus is thin-walled and uninterrupted, i.e., not divided into two lumina; the eggs measure 100×70$\mu$, with a thin shell. The vagina is well developed but its walls are not thick; it traverses 0.4 of the body width internally.

Males were not found. The **tail** is quite long, pointing gradually to the end, making a perfectly conical shape (Figure 32c). The tubular caudal glands are located within the tail; the cuticle thickens at the end of the tail so that the caudal pore is long, while the cone, as in the other species, is inserted into the cuticle. The proportions of the tail are: length 4, width at the level of the cone 0.25.

This species was found in fairly large quantities, but only as females: phyllophores 5.12; oxeas sand of Georgievskii Monastery 7.12; Kruglaya Bay 6.12.

The characteristic structure of the esophagus differentiates this species from the other forms of Symplocostoma, but the structure of the oral cavity is similar to that of the other species; therefore, I do not isolate it in a new genus.

### 33. S. **sabulicola** n.sp.
(Table 5, Figure 33)

$$\text{immature } \text{♀}\ \frac{1.2 \quad 9.6 \quad 20.7 \quad 49 \quad 69^{*} \quad 91.7}{0.8 \quad 2.1 \quad 2.4 \quad 2.4 \quad 1.4}\ 2400$$

$$\alpha=42,\ \beta=5,\ \gamma=12.$$

| Dimensions immature ♀ | Cephalic bristles | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 9 | 29 | 220 | 425 |
| Width | 19 | 22 | 43 | 52 |

173 The **body** tapers slightly anteriorly, only $2^1/_2$ times from the base of the esophagus, so that the first impression is that this species differs from the type of Symplocostoma, and only more detailed examination establishes its membership in the genus. The body tapers almost twofold to the anus. The **cuticle** is smooth, thin, 2$\mu$, with numerous small bristles on it.

The **head** is rounded and truncated, has six well-developed labial papillae and the same number of cephalic bristles. The latter are $5^1/_2\mu$ long, or 0.3 of the head width. The lateral organ lies 4$\mu$ behind the lateral bristles; its orifice is 5$\mu$ wide (about $^1/_4$ of the corresponding body width). The orifice is round; the pouch behind it is of the same length as the orifice (o. l. — Figure 33a). The mouth is very narrow. The **oral cavity** is of typical structure, but the constriction is hardly pronounced, possibly owing to poor preservation. Of the immovable teeth only the right subventral is well developed; the movable spear is adjacent it; the remaining two teeth are very slightly developed. The spear is very narrow and its base does not occupy the entire bottom of the oral cavity as in typical forms of Symplocostoma, but is shifted ventrally (d. mob. — Figure 33a). The maximum width of the oral cavity is 19$\mu$. Posteriorly, it is transformed into the very wide internal tube of the esophagus. The cuticular body is small, 3$\mu$, oval, with a pigment cup behind it. The esophagus is very narrow anteriorly, and lacks muscles, but posteriorly it is well developed.

Only the posterior **ovary** is present; it is reflexed and short. The vagina passes obliquely through half the body width. The tail is conical to its middle and its posterior half is of uniform diameter (Figure 33b). Its proportions are: length 5.7, width at end 0.25. The tubular caudal glands have round bases and are contained within the tail.

Only one immature female — oxeas sand, 18 sajenes, Georgievskii Monastery. This species is unique in Symplocostoma in that the female genital tract is unpaired. In the structure of the anterior end it most approximates S. tenuicolle Eberth.

174

### 34. **Symplocostoma marioni** n.sp.
(Table 5, Figure 34)

$$\text{♀}\ \frac{0.4 \quad 5.6 \quad 16.6 \quad 39 \quad 51 \quad 54 \quad 62 \quad 69 \quad 97.1}{0.7 \quad 1.5 \quad 1.9 \quad 2.3 \quad 1.0}\ 5330$$

$$\alpha=43,\ \beta=6,\ \gamma=34.$$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 8 | 35 | 57 | 285 | 910 |
| Width | 26 | 41 | — | 73 | 95 |

---

* Length of uterus not given.

The **body** narrows almost four times from the end of the esophagus anteriorly, with particularly sharp tapering anteriorly, so that the sides appear rounded (Figure 34a). It tapers more than twofold to the anus. The cuticle is thick, about 4μ; its outer layer is very finely annulated behind the cephalic line with intervals of 0.9μ. The annules lie obliquely. There are bristles also on the body.

The **head** is truncated, lips are absent (Figure 34a). The six labial papillae are developed in the form of short bristles and are disposed normally. Of the ten cephalic bristles, the six largest are 16μ long and the four smaller subventrals are 7μ. The lateral organ is elongate with an anterior round orifice 5μ in diameter ($^{1}/_{5}$ of the corresponding body width); a pouch of the same length with fairly thick walls extends from it posteriorly (o. l. —Figure 34a). At the level of the cephalic line, which is immediately posterior to the lateral organs, the cuticle divides into a thick inner and a thin outer layer, each of which is attached separately to the oral capsule (b—Figure 34a).

The mouth is widely open, 18μ in diameter. The **oral cavity** is very different from that in typical Symplocostoma. Instead of several chitinized rings, characteristic for Symplocostoma, here there is only 175 one (a—Figure 34a), which creates a narrow constriction that divides the oral cavity into two unequal chambers: the anterior is 8μ long, the posterior 26μ long, and the maximum width of both is 19μ. A cuticular ring creates a stiffening around the anterior margin of the oral cavity (an. cut. —Figure 34a). Three teeth project anteriorly from the cuticular ring into the oral cavity. The largest of these is the right subventral, which has an irregular shape (d. subv. —Figure 34a). The mobile spear (d. mob. —Figure 34a) is adjacent to it; the base of the latter is located in the posterior part of the oral cavity. The other two teeth are in the form of small spines (d. d. —Figure 34a). Posteriorly in the oral cavity, three more teeth project that are homologus with the teeth of Oncholaimus (den. —Figure 34a) and the esophageal glands discharge onto them (gl. oes. —Figure 34a). The wall of the oral cavity is gradually transformed posteriorly into the internal chitinized tube of the esophagus, initially forming a mushroom-shaped enlargement (c—Figure 34a), behind which the tube is of uniform diameter. The walls of the tube are thick throughout. Two small cuticular bodies are present opposite the posterior end of the oral cavity, as in the other forms of Symplocostoma. The esophagus expands from 18μ (40% of the body width) anteriorly to 24μ (33%) at the nerve ring and to 70μ (75%) posteriorly. I was unable to detect the position of the **cervical gland**, but its pore lies anteriorly, a short distance from the oral cavity.

The **ovaries** are short, as in the other forms of the genus. The uterus is thin-walled. The vagina is **short**, 0.4 of the body width. The tail tapers conically, does not widen at the end, and its tip is of uniform diameter. Its proportions are: length 3, width at end 0.3.

Only one specimen—an adult female—was found in Cystoseira from the road 5.12.

This species, together with S. antarcticum Linstow and Amphistenus pauli Marion, will possibly have to be isolated in a special genus. I have not done this yet, as I have little material, and the species is furthermore very closely related to Symplocostoma: the oral spear, the cuticular body, and the form of the lateral organs are all similar.

## 176 8. Subfamily **Dorylaimini**

This subfamily consists primarily of freshwater species and only a few genera are marine.

There are both large and small nematodes in this subfamily. Dorylaimus is largest of all freshwater nematodes. The cuticle is smooth (rarely finely annulated on the surface), most frequently thick, usually bearing bristles converted into papillae. The head is often somewhat expanded and bears three or six characteristic lobes upon which the cephalic and labial papillae are set. The lateral organ is cyathiform.* The oral cavity is variously constructed. It passes from the immovable shortened cavity (Mononchus Bastian) to a large cavity provided with a stout spear (Actinolaimus Cobb), from which as a result one spear remains (Dorylaimus). In this group the spear is apparently a simple formation attached to the dorsal sector of the esophagus; sometimes it is very slender (Trichodorus Cobb). In other species the wide spear of Dorylaimus, which is like a sharpened quill, is replaced by slender spears compounded of three separate rods and thickened at the base (Tylencholaimus, etc.). The intermediaries between them and the forms with an immovable oral cavity are genera such as Diphtherophora de Man. The marine Syringolaimus and Dolicholaimus, the freshwater Ironus, and some other genera have a long oral cavity, but a spear is not developed in it; three small denticles are often developed in its stead, and are shed upon molting, like the spear of Dorylaimus. Auxiliary denticles, like the spear, are embedded early in the esophageal wall. Genus Odontopharynx de Man is an interesting form, with an oral cavity that is wide, as in Mononchus and elongated, as in Ironus, etc. The esophagus is usually greatly thickened posteriorly, but it does 177 not form bulbs. The ovaries are reflexed. The spicules are short. The tail is typically long, with a filiform termination, but all the degrees of shortening are represented, up to the rounded tails of many forms of Dorylaimus. In many species of this genus the tail is short only in adult males; adult females and the young of both sexes are long-tailed. Caudal glands are apparently absent in many freshwater genera.

In my view it is quite inadmissible to associate the highly developed Dorylaimus with such reduced forms as Tylenchus and Aphelenchus, as was done by de Man (1884) and repeated without question by Cobb (1913), Hofmänner (1913), Hofmänner and Menzel (1915), even though Bastian (1865) and Bütschli (1873) place these groups at entirely different ends of their systems. Oerley (1886) quite rightly incorporated the latter genera with several others in a special family Rhabditidae (more properly Anguillulidae, according to the oldest genus).

---

* Cobb's indication (1888) that the lateral organ in some Dorylaimus is spiral is not definite and can hardly be believed.

The oral spear of Tylencholaimus, etc., cannot be considered as proof of a relationship between these groups; this is only a parallel formation, which is met frequently in the animal kingdom. As early as 1876 de Man noted the similarity with Dorylaimus in the organization of this genus.

Cobb (1913) proposed a series of new freshwater genera that agreed with the notion of the old genus Dorylaimus, thus making an attempt to divide this wide genus into smaller genera. I am not opposed to the idea in principle, but some of his genera seem to me to be too slightly differentiated and liable to be recombined.

Thus, I ascribe the following genera to this subfamily:

A. Genera with a broad, thick-walled oral cavity.

1) Mononchus Bastian 1865: Trans. Linn. Soc. 25, p. 100; Bütschli 1873: N. Acta 26, No. 5, p. 73; de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 183; 1884: Nemat. Niederl. Fauna, p. 62; Cobb 1893: Macleay Memorial. Vol., p. 1; Jägerskiöld 1909: Süssw.-Fauna Deutschl., Heft. 16, p. 31; Hofmänner 1913: Revue Suisse Zool. 21, p. 631.—In fresh water and damp earth. About 35 species.
178 2) Odontopharynx de Man 1912: Zool. Jahrb. Syst. 33, p. 637; 1 species.

B. Genera with a long oral cavity

3) Aulolaimus de Man 1880; 1884: Nemat. Niederl. Fauna p. 78. One freshwater species. Relationship doubtful.
4) Cephalonema Cobb 1893: Agric. Gaz., N. S. W. 4, p. 825; 1 species from damp earth. Ironus filicauda Daday 1904 from New Guinea possibly also belongs here.
5) Ironus Bastian 1865: loc. cit., p. 103; de Man 1876: loc. cit., p. 83; 1884: loc. cit., p. 69; Jägerskiöld 1909: loc. cit., p. 27; Hofmänner 1913; loc. cit., p. 627.—Freshwater, very common genus; 5—6 species known.
6) Thalassironus de Man 1889: Mém. Soc. Zool. France 2, p. 4.*
7) Dolicholaimus de Man 1888: Mém. Soc. Zool. France 1, p. 31.**
8) Syringolaimus de Man 1888: ibid., p. 34.†

1 (2). Oral cavity lacks teeth anteriorly ........ **Aulolaimus** de Man
2 (1). Teeth present anteriorly in oral cavity.
3 (4). Only one tooth, cephalic end expanded ..... **Cephalonema** Cobb
4 (3). Anteriorly, 3 variously constructed teeth or cuticular bodies.
5 (10). Behind oral cavity esophagus only slightly expanded.
6 (9). Walls of oral cavity thin. Cuticular bodies disposed at its beginning.
7 (8). Tail pointed. Freshwater ................. **Ironus** Bastian
8 (7). Tail conical, rounded at end. Marine ... **Thalassironus** de Man
9 (6). Walls of oral cavity thick, bodies located anterior to it. Teeth small ..................... **Dolicholaimus** de Man
10 (5). Esophagus widens sharply behind end of oral cavity and bears two eyes ....................... **Syringolaimus** de Man

C. Genera with separate rods in the oral cavity—a transition to the following group.

9) Diphtherophora de Man 1880; 1884: Nemat. Niederl. Fauna p. 128. One species, terrestrial.
10) Chaolaimus Cobb 1893: Agric. Gaz. N. S. W. 4, p. 821. One species, terrestrial. Both genera doubtful as the authors had only young molting individuals.

D. Genera with triple spear, swollen at end.

11) Tylolaimophorus de Man 1880; 1884: loc. cit., p. 130. One species, terrestrial.
12) Tylencholaimus de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 119;
179 1884: loc. cit., p. 132; Stefanski 1914: Ném. du Léman, p. 56: 8 freshwater or terrestrial species.
13) Tylencholaimellus Cobb 1915: Trans. Amer. Micr. Soc. 34, p. 21. Judging from the name, it belongs here.
14) Xiphinema Cobb 1913: Journ. Washington Ac. Sci. 3, p. 436; 1—2 species. Very similar to preceding.

E. Genera with plain (dorsal) spine:

a) Spear broad, vestibulum also.

15) Actinolaimus Cobb 1913: loc. cit., p. 439; Steiner 1916: Zool. Anz. 46, p. 328. 5 species. Here belong Doryl. macrolaimus and similar species.
16) Antholaimus Cobb 1913: loc. cit., p. 440; one species—and
17) Discolaimus Cobb 1913: loc. cit., p. 439; one species—it seems to me poorly characterized.

b) Spear broad, vestibulum narrow.

18) Dorylaimus Dujardin 1845: Hist. Nat. des Helminthes p. 231; Bastian 1865: loc. cit., p. 104; Bütschli 1873: loc. cit., p. 19; 1874: Abh. Senck. Ges. 9, p. 19; de Man 1876: loc. cit., p. 88; 1884: loc. cit., p. 154; Cobb 1888: Jen. Zeit. Naturwiss. 26, p. 68; 1891: Proc. Linn. Soc. N. S. W. 6, p. 149; 1893: Macleay Memorial Vol., p. 41; Jägerskiöld 1909: Süsswf. Deutschl., Heft 16, p. 36; Hofmänner 1913: loc. cit., p. 638.—Freshwater genus. About 110—115 species.*
19) Dorylaimellus Cobb 1913: loc. cit., p. 440; one species—and
20) Nygolaimus Cobb 1913: loc. cit., p. 441; one species; it seems to me poorly characterized.

---

* One species: Th. britannicus de Man 1889: loc. cit., rarely in Penzance (Cornwall).

** Two species: (1) D. marinus Dujardin 1888: loc. cit., p. 32, Tables 2, 3, Figure 15, from the English Channel; (2) D. plectolaimus Steiner 1916: Zool. Jahrb. Syst. 39, p. 608, Table 28, c—Figure 25a Two specimens from algae from the White Sea strait.

† One species: S. striatocaudatus de Man 1888: loc. cit., p. 35, Tables 3, 4, Figure 16; from the English Channel.

* Two species known for the sea: (1) D. marinus Dujardin 1845: Hist. des Helminthes, p. 231, Table 3, Figure D; Bastian 1865: loc. cit., p. 110. Among algae—Lorient (Brittany); (2) D. maritimus Ditlevsen 1913: Medd. om Grönland 43, p. 429, Table 18.—Benthic forms on the coasts of Greenland

c) Spear very long, narrow.

21) Trichodorus Cobb 1913: loc. cit., p. 441; 1–2 species, here probably Doryl. elongatus de Man etc.

Several freshwater or terrestrial genera are connected by various features to Dorylaimini. However, their inclusion would make the genus too broad and unhomogeneous. It therefore seems necessary to place these genera in a separate subfamily, Trilobini. Related here are:

1) Trilobus Bastian 1865: Trans. Linn. Soc. 25, p. 99: Bütschli 1873: Nova Acta 26, No. 5, p. 53; de Man 1884: Nemat. Niederl. Fauna p. 74; Jägerskiöld 1909: Süswasserfauna Deutschl., Heft 16, p. 15; Hofmänner 1913: Revue Suisse Zool. 21, p. 616; 13 species, some very common.
180 2) Trischistoma Cobb 1913: Journ. Washington Ac. Sci. 3, p. 444; one species. Seems not to differ in any essential from Trilobus.
3) Alaimus de Man 1880, see p. 48. Also probably should be placed here, and not among Oxystomini, as I thought when writing those sections.
4) Deontolaimus de Man 1880; 1884: Nemat. Niederl. Fauna p. 31; two species—position doubtful.
5) Prismatolaimus de Man 1880; 1884: loc. cit., p. 79; Jägerskiöld 1909: loc. cit., p. 15; Hofmänner 1913: loc. cit., p. 615; 9 species—position doubtful.
6) Bastiania de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 172; 1884: loc. cit., p. 33; 3 species—spiral lateral organs make position doubtful.

## 9. Subfamily **Tripyloidini**

These are medium-sized and small nematodes with thin, smooth cuticle. There are ten cephalic bristles. The **lateral organ is spiral and embedded.** The oral cavity is without specialized structure, being a simple widening of the inner esophageal tube; the latter lacks bulbs.

I relate here the marine genera Tripyloides de Man 1886 and Bathylaimus Cobb 1893,* which are distinguished by a broad two-chambered oral cavity. The freshwater genus Trilobus Bastian 1865 is apparently closely related to this genus, but is differentiated by its cyathiform lateral organ. It is quite possible that Tripyloides together with these genera and some others mentioned above as members of Dorylaimini should be isolated as a common subfamily with another name.

### Genus TRIPYLOIDES de Man 1886

Tripyla p. p. Bütschli 1874: Abh. Senck. Ges. 9, p. 33.
Tripyloides de Man 1886: Anat. Untersuch. , p. 60.

These are small nematodes with a slender body and smooth cuticle. 181 Six labial papillae lie on the head and ten cephalic bristles form a plain circlet. The lateral organ is **spiral, embedded,** and shifted quite far posteriorly. It seems to me that this is merely a modification of the cyathiform organ with the cavity enveloped. **The oral cavity is conoid, with three** fairly irregular **rays** that narrow the lumen and two lateral pouches at its base. The esophagus is straight, without bulbs. The ovaries are paired and reflexed. **The spicules are broad and flat**; The gubernaculum is thin, unpaired, and adjacent to the spicules dorsally; at the anus it forms an expansion provided with two characteristic claws. The tail is long, conoid, and rounded at the end.

The genus was established by de Man (1886) for Bütschli's species Tripyla marina and one more new species. Three very similar species are known:

1) Tr. marinus (Bütschli 1874); Tripyla marina: Abh. Senck. Ges. 9, p. 33, Table 3, c—Figure 12a; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 18, c—Figure 8a—fine sand on the shores of the Kiel Firth (Bütschli); Tvärminne Bay, mud ($^{1}/_{2}$% saline) (G. Schneider).
2) Tr. vulgaris de Man 1886: Anat. Untersuch., p. 61, Table 11; Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 119; Walcheren (Holland)—seawater canal (de Man); Lake Mogil'noe at Kil'din Island (Saveljev). Probably identical with the first.
3) Tr. demani n.sp., see below.

1 (2). Posterior half of oral cavity embraced by esophagus. Relation of length of spicules to width = 4. I failed to find essential differences in the descriptions of de Man, Bütschli, and G. Schneider . . . . . . . . . . . . . . . . . . . **Tr. marinus** (Bütschli)
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Tr. vulgaris** de Man
2 (1). Posterior $^{2}/_{3}$ of oral cavity embraced by esophagus. Relation of length of spicules to width = 3. . . . . . . . . . .**Tr. demani** n. sp.

### 35. **Tripyloides demani** n. sp.

(Table 6, Figure 35)

$$\text{♂}\;\begin{array}{ccccc} - & 7.5 & 13.3 & 20.4 & 93.3 \\ \hline 1.3 & 2.1 & 2.1 & 2.7 & 2.0 \end{array}\;1380$$

$$\alpha = 37;\ \beta = 7^{1}/_{2};\ \gamma = 15.$$

$$\text{♀}\;\begin{array}{ccccccccc} - & 6.6 & 12.9 & 33 & 46.5 & 47 & 50 & 62 & 96.2 \\ \hline 1.0 & 1.8 & 2.0 & & & 2.5 & & & 1.7 \end{array}\;1730$$

$$\alpha = 40;\ \beta = 7^{1}/_{2};\ \gamma = 13.$$

---

* Proc. Linn. Soc. N. S. W. 8, p. 409; one species: B. australis Cobb 1893: loc. cit., p. 409, Figure 9. Port Jackson N. S. W.— and possibly more. Anoplostoma longisetum Steiner 1916: Z. J. Syst. 39, p. 600, Table 25, c—Figure 16a; one female from the White Sea strait, with algae.

| Dimensions ♀* | Cephalic bristles | End of oral cavity | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 7 | 15 | 19 | 115 | 225 |
| Width | 19 | — | 24 | 32 | 35 |

The **body** is of fairly even width, tapering only slightly to the anus and to the end of the esophagus. From this point anteriorly it tapers twofold or slightly less. The **cuticle** is about 1$\mu$ thick and quite smooth. Bristles are few.

The **head** is truncated with no constriction behind the cephalic bristles as is characteristic for Tr. vulgaris de Man. Anteriorly, three grooves on the head create three lobes, which according to de Man are lips; however, these formations seem to me insufficiently specialized to be so designated. The six labial papillae are set in pairs on each lobe. A circlet of ten cephalic bristles follows the papillae. They are 5$\mu$ long, the sublaterals slightly shorter. The lateral organs are 6$\mu$ in diameter, spiral, but not the usual spiral type. The spiral apparently does not lie externally, but is sunken, and a round aperture leads to the outside (see Figure 35a).

The **oral cavity** consists of two chambers: an anterior that is not embraced by musculature and a posterior that is. They are demarcated clearly by a thickening to which the esophagus is attached. Three thick chitinized rays project inside. The general form of the cavity is irregularly conical, 7$\mu$ wide (Figure 35a). At its base are the two lateral pockets characteristic for Tripyloides. The esophagus is straight, expanding only slightly posteriorly. Its width increases from 15$\mu$ anteriorly to 22$\mu$ posteriorly, constantly occupying 70% of the body width.

The **ovaries** are paired and reflexed; their ends are elongate. The uterus was short and contained only one egg. The vagina is very inconspicuous,
183 about $^1/_5$ of the body width.

The single **testis** is short, followed by a sac filled with large sperm. The **spicules** are broad and short in the form of plates (Figures 35b, c) with thickenings in places on their surface. The gubernaculum is unpaired, with a thin lamellar process in the middle of the same length as the spicules (a—Figure 35c), while posteriorly there is a thicker paired part provided with two claws directed posteriorly and laterally. The processes here are better developed than in the northern Tr. vulgaris de Man.

The **tail** is conical, with a fairly long portion of uniform width at the end. The proportions are: length of tail of female 5, of male 3.5; width at end of male and female 0.33; length of spicules and gubernaculum 1.1.

Several specimens of this species were found in clay from the north side 6.12; Streletskaya Bay—deposit on Potamogeton, Zernov 3.10; Zostera from the Chernaya River 5.12.

For the differences from the other species see the key.

---

[*] The dimensions of the male are not given as the specimen was too small.

## II. Family *CHROMADORIDAE*

I relate here fairly diverse forms, but all possessing an annulated cuticle. In many forms the cephalic bristles are divided into two circlets: in the anterior circlet the six bristles are usually converted into papillae; the posterior circlet has four bristles. The lateral organ typically is spiral, rarely has the form of a round or oval pit (Monoposthia, Tripyla), an irregular pouch (Acanthopharyngini), or is completely reduced (Chromadorini). The oral aperture typically lacks lips entirely and is encircled by an elastic cuticle that is folded when the mouth is closed. When the mouth is open **the esophagus may be pushed forward and the oral organs are inverted interiad.** The teeth may serve as hooks or cutting organs, like the spines of various genera of other families. The
184 esophagus very frequently is provided with a bulb with or without an internal cavity, but many forms lack it. **The ovaries are reflexed,** in most cases characteristically short, conical with a blunt cone. The tail in the majority of species is characteristically regularly conical with a long tube at the end (the caudal sucker of Bastian).

I incorporate here the following subfamilies:

1) Acanthopharyngini (Acanthopharynx, Camacolaimus, Acontiolaimus n.g), p. 132.
2) Cyatholaimini (Cyatholaimus, Choanolaimus, Halichoanolaimus, Dignathonema n.g), p. 134.
3) Spilipherini (genera from the Spilophora — Chromadora group provided with spiral or circular lateral organs), p. 150.
4) Chromadorini (genera with reduced lateral organs), p. 171.
5) Draconematini (Draconema = Chaetosoma auct., Rhabdogaster, family Chaetosomatidae auct.), p. 188.

Genus Tripyla Bastian 1865* belongs here also, probably as a special subfamily. This genus has the eversible pharynx as in all forms of Cyatholaimini, Spilipherini, and Chromadorini, and the transversely oval lateral organs as, for example, in Monoposthia de Man. Probably Udonchus Cobb 1913** and Rhabdolaimus de Man 1880† are also members here.

185 All these groups are closely related to each other, except for Acanthopharyngini, the disposition of whose systems is still unclear. Draconematini represents an aberrant branch of the basic group.

---

[*] Trans. Linn. Soc. 25, p.115; Bütschli 1873: Nova Acta Ac. Leop. Car. 36, No.5, p.33; de Man 1884: Nem. Nied. F., p 44; Cobb 1893: Macleay Memor. Vol., p.31; Jägerskiöld 1909: Süsswf. Deutschl. Heft 16, p 7; Hofmänner 1913: Revue Suisse Zool. 21, p.606; Menzel 1914: Arch. Naturg. 80A, Lfg. 3, p.46. Freshwater genus. Better descriptions and drawings: Bütschli 1873, 1876; de Man 1884. Possibly belonging to this or a similar new genus is Chromadora dubia Bütschli 1873: loc. cit., p.72, Table 5, Figure 31; Jägerskiöld 1909: loc. cit., p.36.—Moss in forest around Frankfurt

[**] Journ. Washington Ac. Sci. 3, p.442; one freshwater species from Jamaica

[†] 1884: Nem. Niederl. Fauna p.125; Jägerskiöld 1909: Süssw.-Fauna Deutschl. p.19; Hofmänner 1913: Revue Suisse Zool. 21, p 619; 3 freshwater or terrestrial species.

1 (8). Lateral organ conspicuous: spiral, in form of irregular pouch or circle.
2 (3). Lateral organ in form of irregular pouch . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 1. **Acanthopharyngini**
3 (2). Lateral organ spiral, sometimes with many turns, or circular.
4 (7). No specialized modified thick bristles preanally.
5 (6). All ten cephalic bristles in one circlet . . . . . . . . 2. **Cyatholaimini**
6 (5). Cephalic bristles in two circlets. Anterior has six, in form of papillae or short bristles, posterior has four long bristles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3. **Spilipherini**
7 (4). 2—4 specialized modified ventral rows of bristles preanally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5. **Draconematini**
8 (1). Lateral organ in form of hardly pronounced depression in front of head, sometimes completely inconspicuous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4. **Chromadorini**

## 1. Subfamily **Acanthopharyngini**

These are medium-sized worms with an annulated cuticle. A circlet of labial papillae and two circlets of cephalic bristles are present. The anterior cephalic circlet consists of papillae, the posterior of true bristles. The **lateral organs** are of an aberrant type: they are circular or in the form of a short spiral, **from which a long blind pouch runs posteriad**. The oral cavity is always present: its most characteristic feature is a considerably long **cuticular plate dorsally**. In Acontiolaimus there is a movable dorsal spear inside the oral cavity. **The esophagus is straight, without bulbs**, similar in general structure to the esophagus of Enoplidae. The ovaries are reflexed. The spicules, as far as they are known, are short and curved. The tail is conoid and short.

Three genera are related here:

1) Acanthopharynx Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 34.*
186 2) Camacolaimus de Man 1889: Mém. Soc. Zool. France 2, p. 8.**
3) Acontiolaimus n.g., see p. 133.
4) Dermatolaimus Steiner 1916: Zool. Jahrb. Syst. 39 p. 603.†

---

* Four species: (1) A. perarmatus Marion 1870: loc. cit., p. 34, Table K, Figure 1 (févr., mars au Pharo); (2) A. oculatus Marion 1870: loc. cit., p. 35, Table K, Figure 2 "au milieu des Gelidium corneum sur les rochers du Pharo, avril 1869 (Marion); Sète — canal de Bourdigues (Rouville); (3) A. striatipunctatus Marion (1870): loc. cit., p. 35, Table K, Figure 3 "au large de Montredon, par le travers du château d'If, à 18 brasses de profondeur"; (4) A. affinis Marion 1870: loc. cit., p. 36, Table K, Figure 4 "sur les rochers d'Endoume, avril 1868, mai 1869". Odontobius micans Eberth 1863 is related by Marion to this genus and possibly A. oculatus Marion also belongs to genus Cyatholaimus.

** One species: C. tardus de Man 1889: loc. cit., p. 8; p. 184, Table 5, Figure 2; Steiner 1916: Zool. Jahrb. Syst. 39, p. 606, Table 29, c—Figure 26a. Walcheren (de Man); Kola Gulf (Savel'ev); White Sea strait in algae (Steiner).

† One species: D. ditlevseni Steiner 1916: loc. cit., p. 604, Table 27, d—Figure 21a. White Sea strait on algae.

1 (6). Lateral organ shifted to anterior margin of head.
2 (5). End of dorsal oral plate fixed to posterior end of oral cavity.
3 (4). This end with some spines . . . . . . . . . . **Acanthopharynx** Marion
4 (3). This end without spines . . . . . . . . . . . . . **Camacolaimus** de Man
5 (2). This end consists of movable spear located in oral cavity . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Acontiolaimus** n. gen.
6 (1). Lateral organ shifted quite far from anterior end . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Dermatolaimus** Steiner

## Genus ACONTIOLAIMUS n.g.

Type species: A. zostericola n.sp.

These are small worms with an annulated cuticle. Only the four large bristles of the posterior circlet are well marked on the head. Anterior to them there are probably two circlets of six papillae each—the labial and anterior cephalic (I saw only one). The lateral organ is spiral and **shifted anteriad**. The wide mouth leads to an oral cavity of medium size that is not embraced by muscles. On its dorsal side there is a **clawlike movable tooth**. **The esophagus is straight, and without bulbs**. The ovaries are paired and reflexed. The tail is conical and fairly straight.

This genus is most similar to Camacolaimus de Man in its annulated cuticle, anteriorly-shifted lateral organs, and particularly in the chitinized thickenings on the dorsal ray of the esophagus.

The sole species is:

### 187 36. **Acontiolaimus zostericola** n. sp.

(Table 6, Figure 36)

$$\text{♀}\ \frac{-\quad 6.2\quad 13.6\quad 40\quad 48.5\quad 52\quad 53.5\quad 61\quad 95.2}{0.5\quad 1.4\quad 1.7\qquad\qquad\quad 2.0\qquad\qquad\quad 1.3}\ 2700$$

$$\alpha=50;\ \beta=8;\ \gamma=21.$$

| Dimensions ♀ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 4½ | 145 | 320 |
| Width | 12 | 32 | 38 |

The **body** tapers gradually, slightly to the anus and more slightly to the end of the esophagus, whence it tapers about twofold to the cephalic bristles. The **cuticle** is fairly thick, with an annulated outer layer; the width of the individual annules is about $1.5\mu$, the thickness of the cuticle is about $1.5\mu$. Bristles are almost absent.

The **head** (Figure 36a) is fairly regularly round, hardly thickening anteriorly. Six small labial or anterior cephalic papillae are disposed around the oral aperture, while four large cephalic bristles ($4^1/_2\mu$) lie more posteriorly. The lateral organ at first seems rather unusual, but careful examination shows that it is spiral with $1^1/_2$ turns and only its internal section is wider than usual, which also breaks its regularity (Figure 36a). Its width is about $3\mu$.

The **oral aperture** is large, triangular, not closed by any lips. The **oral cavity** is triangular, fairly wide; a lanceolate tooth arises in its dorsal sector adjacent to the dorsal wall. A long chitinized extension runs from it posteriorly, exactly as in Camacolaimus. Evidently, when this extension is drawn backwards the tooth moves directly to the middle of the oral aperture and may also be shifted anteriorly. A special process from the cuticle surrounding the oral cavity extends anteriorly in 188 the dorsal sector of the esophagus. This stiffens the wall of the oral cavity (a—Figure 36a). The **esophagus** is narrow, $^1/_2-^1/_3$ of the body width, thickening somewhat posteriorly. The **nerve ring** is broad. The large pyriform **excretory gland** is located $50\mu$ behind the end of the esophagus. It is $17\mu$ long, $8\mu$ wide. The excretory pore lies immediately behind the nerve ring. A short, curved, chitinized canal is connected to it.

The **ovaries** are paired, reflexed, and short, containing a few large oocytes. The uterus was still weakly developed, with thick walls. The vagina traverses $^1/_6$ of the body diameter.

The **tail** (Figure 36b) is conoid, $3^1/_2$ times longer than its width at the base; its tube is at the end.

One immature female and another young female were found in Zostera from Chernaya River 5.12.

## 2. Subfamily **Cyatholaimini**

The body is usually quite large and stout. The cuticle is annulated, the annulation created by rows of punctations set within the cuticle; sometimes there is also a weak outer annulation. There are no lateral bulges. On the head six labial papillae are usually present and **ten cephalic bristles arranged in the usual manner,** in one circlet; sometimes these are shortened. **The lateral organ is large, spiral,** usually with many turns. The entrance to the oral cavity is usually closed by lips. The cavity is most primitive in Cyatholaimus, where it is plicated and capable of expanding, as in the following subfamilies. A small dorsal tooth is present in its bottom. In the carnivorous Halichoanolaimus and Dignathonema secondary denticular complexes are observed. The esophagus is usually straight (Cyatholaimus, Halichoanolaimus), but sometimes greatly modified (Dignathonema). The ovaries are paired and reflexed. The male genital apparatus is varied, but usually the spicules are short and slightly curved. Sometimes the gubernaculum is very large and of complex structure (Cyatholaimus, Necticonema). 189 The tail frequently is characteristically conoid with a terminal tube.

The doubtful Necticonema approaches the type genus Cyatholaimus in its spicular apparatus. The lateral organ and the cuticle link Cyatholaimus with Demonema, Choanolaimus, and Halichoanolaimus, which in my opinion (and also in Cobb's) should be regarded as forms of Cyatholaimus that have become adapted to the carnivorous form of life. Cobb's original comparison of Demonema to Enoplus must be rejected, especially as the latter are herbivorous. Dignathonema prove to be quite different, having become considerably more adapted to the carnivorous life. However, the structure of the lateral organs, the cuticle, and the general form of the body and tail link them directly with Halichoanolaimus and Choanolaimus.

The following genera are incorporated here:

1) Necticonema Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 32.[*]
2) Cyatholaimus Bastian 1865, see next page.
3) Demonema Cobb 1893: Proc. Linn. Soc. N. S. W. 8, p. 392.[**]
4) Choanolaimus de Man 1880; 1884: Nematoden der Niederländischen Fauna, p. 73.[†]
5) Halichoanolaimus de Man 1888, see p. 143.
6) Dignathonema n.g., see p. 146.

In addition, the following freshwater genera are connected by virtue of several features:

Nannonchus Cobb 1913: Journ. Washington Acad. Sci. 3, p. 442; Syn.: Parachromadora Micoletzky 1914 ex. p.: Zool. Jahrb. Syst. 36, p. 492[††] and possibly also:
Odontolaimus de Man 1880: Nem. Niederl. Fauna, p. 127[‡]

190
1 (2). Oral cavity very narrow or absent, no specialized thickenings in it . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Necticonema** Marion
2 (1). Oral cavity quite wide or with specialized thickenings.
3 (10). No movable jaws in oral cavity, esophagus not expanded anteriorly.
4 (5). Oral cavity not very wide, folds on its wall, tooth on dorsal ray. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Cyatholaimus** Bastian
5 (4). Oral cavity greatly plicate when mouth closed, or, conversely, very wide with specialized thickenings on its walls. Tail frequently with flagellum.

---

[*] One species: N. prinzi Marion 1870: loc. cit., p. 33, Table I, Figure 2 "à Mallamousque et dans les anses voisines" — near Marseilles.

[**] One species: D. rapax Cobb 1893: loc. cit., p. 393, Figure 5; Naples, in coral bank, 35 m.

[†] One species: Ch. psammophilus de Man 1880, 1884; loc. cit., p. 73, Table 10, Figure 42. In Holland, in sand dune on roots of grass.

[††] Here are: (1) Triodontolaimus lacustris Micoletzky 1913: Sitz.-Ber. Akad. Wiss. Wien 122, Abth. 1; Chromadora (Parachromadora) l., 1914: Zool. Jahrb. Syst. 36, p. 497, Table 17, Figure 18: Austrian Alps in water and in earth (in a forest); (2) N. granulatus Cobb 1913: loc. cit., p. 442. On roots of water plants not far from Washington. It is possible that the species given below in Group E (p. 138, 139) belong here.

[‡] One species: O. chlorurus de Man 1880; 1884: loc. cit., p. 127, Table 20, Figure 85. Holland in earth of forest glades, etc., Germany (Erlangen), Austria (Laibach) [now Ljubljana, Yugoslavia], Switzerland (Altdorf) in earth.

6 (7). Oral cavity not divided into chambers, tightly plicate when mouth closed, but can open widely . . . . . . . . . . **Demonema** Cobb

7 (6). Oral cavity divided into two chambers.

8 (9). No teeth at boundary of two chambers; posterior part of oral cavity supported by plain rings. . . . . . . . . **Choanolaimus** de Man

9 (8). A row of teeth in the form of unbroken ridge present in that part. Specialized complex plates posteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Halichoanolaimus** de Man

10 (3). Special movable jaws of complex structure in anterior part of esophagus . . . . . . . . . . . . . . . . . . . . . . **Dignathonema** n. gen.

## Genus CYATHOLAIMUS Bastian 1865

Trans. Linn. Soc. 25, p. 162.

Bütschli 1874: Abh. Senck. Ges. 9, p. 48.
De Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 109.
De Man 1884: Nemat. Niederl. Fauna, p. 52.
Jägerskiöld 1909: Süsswasserfauna Deutschlands, Heft 16, p. 33.
Hofmänner 1913: Revue Suisse Zool. 21, p. 633.

Type species: C. ocellatus Bastian 1865 (nec de Man 1890)

The body is usually quite short and stout, although exceptions exist. **The cuticle is annulated**, the annules being both external and internal. **A transverse row of punctations** is observed in the middle of the cuticle: this forms a third layer of annulation.*

The head is sharply truncated; its most anterior part is demarcated by 191 a constriction. This part is movable and may be inverted interiad. Anteriorly, the entrance to the triangular oral cavity is located between six thick elevations, each of which is beset with a labial papilla. There are ten cephalic bristles. The lateral organ is large, spiral, usually with many turns. The **oral cavity** is spacious, with **12 pouches** anteriorly which are divided by rays of the cuticle that project internally. When viewed laterally these rays are seen as chitinized rods running along the oral cavity, giving it a characteristic appearance. Posterior to this part a **dorsal** chitinized tooth is located, sometimes a component part of the bottom of the cavity, sometimes projecting internally. The posterior part of the oral cavity is considerably narrower than the anterior part, and is sometimes even completely constricted; thus the tooth becomes narrower at the posterior border of the oral cavity. Eyes with pigment soluble in alcohol are sometimes present. **The esophagus is thick, highly muscular, hardly expands posteriorly, and lacks bulbs.** These forms are polymyarian. **Numerous phagocytic cells** are dispersed in the body cavity, sometimes regularly along the longitudinal fields, sometimes irregularly. These cells are very characteristic and make it possible to recognize the living Cyatholaimus at first glance. The ovaries are paired and reflexed; the uterus is thick-walled and muscular, and **the eggs are very small.** The testes are paired. The spicular apparatus is variously developed. **The spicules are short and broad.** The gubernaculum is very well developed. In the simplest form it consists of a pair of bodies that lies along the spicules, parallel with them and not uniting posteriorly (C. intermedius de Man). There may be a widening at their end, with the position of the anterior processes maintained (C. caecus Bastian), or finally, the anterior processes may be fused as an unpaired organ (C. ocellatus Bastian, C. demani m.), the posterior expansion being retained and covered with characteristic spines. Median papillae are located anterior to the anus in some species. The tail is conoid, sometimes very long or provided with a flagellum. There is a long tube at its end, 192 sometimes so long that it appears to be a specialized appendage of the tail.

The first species of this genus to be made known was Enoplus gracilis Eberth 1863. Genus Cyatholaimus was established by Bastian (1865) and has retained its scope unchanged until the present. Later (de Man 1878, Cobb 1898), long-tailed species of this genus were described, including some freshwater forms (de Man 1876, 1880, 1884), but many of them apparently belong to quite different genera.

The following species have so far been described:

A. Short-tailed species with unpaired anterior extension of the gubernaculum.

1) C. demani nom. nov.: C. ocellatus de Man 1889 (nec Bastian 1865), see p. 141.

2) C. gracilis (Eberth 1863) — Enoplus gr.: Unters. über Nematoden, p. 34, Table 2, Figures 13—19; C. spirophorus de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 23, Table 9, Figure 15. ? Enoplus tridentatus Leydig 1854 (nec Dujardin 1845): Arch. Anat. Phys., p. 292, Table 11, Figures 10—13. Naples (frequently), Nice.

3) C. ocellatus Bastian 1865: Trans. Linn. Soc. 25, p. 163, Table 12, Figures 210—212a (nec de Man 1889). Falmouth on Cladophora.

4) C. punctatus Bastian 1865: Trans. Linn. Soc. 25, p. 164, Table 13, Figures 217, 218; de Man 1890: Mém. Soc. Zool. France 3, p. 180, Table 4, Figure 6. Mud from the harbor — Falmouth (Bastian); very common at St. Vaast, Calvados (de Man).

5)? C. ornatus Bastian 1865: Trans. Linn. Soc. 25, p. 163, Table 13, Figures 215, 216. Falmouth in green algae.

B. Short-tailed species with paired anterior extensions of the gubernaculum.

6) C. caecus Bastian 1865: Trans. Linn. Soc. 25, p. 163, Table 13, Figures 213, 214; de Man 1889: Mém. Soc. Zool. France 2, p. 204, Table 7, Figure 10; Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 23. Steiner 1916: Zool. Jahrb. Syst. 39 p. 586. Mud from the harbor — Falmouth (Bastian); very common

---

* This description relates strictly to the Black Sea form C. demani m., but a similar cuticular structure is probably present in other species of this genus also.

in Cornwall, Walcheren, rocks at Calvados (de Man); Lake Mogil'noe on Kil'din Island (Savel'ev). White Sea strait on algae (Steiner); Sète — canal de Bourdigues (Rouville). Sabang on Sumatra, mud with diatoms (Steiner).

7) C. striatus Bastian 1865: Trans. Linn. Soc. 25, p. 164, Table 13, Figures 219, 220: Mud from harbor at Falmouth.

8) C. quarnerensis Daday 1901: Természetrajzi Füzetek 24, p. 436, Table 21, Figures 4—8. Fiume, patches of algae on the pier.

9) C. elongatus de Man 1907: Mém. Soc. Zool. France 20, p. 70, Table 4, Figure 14; Veere, Yerseke on the coast of Holland, Kola Gulf (Savel'ev).

10) C. intermedius de Man 1880; C. dubiosus de Man (nec Bütschli
193 1874) 1876: Tijd. Nederl. Dierk. Ver. 2, p. 84, Table 10,
Figure 39; C. i. 1884: Nemat. Niederl. Fauna, p. 53, Table 6, Figure 25. — Holland in damp earth, dunes, meadows, forests (de Man); Denmark — on roots of weeds in small ponds (Ditlevsen).

It is possible that Acanthopharynx oculatus Marion 1870 (see p. 132) and Odontobius micans Eberth 1863 (Unters. üb. Nematoden p. 28, Table 1, Figures 1—5) from Nice also belong to this group.

C. Species with long tails but without a flagellum.

11) C. dubiosus Bütschli 1874: Abh. Senck. Ges. 9, p. 48, Table 7, Figure 31; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 23, Figure 11 (nec de Man 1876). Kiel Firth, some sajenes (Bütschli); Tvärminne Bay — Gulf of Finland — mud ($^1/_2$% saline-Schneider).

12) C. proximus Bütschli 1874: Abh. Senck. Ges. 9, p. 49, Table 7, Figure 30. — Kiel Firth and coast — some sajenes.

13) C. exilis Cobb 1898: Proc. Linn. Soc. N. S.W. 23, p. 400 — sand around the tide mark, Port Jackson, N. S. W.

D. Species with long tails provided with a flagellum.

14) C. trichurus Cobb 1898: Proc. Linn. Soc. N. S.W. 23, p. 398 — sand around the tidemark, Port Jackson, N. S. W.

15) C. minor Cobb 1898: ibid., p. 402 — in the bay, depth of 4—6 sajenes, sand at the same place.

16) C. tenuicaudatus Saveljev 1912: Tr. Soc. Natur. St. Pétersbourg 43, livr. 1, p. 122 — Kola Gulf.

17) C. longicaudatus de Man 1878: Tijd. Nederl. Dierk. Vereen 3, p. 111, Table 9, Figure 16 — Naples.

18) C. heterurus Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 400 — in sand around the tidemark at Port Jackson N. S. W., possibly a synonym of the foregoing.

E. Species with a deep oral cavity and esophagus expanded at the end.

Only freshwater species are included in this group. Some of them have bulbs. The structure of the oral cavity is so different from the typical that either a new genus is required or these species should be incorporated into genus Nannonchus Cobb (p. 189).

19) C. terricola de Man 1880; 1884: Nem. Nied. Fauna, p. 54, Table 7, Figure 84. Holland — earth of meadows and forests (de Man); Germany: Erlangen (de Man); Jena in moss (Cobb); around Bremen in earth on the coast of the lake, adults in 9, 3 (Brakenhoff). Switzerland in various lakes (de Man, Hofmänner).

20) C. ruricola de Man 1880; 1884: Nem. Nied. Fauna, p. 55, Table 7, Figure 27; "eigenartige Nematode" Bütschli 1873: N. Acta 23, p. 72; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 483. Stefanski 1914: Ném. du Léman p. 29. Holland — earth of meadows and forests (de Man); Germany — Weimar River (de Man) Main River (Bütschli); Switzerland — roots of moss on the temporarily flooded coast of Lac de Brêt (Hofmänner); in moss around Geneva (Steiner); Austria — Lake Lunzersee in water moss; Chernovtsy (Micoletzky).

194 21) C. micoletzkii Stefanski 1915: Zool. Anz. 45, p. 348; C. sp.
Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 485, Table 17, Figure 27 Lunz.; Charna, tributary of Pilitsa (Stefanski).

22) C. steineri nom. nov. pro C. ornatus Steiner 1916 (nec Bastian 1865): Zool. Anz. 47 p. 56, c — Figure 3a.

23) C. arcticus nom. nov. pro C. micoletzkii Steiner 1916 (nec Stefanski 1915) ibid. p. 58, c — Figure 4a. Both species from Novaya Zemlya — moss at Matochkin Shar.

C. cotylophorus Steiner 1916: Zool. Jahrb. Syst. 39 p. 587, Table 27, g — Figure 19a White Sea strait in algae — probably belongs to this genus, may be similar to Halichoanolaimus. If the lateral organs are definitely absent it may even belong to another subfamily.

C. brevicollis Cobb 1898 is not Cyatholaimus but belongs to genus Chromadorina; see p. 162.

C. tenax (de Man 1876); Monhystera tenax: Tijd. Ned. Dierk. Ver. 2, p. 99, Cyath. tenax 1884: Nem. Nied. F., p. 56, Table 7, Figure 28; Jägerskiöld 1909: Süsswasserfauna Deutschlands, Heft 16, p. 33. Freshwater species: Russia: Moscow, around pond in spruce forest (de Man); Norway: Bygdö near Christianiya t (de Man); Germany: Erlangen t (de Man); Switzerland: near Lucerne t (de Man); Léman 280 m. p. (Hofmänner); Austria: Laibach t (de Man); on Phragmites near Saltzburg on Chara of Halstättersee p. (Micoletzky); Hungary [now Czechoslovakia] — lake in Tatra p. (Daday); Holland: meadow earth all year round t only females (de Man); France — Montpellier (de Man).

C. geophila de Man 1884: Nem. Nied. F., p. 56. Earth with brackish water: Walcheren, Holland. The last two species with circular lateral organs are evidently not forms of Cyatholaimus but belong to a new genus. Unfortunately not one of the numerous authors who have observed them since de Man has undertaken the task of preparing a more detailed description.

In many cases definition is possible only according to the males, in which there is a very characteristic gubernaculum. All the other features are usually inadequate. Group E is not included in the key.

1 (26). Tail without filiform end.

2 (3). Tail 5 times longer than its width at anus . . . . . . **C. exilis** Cobb

3 (2). Not longer than $3^{1}/_{2}$ times.

4 (23). Tail not swollen at end.

5 (6). Anterior end of body tapers from end of esophagus more than twofold . . . . . . . . . . . **C. dubiosus** Bütschli

6 (5). Less than twofold.

7 (8). Only the female known; short cephalic bristles; large eyes; tail short . . . . . . . . . . . **C. ornatus** Bastian

8 (7). Males.

9 (16). In gubernaculum unpaired part between spicules. Indentations present on posterior of paired part.

10 (13). This part longer than spicules.

11 (12). Its upper end has parallel sides. Indentations directed laterally . . . . . . . . . . . **C. gracilis** (Eberth)

195 12 (11). Anterior processes of gubernaculum divide at side. Indentations on paired part directed more posteriorly . . . . . . . . . . . **C. demani** nom. nov.

13 (10). This part is shorter than spicules or equal to them.

14 (15). Middle part equal to length of spicules, posterior parts accrete . . . . . . . . . . . **C. punctatus** Bastian

15 (14). Middle part shorter than spicules, posterior parts separated . . . . . . . . . . . **C. ocellatus** Bastian

16 (9). Anterior part of gubernaculum in form of two separate plates.

17 (18). Spines on posterior parts of gubernaculum absent . . . . . . . . . . . **C. intermedius** de Man

18 (17). Spines present.

19 (20). Gubernaculum shorter than spicules.

20 (19). Gubernaculum longer than spicules.

21 (22). Some large spines in posterior parts of gubernaculum . . . . . . . . . . . **C. caecus** Bastian

22 (21). Many small spines . . . . . . . . . . . **C. elongatus** de Man

23 (4). Tail swollen at end.

24 (25). Swelling at extreme tip, very slight . . . . . . . . . . . **C. proximus** Bütschli

25 (24). Swelling pronounced, on $^{1}/_{3}$ of tail . . . . . **C. quarnerensis** Daday

26 (1). Long tail with filiform end.

27 (28). Only anterior $^{1}/_{5}$ of tail conoid. Overall length of tail about $^{1}/_{5}$ of body length. Not distinguished by description . . . . . . . . . . . **C. longicaudatus** de Man

. . . . . . . . . . . **C. heterurus** Cobb

28 (27). Anterior $^{1}/_{2}-^{1}/_{3}$ of tail conoid, its overall length less.

29 (32). Cephalic bristles half head width, half of tail filiform.

30 (31). Gubernaculum equal in length to spicules; 2.6 mm. . . . . . . . . . . . **C. trichurus** Cobb

31 (30). Gubernaculum $^{3}/_{4}$ of length of spicules; 1.3 mm. . . . . . . . . . . . **C. minor** Cobb

32 (29). Cephalic bristles shorter, $^{2}/_{3}$ of tail filiform . . . . . . . . . . . **C. tenuicaudatus** Saveljev

### 37. **Cyatholaimus demani** nom. nov.

(Table 5, Figure 37)

C. ocellatus de Man 1889: Mém. Soc. Zool. France 2, p. 201, Tables 6, 7, Figure 9.
Golovin 1901: Observations on Nematodes, p. 101, Table 2, Figure 4, nec C. ocellatus Bastian 1865.

♂ $\dfrac{-\quad 6.5\quad 11.2\quad 23.5\quad 44.0\quad 91.8}{1.5\quad 2.5\quad 2.5\qquad 3.5\qquad 3.2}$ 2550

$\alpha=28;\ \beta=9;\ \gamma=12.$

♀ $\dfrac{-\quad 5.8\quad 10.0\quad 32\quad 40\quad 48.5\quad 60.5\quad 68.5\quad 92.0}{1.4\quad 2.6\quad 2.6\qquad\qquad 4.0\qquad\qquad 2.7}$ 2850

$\alpha=25;\ \beta=10;\ \gamma=12^{1}/_{2}.$

196

| Dimensions ♂ | End of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 16 | 145 | 175 | 280 |
| Width | 38 | — | 65 | 68 |
| ♀ | | | | |
| Length | 16 | 145 | 180 | 285 |
| Width | 42 | 68 | 68 | 75 |

The Black Sea specimens are somewhat larger than the northern ones described by de Man.

The **body** tapers less than twofold to the end of the esophagus and to the anus, the latter tapering being less pronounced in the male. Anterior to the end of the esophagus the body tapers less than twofold. The **cuticle** is distinctly annulated, conforming fully to de Man's description. Two layers are distinguished in it, the outer rather thinner than the inner. The outer layer is annulated, with the intervals between the annules only slightly depressed. Near midbody the annules are $3\mu$ apart, anteriorly slightly more. According to de Man's data, the annules in the northern C. ocellatus are somewhat more than $5\mu$ at midbody. On the boundary between the inner and outer layers an annular row of mounds corresponds to each annule. There are **four** rows on the inner layer for each outer annule. Finally, a marked annulation is observed on the inner boundary of the cuticle – there being two inner annules for each outer ($1^{1}/_{2}\mu$ apart). A row of circular pores, probably sensory papillae, is observed along the lateral lines. Fairly numerous bristles are disposed against the longitudinal fields.

The structure of the **head** (Figure 37a) is so similar to that described by de Man that I may be brief. The cephalic bristles are $11\mu$ long, or $^{1}/_{4}$ of the head width. The large spiral ($3^{1}/_{2}$ turns) lateral organs in the male are $15\mu$ wide, or $^{1}/_{3}$ of the corresponding diameter of the body, and in the female slightly less, shifted rather more posteriad than in de Man's
197 drawing. I did not observe **eyes** on the preparations but a pigment may have dissolved on processing. The **esophagus** hardly expands posteriorly. The pyriform **cervical gland** is about $100\mu$ long and $25\mu$ wide and is located not far behind the end of the esophagus.

The **ovaries** at first lie in many rows, but then become a single row. The deposition of vitellum occurs in 1 – 2 anterior oogonia. The uterus is wide, thick-walled, with an unbroken lumen. The vagina traverses $^{1}/_{3}$ of the body width internally. The eggs are round with a thick shell, very small compared with the body diameter – 45$\mu$. In coquina of Georgievskii Monastery I succeeded in finding many females whose eggs had developed within the uterus; tiny worms could be seen curled up within the eggshell.

There are two **testes**. The **spicules** (55$\mu$) are small and shorter than the gubernaculum (75$\mu$) (sp. – Figures 37b, c). The latter consists of a long anterior unpaired part (a – Figure 37b) and two posterior paired parts beset with four spines turned outwards and posteriorly. One of these projects from the lower surface and the remaining three from the posterior surface of these lobes (b – Figure 37b).

The tail is conoid, terminating in a long tube (about 15$\mu$), through which the caudal glands discharge.

The proportions of the posterior end are: length of tail of male 2.6, of female 3.2; width opposite tube $^{1}/_{8}$; spicules 0.7; gubernaculum 0.95.

This species is fairly common around Sevastopol. It was found in Cystoseira from the road (not deep) 5.12, few; deep Cystoseira, immature and mature males and females 6 – 7.12; mussels from under the station 6.12, adult males and females, numerous. Nassarius from mud of Artilleriiskaya Bay 1.12, male and female young; Ulva from New Holland 7.12, few adult; Zostera 5.12, male, female, $\infty$ adults; Potamogeton of Streletskaya Bay 3.19, adult male and female, fairly numerous; oxeas sand from Peschanaya Bay 7.12, female; algae in sand at the same place 6.12, few; oysterbeds 6.12, adult males, few females; coquina of Georgievskii Monastery 7.12, 13, few; phyllophores 6.12, few. Found by Golovin for the first time for the Black Sea – few on mussels
198 in Sevastopol and Balaklava.

**Geographical distribution:** North Sea: Falmouth on Cladophora (Bastian); Cornwall, Walcheren – (de Man).

This species fits de Man's description quite accurately, although some differences are observed: the structure of the cuticle is otherwise and the lateral organs are shifted posteriad. However, I took the exact similarity in the structure of the gubernaculum as a sign of the identity of the two species. C. ocellatus, described by Bastian, has a gubernaculum that is **shorter than the spicules** and therefore does not correspond with the species described by de Man under this name. C. gracilis Eberth 1863 and C. spirophorus de Man 1878 are apparently synonyms. They differ from C. demani by the dissimilarity of the upper ends of the medial parts of the gubernaculum.

I found two other forms of Cyatholaimus, which I do not describe because of insufficient material.

1) A small species with a tooth projecting more anteriorly than in C. caecus in de Man's drawing (Mém. Soc. Zool. 2, Table 7, Figure 10). One adult female in mussel mud.

2) A long-tailed species – some badly preserved specimens. Oxeas sand of Peschanaya Bay 5 – 6.12.

## Genus HALICHOANOLAIMUS de Man 1886

de Man 1888: Mém. Soc. Zool. France 1, p. 36.

Type species: H. robustus (Bastian 1865) de Man 1888

The body is stout with a broad head. Annular rows of punctations are present on the inner layer of the cuticle that produce an impressed annulation. The bristles are short.

The head is sharply truncated. The entrance to the oral aperture is closed by six lamellar lips, on each of which a labial papilla is set. The
199 cephalic bristles or papillae lie in a plain circlet. The lateral organ is spiral, usually large. Inside the head there is (? always) a cephalic capsule under the surface. **The oral capsule is wide, divided into two chambers,** both of which are triangular on cross section. The **anterior chamber** has four thickenings of cuticle on each wall. It is separated from the posterior by a **special ridge of chitinized teeth** on the wall of each sector of the oral cavity. Lateral denticles are arranged symmetrically on each sector; an anterior asymmetrical denticle is longer than the others. **The posterior chamber of the oral capsule is stiffened by three specialized plates** of different form in different species. The esophagus is very muscular, hardly expanding posteriorly. The intestine consists of very large cells.

The ovaries are short, the eggs small. The spicules are short, and arched; the gubernaculum is small; preanal papillae are sometimes present. The tail is slender at the end, sometimes with a long filiform appendage.

The species of this genus are carnivorous and the spines in the oral cavity serve for the trapping of prey.

The genus was established by de Man for Spilophora robusta Bastian. The genus is well differentiated; of the other genera its nearest relative is the freshwater Choanolaimus, as de Man pointed out. Cyatholaimus is also closely related to it: Halichoanolaimus is its "exaggeration," in Cobb's expression.

The following species are now known:

1) H. minor Saveljev 1912: Tr. Soc. Natur. St. Pétersbourg 43, livr. 1, p. 121. – Kola Gulf, Ekaterininskaya Harbor, some meters.
2) H. filicauda n. sp., see p. 145.
3) H. dolichurus Saveljev 1912: loc. cit., p. 121 – together with H. minor.
4) H. robustus (Bastian 1865) Spilophora r.: Trans. Linn. Soc. 25, P. 166, Table 13, Figures 226, 227; Bütschli 1874: Abh. Senck. Ges. 9, p. 46, Table 7, b – Figure 29a; H. r. de Man 1888: Mém. Soc. Zool. France 1, p. 38, Table 4, Figure 17. Mud from the harbor – Falmouth (Bastian); Kiel Firth, some sajenes (Bütschli); Walcheren (de Man), Kola Gulf (Savel'ev).
5) H. australis Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 404. Sand at the tidemark, Port Jackson, N. S. W.
6) H. clavicauda n. sp., see next page.

200 7) H. rapax Savel'ev 1912: loc. cit., p. 122. — Kola Gulf, Lake Mogil'noe, Pala Inlet; sand. This species should possibly be isolated in a special genus.

Apart from these, Spilophora punctata Linstow 1900 (Fauna Arctica 1, p. 127, Table 7, Figure 38) from Spitsbergen either belongs to this genus or should constitute a new similar genus. The same concerning Cyatholaimus cotylophorus Steiner 1916: see p. 139.

1 (6). Tail with long filiform termination.
2 (5). Filiform part accounts for $^4/_5$ — $^5/_6$ of length of tail.
3 (4). Lateral organ half head width with 5 turns 1,500 $\mu$ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **H. minor** Saveljev
4 (3). Lateral organ half head width, $3^1/_2$ turns; 3,100 $\mu$ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **H. filicauda** n. sp.
5 (2). Filiform part of tail accounts for $^8/_9$ of tail length. Lateral organ $^1/_6$ of head, 4 turns, 3,500 $\mu$ . . . . . . **H. dolichurus** Saveljev
6 (1). Tail without terminal filiform part.
7 (10). Tail not pointed at end.
8 (9). Two chambers of oral cavity of uniform width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **H. robustus** (Bastian)
9 (8). Posterior chamber twice narrower . . . . . . . . **H. australis** Cobb
10 (7). Tail thickened at end.
11 (12). Lateral organs with $4^1/_2$ turns. . . . . . . . . . . **H. clavicauda** n. sp.
12 (11). Lateral organs with two wide turns . . . . . . . . . **H. rapax** Saveljev

### 38. **Halichoanolaimus clavicauda** n. sp.
(Tables 5, 6, Figure 38)

$$\text{young}\ \text{♂}\ \frac{1.7\quad 4.3\quad 10.7\quad ?\quad 94.3}{1.6^{*}\quad 2.9\quad 2.9\quad 3.4\quad 2.7}\ 1860$$

$$\alpha=30;\ \beta=9^1/_2;\ \gamma=17.$$

$$\text{♀}\ \frac{1.5\quad 4.1\quad 10.0\quad 44.5\quad 49.5\quad 52\quad 60.5\quad 67\quad 96.2}{1.4^{*}\quad 2.1\quad 2.2\qquad\qquad\qquad 2.8\qquad\qquad\qquad 1.3}\ 2480$$

$$\alpha=36;\ \beta=10;\ \gamma=25.$$

| Dimensions<br>♂ | Cephalic bristles | 1st chamber of oral cavity | 2nd chamber of oral cavity | Nerve ring | Excretory pore | End of esophagus |
|---|---|---|---|---|---|---|
| Length | – | 15 | 32 | 87 | ? | 192 |
| Width | 30 | 40 | 46 | 51 | – | 55 |
| ♀ | | | | | | |
| Length | – | 19 | 36 | 103 | 117 | 248 |
| Width | 27 | 40 | 49 | 52 | – | 54 |

201 The **body** tapers twofold anteriorly from the end of the esophagus, twofold from midbody to the anus in the female, only by $^1/_4$ in the male. The **cuticle**, as in Cyatholaimus, consists of two layers; their common thickness is about 4 $\mu$. The outer layer is apparently smooth, while the inner bears punctations on its two surfaces. The punctations are constructed in transverse annules. The distance between the annules is about 1.5 — 2 $\mu$, depending on the part of the body. The few bristles on the body are mainly subventral and short.

The **head** is sharply truncated, with six lips of structure as in H. filicauda (see p. 203). They are beset with six labial papillae, behind which is a circlet of ten cephalic bristles. The longer bristles — the four subventrals — are 4 $\mu$ long and the remaining six are each 2 $\mu$ long. The lateral organ in the female is large (13 $\mu$), occupying about $^1/_3$ of the corresponding width of the body (in males it is somewhat more than $^1/_3$ — 17 $\mu$). It is spiral with $4^1/_2$ turns. Posterior to the lateral organ, above and below, two short bristles are set (s. ceph. acc. — Figure 38a).

The **cephalic capsule** is as in H. filicauda. The **oral capsule** is a complex structure. Its first chamber is triangular; anteriorly, it is encircled by the ring of the cephalic capsule and posteriorly, a denticular ridge from each of the esophageal sectors is present. Six of the seven teeth that compose the comb are arranged symmetrically more posteriorly (a — Figure 38a), while the seventh lies in the middle and projects more anteriorly (b — Figure 38a). The posterior chamber of the oral capsule is stiffened by three plates. Viewed laterally each plate is seen to be thicker anteriorly (d — Figure 38a), and thinner along the posterior edge, where the tube of the esophagus is attached to it. From above (c — Figure 38a) it is seen that these plates are not continuous, do not meet anteriorly, and bear four processes. The lateral processes are part of the anterior chamber of the oral capsule, while the two median ones do not reach it. The overall length of the capsule in the adult female is 32 $\mu$, of which the anterior chamber accounts for 15 $\mu$.

202 The **esophagus** is very thick, taking up more than half the body width and posteriorly hardly expands, or not at all, measuring 35 — 40 $\mu$. The cervical pore is located slightly posterior to the nerve ring. The **intestine** consists of large cells. The **ovaries** are very short, paired, and reflexed. Almost ripe eggs measure 54 × 43 $\mu$.

The **spicules** (Figure 38c) are 70 $\mu$ long, greatly curved, with an irregular manubrium at the base. Specialized structures are seen at the end. The **gubernaculum** (24 $\mu$) is adjacent to the spicules dorsally and also extends between them to the ventral side. I found no median preanal papillae.

The **tail** is elongated, conoid, slightly swollen at the end. The caudal glands are accommodated within the tail; at the end there is a long tube, about 15 $\mu$. The proportions are: length of tail in male 2.3, in female 2.7; width at end 0.22 in male, 0.28 in female; spicules 1.5; gubernaculum 0.6.

The species was found in deep sand in Peschanaya Bay; male and female 6 and 7.12.

### 39. **Halichoanolaimus filicauda** n. sp.
(Table 6, Figure 39)

$$\text{♂}\ \frac{1.3\quad 5.4\quad 10.0\quad 31^{*}\quad 39^{**}\quad 47^{\dagger}\quad 89.0}{1.2\quad 2.3\quad 2.6\qquad\qquad 2.6\qquad\qquad 1.7}\ 3100$$

$$\alpha=38;\ \beta=10;\ \gamma=9.$$

---

* Width at margins of head.

* Anterior end of anterior testis.

** Between them.

† Posterior end of posterior testis.

$$♀\ \frac{1.6\quad 5.3\quad 12.0\quad 33.5\quad 37.0\quad 45.5\quad 58.0\quad 61.5\quad 88.5}{1.5\quad 2.6\quad 3.0\qquad\qquad\qquad 4.0\qquad\qquad\qquad 1.6}\ 3100$$

$\alpha=25;\ \beta=8;\ \gamma=7.$

| Dimensions ♀ | Cephalic bristles | 1st chamber of oral cavity | 2nd chamber of oral cavity | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | – | 24 | 46 | 143 | 155 | 380 |
| Width | 43 | 54 | 60 | – | 76 | 89 |
| ♂ | | | | | | |
| Length | – | 22 | 45 | 143 | 167 | 308 |
| Width | 38 | 46 | 51 | – | 70 | 81 |

The **body** is very stout, widening greatly in female at midbody, tapering
203 to the anus more than twofold, to the end of the esophagus by $^1/_4$, and hence to the anterior end twofold. The **cuticle** has an overall thickness of about $3^1/_2\mu$; it has two layers, the outer accounting for $^1/_4$ of the thickness. Punctations arranged in transverse rows lie externally in the middle, giving the impression of a major annulation (see Figure 39a). The rows are $2^1/_2\mu$ apart. On the inner surface weakly developed true annules are observed with intervals of $2\mu$ between them. All the bristles on the body are short and converted into papillae.

The **head** is sharply truncated, so that anteriorly it has a fairly wide flat surface. Anteriorly, the entrance to the oral aperture is closed by six strongly developed **lips**, each consisting of thin chitinized plates (a—Figure 39c) that are split in the middle, leaving a space for plasmatic material (b—Figure 39c). A small labial papilla is set in the middle of this area (p. lab. —Figure 39c). The nerves of this papilla are contained in a chitinized tube which bends downwards and runs through the cephalic capsule (n. p. lab. —Figure 39c). Ten very short cephalic bristles are disposed normally (s. ceph. —Figures 39a, c). The lateral organ lies directly at the level of the boundary between the two chambers of the oral cavity, i.e., shifted more anteriorly than in the preceding species. It is large, spiral, with $3^1/_2$ turns, of equal size in male and female ($14-15\mu$), or $^1/_4$ of the head width (see Figures 39a, b). On the right of Figure 39b it is clearly seen that its internal turns are the smallest, while the external ones are deeper. Its outline has the form of an unbroken line.

The **cephalic capsule** is a chitinized ring that encircles the anterior part of the oral capsule. Laterally, it appears narrow, as it is widest in the plane perpendicular to the longitudinal axis of the body (c. ceph. —Figures 39b, c). Its structure is distinct only when viewed from the front (Figure 39c). From here it is seen that it bears 16 processes directed
204 laterally: three pairs of processes are set on the lateral surface, two processes are located medially and two pairs of short processes are submedian. Internally, six of the processes stiffen the angles between the lips (c—Figure 39e). Strong musculature is attached to them posteriorly. This serves to move the lips and the anterior part of the oral cavity.

The **oral cavity** is also a very complex structure. It consists of two chambers (Figures 39a, b). In the anterior chamber each of the three walls bears four longitudinal supporting columns which are seen slightly obliquely in profile on Figure 39a (a), in section on Figure 39d (a), and from above on Figure 39b (a). Anteriorly, these columnar bulges diverge and additional narrow bulges arise between the central ones (b—Figure 39b). The posterior chamber is separated from this anterior part by a constriction. On each of the three surfaces of the posterior part there is a ridge consisting of 11 denticles (c—Figure 39b). Five denticles are arranged symmetrically (b—Figure 39d) on each side of the asymmetrical central denticle (c—Figure 39d), which is more pointed and stands rather more anteriorly than the others. The posterior chamber is widest posteriorly and wider than in the other species (Figure 39b). Its walls are enclosed by muscles and stiffened by special chitinized plates, which are a direct continuation of the walls of the anterior chamber of the oral capsule (d—Figure 39b). The walls have the general form of a half oval with the truncated end turned outwards. Their lateral parts and one chord in the middle are chitinized. The bottom of the chamber is also stiffened by special chitinized plates (c—Figure 39b). Its overall length is $45\mu$, of which the anterior chamber takes up $25\mu$. The width of the anterior chamber is $25\mu$, of the posterior about $33\mu$.

There are no **eyes.** The **esophagus** is cylindrical, very muscular, occupying anteriorly half the body width, while posteriorly it expands to three-quarters of it. Opposite the posterior part of the oral cavity it expands slightly. The small **cervical gland** is located quite far behind the end of the esophagus; the excretory pore is exactly at the level of the nerve ring. The **intestine** consists of very large cells in 3—4 rows (Figure 39e). The hindgut is very short.

The **ovaries** are short and reflexed. The uterus is wide, with an
205 unbroken lumen and thick walls. The eggs lie in it freely, as in Cyatholaimus; they have a thick shell, and are round or slightly elongate, $85\mu$ (or correspondingly narrower and longer). The vagina has thick walls and traverses $^1/_3$ of the body width internally.

In the male the **testes** are paired, with large cells. The posterior recurves posteriorly. The ejaculatory duct is quite long. The spicules (Figure 39h) are $95\mu$ long, and greatly curved. A specialized plate (a— Figure 39h) projects internally at the basal end; chitinized strips are observed on the surface of the terminal portion, while on the under surface there are mounds (b—Figure 39h). The gubernaculum is not well developed ($54\mu$); it is adjacent to the terminal parts of the spicules dorsally and laterally (gub.—Figure 39h). Anterior to the anus in the midline there are 6—9 papillae (pap.—Figure 39h). Strictly these are very short bristles with their base inserted into the cuticle. There are also two or three pairs of papillae in the middle of the tail.

The anterior $^1/_6$ of the **tail** tapers sharply conically, while the posterior $^5/_6$ are filiform (Figure 39e). A fairly long terminal tube lies at the end (Figure 39f). The proportions are: length of tail in male and female 6.0; conical part 1.0; filiform part 4.5—5.0; width at end $^1/_9$; spicules 1.7; gubernaculum 0.9; distance from anus to anterior papilla in male 2.7.

Very many specimens were encountered in Zostera from the Chernaya River 5, 7.12.

## Genus DIGNATHONEMA n. g.

Type species: D. bulbosa n. sp.

These are stout nematodes. The cuticle is annulated, the annules formed of transverse rows of punctations, as in Halichoanolaimus. The head is round, with **two large lateral lips** whose apices are beset with large 206 lateral labial papillae. The cephalic bristles are short, lying in a plain circlet. The lateral organ is large and spiral. The anterior portion of the esophagus is expanded and contains the oral armature, which consists of **two subventral jaws** with a hook at the end turned inward. Two lateral pieces with some hooks on each are adjacent to them. The dorsal sector is more weakly developed and lacks jaws. Posteriorly, the esophagus expands greatly. The ovaries are short and reflexed. Males are unknown. The tail is conoid and short.

This new genus is most reminiscent of Cyatholaimus and Halichoanolaimus in the structure of the cuticle and lateral organs. The intestine also is similar to that of the last named. This is a very specialized type as a result of its carnivorous form of life. The sole species is:

### 40. **Dignathonema bulbosa** n. sp.

(Table 6, Figure 40)

$$\text{♀}\ \begin{array}{ccccccccc} - & 2.9 & 5.4 & 44 & 50 & 56 & 62 & 69 & 98.2 \\ \hline 1.8 & 2.0 & 2.0 & & & 2.5 & & & 2.0 \end{array}\ 4340$$

$$\alpha=40;\ \beta=19;\ \gamma=56.$$

| Dimensions ♀ | Cephalic bristles | End of jaws | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | – | 60 | 175 | 300 |
| Width | 67 | 105 | 105 | 105 |

The **body** is almost of even thickness and only slightly expands at midbody. Anteriorly, narrowing occurs only at the extreme anterior end. The **cuticle** is about 3$\mu$ thick, constructed as in Halichoanolaimus: the outer layer is smooth, while a weak annulation is observed on the inner, due to the presence of transversely disposed rows of punctations 2.2$\mu$ apart. The bristle armature is converted into papillae.

The **head** appears rounded, but the regularity is broken by two protruding lips, the dorsal lip being reduced (lab. –Figure 40a, see also 207 Figure 40c). Each lip bears two papillae: one highly developed on the apex (p. l. lat. –Figures 40a, c) and one less developed at the base subventrally (p. l. sv. –Figure 40c). Subdorsal papillae do not lie on the lip itself, but somewhat anterior to its end (p. l. sd. –Figure 40c), which indicates that they belong to the lost dorsal lip. All the papillae are well developed and provided with a chitinized canal containing their nerves. The cephalic bristles are weakly developed, probably because their function has been taken over by the labial papillae. They are ten in number and are disposed in a plain circlet at the anterior margin of the head. The sublaterals (s. c. sl. –Figure 40c) are longer than the other six, of which the laterals are the shortest (s. cl. l. –Figure 40c). The lateral organ is very large, up to 30$\mu$, or about $^1/_3$ of the head width; it is spiral with $3^1/_2$ turns.

The **cephalic capsule** is located inside the head at the base of the lips: this is a cuticular ring to which muscles that serve to extend the head are attached (c. ceph. –Figures 40a, b). The **oral aperture** (os is its demarcating line on Figure 40c) has a general rectangular shape and is bordered by the lips described above. The **oral armature** is very complex. The esophagus in the oral region has an oval outline. Its upper sector is compressed and the two lower ones are considerably better developed than the dorsal (sect. sv. –Figure 40c). All the anterior part of the esophagus is invested externally with a thick capsule that is wider laterally and serves to impart stability to the entire gnathous apparatus (c. oes. –Figures 40b, c). This capsule therefore has the same function as the ring of the cephalic capsule in Enoplus, but there it has developed in an entirely different manner. **Two** jaws arising from the subventral sectors project into the mouth. Each of them bears a point at its end with a hook curved inward (md. c. –Figures 40a, c) next to which are two mounds, each bearing five punctations on their internal surface (md. l. –Figures 40a, c). Posteriorly, each jaw extends as a long appendage to which powerful muscles are attached (md. –Figures 40a, b).

208 As stated, the dorsal sector is far less developed than the two ventrals (sect. d. –Figure 40c). There are also a small median and two lateral teeth on it. The laterals (d. sd. –Figure 40c) are very reminiscent in structure of the reduced lateral processes of the large jaws: these are also mounds with several processes.

The entire gnathous apparatus is embraced by the muscular **esophagus**, which is here very well developed and much expanded anteriorly. Numerous muscle fibers are attached to the end of the jaws (Figures 40a, b). Apart from these, the weakly developed muscles of the dorsal sector and the longitudinal muscles forming the most external layer of the masticatory bulb (seen on Figure 40b) are present. The overall width of the bulb reaches 80$\mu$, about 0.75 of the body width. Behind the bulb there is a narrow portion 30$\mu$ thick, about 0.3 of the body width, which expands greatly posteriorly to 70$\mu$, or 0.7 of the body width, but a distinct posterior bulb is not formed (Figure 40f). The **nerve ring** is thin. I could not find the cervical gland, while the **cervical pore** is located immediately behind the nerve ring.

The **intestine** (Figure 40d) consists of large cells with a weakly developed protoplasm, so that they appear empty, and only a few, filled with plasmatic substance, are darker and larger than the others. The intestine begins as a narrow neck; at its base are four cells of glandular appearance.

The **ovary** is quite long and reflexed; two of the oogonia in its upper part are far larger than the others. The uterus is small, thick-walled with few eggs, which are large, measuring 190×130; they are slightly elongated, with a thick shell. The vagina occupies about $^1/_4$ of the body diameter.

The **tail** (Figure 40e) is short, tapering evenly to a point; its relative length is 1.2. The caudal glands occupy its entire cavity. The caudal pore is short, corresponding to the short form of the tail.

209 This interesting species was found in oxeas sand of Georgievskii Monastery 7.12, 13 and in Zostera from the Chernaya River 5.12, the northern part 6.12. Unfortunately only females were encountered.

D. bulbosa is carnivorous, as the structure of the gnathous apparatus indicates. Parts of swallowed nematodes may be present in its intestine.

## 3. Subfamily **Spilipherini**

These are small and medium-sized nematodes with an annulated cuticle, often of very complex structure. A circlet of labial papillae lies on the head, behind which are ten cephalic papillae and bristles which are **always disposed in two circlets**: The anterior consists of six cephalic papillae (median and subventral), rarely short, true bristles, and the posterior of four true bristles, also rarely converted into papillae. The lateral organs are spiral (apart from Monoposthia and some freshwater genera), either with several turns or more simple. In the majority of cases they are shifted anteriad, but may remain posterior (Monoposthia, Desmodora). The oral cavity is small but always present. There is a dorsal tooth, sometimes very well developed (Hypodontolaimus, Onyx), rarely accompanied by two ventral teeth (Ethmolaimus, Spiliphera). The esophagus always has a bulb, sometimes very conspicuous, sometimes double (Metachromadora). In addition there frequently is an anterior expansion around the oral cavity (Metachromadora, Hypodontolaimus, Monoposthia). The ovaries are reflexed. The spicules are short, curved, and simple. Sometimes there is a row of median papillae anterior to the anus. The tail is usually regularly conoid; its end lacks a cuticular ring and is provided with a distinct terminal tube for the caudal glands (except Spira).

This subfamily, like the following—Chromadorini—consists chiefly
210 of forms originally related by Bastian and Bütschli to genera Chromadora and Spiliphera. Later, de Man isolated from these unwieldy genera several aberrant forms: Desmodora, Monoposthia, Hypodontolaimus; among these I incorporate here; Euchromadora from Chromadorini; Halichoanolaimus from Cyatholaimini. He related all the remaining forms to genera Spilophora and Chromadora, placing in the former those species lacking median preanal papillae and in the latter those possessing them. This distinction is artificial and therefore similar species are encountered in different genera and many aberrant forms prove to be contained here (e.g., Chromadora (Chromadoropsis) vivipara de Man). Steiner (1916, p. 525) finds this to be the case also, but does nothing to rectify the situation. De Man himself was aware of the inadequacy of this rule, since, for example, he included Chromadora bioculata m. Schultze, which lacks preanal papillae, in Chromadora, and not in Spiliphera. Jägerskiöld (1909) suggested simply combining these two genera.

I propose the following scheme of classification:

1) Cyatholaimini: plain circlet of cephalic bristles and spiral lateral organs (see above).
2) Spilipherini: two circlets of cephalic bristles, distinctly spiral lateral organs. Type species: Spiliphera elegans Bastian (similar to Sp. gracilicauda de Man).
3) Chromadorini: two circlets of cephalic bristles, lateral organs indistinct or in the form of transverse slit. Type species: Chromadora nudicapitata Bastian (de Man) (see p. 171).

Thus, the majority of species related up to now to Spiliphera are placed in another subfamily, and only a few remain in this latter genus (see p. 152).

By this means, the following genera are related to Spilipherini:

1) Hypodontolaimus de Man 1886; 1888: Mém. Soc. Zool. France 1,
211 p. 39, Jägerskiöld 1905: Zool. Anz. 27, p. 417. It is difficult to agree with Steiner (1916, p. 524) that this genus "scheint . . . die Berechtigung als Genus verloren zu haben." Although Jägerskiöld points out that de Man's opinion as to the ventral position of the tooth is erroneous, the form and size of the latter are nevertheless so characteristic as to make it impossible to consider abolishing the genus; it is sufficient to introduce the necessary modifications into its characterization.*
2) Onyx Cobb, see p. 153.
3) Metachromadora n. g., see p. 156.
4) Chromadoropsis n. g. is similar to the forgoing in the double bulb of the esophagus but differs in the finer annulation and in that the lateral organs are constructed as normal, i.e., not lying at the bases of cuticular plates.**
5) Desmodora de Man 1889: Mém. Soc. Zool. France 2, p. 9. Steiner 1916: Zool. Jahrb. Syst. 39 p. 545.†

---

* Three species: (1) H. inaequalis (Bastian 1865) Spilophora i.: Trans. Linn. Soc. 25, p.166, Table 13, Figures 223—225; nec Bütschli 1874; Hyp. i.: de Man 1888: Mém. Soc. Zool. France 1, p.41, Table 4, Figure 18; Jägerskiöld 1905: Zool. Anz. 27, p. 417, Figure. English Channel—Falmouth, mud from the harbor (Bastian); North Sea—seawater canal on Walcheren Island (de Man); coasts of Denmark in Ulva and Enteromorpha (Ditlevsen); Kristinenberg in sand (Jägerskiöld); (2) H. bütschlii nom. nov.; H. inaequalis Bütschli 1874 (nec Bastian 1865): Abh. Senck. Ges. 9, p. 44, Tables 5,6, Figure 23; coastal strip of Kiel Firth, also in freshwater parts; (3) H. balticus (G. Schneider 1906): Chromadora b.: Acta Soc. F. F. Fenn. 27, No. 7, p. 30, Figure 14 (nec H. inaequalis Bütschli). Mud from the Tvärminne Bay, Finland; H. arabicus Cobb 1891: Proc. Linn. Soc. N.S.W. 5, p. 465. From Aden—related to another genus, possibly Chromadorella m. Cobb (1914) adds other new species, but I was unable to obtain this work.

** One species: Ch. vivipara de Man 1907: Mém. Soc. Zool. France 20, p. 67, Tables 3,4, Figure 13; in summer on Yerseke Island (de Man); Kola Gulf (Savel'ev). Known to me from the same place.

† Six species: (1) D. communis (Bütschli 1874) Spilophora c.: Abh. Senck. Ges. 9, p. 46, Tables 6,7, Figure 27. Kiel Firth, sand, some sajenes with Paroncholaimus vulgaris Bastian; (2) D. serpentulus de Man 1889: Mém. Soc. Zool. France 2, p.188, Table 5, Figure 4; Steiner 1916: Zool. Jahrb. Syst. 39, p. 546; in seawater canal on Walcheren Island; St. Vaast, among algae (de Man); Kola Gulf; Lake Mogil'noe (Savel'ev); White Sea strait in algae (Steiner); (3) D. scaldensis de Man 1889: loc. cit., p. 190, Table 5, Figure 9—Walcheren, Vlissingen (de Man); Lake Mogil'noe (Savel'ev; possibly the indication relates to D. poseidoni Steiner); (4) D. nudicapitata Cobb 1891: Proc. Linn. Soc. N.S.W. 5, p. 465—sand at low tide, Aden; (5) D. poseidoni Steiner 1916: Zool. Jahrb. Syst. 39, p.547, Table 22, d—Figure 9a; White sea strait, among algae; (6) D. bullata Steiner 1916: loc. cit., p. 549, Table 22, d—Figure 10a—the same place. In addition: (7) Desmodora sp. Rouville 1905: CR. Ass. Franç. Avanc. Sci, 1904, p. 794. Sète canal de Bourdigues; there may also be: (8) Chromadora cincta Villot 1875: Arch. Zool. Exp. (1) 4, p. 464, Table 9, Figure 12; Roscoff. The following two species, judging from the structure of the cuticle, do not belong here; Steiner is of the same opinion (1916, p.545) D. angusticollis Daday 1901: Termész. Füz. 24, p. 444, Table 22, Figures 4—7; Rouville 1905: Cr. Ass. Franc. Av. Sci. 1904, p.793: Buccari algae on stones on the coast; Sète, canal de Bourdigues; D. papillata Daday 1901: loc. cit., p. 445, Table 22, Figures 8,9. Fiume, on patches of algae on the pier.

212 6) Spiliphera (auct. ex. p.); Bastian 1865: Trans. Linn. Soc. 25, p. 165; Bütschli 1874; Abh. Senck. Ges. 9, p. 44; em. de Man 1886: Anat. Unters. p. 66; 1888: Mém. Soc. Zool. France 1, p. 44; 1889: ibid. 2, p. 9. The following characterization may be suggested for this genus: cuticle annulated, with punctations; lateral organ spiral; large dorsal tooth and other thickenings around it, from which special chitinized processes proceed.* For names see Appendix.

7) Achromadora Cobb 1913: Journ. Washington Acad. Sci. 3, p. 441. Freshwater and terrestrial genus.**

8) Ethmolaimus de Man 1880; 1884: Nemat. Niederl. Fauna, p. 61; Hofmänner 1913: Revue Suisse Zool. 21, p. 634. – Freshwater genus.†

9) ? Microlaimus de Man 1880; 1884: Nem. Nied. F. p. 51; Steiner 1916: Z. J. Syst. 39, p. 589††

213 10) Chromadorina n. g., see p. 162.

11) Chromaspirina n. g., see p. 164.

12) Spirina nom. nov. pro Spira Bastian 1865, see p. 165.

13) Laxus Cobb 1893: Proc. Linn. Soc. N. S. W. 8, p. 413.‡ Apparently its very close relative.

14) ? Monoposthia de Man, see p. 169

---

* Three species: (1) Sp. elegans Bastian 1865: Trans. Linn. Soc. 25, p.165, Table 13, Figures 221, 222. Mud from harbor – Falmouth; (2) Sp. gracilicauda de Man 1893 with a variety of dolichura de Man 1893: Mém. Soc. Zool. France 6, p.91, Table 5, Figure 6 – fairly common on algae on rocks, Falmouth; (3) Sp. giardi Rouville 1903: Cr. Ass. Franç. Avanc. Sci. 1904, p.795; Sète, canal de Bourdigues.

** Here are: (1) Chromadora lehberti G. Schneider 1906: Zool. Anz. 29, p.680, Figures 1, 2. Obersee around Revel; (2) Chromadora minima Cobb 1893: Macleay Memor. Volume, p.13; 1893: Agric. Gaz. N.S.W.4, p.820, Figure 38; Achromadora m. 1913: Journ. Washington Acad. Sci. 3, p.441. On banana roots at Fiji; on sugar cane roots N.S.W.: type genus; (3) Chromadora musae Cobb 1893: Macleay Memorial Volume, p. 14; banana roots, Fiji.

† Five species: (1) E. pratensis de Man 1880; 1884: loc. cit., p. 61, Tables 8, 34, Figure 33, t – Holland; (2) E. (?) tatricus Daday 1897: Zool. Jahrb. Syst. 10, p.107, Table 13, Figure 12 – Lake in Tatra region, Hungary; (3) E. revaliensis (G. Schneider 1906) Chromadora r.: Z.Anz. 29, p.681, Figures 3 – 5; E.r.: Steiner 1913: Arch. Hydrobiol, Planktonk. 8, p.454, Figures 4 – 6; Hofmänner 1915: Revue Suisse Zool. 23, p.140, Table 4, Figure 6; Table 5, Figures 8, 9. Obersee around Revel; Lakes Zurich and Geneva; (4) E. lemani Hofmänner 1913: Revue Suisse Zool. 21, p.635, Table 16, Figures 14, 15; 1915: ibid. 23, p. 139, Table 4, Figure 5. Lakes Lugano and Geneva; (5) E. foreli Hofmänner 1913) Chromadora f.: loc.cit., 21, p.637, Table 16, Figures 12, 13; E.f.: ibid. 23, p.138, Table 4, Figure 7; (6) E. alpinus (Micoletzky 1913) Triodontolaimus a.: S. Ber. Ak. Wiss. Wien, 1 Abt., Bd. 122; Chromadora (Parachromadora) a: 1914: Z.J.Syst. 36, p.494, Tables 17, 18, Figure 29; (7) E. arcticus Steiner 1916: Zool. Anz. 47, p.60, b – Figure 5a; Novaya Zemlya, moss at Matochkin Shar. Here also possibly belongs: Chromadora tatrica Daday 1897: loc. cit., p.103, Table 11, Figures 16 – 18.

†† Here are: (1) M. globiceps de Man 1880; 1884: loc.cit., p.52, Table 6, Figure 24; nec G. Schneider; earth soaked with brackish water, Walcheren, III, VIII; (2) M. menzeli Hofmänner 1914; Z.Anz. 44, p.84, Figure 6; 1915, Revue Suisse Zool. 23, p.135, Table 5, Figures 15, 16; lakes in Switzerland; (3) M. borealis Steiner 1916: Z.J.Syst. 39, p.590, Table 27, Figures 20a, c; ? M. globiceps G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No.7, p. 21, b – Figure 10a; algae from the White Sea strait; ? Tvärminne (Gulf of Finland) in mud.

‡ Two species: (1) L. contortus Cobb 1893: loc.cit., p.414. Marine sand in Naples; (2) L. longus Cobb 1893: loc.cit., p. 416, Figure 11 – sand, Port Jackson N.S.W.

1 (23). Two spicules. Lateral organs spiral or large, circular.
2 (20). Oral cavity fairly wide with distinct teeth.
3 (6). Dorsal tooth constructed like movable spear.
4 (5). Spear very large, appears shifted from ventral side. Cuticle of annules with punctations . . . . . . . . **Hypodontolaimus** de Man
5 (4). Spear not large. Cuticle of narrow annules without punctations. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Onyx** Cobb
6 (3). Tooth not spearlike.
7 (18, 19). Head appears truncated anteriorly.
8 (13). Cuticular annules smooth without punctations.
9 (10). Lateral organs lie on specialized cuticular plate. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Metachromadora** n. g.
10 (9). Lateral organs spiral, usual type.
11 (12). Lateral organ shifted to extreme anterior end . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chromadorina** n. sp.
12 (11). Lateral organ shifted posteriorly . . . . . . . . **Desmodora** de Man
13 (8). Cuticular annules with punctations.
14 (17). Teeth in oral cavity pronounced, set directly against eyes; esophagus distinctly expanded anteriorly.
15 (16). Oral cavity conical, cuticular processes extend posteriorly from teeth into musculature of esophagus . . . . . . . . **Spiliphera** Bastian
16 (15). Oral cavity large, cylindrical, with three teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Ethmolaimus** de Man
17 (14). Teeth small, esophagus hardly expanded anteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chromadorina** n. sp.
18 (7, 19). Head uniformly round . . . . . . . . . . . . . . . **Chromaspira** n. g.
19 (7, 18). Head expanded, lateral organ circular, posterior to oral cavity . . . . . . . . . . . . . . . . . . . . . . . . . . **Microlaimus** de Man
20 (2). Oral cavity very small, with tiny teeth (in Laxus may be entirely absent). Esophagus very short.
21 (22). Lateral organs at first seem circular, incised with edge . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Spirina** nom. nov.
22 (21). Lateral organs distinctly spiral . . . . . . . . . . . . . . **Laxus** Cobb
23 (1). Only one spicule; lateral organs small, circular. Cuticle annulated, without punctations, with longitudinal rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Monoposthia** de Man

214

## Genus ONYX Cobb 1891

Proc. Linn. Soc. N. S. W. 6, p. 146.

Type species: O. perfectus Cobb 1891

This genus was established by Cobb for one very characteristic species and is distinguished by the following features:

They are nematodes of small dimensions. The cuticle is finely annulated, without punctations. The bristles are long and flexible. The head is rounded when the mouth is closed. Ten cephalic bristles are present, six short and four long. The lateral organ is large and spiral. The lips are in the form of 12 rods, narrowing from the posterior end, and are capable of spreading widely. The small oral cavity is cup-shaped. A movable dorsal spear with a chitinized tip projects into it posteriorly: The oral cavity and spear are covered by musculature, which constitutes the anterior expansion of the esophagus. The expansion is followed by a narrow portion, and a large longitudinal bulb is located posterior to this. The ovaries are paired and reflexed, the spicules curved and pronounced. The gubernaculum is spoon-shaped. The tail is conoid and the annulation ceases before reaching its end. The tube lies at the end of the tail.

Cobb compared this genus to Dorylaimus, but this similarity is purely superficial. Dorylaimus is differentiated from this genus by the absence of bristles, the cyathiform lateral organ, the different structure of the genital tracts, and the completely different structure of the spear and its mechanism, which was elucidated by Cobb himself. The differences are so great that I have placed the two genera in different families. The arrangement of the cuticle on the head is very similar to Metachromadora.

The sole species is:

### 41. **Onyx perfectus** Cobb 1891

(Table 6, Figure 41)

Proc. Linn. Soc. N. S. W. 6, p. 153, Figures 4, 5, 8.

$$♂\ \frac{-\quad 6.4\quad 13.6\quad 43\quad 58\quad 94.7}{1.7^{**}\ 2.1\quad 2.4\quad 2.7\quad 2.1}\ 2025$$

$$\alpha=37;\ \beta=7;\ \gamma=19.$$

$$♀\ \frac{-\quad 6.8\quad 13.3\quad 40^{*}\quad 64\quad 80^{*}\quad 94.2}{1.8^{**}\quad 2.2\quad 2.4\quad 3.1\quad 1.8}\ 2100$$

$$\alpha=32;\ \beta=7^1/_2;\ \gamma=17.$$

215

| Dimensions with mouth withdrawn | Cephalic bristles | Middle of lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length ♂ | – | 10 | 125 | 265 |
| Width | 25 | 34 | 43 | 46 |
| Length ♀ | – | 11 | 145 | 285 |
| Width | 27 | 38 | 46 | 50 |

The **body** tapers slightly to the beginning of the esophagus, somewhat more markedly to the anus. In the esophageal region the tapering is almost twofold to the cephalic bristles. The **cuticle** is $1^1/_2-2^1/_2\mu$ thick, finely annulated externally, the annules being $0.7-0.8\mu$ wide. They are smooth, without punctations. Long, slender and supple bristles, reaching $10-20\mu$ in length, are observed over the entire body and are particularly numerous at the anterior end (Figure 41a). All the bristles are set in special pits in the cuticle that are well marked in profile (see Figure 41a, on the right).

The **head** is perfectly round when the mouth is closed (Figure 41b). The lips are narrow, and the labial papillae extend as short bristles between them, so that anteriorly 12 lips are seen, tightly pressed together at the anterior end when the mouth is closed (lab. – Figure 41b), but opened into a tube when it is open (lab. – Figure 41a). Cobb draws them as ornamentations of the cuticle, which is of course inaccurate. When open the mouth is $6\mu$ wide. The cephalic bristles are ten in number: the six anterior are short, $7^1/_2\mu$ (s. c. ant. – Figure 41a), and the four posterior are very long ($22\mu$) and are the longest bristles on the head, equal almost to the head width (s. c. post. – Figure 41a). Numerous cervical bristles are disposed behind them (s. cerv. – Figure 41a). The lateral organ is conspicuous, spiral with two small turns, having in the male a diameter of $12\mu$ or about $^1/_3$ of the head width; in the female it is somewhat less 216 (about $9^1/_2\mu$ or $^1/_4$ of the head width). The transverse annules of the cuticle lose their regularity, running around the lateral organ, while on the median sides of the head their ends abut upon the posterior margin of an area on the anterior surface of the head completely devoid of annules.

The **vestibule** is located between the extensions of the 12 lips and labial papillae. When the mouth is closed its cavity is narrow and straight, and the posterior portions of the lips constrict the oral cavity lying behind them (see Figure 41b). When the mouth is open (Figure 41a) the vestibule assumes a funnel shape. The **oral capsule** is cup-shaped with thin lateral walls (c. or. – Figure 41a). The ends of the rays of the vestibule project backwards into the oral capsule, thereby narrowing its lumen. The capsule is $12\mu$ wide and $6\mu$ deep. Posteriorly, a large dorsal tooth, here converted into a movable spear, projects into it. It is possible that this spear, as Cobb suggests, may protrude from the mouth and pierce the objects to which the nematode is attached by its open vestibular funnel. The length of the chitinized thimblelike tip covering the end of the spear is $8\mu$, its width is $5^1/_2\mu$. The spear may extend as a special formation also posteriorly to the tip, as Cobb thinks. I saw only one auxiliary tip posterior to the main one; usually these are absent. Cobb found as many as three, sometimes fairly large.

Around the oral cavity there is special musculature directed generally longitudinally and serving for the movement of the oral apparatus. This musculature forms the anterior expansion of the esophagus, attaining a width of $27\mu$ (about $^2/_3$ of the entire body width). It is followed by a narrow portion of the esophagus of usual structure, about $20\mu$ wide (less than half the body width); posterior to this there is a long true bulb $35\mu$ wide (about $^2/_3$ of the body width). The first swelling accounts for 30% of the esophagus length, the central portion 33%, and the posterior bulb 37%. The esophageal glands are particularly well developed in the bulb, 217 opening in the lumen of the esophagus not far posterior to the oral cavity.

The **ovaries** are paired and reflexed; in one case I observed that the anterior ovary was far longer than the posterior. The uterus is thick-walled. The eggs are large, $110\times60\mu$; I found development stages already inside the uterus. The vagina traverses internally 0.4 of the body width.

There are apparently two **testes**. Their ends are reflexed and filled with small cells which rapidly enlarge in volume and are tightly packed together. The diameter of the sperm, which are provided with a distinct nucleus, is $^1/_4-^1/_5$ of that of the mother cells from which they are derived

---

* Only the overall length of the genital tract is indicated.

** Opposite the lateral organ.

(Cobb). The vas deferens consists, as usual, of two rows of compact cells and is well developed. The **spicules** (Figures 41c, d) are 65 — 70$\mu$ long, thick-walled, curved, and have a pronounced knob with a longitudinal constriction inside; at the end the spicules are evenly pointed. The **gubernaculum** is 35 — 40$\mu$ long, paired, spoon-shaped, and embraces the terminal part of the spicules; its anterior part is fairly thick (a — Figure 41d), while the lateral parts on the spicules are thin and provided with appendages (b — Figure 41d). Anterior to the anus there is a row of 18 — 22 (28 according to Cobb) papillae of very characteristic structure (Figure 41c). Each papilla (Figure 41e) is a slightly S-shaped pivot going deep into the body; its total length is 16 — 19$\mu$. A spoon-shaped enlargement at the end, however, is directed through an opening externally. According to Cobb's observations, this row is hardly longer than double the length of the tail. The posterior papillae, which may project and clasp the female on copulation, are set more frequently. In his description Cobb says nothing about their form, and the figures provide only hints of it, but this is probably due to oversight. Two postanal subventral rows of short bristles (Figure 41c), are not noted by Cobb either: he mentions only the bristles at the middle of the tail.

The **tail** is just longer in the female than in the male, gradually tapering
218 conically posteriorly (Figure 41c); the annulation ceases 25$\mu$ from the tip
and the terminal tube is about 9$\mu$ long. The tip of the tail is slightly swollen — more than is drawn in Cobb's figure (see Figure 41c here and Figure 8 — II, p. 154 in Cobb). The caudal glands are located inside the tail. There is no cone. The proportions are: length of tail in female 3.5 — 3.8, in male 2.2 — 2.5; spicules 1.5; gubernaculum 0.9; length of row of preanal papillae 6.8 — 7.5.

This species was found only in oxeas sand: Peschanaya Bay 5, 6, 7.12, few specimens; Georgievskii Monastery, many specimens 7.12, 13; particularly from a depth of 18 sajenes. In Naples Cobb found it also in oxeas sand. The absence of large marine algae on the sand prompted him to suggest that Onyx attaches to animals, which seems doubtful to me.

In spite of the many differences mentioned above I have decided to identify this species with Cobb's since the differences are so slight as to be attributable to inaccuracy of observation and drawing: in all other respects my forms of Onyx are exactly similar to those of Cobb.

## Genus METACHROMADORA n. g.

Type genus: M. macroutera n. sp.

These are nematodes of medium size. **In the female the body is greatly swollen** in its posterior half, where the genital tract is located. The **cuticle** consists of two layers, the outer compsed of **smooth annules** and sometimes taking up almost the entire thickness; special narrow annules are present on the head; lateral elevations are present; the extreme anterior surface of the head is not annulated; Six labial papillae are located around the oral aperture; more posteriorly there are six cephalic bristles. **The lateral organs are large and spiral, located on special thick cuticular plates shifted far anteriorly.** The oral cavity is small,
219 thick-walled, **with a movable dorsal tooth,** and embraced by specialized
musculature. Posteriorly, the esophagus is a large, long bulb. The ovaries are short, joined to the uterus, which is very spacious with thick walls. There is one testis. The spicules are short and the gubernaculum is adjacent to them. In the female preanally in the midline there is a special mound of thickened cuticle beset with papillae. The tail is conoid.

I found two species characterized by these features in the Black Sea. The following genera may be indicated as being most similar to them: Desmodora de Man, which differs in the absence of cuticular annules on the head and by the lateral organs; Chromadoropsis n.g.* is very similar to Metachromadora in the structure of the oral cavity and bulb, but differs in the structure of the cuticle (it is very finely annulated, as distinct from the coarsely annulated cuticle of Metachromadora) and in the structure of the lateral organs. In addition, genus Onyx Cobb is similar to our genus in many features, but it has a differently shaped head and a different distribution of the cephalic bristles.

The two species are:

1) M. macroutera n. sp., see below.
2) M. cystoseirae n. sp., see p. 160.

1 (2). Body tapers anteriorly from end of esophagus less than twofold, margin of lateral organ not very thick . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. macroutera** n. sp.
2 (1). Body tapers more than twofold. Margin of lateral organ so thick that spiral appears to be located on a specialized shield . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **M. cystoseirae** n. sp.

### 42. **Metachromadora macroutera** n. sp.
(Table 6, 7, Figure 42)

$$♂\text{(Peschanaya Bay)}\ \frac{\text{—}\quad 5.0\quad 12.0\quad 41^{\ddagger}\quad 64^{\ddagger\ddagger}\quad 93.4}{1.9\quad 2.5\quad 2.8\quad 2.8^{\dagger}\quad 3.1^{\dagger\dagger}\quad 2.4}\ 2400$$

$$\alpha=32;\ \beta=8^{1}/_{3};\ \gamma=15.$$

220

$$♂\text{(Georgievskii Monastery)}\ \frac{\text{—}\quad 5.1\quad 11.1\quad 45^{\dagger\dagger}\quad 66.5^{\ddagger}\quad 94.0}{1.7\quad 2.3\quad 2.6\quad 1.4^{**}\quad 3.2^{\dagger}\quad 2.3}\ 2625$$

$$\alpha=31;\ \beta=9;\ \gamma=17.$$

$$♀\text{(Peschanaya Bay)}\ \frac{\text{—}\quad 5.3\quad 11.8\quad 60^{\ddagger\ddagger}\quad 74.5\quad 90\quad 94.0}{1.8\quad 2.5\quad 3.0\quad 2.7^{**}\quad 5.7\quad 2.2}\ 2550$$

$$\alpha=18;\ \beta=8^{1}/_{2};\ \gamma=17.$$

---

* Established by me for Chromadora vivipara de Man, see p. 151.

** Diameter of the body between the esophagus and the genital tracts

† Maximum diameter.

†† Beginning of testis.

‡ End of testis.

‡‡ Only the overall length of the genital tracts is given.

| Dimensions ♂ | Cephalic bristles | End of coarse annulation of cuticle | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | – | 16 | 24 | 145 | 290 |
| Width | 28 | 40 | 42 | 65 | 70 |

The dimensions of the female do not differ greatly.

The **body** widens greatly in the middle, particularly in the female, where it is double the width of the body at the beginning of the esophagus. The expansion is very sharp, so that this part of the body appears much swollen (Figure 42i) and facilitates recognition of this species under a magnifying glass. In the male the expansion is less pronounced. The body frequently but not always narrows between the end of the esophagus and the beginning of the genital tracts, sometimes very sharply (cf. formula of male from Georgievskii Monastery). The body tapers from the end of the esophagus anteriorly $1^{1}/_{2}$ times.

The **cuticle** consists of two layers: the inner is smooth but the outer is composed of clearly separated annules completely lacking punctations; sometimes it occupies the entire thickness of the cuticle. At the anterior end these annules are $1.4\mu$ wide, in the middle and on the dorsal side posteriorly $1.0\mu$, on the ventral side posteriorly $0.6\mu$ postanally, and $1.2\mu$ preanally in the male. Sometimes the annules are incomplete and wedged out by the two neighboring annules (a—Figure 41b), or they circumvent a 221 papilla. On the sides of the head anteriorly the annules are far narrower and curve to form arcs with the ends anteriorly and with the centers in the median plane (Figures 42b, c, d). There follows a group of wider annules which at the nerve ring are transformed into normal annules. Laterally, there is an elevation consisting of a fold of cuticle beginning from the posterior end of the esophagus and terminating slightly in front of the anus. The annules remain unbroken on it. The thickness of the cuticle anteriorly is about $4\mu$, at midbody $3^{1}/_{2}\mu$, posteriorly $4\mu$. On the ventral side of the male it is up to $6^{1}/_{2}\mu$ in the region of the elevation, $2^{1}/_{2}\mu$ on the tail. The bristles are quite numerous and long.

The **head** appears generally truncated. The cephalic bristles are disposed in two circlets: the anterior of six very short bristles, almost papillae (s. c. ant. —Figures 42c, d), and the posterior (s. c. post—Figures 42b, c, d) of four fairly long bristles, $9\mu$ long, or $^{1}/_{3}$ of the corresponding body width. The lateral organ is very large—$19\mu$ long and wide, or $^{2}/_{5}$ of the corresponding body width. It consists of a thick chitinized plate, within which lies a small spiral that opens to the outside with $1^{1}/_{2}$ turns. This spiral is indistinct, so that at first the organ appears circular with a large median elevation, and only on more careful inspection is the spiral detected (see Figure 42b—lateral aspect and Figures 42c, d, e—sections). Two small bristles $6\mu$ long lie laterally on the dorsal sides.

In the resting position the **mouth** anteriorly is small aperture (os—Figure 42d), into which six fairly well-developed labial papillae project (p. lab.—Figure 42d); its margins are plicate. It is located in a depression that is present on the entire anterior end of the worm. Externally, the margins of this depression are beset with four large cephalic bristles, and internally there are six large bristles (see Figures 42b, c, d). A plicate tube follows the oral aperture: this is the **vestibule**; each of its three sides (corresponding to the three sectors of the esophagus) bears four waveform 222 projections directed into the oral cavity (vest.—Figures 42b, c, e). Its walls are fairly thin. A small, round, cup-shaped oral cavity with thick walls (c. or. —Figures 42b, c, e) follows. A well-developed tooth that is characteristic for the majority of Chromadorini (den. —Figures 42b, c, e) arises on the dorsal side. Posteriorly, the walls of the cavity are transformed directly into the tube of the esophagus. Laterally, the oral cavity is covered by two layers of the muscular esophagus. The inner layer consists of longitudinal fibers, rectangular on section, which are adjacent to the internal wall of the esophagus (m. int. —Figure 42e, drawn at the level of the oral cavity). Five such fibers extend through each sector of the esophagus. The outer layer consists of fibers which at the level of the oral cavity are quite flat and invest the adjacent layer of inner muscles (m. ext$_1$ — Figure 42e), while anteriorly at the level of the vestibule they are rounded in section and do not constitute a continuous layer (m. ext$_2$—Figure 42e). Four such fibers extend in each sector. Both layers of muscle fibers are attached to the most anterior part of the vestibule so that the oral cavity and almost the entire vestibule are embraced by musculature. The width of the oral cavity is $18\mu$, its depth $8\mu$. The mouth may be opened widely. In the normal position of the mouth the lateral organs lie **obliquely** to the longitudinal axis of the body and all the anterior, finely annulated part of the body is bent internally. However, when the mouth is open, the walls of all the anterior parts are bent out and straightened, the lateral organ becomes **parallel** with the longitudinal axis of the body, and the folds of the vestible become widely stretched. I do not know if the tooth in this condition can protrude entirely outside, but in any event it is shifted considerably anteriorly. On the other hand, when the anterior end is drawn deeply within, the lateral organs become almost perpendicular to the longitudinal axis. The muscles described above evidently serve to draw back the anterior parts of the body and to project the oral organs to the outside.

223 In the **esophagus** (Figure 42a) three parts are distinguished. The anterior part embraces the oral cavity and extends behind it, accounting for 20% of the overall length. This part is characterized by the presence of the aforementioned muscles, distinctly separate from each other, running longitudinally; its maximum width is $30\mu$. The second portion is narrow, of normal structure, $25\mu$ wide, occupying $40\mu$ of the total length of the esophagus. Finally, the posterior 40% is taken up by a massive, long bulb with a double arrangement of the muscles, $55\mu$ wide (80% of the body width). Posteriorly, a narrow constriction separates the intestine from the end of the esophagus. The **cervical gland** is small, located behind the end of the esophagus, and its pore is opposite the nerve ring; the latter encircles the posterior $^{1}/_{3}$ of the narrow portion of the esophagus.

The **female genital apparatus** is massive, so that the body is greatly swollen around it. The ovaries are paired, reflexed, and very short, so that they lie almost perpendicular to the longitudinal axis of the animal.

The uterus is very wide with a common lumen. Its walls consist of very large cells with evidently shrunk nuclei. The eggs are round, small ($70\mu$) in comparison with the general width of the uterus, with a thick shell.

The **testis** is short and narrow (a—Figure 42k), containing a cluster of small dense cells, which gradually expand posteriorly to $15\mu$ and pass into the seminal vesicle (b—Figure 42k). Here they become vacuous, forming cavities reminiscent in general form of the uterine lumen in the female. I did not observe subsequent stages of development of the sperm. The cavity of the tract then changes from irregular to narrowly tubular and the seminal vesicle is transformed into the vas deferens. Its first part is composed of light cells lying in several rows, the direct continuation, as it were, of the large cells of the seminal vesicle (c—Figure 42k). In
224 the following part (d—Figure 42k) the cells are packed with granules, become darker in color, and are disposed at first in two rows, narrow parts alternating with wide parts: the narrow part above, the wide part below, and so on. The end of this portion is characterized by a regular disposition of cells packed like two piles of coins. More posteriorly these piles, whose cells have become lighter, are covered by a layer of obliquely running musculature (e—Figure 42k), and form a narrower ejaculatory duct. The spicules (Figure 42f) are two in number, uniform ($60\mu$ long), curved, with a double knob at the base; one part of it is directed anteriad, the other laterally. The ends of the spicules are pointed. Their velum is quite well developed. Two thin parts of the gubernaculum, $28\mu$ long, are adjacent to each spicule dorsally. Their anterior end is pointed. The supplementary bristle armature in the male is very complex. Two mounds lie in the midline on the tail (a—Figures f, h) and are pierced by sensory pores. Preanally, there is a narrow elevation of cuticle $7\mu$ thick. This runs anteriorly to the beginning of the testis and is beset with a row of 26—48 papillae (pap.—Figure 42f). Each papilla (Figure 42g) consists of a chitinized button on the surface of the cuticle with a contiguous short pivot, also chitinized, leading to a pore where the nervous apparatus terminates. In addition, there are six longitudinal rows of long (about $8\mu$) bristles that run anteriorly for the same distance as the aforementioned bulge and posteriorly to the end of the tail; two of the rows are subventral, (s. subv.—Figure 42f), two lateral (s. lat.—Figure 42f), and two subdorsal (s. subd.—Figure 42f). The last-named rows are less regular and do not reach the tip of the tail.

The **tail**, as in the majority of Spilophorini, is regularly conoid and quite long. The annulation of the cuticle ceases $30-35\mu$ from the end, the last annules being irregular (b—Figures 42f, h). The caudal glands are accommodated within the tail and there are no cones. The tube at
225 the end of the tail is long—$8\mu$ (see Figure 42h). The proportions are: length of tail of male 2.3, of female 3.0; width at end of annules in male 0.24, in female 0.3; length of spicules 1.0; gubernaculum 0.5; space occupied by papillae 12—15.

M. macroutera n. sp. is one of the most characteristic species of oxeas sand and coquina. There were many of them in summer and winter in all samples from both Kruglaya Bay and Georgievskii Monastery, 9 sajenes and 18 sajenes. One chance specimen was encountered in oyster banks 6.12.

## 43. Metachromadora **cystoseirae** n. sp.

(Table 7, Figure 43)

$$\text{♀}\ \frac{\begin{array}{ccccccc} — & 6.0 & 12 & 63^{1)} & 74 & 87^{*} & 93.5 \end{array}}{\begin{array}{ccccccc} 1.4 & 3.0 & 3.1 & & 5.3 & & 2.4 \end{array}}\ 2550$$

$$\alpha = 19;\ \beta = 8;\ \gamma = 15.$$

| Dimensions<br>♀ | Cephalic bristles | End of lateral organ | Cervical pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 12 | 22 | 80 | 110 | 280 |
| Width | 35 | — | 60 | 60 | 85 |

As in the forgoing species, the body of the female is greatly swollen around the genital organs and sharply narrowed elsewhere: to half near the anus and to 0.6 at the end of the esophagus. From here anteriorly, the body tapers $2^1/_2$ times, more than in the preceding species. The **cuticle** consists of exactly the same form of annules. Anteriorly, it is $3\mu$ thick and in the other regions it is a little more than $2\mu$. The annules are $1.6\mu$ wide anteriorly, $1.2\mu$ at the beginning of the esophagus, $1.4\mu$ posteriorly. An elevation of cuticle extends along the lateral line from the posterior end of the esophagus almost to the anus.

The **head** (Figure 43) is truncated; Lips are absent. The labial bristles are disposed directly around the oral aperture. The cephalic bristles lie
226 in two circlets: the anterior of 6 papillae and the posterior of four true bristles $10\mu$ long, or about $^1/_4$ of the head width. The lateral organ is similar to that in M. macroutera, but is distinguishable from it. Its spiral is narrower than in the forgoing species, which causes the cuticular plate on which it lies to appear wider (see Figure 43). Its width is $15\mu$, or 0.4 of the corresponding body width. A vestibule (vest.—Figure 43) with plicate walls leads to an **oral capsule** with fairly thick walls and a dorsal tooth; the capsule is constructed as in the forgoing species, but with thinner walls (see Figure 43 and c. or.—Figure 42b).

The **esophagus** is constructed as in the forgoing species: it is expanded anteriorly around the oral cavity ($27\mu$), then a narrow portion ($22\mu$) follows, and the posterior 40% of the total length is taken up by a large bulb $35\mu$ wide with an elongated lumen. It is considerably less developed than in the forgoing species, occupying only 0.4 of the width of the body in the corresponding part. The small **cervical gland** is located behind the end of the esophagus and its pore is anterior to the nerve ring.

The **female genital tract** is developed exactly as in the forgoing species. The **tail** is conoid also, and its posterior part, devoid of annules, is $25\mu$ long. Its proportions are: length 3.0, width at terminal tube 0.1.

Only one female, still without eggs, was found in Cystoseira from a small area of the road 6.12.

This species is easily differentiated from M. macroutera n. sp. by its narrower anterior end and the different form of its lateral organs.

---

* The total length of genital tracts is indicated.

## Genus CHROMADORINA n.g.

Type species: Chr. obtusa n. sp.

These are small nematodes with an annulated cuticle. **Punctations are observed on the annules,** and they are sometimes distributed in longitudinal rows along the lateral surface of the body. Six short labial papillae are concealed within the vestibule. Six cephalic papillae and
227 four long cephalic bristles are present. **The lateral organ is spiral.** The vestibule is plicate, **the oral cavity is conical with a movable dorsal** tooth, devoid of chitinized processes, running posteriorly into the esophageal wall. There is a distinct bulb. The ovaries are paired and reflexed. The spicules are curved and short, with a gubernaculum covering them. There are preanal papillae. The tail is conoid, with a terminal tube, the annulation not reaching the end. One species is in the Black Sea.

This genus is most similar to Spilophora s. str., but differs from it by the absence of cuticular processes attached to the oral cavity.*

So far only three species are related here:

1) Chr. obtusa n. sp., see below
2) Chr. brevicollis (Cobb 1898); Cyatholaimus br.: Proc. Linn. Soc. N.S.W. 23, p. 403. Sand at the tidemark at Port Jackson N.S.W.
3) Chr. microlaima (de Man 1889); Chromadora m.: Mém. Soc. Zool. France 2, p. 199, Table 6, Figure 8. Seawater canal on Walcheren Island; White Sea strait on algae (Steiner).

It is likely that some species now related to Chromadora will also prove to belong here.

1 (2, 3). Three longitudinal rows of punctations laterally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. brevicollis** Cobb
2 (1, 3). Two longitudinal rows of punctations laterally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. microlaima** de Man
3 (1, 2). No longitudinal rows of punctations . . . . . . **Chr. obtusa** n. sp.

### 44. **Chromadorina obtusa** n. sp.
(Table 7, Figure 44)

$$\sigma\text{ (immature) }\frac{\begin{array}{cccccc}\text{—} & 10.4 & 18.4 & 36.5 & 55 & 85.6\end{array}}{\begin{array}{ccccc}1.8 & 3.8 & 4.2 & 5.2 & 4.8\end{array}}\ 675$$

$$\alpha=19;\ \beta=5.5;\ \gamma=7.$$

$$♀\text{ (immature) }\frac{\begin{array}{ccccccc}\text{—} & 9.3 & 15.5 & 38 & 47 & 59 & 89\end{array}}{\begin{array}{ccccc}1.9 & 3.8 & 4.5 & 5.9 & 4.0\end{array}}\ 780$$

$$\alpha=17,\ \beta=6^1/_2,\ \gamma=9.$$

228

| Dimensions ♀ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 5 | 70 | 120 |
| Width | 14 | 30 | 35 |

The short **body** expands greatly in the middle and tapers less than $1^1/_2$ times to the anus and the end of the esophagus, whence anteriorly it tapers more than twofold to the anterior end. The **cuticle** is thin, anteriorly $1\mu$, more posteriorly reaching $1.6\mu$. It is composed of annules $1.1-1.2\mu$ apart. Rows of punctations are located between the annules. The outer surface is smooth, not annulated (see Figure 44b). Quite numerous submedian bristles lie along the body.

The **head** is roundly truncated (Figure 44b). I could not find labial and cephalic papillae. There are four cephalic bristles $6\mu$ long (somewhat less than half the head width). The lateral organ is spiral with $1^1/_2$ turns, about $3-4\mu$ in diameter, located far anteriorly among the cephalic bristles (see Figure 44b).

A small oral cavity follows the plicated vestibule, which is $4\mu$ long. The anterior chamber of the cavity is cup-shaped, $2^1/_2\mu$ long, $5\mu$ wide, with a large curved movable tooth in its bottom $3^1/_2\mu$ long (den. – Figure 44b). There may be two more small immovable subventral teeth. Behind the teeth the oral cavity continues conically for $5^1/_2-6\mu$ posteriorly. Anteriorly, the esophagus incorporates special muscles that serve to move the oral parts. The anterior portion of the esophagus is about $10-12\mu$ wide, while posteriorly it expands into a large bulb $25\mu$ wide, lacking an internal cavity (see Figure 44a). The **cervical gland** is large, elongate, $37\times14\mu$, located immediately posterior to the cone of the esophagus. The cervical pore lies immediately behind the nerve ring.

The **ovaries** are paired and reflexed. The vagina traverses $^2/_7$ of the
229 corresponding body width. The **spicules** (Figure 44) are quite slender, $32\mu$ long, with a small manubrium and velum. The gubernaculum is double, $30\mu$ long, and in the shape of a spoon covering the spicules laterally; in the middle the two halves apparently fuse. Posteriorly, there are two points extending to the sides. Two small median papillae are located preanally.

The **tail** is conical, swollen at the end. In the male (Figure 44d) this swelling is hardly noticeable, while in the female (Figure 44c) it is distinct. Three large caudal glands occupy almost the entire cavity of the tail. Their ducts widen into reservoirs anterior to the cone (r. – Figures 44c, d). The terminal tube is $6-8\mu$ long.

The proportions are: length of tail of female 4.0, of male 3.2; width of terminal swelling in female 0.6, in male 0.4; width at tube $^1/_6$; spicules 1.1; gubernaculum 1.0; distance from anus to anterior papilla 1.0.

This species was found in large quantities in Cystoseira from rocks at Georgievskii Monastery 7.12, in smaller quantities in deep Cystoseira from the road and from Shmit Bay 6–7.12. All the females were still immature.

---

* "Apophyses chitineuses" of de Man. Mém. Soc. Zool. France 6, p. 91, Table 5, Figure 6a.

## Genus CHROMASPIRINA n. g.

Type species: Chr. pontica n. sp.

These are small filiform worms with rounded head and annulated cuticle. All three rows of bristles on the head (6 labial, 6 anterior cephalic, 4 posterior cephalic) are well expressed and are short true bristles. The lateral organ is similar to Spirina — a hardly pronounced spiral. The oral aperture is encircled by an elevation of cuticle, inside which a vestibule with plicate walls originates and continues inside the head. The oral cavity is well expressed, with a large, pointed, anteriorly-directed dorsal tooth and two small teeth. The esophagus gradually expands posteriorly but does not form a bulb. The ovaries are paired and reflexed. The testis is single, the spicules are broad with a pronounced velum, and the gubernaculum is of complex structure. The tail is conoid, 230 tapering at the end.

The round head and well-developed cephalic bristles place our genus close to Onyx. However, the movable tooth in Onyx is here made firmly fast, the lateral organs are a spiral with hardly one turn, while the cuticle is not as annulated. The two last features as well as the short esophagus and structure of the end of the tail make the genus similar to Spirina.

The sole species is:

### 45. **Chromaspirina pontica** n. sp.

(Table 7, Figure 45)

$$\text{♂}\ \frac{—\quad 3.9\quad 8.3\quad 20.5\quad 49.5\quad 87\quad 96.3}{0.9\quad 1.7\quad 1.8\qquad\quad 1.8\qquad\quad 1.8}\ 2650$$

$$\alpha=60;\ \beta=12;\ \gamma=30.$$

$$\text{♀}\ \frac{—\quad 3.7\quad 7.3\quad 44\quad 49\quad 58.5\quad 71.5\quad 80.5\quad 96.4}{0.9\quad 1.7\quad 1.7\qquad\qquad 1.9\qquad\qquad 1.4}\ 2800$$

$$\alpha=53;\ \beta=14;\ \gamma=30.$$

| Dimensions ♀ | Anterior bristles | Posterior bristles | Excretory pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 9 | 41 | 93 | 190 |
| Width | 24 | 31 | — | 47 | 47 |

The **body** of this species is filiform and has almost the same diameter from the nerve ring to the anus. From the nerve ring to the cephalic bristles it tapers approximately twofold. The **cuticle** is fairly thick ($2^1/_2\mu$); the inner layer has a marked annulation with intervals between the annules of $1^1/_2\mu$. There are fairly numerous bristles, sometimes quite long, over the entire body.

The **head** (Figure 45a) is evenly rounded. Along the margins of the mouth a small striated elevation is observed. Externally, it is beset with six short labial bristles ($2^1/_2\mu$), behind which is a circlet of six longer ($4\mu$) anterior cephalic bristles; posterior to these, opposite the anterior margin of the lateral organ, are four posterior cephalic bristles $5\mu$ long. 231 The lateral organ, as in Spirina, is spiral with one small turn. The spiral is open on the dorsal side. Here, however, its true structure is far more easily examined than in Spirina. Its diameter is $9\mu$, or $^2/_7$ of the corresponding diameter of the head.

The **vestibule** is quite broad, $4\mu$ long. The **oral capsule** is small but well marked; it is $5\mu$ long and $4\mu$ wide. Three teeth are located inside: one large dorsal (den. — Figure 45a) running from the bottom of the capsule almost to the anterior tip, and two small subventrals. The **esophagus** widens slightly anteriorly, then extends posteriorly almost without change in diameter (about $25\mu$ at a body width of $45-50\mu$); posteriorly, it expands $1^1/_2$ times without forming a bulb. The **nerve ring** lies half way along it and the cervical pore is located opposite its anterior part. The very narrow **intestine** consists of two rows of cells which project as denticles into its lumen.

The **ovary** is paired and reflexed. The uterus is thick-walled and has an unbroken cavity. The eggs measure $130\times45-50\mu$. The vagina has thick walls and traverses internally half the body width.

There is one very long **testis**. The vas deferens consists of very narrow cells and the ejaculatory duct is short. The sperm are $6\mu$ in diameter. The spicules (Figure 45c) are as broad as in Spirina, but are differentiated by the absence of a knob and the well-developed velum; their length is $55\mu$. The gubernaculum covers their ends and is also well developed, about $45\mu$ long. None of its stiffenings seems to extend beyond the limits of the spicule pouch.

The **tail** (Figure 45b) is conoid, with no terminal tube: at the end there is a small conical process like the end of a lemon, possibly somewhat longer than that drawn in the figure. The glands do not extend outside the tail. The proportions are: length of tail of female 2.7, of male 2.1; width at end 0.2; spicules 1.2; gubernaculum 1.0.

This species was found in large quantities in Zostera 5, 7.12 from the Chernaya River and from the north side.

232

## Genus SPIRINA nom. nov.

Spira Bastian 1865: Trans. Linn. Soc. 25, p. 159 (nom. praeocc.:
Brown 1838 mollusca).
— Villot 1875: Arch. Z. Exp. (1) 4, p. 463.
— de Man 1890: Mém. Soc. Zool. France 3, p. 174.
nec de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 106.

Type species: Sp. parasitifera (Bastian 1865)

A characterization of this small, very natural group has already been given by de Man, and I have hardly had to add anything to it.

These are small worms with a finely annulated cuticle. The labial bristles are located at the entrance to the vestibule, and the cephalic bristles are probably in two circlets, as in Spilipherini. The lateral organ is a small spiral with almost one turn; at first appears circular with an indented margin.* The oral cavity is very small with a very small dorsal tooth. The esophagus is short and narrow in relation to the body; posteriorly, it expands into a pronounced bulb that lacks an internal cavity. The ovaries are paired and reflexed; the uterus is wide with an unbroken cavity. There is one testis. The spicules have a wide knob and well-developed velum. The gubernaculum is small, adjacent to the ends of the spicules. The tail is conoid, pointed at the end, without a terminal tube; its extreme tip is characterized by a dorsal bend.

This genus in its head structure and genital structure is very similar to Chromadorina and other genera of this group. De Man considers it a relative of the brackish-water genus Microlaimus de Man.

The genus was established by Bastian as early as 1865 and fully 233 characterized by de Man (1890), who previously (1889) had isolated from it into a new genus, Araeolaimus, two species with straight ovaries that he described earlier from the Mediterranean. Thus, the following species, which originally were described as Spira, are now related to Spirina.

1) Sp. parasitifera Bastian 1865: Trans. Linn. Soc. 25, p. 159, Table 13, Figures 201—203; de Man 1890: Mém. Soc. Zool. France 3, p. 175, Table 3, Figure 3. Falmouth, sand and gravel at low tide (Bastian); common at Calvados, English Channel (de Man); Kola Gulf, Lake Mogil'noe (Savel'ev); White Sea strait on algae (Steiner); ? Sète—canal de Bourdigues (Rouville).
2) Sp. sabulicola n. sp., see next page.
3) Sp. zosterae n. sp., see p. 167.
4) Sp. laevis Bastian 1865: Trans. Linn. Soc. 25, p. 160, Table 13, Figures 204—206. Falmouth—in sand under roots of algae.
5) Sp. similis Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 390. — sand at low tide, Port Jackson. N. S. W.
6) ? Sp. schneideri Villot 1875: Arch. Zool. Exper. (1) 4, p. 464, Table 11, c—Figure 11a. Roscoff sur Terebelles. Possibly belongs to another genus.

1 (10). Tail several times longer than width at base.
2 (5). Lateral organ equal to almost half corresponding head width.
3 (4). Cephalic bristles lie at anterior margin of lateral organ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Sp. parasitifera** Bastian
4 (3). Cephalic bristles disposed at posterior margin of lateral organ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Sp. sabulicola** n. sp.
5 (2). Lateral organ $^1/_4$ to $^1/_3$ of head width.
6 (9). Length of spicules = 1.2—1.5 of diameter at anus. Bulb not more than $^3/_4$ of corresponding body width.
7 (8). Manubrium of spicules greatly expanded and more or less rounded. Spicules equal to 1.2 of diameter at anus. Bulb pronounced . . . . . . . . . . . . . . . . . . . . . . . . **Sp. zosterae** n. sp.
8 (7). Manubrium of spicules not greatly widened, angular. Spicules 1.5 of diameter at anus. Bulb not very pronounced . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Sp. laevis** Bastian
9 (6). Length of spicules twice greater than diameter at anus. Bulb occupies $^5/_6$ of corresponding body width. . . . . **Sp. similis** Cobb
10 (1). Width of tail equal to its length. . . . . . . . . . **Sp. schneideri** Villot

## 46. **Spirina sabulicola** n. sp.

(Table 7, Figure 46)

$$\text{♀}\ \frac{-\quad 4.1\quad 6.8\quad 40\quad 44\quad 53\quad 56.5\quad 65\quad 93.1}{0.9\quad 2.3\quad 2.4\qquad\qquad\qquad 2.9\qquad\qquad\qquad 1.5}\ 1800$$

$\alpha = 35$; $\beta = 15$; $\gamma = 15$.

234

| Dimensions ♀ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 6 | 62 | 103 |
| Width | 18 | 43 | 45 |

The **body** of the female tapers from the middle to the end of the esophagus only slightly, to the anus almost twofold, and from the end of the esophagus anteriorly almost three times, more markedly than in the following species. The **cuticle** is $1^1/_2\mu$ thick, its outer layer very finely annulated with annules about $6\mu$ wide. There are many bristles of diverse lengths. Particularly large bristles (up to $12\mu$) are encountered in the anterior part of the body.

The **head** is truncated. Six short cephalic bristles are observed at the entrance to the vestibule (p. ceph.—Figure 46a); four long bristles, $5\mu$ long, or more than $^1/_4$ of the width of the head, are present at the posterior margin of the lateral organ. The lateral organs are $7^1/_2\mu$ wide, somewhat less than half the head width and very greatly shifted anteriorly. Their form is a concealed spiral, as in the other forms of Spirina. They are larger than in other species.

The **vestibule** (see Figure 46a) is transformed insensibly into the narrowed oral cavity, inside which there is a very small dorsal tooth. The **esophagus** is short and slender ($11\mu$), but the bulb widens sharply to $26\mu$.

The **ovaries** are paired and reflexed. In my specimen the anterior ovary was very short and the posterior longer, as it contained many semiripe eggs. There were no ripe eggs.

The **tail** is longer than in the other species, four times longer than wide. It is conoid with a reflexed pointed tip (Figure 46b).

Two females were found, one in sand of Peschanaya Bay 7.12, the other in oyster banks 6.12.

Our species is easily differentiated from the very similar Sp. parasitifera Bastian by the position of the cephalic bristles, which here are disposed at the **posterior** margin of the lateral organs, while in Bastian's species they are located on the **anterior** margin.

235

## 47. **Spirina zosterae** n. sp.

(Table 7, Figure 47)

$$\text{♂}\ \frac{-\quad 3.3\quad 5.4\quad 32\quad 54\quad 73\quad 95}{0.7\quad 1.6\quad 1.7\qquad\qquad 2.6\qquad\qquad 1.8}\ 2630$$

$\alpha = 40—45$; $\beta = 19—22$; $\gamma = 20—22$.

---

* This is how de Man puts it, but Cobb (1898, see below) considers that its internal elevation is a small spiral

$$\text{♀}\ \frac{\begin{array}{ccccccccc} — & 3.4 & 5.6 & 39 & 43.5 & 53.5 & 62.5 & 66 & 95.6 \end{array}}{\begin{array}{ccccccccc} 0.7 & 1.7 & 2.0 & & & 2.9 & & & 1.6 \end{array}}\ 2720$$

$$\alpha=34;\ \beta=19;\ \gamma=23.$$

| Dimensions | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| ♂ | | | |
| Length | 7 | 80 | 135 |
| Width | 15 | 36 | 40 |
| ♀ | | | |
| Length | 5 | 80 | 130 |
| Width | 15 | 40 | 46 |

The **body** tapers about $1^1/_2$ times from the middle to the end of the esophagus, somewhat less to the anus; it tapers anteriorly from the end of the esophagus $2^1/_2-3$ times. The **cuticle** is thin (about 1.5μ), its outer layer is very finely annulated with intervals between the annules of approximately $^1/_2\mu$. I observed separate bristles only at the anterior end of the body.

The **head** is roundly truncated. It appears more flattened anteriorly when the **oral** cavity is drawn deep inside. Owing to the small size of the specimen I could not detect either labial or anterior cephalic bristles. The posterior cephalic bristles are quite long (6μ), or about $^1/_3$ of the head width. The lateral organ has the form characteristic for Spirina: it first appears circular with an excavation running from the dorsal side to the middle: closer inspection, however, shows that the organ is of the typical spiral form (see Figure 47b). Its outer contours are thickened, but inside the slit they are very narrow. Owing to this, only the outer contours are seen at first and the impression of a circular indented organ, as described by de Man in Sp. parasitifera Bastian, is obtained.
236 Its width is 6μ, about $^1/_4$ of the corresponding body width.

The **oral cavity**, as in the type species, is very narrow. It is adjacent to the small vestibule, and a very small tooth is present in its dorsal side (see Figure 47b). It hardly widens under the lips.

The **esophagus** (Figure 47a) is of almost even diameter (12–14μ) from the oral cavity to the posterior part, but it expands into a bulb (30μ diameter) at the posterior end. It is narrow and short in respect of the body width. The **nerve ring** is located somewhat posterior to the middle of the esophagus. The **lateral fields** are very strongly developed, so that the musculature is weakly developed, consisting of large cells. The **intestine** is narrow, thin, particularly at its origin, where it is contiguous with the esophagus.

The **ovaries** are paired, reflexed and very short. The uterus has thick glandular walls and an unbroken cavity. The eggs measure 90–110×45–50μ. The vagina has thin walls and traverses $^2/_5$ of the body width.

There is one very short **testis**, opening into a wide seminal vesicle filled with large sperm about 190μ long. The vas deferens proceeds from this chamber for 130μ, full of small sperm; the posterior 160μ of its length are covered with muscles and thus is the ejaculatory duct. The spicules are considerably wider than in Sp. parasitifera Bastian (Figures 47c, d). There is a broad knob with an irregular lumen at the base. The remainder of the spicule is divided into the narrower body proper and a wide and thick velum (see Figure 47d). The length of the spicules is 60μ. The **gubernaculum** is small, paired, adjacent dorsally to the ends of the spicules and partially embracing them; its length is 22μ. I did not observe any supplementary bristles or papillae.

The **tail** is conoid (Figure 47c), wider and shorter than in Sp. parasitifera Bastian, and its tip is slightly but very characteristically bent
237 upwards. The three tubular caudal glands are accommodated within it. Three indistinct cones corresponding to them are directly adjacent to the caudal pore. The absence of a terminal tube is also very characteristic. The proportions at the posterior end are: length of tail of male and female 3.0; length of spicules 1.3; gubernaculum 0.5.

This species is very common in Zostera from the Chernaya River and from other places 5, 7.12.

Sp. zosterae n. sp. is very similar to Sp. parasitifera Bastian, but it is somewhat wider in the middle, and the spicules and tail are markedly shorter.

## Genus MONOPOSTHIA de Man 1889

Mém. Soc. Zool. France 2, p. 9.

Steiner 1916: Zool. Jahrb. Syst. 39, p. 551.

Type species: M. costata (Bastian 1865) de Man 1889

These are small nematodes. **The cuticle consists of smooth annules along which run longitudinal rays** upon which the individual parts of the annules of hard armor articulate (Steiner). There are 12 papillae on the head—six labial and six anterior cephalic; there are 4 cephalic bristles. **The lateral organs are round** and small. The esophagus has a bulb. A small dorsal tooth is present in the oral cavity. The anterior ovary alone is present. **The female genital pore is shifted far posteriad**, almost to the anus. **The spicule is single, short, and wide.*** The tail is conoid.

2 species: 1) M. costata Bastian 1865 with 20 longitudinal rays, see below.
2) M. mielcki Steiner 1916 with 6 longitudinal rays: Zool. Jahrb. Syst. 39, p. 554, Table 23, 1—Figure 12a; White Sea strait on algae.

### 48. Monoposthia costata (Bastian 1865)
(Table 7, Figure 48)

Spiliphera c. Bastian 1865: Trans. Linn. Soc. 25, p. 166, Table 13, Figures 228, 229.

---

* In M. mielcki Steiner describes two; see footnote on the next page.

Spilophora c. Bütschli 1874: Abh. Senck. Ges. 9, p. 45, Table 5, d—Figure 22a.
M. c. de Man 1889: Mem. Soc. Zool. 2, p. 192, Tables 5, 6, Figure 6.
? M. c. Steiner 1916: Zool. Jahrb. Syst. 39, p. 552, Table 33, b—Figure 11a.

238

$$\text{immature } \sigma \; \frac{-\quad 7.9\quad 14\quad 17^{*}\quad 90}{1.8\quad 3.1\quad 3.3\quad 3.3\quad 3.3}\; 1130$$

$$\alpha=30;\ \beta=7;\ \gamma=10.$$

$$\text{immature } \female \; \frac{-\quad 9.0\quad 17\quad 34\quad 51}{1.7\quad 3.3\quad 3.9\qquad\qquad}\frac{79\quad 91}{4.9\quad 2.6}\; 1110$$

$$\alpha=20;\ \beta=6;\ \gamma=11.$$

| Dimensions ♀ | Cephalic bristles | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 6 | 12 | 105 | 180 |
| Width | 19 | 21 | 35 | 40 |

In the following I only give the measurement data and refer the reader to de Man for the description. The tapering of the **body** is even over the whole extent anteriorly and posteriorly. The tapering from the end of the esophagus anteriorly is almost twofold. The lateral ray of the **cuticle** does not extend to the lateral organ. As in Spirina and some other nematodes, the cuticle is covered with algae and bacteria.

On the **head** are two rows of papillae, a labial circlet and a cephalic circlet, and four cephalic bristles of length 11 μ, somewhat greater than the width of the head. The lateral organ is round, interrupts the third annule of the cuticle, 4 μ, or $^1/_5$ of the body width. The oral cavity is 8 μ wide; its bottom is 9 μ from the anterior end. A small acute-angled dorsal tooth lies in it. The anterior expansion of the esophagus reaches 17 μ (0.6 of the body width, 0.2 of the length of the esophagus); in the middle it is 13 μ (0.3 and 0.4), and its posterior bulb is 31 μ wide (0.75 and 0.4).

The spicule is compound, an accretion of two, divided in its anterior part, 32 μ long.[**] The proportions are: length of tail in female 3.5, in male 3; spicules 0.9 and a true spicule of normal structure is located in front of it. My material did not make it possible to reach any definite conclusion.

239 A few young males and females were found in Zostera 5.12 and in Corallina 7.12. In life the worms appear gray because of the thick cuticle. M. costata is widespread in the northern European seas. **Baltic Sea:** Kiel Firth, some sajenes in sand with Onch. vulgaris (Bütschli); North Sea: Arendal (Norwegian coast) in similar conditions (Bütschli); Holland: Walcheren (de Man). **English Channel:** rocks of Calvados (de Man); mud from the harbor, Falmouth (Bastian); **Arctic Ocean:** Kola Gulf, Lake Mogil'noe (Savel'ev); White Sea strait on algae (Steiner). The Arctic Ocean species will possibly prove to be new.

---

[*] Beginning of genital tracts.

[**] According to Steiner this spicule is in fact the gubernaculum.

## 4. Subfamily **Chromadorini**

These are small nematodes with an annular cuticle sometimes very complex in structure. Lips are absent; there are six labial and six cephalic papillae, and four cephalic bristles. **The lateral organ is indistinct, in the form of a transverse slit, or entirely lost.** The oral cavity is clearly demarcated, small, wholly embraced by the esophagus. The esophagus in the majority of species has a bulb, although sometimes this is absent (Graphonema, Euchromadora). The ovaries are paired. The cavity of the uterus is not divided. The spicules are short. The tail is conoid with a long tube, as in the majority of Spilipherini.

As distinct from the latter, to which they are very similar, Chromadorini are devoid of spiral lateral organs.

The following genera are incorporated here:

1) Euchromadora de Man 1886: see p. 172.
2) Rhabdotoderma Marion 1870: Ann. Sci. Nat. Zool. (5) 13, Art. 14, p. 31.[*]
3) Graphonema Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 406.[**]
4) Chromadora (Bastian 1865): sensu Filipjev, see p. 174.
5) Chromadorella n. g., see p. 184.
6) Chromadorissa Filipjev 1917: Revue Russe Zool.[†]
7) Spilipherella n. g., see p. 186.

240 Apart from these, several new genera permit a re-examination to be made of many species described as Spilophora and Chromadora but which do not fit the limited diagnosis that I gave for these genera (see p. 152). These are not taken into consideration in the following key.

1 (6). Bulb absent, as well as special punctations laterally.
2 (5). Cuticle consists of separate annules, is of different structure in different parts of the body.
3 (4). In places annules bear rows of specialized rods . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Euchromadora** de Man
4 (3). Annules plain . . . . . . . . . . . . . . . . . . . **Rhabdotoderma** Marion
5 (2). Cuticle consists of plain annules with punctations. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Graphonema** Cobb
6 (1). Bulb present; longitudinal rows of punctations laterally.
7 (10). Bulb plain (rarely double, when it has a slight, very gradual swelling).
8 (9). One dorsal tooth . . . . . . . . **Chromadora** Bastian (sensu Filipjev)

---

[*] One species: (1) Rh. morstatti Marion 1870: loc. cit., p. 31, Plate J, Figure 1 "assez fréquemment à la batterie d'Endoume, au Pharo et a la Joliette," around Marseilles.

[**] One species: (1) Gr. vulgaris Cobb 1898: ibid. Very common in sand and algae on the coasts of Australia.

[†] Two species: (1) Chr. beklemishevi Filipjev 1917: loc. cit. Drawing and description not yet published. Baku, on Sagina; (2) Monhystera bulbosa Grimm 1876: Proceedings of the Aral-Caspian expedition, No. 2, p. 102, Table 4, Figure 6. Mud from Bakinskii Bay.

9 (8). Three teeth ...................... **Chromadorella** n. g.
10 (7). Bulb double.
11 (12). Internally, bulb lacks distinct lenticular cavities. Terminal tube of caudal glands of usual structure .............................................. **Chromadorissa** Filipjev
12 (11). Internally, bulb with distinct lenticular cavities. Tail pointed at end. Caudal pore not located at tip ....... **Spilipherella** n. g.

## Genus EUCHROMADORA de Man 1886

Anatomische Untersuchungen über freilebende Nordsee-Nematoden, p. 67.

Type species: Eu. vulgaris (Bastian 1865) de Man 1886*

241 This small genus is characterized by the following features:

The cuticle is thick, distinctly annulated, most of the annules being covered by special longitudinal cuticular rods. Six elevations bearing six labial papillae are present on the truncated head. The cephalic bristles are disposed in two circlets: the anterior of six cephalic papillae, the posterior of four true bristles. The lateral organs are narrow, indistinct, transverse formations. A movable dorsal tooth lies in the oral cavity, which may be extended, whereupon the tooth protrudes anteriorly and may pierce the plants on which Euchromadora feeds. The esophagus expands posteriorly, but a bulb is not formed. The ovaries are paired and reflexed; the uterus is thick-walled, its cavity is common and the eggs are small. The spicules are curved, sometimes unequal: in the Black Sea species, however, they are almost equal, and de Man was incorrect in including this feature in his generic diagnosis. The gubernaculum is of three parts, the lateral parts reminiscent in form of spicules. Preanal papillae are absent. The tail is long and slightly tapering to the end.

Genus Euchromadora is well characterized chiefly by the structure of the cuticle, but the inequality of the spicules is not a characteristic feature as suggested by de Man. Steiner (1916, pp. 525, 532) even doubts that the genus is sufficiently specialized. However, the structure of the cuticle is so characteristic that the genus has remained completely isolated.

The genus was established by de Man for Bastian's species Chromadora vulgaris.

---

* De Man, of course, was not quite correct in taking this species, which probably was the type species of genus Chromadora Bastian 1865, as the type species of his new genus (see Stiles and Hassall 1905, p. 94). However: (1) In practice he was correct, since he isolated only Chr. vulgaris from the remaining species of the genus, and this therefore was the only species that underwent a change of name, while the many remaining species were retained in the old genus. (2) Only in 1905 did Bastian conclusively indicate Chr. vulgaris as the type of this genus (a letter published by Stiles) and this could not have been known to de Man, who had described his new genus in 1886. (3) When the type species is not indicated by the author of a genus, an author who proposes a new genus may select any species as the type of the former genus, and his choice is binding. (4) Since Chr. vulgaris Bastian must definitely be considered the type species of the new genus created for it, as the type species of Chromadora we should take Chr. nudicapitata Bastian, a species that Bastian described after Chr. vulgaris.

---

The following three species are known:

1) Eu. vulgaris (Bastian 1865). Chromadora v.: Trans. Linn. Soc. 25, p. 167, Table 13, Figures 233—235; Eu. v. de Man 1886: Anat. Untersuch. p. 69, Tables 12, 13; on Cladophora at Falmouth (Bastian), in a seawater canal on Walcheren Island (Holland, de Man).
2) Eu. striata (Eberth 1863), see below.
3) Eu. africana Linstow 1908: Denkschr. med.-naturw. Ges. Jena 13, p. 28. —Atlantic coast of South Africa. The description was not available to me. Also very similar to this genus is Spilophora loricata Steiner 1916: Zool. Jahrb. Syst. 39, p. 526, Table 19, n—Figure 3a, White Sea strait on algae.

242 1 (2). Spicules unequal; lateral parts of gubernaculum have knobs with sharp hook at end.............. **Eu. vulgaris** (Bastian)
2 (1). Spicules almost equal; lateral parts of gubernaculum without knobs, end slightly curved. ........... **Eu. striata** (Eberth)

### 49. Euchromadora striata (Eberth 1863)
(Table 7, Figure 47)

Odontobius striatus Eberth: Untersuchungen über Nematoden p. 30, Table 1, Figures 21—27.

$$\text{♂}\ \frac{\text{— 6.3 15.0 40 51 56 91}}{\text{1.5 2.1 2.3 3.4 2.2}}\ 2060$$

$$\alpha=29;\ \beta=6^{2}/_{3};\ \gamma=11.$$

$$\text{♀}\ \frac{\text{— 5.7 15 29 39 48 57 70 87.5}}{\text{1.3 2.5 2.8 4.6 2.4}}\ 2050$$

$$\alpha=22;\ \beta=6^{2}/_{3};\ \gamma=8.$$

| Dimensions<br>♂ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 8 | 130 | 310 |
| Width | 30 | 43 | 46 |
| ♀ | | | |
| Length | 8 | 115 | 310 |
| Width | 35 | 50 | 57 |

This species is very similar to E. vulgaris (Bastian), and I have constantly had recourse to the excellent description of this form provided by de Man.

The **body** expands greatly in the middle, especially in the female, tapering to the anus and to the beginning of the esophagus twofold in the latter, $1^{1}/_{2}$ times in the male. Anteriorly, from the end of the esophagus (to the end of the annules) the body tapers approximately twofold. The **cuticle** has a complex structure quite similar to that of Eu. vulgaris Bastian.* The cuticle is entirely annulated (with annules $5^{1}/_{2}\mu$ wide at midbody), a large lateral part of the annules is provided with special rods,

---

* De Man, loc. cit., pp. 69—71.

243 while on the ventral and dorsal sides there are areas free of them. In the anterior region of the body an intermediary field of rods arises on these areas. The four fields meet anteriorly. Originating laterally at the end of the esophagus there are special bodies which posteriorly take on the form of complex brackets, as they were drawn by Eberth. This is linked with the cleavage of the original annules, as de Man pointed out. In our species this is even more clearly marked than in Eu. vulgaris. Some long bristles are set in the subventral lines.

The **head** is constructed as in Eu. vulgaris. The cephalic bristles are $12-13\mu$ long, or $^{1}/_{3}-^{2}/_{5}$ of the head width. De Man* draws two slits on the sides of the head but does not describe them in detail. I think that these are the lateral organs. In one preparation I saw a posterior as well as an anterior margin of the slit. The tooth in the mouth is more blunt than in the northern species, and the chitin on it is thicker. I did not observe eyes: the pigment probably dissolved in the alcohol.

The **ovaries** are reflexed and paired, the uterus has thick walls and a common lumen. There is one testis. The **spicules** (Figure 49a) are thicker than in the northern species; they are larger ($70\mu$) and very slightly unequal, the right spicule being just smaller. (sp. d. — Figure 49a). The gubernaculum is $35\mu$ long, its lateral parts are $38\mu$, and its structure is exactly as in Eu. vulgaris except that the hook in the lateral parts (gub. l. — Figure 49a) is not so pronounced and their bases are devoid of knobs. Two pairs of bristles are located preanally, the anterior $20\mu$ from the anus. The dimensions given are very constant. The proportions are: length of tail of female 5.4, of male 3.4 — 4.2; width at end 0.3 — 0.4; spicules 1.4; gubernaculum 0.7.

This is a fairly common species: shallow and deep Cystoseira
244 6, 7.12, many; mussels 1.12, 6.12, some; Ulva 6.12, many; Zostera 5.12; saccocirrous sand, 1.12; sand, 18 sajenes at Georgievskii Monastery 7.12, some specimens. Mature individuals found in winter and summer.

The species was described by Eberth from Nice, but has not been found there since. De Man (1886) related it to genus Euchromadora on the basis of Eberth's description.

By the structure of the gubernaculum, the only slight inequality of the spicules, and their greater size, this species is easily differentiated from Eu. vulgaris Bastian.

## Genus CHROMADORA Bastian 1865

Chromadora ex p.: Bastian 1865: Trans. Linn. Soc. 25, p. 167.
Spilophora ex p. Bütschli 1874: Abh. Senck. Ges. 9, p. 44 (nec Chromadora Bütschli ibid. p. 47).
Spilophora de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 162; 1884: Nem. Niederl. Fauna p. 57; nec Chromadora de Man 1878: Tijd. Nederl. Dierk. Vereen, 3, p. 112; 1884: loc. cit., p. 57.
Chromadora sensu de Man et auct ex p. — Spilophora sensu de Man et auct ex p. 1886: Anat. Unters. p. 66; 1888: Mém. Soc. Zool. France 1, p. 44, 47; Cobb 1888: Jen. Zeit. f. Naturwiss. 23, p. 72; 1894: Proc. Linn. Soc. N. S. W. 8, p. 395; Jägerskiöld 1909: Süsswasserfauna Deutschlands Heft. 16, p. 33; Hofmänner 1913: Revue Suisse de Zoologie 21, p. 636.

Type species: Chr. nudicapitata Bastian 1865, de Man 1888**

These are small nematodes. The **cuticle** consists of **separate annules**, which are not smooth but are either indented at the edges or **bear internally rows of punctations. Laterally, the punctations are large** and form two, three, or four regular longitudinal rows, or there are specialized structures within a lateral elevation. The head is truncated; the nature of the annules is usually modified anteriorly. Six labial papillae are concealed in the vestibule. Six cephalic papillae are present also, disposed on the anterior surface of the head, sometimes in the form of short bristles. There are four posterior cephalic bristles. The 245 lateral organ is a narrow, rarely wider (Chr. poecilosoma de Man, poecilosomoides n.sp.) slit, usually completely inconspicuous. The funnel-shaped or straight plicate vestibule is directly adjacent to the oral aperture. The oral cavity is small and embraced by special muscles of the esophagus which sometimes form a swelling around it. **One slightly movable tooth** arising from the dorsal sector of the esophagus stands at the bottom of the cup-shaped oral cavity. Sometimes, small immovable denticles are present in the ventral sectors of the esophagus. Posteriorly, the esophagus widens to a bulb of varying structure. The female genital tract is paired and the ovaries are reflexed. The spicules are short and arched, and the structure of the gubernaculum is very varied. Various numbers of median ventral papillae are sometimes anterior to the anus. The tail is of a characteristic conoid form, with a special tube for the caudal glands at the end. Almost all the species related here are marine.

Bastian differentiated Chromadora from Spiliphera by the three teeth in the oral cavity. However, this feature proved to be untrue for many of his species of Chromadora. De Man suggested that species with preanal papillae belonged to the former and species without them to the latter. Chiefly on the basis of the structure of the head, I attempted above (see p. 150) to isolate several forms from these genera in a special subfamily. A group of many heterogeneous species from which further isolation is made still remains. Summarizing the diagnosis given above, I consider true Chromadora to be only species **with one tooth, a plain bulb, and specially differentiated punctations laterally or lateral elevations.** The group thus distinguished is nevertheless still very heterogeneous and requires further division.

The closest relatives of Chromadora among other genera are Euchromadora de Man, which is differentiated by the special structure of the cuticle (see pp. 172, 173): Chromadorella n.g., with three 246 movable teeth in the conical oral cavity; Spilophorella n.g., distinguished by the double lumen of the bulb and length of the caudal tube;

---

* Loc cit , Vol. XII, p 13, a – 14.

** Concerning the selection of the type species of this genus see p. 171.

Chromadorissa m., also with a double bulb, but the usual caudal tube; Graphonema Cobb, lacking a bulb.

Thus, the following species are related here:

α. Species with two longitudinal rows of punctations.

1) Chr. (Spilophora) setosa (Bütschli 1874): Abh. Senck. Ges. 9, p. 45, Table 6, b—Figure 25a. Coastal zone of Kiel Firth. Grimm mentions it for Libava, sand 5—20 f.
2) Chr. (Spilophora) geophila (de Man 1876): Tijd. Nederl. Dierk. Vereen. 2, p. 162, Table 10, Figure 40; 1880: ibid. 5, p. 19; 1884: Nematoden. d. Niederl. Fauna p. 58, Table 7, Figure 29; Ditlevsen 1911: Vidensk. Meddelser Naturhist. Fören. Köbenhavn 63, p. 222, Table 4, Figures 32, 34: Walcheren Island (Holland). Earth soaked with brackish water (de Man); in earth around Öresund in Denmark (Ditlevsen). The Danish specimens may belong to another species.
3) Chr. sabulicola n. sp., see p. 180.
4) Chr. cephalata Steiner 1916: Zool. Jahrb. Syst. 39, p. 543, Table 22, e—Figure 8a. Algae from the White Sea strait.

1 (2). Cephalic bristles very long, far greater than head width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. setosa** (Bütschli)
2 (1). Cephalic bristles shorter than head width.
3 (4). Cuticle finely annulated, preanal papillae absent in male . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. geophila** (de Man)
4 (3). Cuticle coarsely annulated, preanal papillae present.
5 (6). Body tapers anteriorly $1^{1}/_{2}$ times from end of esophagus. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. sabulicola** n. sp.
6 (5). More than twofold . . . . . . . . . . . . . . . . . . **Chr. cephalata** Steiner

β. Species with three longitudinal rows of punctations.

5) Chr. natans Bastian 1865: Trans. Linn. Soc. 25, p. 168, Table 13, Figures 236—238; Daday 1901: Termész. Füzetek 24, p. 451, Table 23, Figures 6—10. English Channel: Falmouth (Bastian); Adriatic Sea: Buccari among patches of algae on the coast (Daday); Mediterranean Sea: Sète, canal de Bourdigues (Rouville); possibly Bastian's species and not identical with Daday's.

γ. Species with four longitudinal rows of punctations.

6) Chr. macrolaima de Man 1889: Mém. Soc. Zool. France 2, p. 197, Table 6, Figure 7. Seawater canal on Walcheren Island—Holland.
7) Chr. nudicapitata Bastian 1865: Trans. Linn. Soc. 25, p. 168, Table 13, Figures 230—232; de Man 1888: Mém. Soc. Zool. France 1, p. 47, Tables 3, 4, Figure 20. Among Cladophora at Falmouth (Bastian), very usual on the coast of Walcheren Island (de Man).
8) Chr. quadrilinea n. sp., see p. 181.
9) Chr. (Spilophora) parva (de Man 1893): Mém. Soc. Zool.
France 6, p. 89, Table 5. Fairly common at Falmouth in algae
on rocks. Caudal tube of this species is constructed as in
247 Spilophorella; possibly this species also belongs to that genus,
whose diagnosis would then be altered.

1 (2). Oral cavity and tooth very large . . . . . **Chr. macrolaima** de Man
2 (1). Both these parts of normal size (see Figure 49a).
3 (6). Caudal tube blunt.
4 (5). Bulb takes up $^{1}/_{4}$ of length of esophagus, spicules somewhat shorter than $^{1}/_{4}$ of tail. . . . . . . . . . . . **Chr. nudicapitata** Bastian
5 (4). Bulb about $^{1}/_{5}$ of length of esophagus, spicules about $^{1}/_{3}$ of tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. quadrilinea** n. sp.
6 (3). Caudal tube pointed. . . . . . . . . . . . . . . . . . . . **Chr. parva** de Man

δ. Indistinct punctations over the entire body; sometimes specialized structures inside the lateral elevations; the bulb is weakly developed.

10) Chr. craspedota Steiner 1916: Z. Jahrb. Syst. 39, p. 534, Table 21, n—Figure 6a; White Sea strait, on algae.
11) Chr. poecilosoma de Man 1893: Mém. Soc. Zool. France 6, p. 96, Table 6, Figure 7; Falmouth, Walcheren—sand at low tide, common.
12) Chr. poecilosomoides n. sp., see p. 183.

1 (2). Lateral elevation supported by special cuticular forks . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. craspedota** Steiner
2 (1). Such forks absent.
3 (4). Lateral punctations of cuticle originate right at head, posteriorly are indistinct. . . . . . . . . . . . . . . . . . . . **Chr. poecilosoma** de Man
4 (3). Lateral punctations begin opposite end of esophagus, distinct to end of lateral elevation on tail. . . **Chr. poecilosomoides** n. sp.

Apart from these 12 species many others have been described as Spilophora or Chromadora. These do not conform with the diagnosis given above and are not included in any of the genera of Chromadorini as I know them. Consequently, a series of new genera should be created out of this mass of forms.

α. Species with one large tooth in a **conical** oral cavity; chiefly freshwater.

1) Spilophora adriatica Daday 1901: Termész. Füzetek 24, p. 447, Table 22, Figures 10—14; Table 23, Figure 1. Adriatic Sea—Fiume among patches of algae on the pier.
2) Chromadora bioculata (Max Schultze 1873) Rhabditis b.: in Carus Icones Zootomicae Table 8, Figure 2. Chr. b.: Bütschli 1873: Nova Acta 26, No. 5, p. 70, Table 5, Figure 32; Table 6, Figure 37; de Man 1880: Tijd. Nederl. Dierk. Ver. 5, p. 20; 1884: Nemat. Niederl. Fauna p. 60, Table 8, Figure 32; 1907: Ann. biol. lacustre 2, p. 14, Table 1, Figure 2, Jägerskiöld 1909: Süsswasserfauna Deutschlands, Heft 16, p. 35; Hofmänner 1913:

Revue Suisse Zool. 21, p. 636; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 485, Tables 12, 13, k—Figure 9a. Stefanski 1914: Ném. du Léman p. 31; Germany: Main (Bütschli); Mark (Jägerskiöld); Russia: Obersee, near Revel [now Tallin], usually in mud (G. Schneider); Holland: in mud (de Man); Hungary: on sponges and Sagina—Lake Balaton, lake in Tatra (Daday); Austria: common in mud, on overgrown stones, Lake Lunzersee, Salzburg, Chernovtsy (Micoletzky); Switzerland: Lake Geneva, Neuchâtel, common in aquatic moss, on stones, in wood up to 70 m deep (Hofmänner, Hofmänner and Menzel, Stefanski); France: very common on stones in the Seine near Paris.

3) Chr. viridis Linstow 1877: Arch. Natur. 42, p. 14, Table 20, Figures 34, 35; Jägerskiöld 1909: Süsswasserfauna Deutschlands, Heft 15, p. 34—Ratzeburg Lake near Hamburg.

4) Chr. oerleyi de Man 1881: Tijd. Nederl. Dierk. Ver. 5, p. 139; 1884: Nemat. Niederl. Fauna p. 59, Table 8, Figure 31. Russia: Lake Bologoe, among Chara (Plotnikov); Denmark: among plants at water's edge (Ditlevsen); Holland: September; earth with brackish water, Walcheren (de Man).

5) Chr. lehberti G. Schneider 1906: Zool. Anz. 29, p. 680, Figures 1, 2. Obersee, near Revel.

6) Spilophora ophrydii Stefanski 1914: Ném. du Léman p. 30, Table 1, b—Figure 9a. In colonies of Ophrydium in Lake Geneva.

The last two species may possibly belong to genus Achromadora Cobb.

β. Species possessing one large tooth in a **cup-shaped** oral cavity; chiefly freshwater.

7) Chr. leuckarti de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 165, Table 10, Figure 41; 1884: Nemat. Niederl. Fauna p. 58, Table 8, Figure 30; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 491; Brakenhoff 1914: Abh. naturhist. Verein Bremen. 22, p. 274; Steiner 1916: Zool. Anz. 46, p. 338. Russia: Bologoe, among Chara 5 VIII 1899 (Plotnikov). Germany: quite common around Bremen in various bodies of water (Brakenhoff); Holland: fresh water (on algae) and brackish water and earth of meadows and flooding (de Man); Denmark (Ditlevsen); Austria; Mur River in Styria (Micoletzky); Tunis: coastal mud with Spirogyra (Steiner).

8) Chr. ratzeburgensis Linstow 1876: Arch. Naturg. 42, p. 13; Chr. bulbosa Daday 1894: Math. termtud. Ertesitö 12, p. 133; 1897: Res. wiss. Erforsch. Balatonsees p. 13, Table 1, Figures 19—23; Zool. Jahrb. Syst. 10, p. 106, Table 12, Figures 9—13; Chr. r.: de Man 1907: Ann. biol. lacustre 2, p. 12, Table 1, Figure 1; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 488, Tables 11, 12, Figure 8; Brakenhoff 1914: Abh. naturh. Ver. Bremen 22, p. 275; Russia: Bologoe, on water plants (Plotnikov); Germany: Ratzeburg Lake (Linstow), Gr. Plöner See (Zacharias); Weser, adults in September (Brakenhoff); Austria: common coastal form (on Chara and on stones) in lakes of the eastern Alps (Micoletzky); France: Seine near Paris (de Man).

9) Chr. tyroliensis Stefanski 1916: Zool. Anz. 46, p. 378, c—Figure 1a. Inn River: muddy sand, stones, marshes.

10) Spilophora (Chr. sensu de Man) impatiens Cobb 1888: Jen. Zt. Naturw. 23, p. 72, Table 6, Figures 26, 28—often in spring in moss near springs, Jena, Kinitz.

11) Spil. tentabunda de Man 1890: Mém. Soc. Zool. France 3, p. 177, Tables 3, 4, Figure 4. Marine form: "St. Aubin, Normandie, assez rare."

12) Chromadora tenuis G. Schneider 1906: Z. Anz. 29, p. 626; Acta Soc. F. Fl. Fenn. No. 7, p. 28, Figure 12. Mud of Tvärminne Bay in Finland.

13) Chr. heterophya Steiner 1916: Zool. Jahrb. Syst. 39, p. 542, Table 21, d—Figure 7a. White Sea strait, in algae.

14) Chr. hyalocephala Steiner 1916: loc. cit., p. 541, Table 20, c—Figure 4a, the same place. Probably belonging here:

15) Chr. balatonica Daday 1904; 1897: Zool. Jahrb. Syst. 10, p. 104, Table 12, Figures 1—3. Balaton, sandy coast.

γ. Species with three teeth in the mouth; possibly some of them should be related to Chromadorella n. g.; only marine.

16) Chr. minor Cobb 1894: Proc. Linn. Soc. N. S. W. 8, p. 394, Figure 6. Port Jackson N. S. W. Among algae.

17) Chr. germanica Bütschli 1874: Abh. Senck. Ges. 9, p. 48, Table 6, Figure 25. Mud from Kiel Firth.

18) Chr. neapolitana de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 113, Table 9, Figure 17. Naples. The almost complete absence of a bulb is interesting. Should possibly be incorporated in genus Graphonema Cobb.

19) Chr. (Spilophora sensu de Man) sabelloides Bastian 1865: Trans. Linn. Soc. 25, p. 169, Table 13, Figures 245, 246. Marine mud, Falmouth. The worms live in tubes formed by adhesion of grit and diatoms.

20) Chr. (Sp. sensu de Man) coeca Bastian 1865: loc. cit., p. 169, Table 13, Figures 239—241; Sp. c. G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 26. Mud from the harbor—Falmouth (Bastian); mud from Tvärminne Bay, Finland (G. Schneider). De Man (Mém. Soc. Zool. France 2, p. 192) suggests that the two foregoing species are related to genus Desmodora. Here apparently belong the insufficiently known species:

21) Chr. laeta de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 115, Table 9, Figure 19; Daday 1901: Term. Füzetek. 24, p. 449, Table 23, Figures 2—5. Naples, Buccari (North Adriatic) in patches of algae.

22) Chr. flamoniensis Daday 1901: loc. cit., p. 453, Table 23, Figures 15—18. Buccari, together with the preceding.

23) Chr. quarnerensis Daday 1901: loc. cit., p. 454, Table 23, Figures 11—14. Same place.

δ. Inadequately described species doubtlessly related to this group:

24) Chr. chlorophthalma de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 114, Table 9, Figure 18. Naples (comparable to Chr. natans (Bastian).

25) Chr. erythrophthalma G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 19, Figure 13. Mud from Tvärminne Bay in Finland, comparable to Chr. chlorophthalma de Man and Chr. oerleyi de Man.

250 26) Chr. bathybia Daday 1894; 1897: Zool. Jahrb. Syst. 10, p. 105, Table 12, Figures 4–9. Balaton, and other lakes of Hungary.

ε. Species not closely related to Chromadora.

27) Chr. papuana Daday 1899: Term. Füz, 24, p. 6, Table 1, Figures 7, 8. Sago swamp in New Guinea.

28) Chr. dubiosa Daday 1904: Zool. Jahrb. Syst. 19, p. 481, Table 27, Figures 4, 5. Turkestan–Przhevalsk, in fresh water.

29) Chr. salinarum Linstow 1901: Arch. Mikr. Anat. 58, p. 195, Table 9, Figures 20–23. Water from a salty source, Nauheim.

30) Chr. papillata Bastian 1865: Trans. Linn. Soc. 25, p. 170, Table 13, Figures 247, 248. Marine form: mud from the harbor–Falmouth.

### 50. **Chromadora sabulicola** n. sp.
(Table 8, Figure 50)

$$♂\ \frac{\begin{array}{ccccc} — & 6.9 & 12.2 & — & 90.4 \end{array}}{\begin{array}{ccccc} 1.9 & 2.5 & 3.1 & 3.5 & 3.0 \end{array}}\ 1690$$

$$\alpha=29;\ \beta=8;\ \gamma=10^1/_2.$$

$$\text{young}\ ♀\ \frac{\begin{array}{ccccc} — & 5.7 & 9.7 & 46 & 89 \end{array}}{\begin{array}{ccccc} 1.6 & 2.1 & 2.6 & 3.0 & 2.3 \end{array}}\ 1920$$

$$\alpha=33;\ \beta=10^1/_2;\ \gamma=9.$$

| Dimensions ♂ | Anterior end | End of annules | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | – | 14 | 110 | 195 |
| Width | 31 | – | 47 | 51 |

The **body** is quite wide, slightly swollen in the middle, tapering somewhat to the anus and to the end of the esophagus, whence anteriorly it tapers only $1^1/_2$ times. The **cuticle** posteriorly (Figure 50c) consists of separate annules at whose sides are two rows of large punctations which soon diminish and are absent over a considerable part of the median surfaces. The cuticle here is $2-2^1/_2\mu$ thick, and the intervals between the annules are from $2.1\mu$ at the tail to $3.2\mu$ at midbody. More anteriorly, near the posterior end of the esophagus, the cuticle changes its structure quite markedly. The annules here are in the form of indented plates with anterior and posterior projections (Figure 50b). This indentation is interrupted laterally (l. lat. –Figure 50b), where a smooth portion lies 251 between the two rows of large punctations and along the submedian lines l. sm. –Figure 50b). The notches on the annules become less sharp anteriorly (Figure 50a), and at the extreme anterior end separate annules disappear entirely and only transverse rows of punctations remain. The boundaries of these rows are marked by a line that curves anteriad to the dorsal and ventral sides from the lateral rows of punctations (Figure 50a). The smooth submedian fields are gradually wedged out anteriorly, as in Euchromadora. The thickness of the cuticle anteriorly reaches $3^1/_2\mu$ and the annules are about $3\mu$ apart.

The **head** is quite rounded, elongate, and appears truncated. There are six short and four long cephalic bristles. I observed faint indications of lateral organs between the rows of punctations on the head (o. l. –Figure 50a). The plicate vestibulum (with apparently 12 folds) is located in front of the oral cavity, which is fairly spacious and contains a dorsal tooth at its bottom (d. d. –Figure 50a). This may be drawn downwards by special muscles. In addition there are two small subventral teeth which are evidently immovable. Above the dorsal tooth the largest pouch of the oral cavity extends posteriorly. The depth of the oral cavity when folded is $7\mu$, its width is $12\mu$, and the tooth is about $5\mu$. Behind the oral musculature ($25\mu$ wide) the **esophagus** narrows to $17\mu$, and posteriorly expands into a small bulb ($30\mu$ wide, $33\mu$ long – 15% of the total length of the esophagus) with an internal lenticular cavity. Numerous phagocytic cells are observed in the body cavity.

The ovaries are long and the uterus was still undeveloped.

The **spicules** (Figure 50d) are fairly stout, curved, have an indistinct manubrium and recurved end and are $60\mu$ long. Two gubernacula in the form of irregular tubes, also with recurved ends, are $27\mu$ long. There are nine protrusible preanal papillae.

The **tail** (Figure 50d) is conoid, pointed to the end, with a tube at
252 the end. The proportions are: length of tail 3.0, width at beginning of tube 0.08; spicules 1.0; gubernaculum 0.5; distance from anus to anterior papilla 2.2.

I encountered one male specimen in oxeas sand in Kruglaya Bay 6.12, a female in coquina (27 sajenes) at Georgievskii Monastery 7.12.

Chr. cephalata Steiner is very similar to this species, but it is half its size and tapers more markedly anteriorly.

### 51. **Chromadora quadrilinea** n. sp.
(Table 8, Figure 51)

$$♂\ \frac{— \quad 10.0 \quad 17 \quad 31 \quad 57 \quad 87}{1.6 \quad 3.6 \quad 3.9 \quad 4.7 \quad 3.6}\ 760$$

$$\alpha=21;\ \beta=6;\ \gamma=8.$$

$$♀\ \frac{— \quad 9.1 \quad 15.8 \quad 27 \quad 35.5 \quad 49 \quad 60 \quad 71 \quad 85.5}{1.3 \quad 3.0 \quad 3.6 \quad 5.5 \quad 3.0}\ 890$$

$$\alpha=19;\ \beta=7;\ \gamma=7.$$

| Dimensions<br>♂ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | – | 73 | 125 |
| Width | 12 | 26 | 30 |
| ♀ | | | |
| Length | – | 65 | 135 |
| Width | 12 | 26 | 31 |

The **body** is greatly swollen in the middle, tapers $1^1/_2$ times to the end of the esophagus, and more than this to the anus in the female. Anteriorly, from the end of the esophagus it tapers more than twofold. The **cuticle** is clearly annulated, each annule bearing a row of punctations (see Figure 51a). Four lateral punctations are more pronounced than the others and create four longitudinal rows, of which the two median are the larger and the
253 lateral are smaller. The thickness of the cuticle is about $1.7-2\mu$. The annules anteriorly are separated by intervals of $1.7\mu$, and at midbody of only $1.3\mu$. The few bristles are set along the subventral lines.

The **head** is rounded and truncated. I did not see labial papillae, which probably are concealed in the vestibule. There are six short cephalic papillae. The four cephalic bristles are very long for Chromadorini ($8\mu$, or $^3/_4$ of the head width). The lateral organs are inconspicuous. The plicate vestibule is $3\mu$ long. The **oral cavity** is small, $3\mu$ deep and $6\mu$ wide. Dorsally, there is a fairly large tooth $1.7\mu$ long. The **esophagus** embraces the oral cavity, forming an expansion which is followed by a narrowed part (see Figures 51a, b) of constant diameter of about $10\mu$. Posteriorly, the esophagus expands to a bulb $25\mu$ wide and long. The latter is clearly marked, but not very large, lacking an internal cavity.

The **ovaries** are paired, quite long, and conical. The uterus is spacious with an unbroken lumen in which were eight large longitudinally-flattened eggs measuring $40\times25\mu$. The vagina transverses up to $^1/_5$ of the body width internally.

There is one **testis,** followed by a wide cavity with large cells along the wall, i.e., exactly as in Metachromadora macroutera m., to which the vas deferens is connected posteriorly. The **spicules** (Figure 51d) are slender, evenly curved, $28\mu$ long. The gubernaculum ($25\mu$ long) is a fairly complex structure. In general it consists of two spoon-shaped bodies that cover the ends of the spicules. At the front each body has a process directed anteriorly (a—Figure 51d); at the end, along each side of the anus, there is a flat expansion (b—Figure 51d). In front of the anus in the male there are six large papillae in the form of flat chitinized caps $4^1/_2\mu$ in diameter.

The **tail** (Figure 51c) is very similar to that of Chr. poecilosomoides m. in that the tapering in the anterior half is sharper than in the posterior, and the end is pointed and provided with a tube $5\mu$ long. In the female the body at the anus is narrower and
254 therefore the tail is also relatively longer. The proportions are: length of tail in male 4.0, in female 4.8; width at end of male and female 0.2; spicules 1.1; gubernaculum 1.0; distance from anus to anterior papilla 4.2.

Male and adult female of this species were found in mussels from under the station 6.12.

Chromadora natans (? Bastian) Daday is apparently a close relative of this species, but Daday draws three rather than four longitudinal rows of punctations (which may also be wrong). Furthermore, the spicules in this species are otherwise. Chr. nudicapitata Bastian is in de Man's opinion also very similar to our species, but the bulb is somewhat smaller, the spicules are larger, and the gubernaculum is different. Apart from this, there is in the male a large papilla half way along the tail in line with the preanal papillae.

### 52. **Chromadora poecilosomoides** n. sp.

(Table 8, Figure 52)

$$\text{♂}\ \frac{\begin{array}{ccccc} - & 4.5 & 11.3 & 24^{*} & 88.7 \end{array}}{\begin{array}{ccccc} 1.0 & 1.9 & 2.0 & 3.0 & 2.4 \end{array}}\ 1100$$

$$\alpha=33;\ \beta=19;\ \gamma=8.$$

$$\text{♀}\ \begin{array}{ccccccccc} - & 6.6 & 10.9 & 27 & 34.5 & 43 & 55 & 63 & 83 \\ \hline 0.9 & 2.1 & 2.3 & & & 3.6 & & & 2.0 \end{array}\ 1200$$

$$\alpha=28;\ \beta=9^1/_2;\ \gamma=6.$$

| Dimensions<br>♂ | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | 4 | 50 | 124 |
| Width | 11 | 21 | 22 |

The **body** is slender, markedly tapering to the anus, in the female almost twofold, in the male less. From the end of the esophagus to the anterior end the tapering is twofold in the male, somewhat more in the female. The **cuticle** is composed of annules. Anteriorly, the annules are unbroken and consist of rounded bodies (Figure 52a); near the end of the esophagus, at midbody, a depression begins to form in the bodies (Figure 52b) and a lateral elevation originates along whose sides the
255 cuticular bodies remain approximately unaltered. More posteriorly, however, the cuticle changes its structure (Figure 50c): the lateral elevation becomes more strongly developed, and two rows of cuticular punctations are disposed at its sides. Between these punctations on the elevation there are only narrow cross-pieces. The cuticular annules adjacent to the punctations are composed of fairly broad plates with a greatly indented posterior margin. Between the annules there are additional rows of punctations which are not interrupted by smooth spaces on the ventral or dorsal sides. The lateral elevation extends only half way along the tail, where it terminates. The annules behind the elevation are again unbroken and devoid of specialized points laterally. Anteriorly, the annules are close together with intervals of $1.5\mu$ between them, while at midbody the intervals are of $2.8\mu$; on the tail they are $2.5\mu$ apart. The thickness of the cuticle changes slightly: anteriorly, it is thicker ($1.6\mu$), at midbody it is $1.2\mu$, and ventrally on the tail it is $2.2\mu$ thick. A few bristles are concentrated subventrally.

---

* Anterior end of testis.

The **head** anteriorly is rounded, as distinct from the majority of other forms of Chromadora. I could not detect labial or cephalic papillae. The four cephalic bristles are long (up to 6 μ or more than half the head width). The lateral organ here is a transverse slit among the cephalic bristles, as in Chr. poecilosoma de Man. The short, plicate vestibule is followed by a small oral cavity, at whose bottom a small dorsal tooth is located. The cavity is 6 μ wide and 3 μ deep. The esophagus expands slightly (see Figure 52a), after which there is a narrow portion about 8 μ wide, while posteriorly there is a small bulb (15 μ wide) without a lenticular cavity. The long and narrow cervical gland is located 80 μ behind the end of the esophagus; it is 75 μ long and 6 μ wide.

The **ovaries** are fairly long, and the uterus has a common lumen. The eggs are large, 50×25 μ.

The **testis** is apparently single. The bursal musculature consists of a
256 small number of muscle fibers (see Figure 52e). The **spicules** (30 μ long) have a broad, sharply curved body with an indistinct manubrium and apparently a velum (Figure 52f). The gubernaculum is double, 22 μ long, each of its parts externally covering the end of one of the spicules (see Figure 52f). Preanally, there are 7–9 weakly expressed median papillae.

The **tail** (Figure 52e) is long, tapering more sharply in the basal than in the terminal half. The extreme tip is devoid of annulation and bears a 6 μ-long tube of the caudal glands. The latter are accommodated within the tail, occupying only an inconsiderable part of its cavity. The proportions are: length of tail in female 5.5, in male 5; width at end of male and female 0.15; length of spicules 1.2; gubernaculum 0.85; distance from anus to anterior papilla 4.5.

This species is common in the Black Sea: oxeas sand of Kruglaya Bay 1.12, 6.12, 7.12, seaweed on the sand, many 6.12; Georgievskii Monastery 7.13. Coastal shingle at Georgievskii Monastery 7.12, male; Nassarius from mud from Artilleriiskaya Bay 1.12, few.

This species is very similar to Chr. poecilosoma de Man in the structure of the head, the bulb, the tail, and the male genital apparatus, but is easily differentiated from it by the structure of the cuticle: in de Man's species the lateral punctations run to the extreme anterior end, while in mine they cease at the posterior end of the esophagus.

## Genus CHROMADORELLA n.g.

Type species: Chr. filiformis Bastian 1865 (de Man 1890)

This genus is very similar to Chromadora as I understand it, but differentiated from it by the presence of **three small movable teeth** in the conical oral cavity. The esophagus gradually expands posteriorly, forming a longitudinal bulb not sharply differentiated from the slender portion of the esophagus. Usually its cavity is double. In three species the cuticle has two longitudinal rows of punctations laterally. The five species are:

257 1) Chr. filiformis (Bastian 1865); Chromadora f.: Trans. Linn. Soc. 25, p. 169, Table 13, Figures 242–244; de Man 1890: Mém. Soc. Zool. France 3, p. 178, Table 4, Figure 5. In algae at Falmouth (Bastian), St. Vaast—Normandy, very common (de Man). Sumatra, Sabang, mud with diatoms (Steiner).
2) ? Chr. sumatrana (Steiner 1916): Zool. Jahrb. Syst. 38, p. 231, Table 23, Figures 12–17. Sumatra (together with the forgoing).
3) ? Chr. sabangensis (Steiner 1916): ibid., p. 233, Tables 23, 24, Figures 18–22; the same place.
4) Chr. mytilicola n. sp., see below.
5) Chr. macrolaimoides (Steiner 1916): loc. cit., p. 234, Table 23, Figures 23–27. Sumatra.

In addition, several species provided with three teeth and listed on p. 179 may be related here. I do not include them here directly because their cuticle is devoid of lateral punctations.

1 (6). Body hardly tapers anteriorly from end of esophagus. Bulb double, hardly expressed.
2 (3). Two longitudinal rows of punctations laterally. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. filiformis** Bastian
3 (2). No specialized punctations laterally.
4 (5). Cuticular bodies anteriorly oval, oral cavity and tooth quite considerable. Bulb occupies almost half length of esophagus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. sumatrana** Steiner
5 (4). Cuticular bodies anteriorly in form of narrow rods. Oral cavity and tooth very small. Bulb about 1/4 of length of esophagus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. sabangensis** Steiner
6 (1). Tapers more than twofold. Bulb considerable.
7 (8). Two longitudinal rows of punctations . . . . **Chr. mytilicola** n. sp.
8 (7). Four longitudinal rows of punctations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Chr. macrolaimoides** Steiner

### 53. **Chromadorella mytilicola** n. sp.

(Table 8, Figure 53)

$$\text{♀}^{*}\ \frac{—\quad 6.8\quad 14.0\quad 47\quad 85}{1.9\quad 3.2\quad 4.3\quad 7.0\quad 3.2}\ 1000$$

$$\alpha = 14;\ \beta = 7;\ \gamma = 6^2/_3.$$

| Dimensions | Anterior end | Beginning of annules | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | — | 10 | 70 | 134 |
| Width ** | 17 | 18 | 35 | 45 |

---

* Length of genital tracts could not be determined.

** This width is greater than the actual as the specimen was compressed.

258 The **body** is very greatly swollen in the middle, tapers twofold to the anus, somewhat less to the end of the esophagus. From this point anteriorly it tapers more than twofold fairly evenly. The **cuticle** is 1.5$\mu$ thick anteriorly, about $1^{1}/_{4}\,\mu$ posteriorly. It consists of annules which laterally bear two rows of punctations. Anteriorly (see Figure 53a), these annules are unbroken and have an indented margin, while posteriorly (Figure 53b), rows of punctations are observed in them. Anteriorly, the cross-pieces between these rows are smooth, but posteriorly they gradually become indented and unequal (Figure 53c). On the dorsal and ventral sides the rows are not interrupted, at least not at midbody. Anteriorly, on the head, the annules are not whole, but are broken up into rows of small punctations (Figure 53a).

The **head** is truncated; I did not observe labial papillae. The cephalic bristles lie in two circlets, the anterior of six short bristles 1.3$\mu$ long, the posterior of four long bristles 6$\mu$ long, or $^{1}/_{3}$ of the head width. I did not find the lateral organ. I could not detect a vestibule and the oral cavity is small with very thin walls; three small movable teeth are located in it, as in Chr. filiformis Bastian according to de Man. The depth of the cavity is about 3$\mu$, its width is 5$\mu$, and the tooth is about 2$\mu$ long. Anteriorly, the **esophagus** is 15$\mu$ thick, posteriorly it expands into a conical bulb about 30$\mu$ wide.

The eggs are large, 53×40$\mu$. The vulva is round-oval, with bristles projecting into it.

The **tail** (Figure 53c) is conoid and pointed, and its end is slightly set off by a constriction and highly reminiscent of the aforementioned Chr. filiformis Bastian. The punctations terminate 19$\mu$ from the end. The tube is 5$\mu$ long. The proportions are: length of tail 5.5.

One female in mussels 6.12.

This species is very similar to Chromadora filiformis Bastian in the structure of the head, in the anterior circlet of cephalic bristles being true bristles and not papillae, the oral cavity with three teeth, and the tail; it is easily differentiated from it, however, by the stout body
259 and the shorter portion on the head devoid of annules. Chr. macrolaimoides Steiner is even more similar with four rows of lateral punctations instead of two.

## Genus SPILOPHORELLA n.g.

Type species: Sp. paradoxa de Man 1888

These are small nematodes, tapering greatly anteriorly. The cuticle consists of unbroken annules on which there are punctations. In particular, there are **two distinct rows of punctations laterally.** G. Schneider makes the interesting observation that in Sp. paradoxa de Man the cuticle between the two rows of punctations stains a dark color with methylene blue. The cephalic bristles are in two rows — an anterior of six papillae, and a posterior of four bristles. The lateral organ is inconsiderable. **The vestibule is deep and funnel-shaped.** The oral cavity is small with one tooth **at its bottom. The bulb of the esophagus has a double lenticular lumen** (in Sp. ceylonensis Cobb it is triple). The ovaries are paired and reflexed, the eggs are large. The gubernaculum is a complex structure (in the males known). The tail is long, **pointed at the end**; the caudal glands open **before its end**:

Three species are related here:

1) Sp. euxina n.sp., see below.
2) Sp. paradoxa de Man 1888: Mém. Soc. Zool. France 1, p. 45, Table 4, Figure 19; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 25. Quite frequent on the coast of Walcheren Island — Holland (de Man), some specimens in mud at Tvärminne Bay (G. Schneider).
3) Sp. ceylonensis Cobb 1891: Proc. Linn. Soc. N. S. W. 5, p. 467; on roots of algae and in sand at Aden and in Ceylon.

The caudal tube, which is the most characteristic feature of this genus, is constructed in the same way in Spilophora parva de Man (see p. 177). This species should also possibly be included, with a corresponding broadening of the generic diagnosis.

1 (4). Bulb double.
2 (3). Lateral punctations large, cuticular annules narrow dorsally and ventrally . . . . . . . . . . . . . . . . . . . . . . . . **Sp. euxina** n. sp.
3 (2). Lateral punctations small, cuticular annules widen dorsally and ventrally. . . . . . . . . . . . . . . . . . . . . **Sp. paradoxa** de Man
4 (1). Bulb triple . . . . . . . . . . . . . . . . . . . . . . **Sp. ceylonensis** Cobb

260
### 54. Spilophorella euxina n.sp.
(Table 8, Figure 54)

$$\text{immature}\,♀\ \frac{-\quad 11.8\quad 18.5\quad 30^{*}\quad 46\quad 64^{*}\quad 84}{1.3\quad 3.6\quad 4.6\qquad\quad 5.5\qquad\quad 2.6}\ 970$$

$$\alpha = 18;\quad \beta = 5^{1}/_{3};\quad \gamma = 7.$$

| Immature ♀ | Anterior end | Nerve ring | End of esophagus |
|---|---|---|---|
| Length | — | 115 | 185 |
| Width | 12 | 35 | 45 |

The **body** of this species is very greatly swollen in the middle, tapers twofold to the anus and only slightly to the end of the esophagus, whence anteriorly it tapers $3^{1}/_{2}$ times, chiefly in the preneural region. The **cuticle** (see Figure 54a) consists of annules with alternate smooth spaces. Each annule is composed of small punctations, the largest located laterally and forming two regular rows running along the entire body (see Figures 54a, c). Between these rows there is a smooth space with no punctations, raised like an elevation over the surface of the body. The annules narrow to the ventral and dorsal sides but are not interrupted. In Sp. paradoxa de Man the reverse is the case: the punctations are small and the **annules**

---

* Only the overall length of the genital tract is given.

**widen** to the dorsal and ventral sides. The thickness of the cuticle is 1.5μ and increases to 2.5μ posteriorly. The intervals between the annules increase from 2.2 to 2.6μ (in the middle). I did not see bristles.

The **head** is truncated and projects anteriorly with six cephalic papillae (p. ceph. —Figure 54a). I did not detect the four cephalic bristles and lateral organs. Four large supplementary cephalic bristles, 6μ long, lie somewhat posteriorly (s. subc. —Figure 54a). They are shorter in Sp. paradoxa de Man.

Inside the head the vestibule is in the form of a wide funnel. De Man 261 draws three rows of folds here in Sp. paradoxa which probably are present in my species also, but I could distinguish them only in the posterior part of the vestibule (the length of this part is $2\frac{1}{2}\mu$) (vest. — Figure 54a). A cup-shaped oral cavity with fairly thick walls and one dorsal tooth follows and is succeeded immediately by the esophageal tube. According to de Man the tooth is movable. The depth of the cavity is $2\frac{1}{2}\mu$, its width is 5μ. Around and posterior to the oral cavity are oral muscles that move it forward. De Man's "appareil valvulaire" is simply the posterior border of this musculature, which anteriorly forms a small expansion of the esophagus (10μ); behind this, the organ narrows slightly and then gradually expands once more, attaining 15μ at the nerve ring. Posterior to this, a distinct bulb about 50μ long (28% of the overall length) and 30μ wide is formed (Figure 54b). This is double and contains two lenticular cavities, the smaller anterior measuring 15×6μ, the posterior measuring 21×9μ. A special slit, also drawn by de Man, lies between them.

The ovaries are double, reflexed, and long. The uterus is spacious with an unbroken lumen. Eggs were absent in the uterus but those located at the end of the ovary are large, measuring 50×25μ.

The **tail** (Figure 54c) is very long and pointed to the end. The aperture of the caudal glands is located at its end, but does not extend onto its dorsal side (por. caud. —Figure 54c). The proportions are: length of tail 6.7; width at pore 0.2.

Only one not fully mature female was found in Georgievskii Monastery: coquina from a depth of 27 sajenes.

The structure of the cuticle makes it easy to differentiate this species from Sp. paradoxa de Man.

## 5. Subfamily **Draconematini** (**Chaetosomatidae** auct., **Nematoda reptantia** Metshnikov, **Nematochaetae** Schepotieff)

This subfamily contains the aberrant genera Draconema Cobb 262 (Chaetosoma auct.) and Rhabdogaster Metshnikov. The anterior part of the body containing the esophagus is greatly swollen, tapers sharply posteriorly with a slender neck following. A gradual enlargement corresponds to the region of the genital tract. The cuticle consists of smooth annules, but these are absent on the anterior and posterior ends. The bristles are long. There are two to four rows of specially modified stout bristles on the ventral side anterior to the anus in both sexes. The ovaries are paired and reflexed; the uterus is spacious with thick walls and a common cavity. The tail is pointed. According to the descriptions of Mechnikov and Shchepot'ev, these worms perform a very characteristic form of locomotion, in the manner of a caterpillar, gripping first with the cephalic bristles and then with the posterior. Steiner had hardly any basis for doubting this observation. Cobb's suggestion that these worms live in tubes was also made without particular foundation.

Concerning the relationship of this group with other nematodes, Metachromadora m. and Desmodora de Man offer many points of comparison. In both forms the cuticle consists of smooth annules, which also are larger on the head; this is characteristic for many other forms of Chromadoridae.[*] Even the form of the body in Metachromadora is sometimes highly reminiscent of Chaetosoma. The neck is frequently rather narrow and opposite the genital organs the body is much swollen, particularly in females. Steiner also indicates one form of Desmodora with a similar body shape. The female genital tract has additional comparable features: there are similar long, reflexed ovaries with numerous oogonia, and a similar thick-walled uterus with a common lumen. These facts also lead me to consider Chaetosoma as highly specialized forms of Chromadoridae, adapted to a particular means of locomotion. They therefore cannot be placed outside the system, as they have been up to now: Mechnikov set them off against the remaining 263 free-living nematodes; Shchepot'ev considered them a connecting link in the chain of Rotatoria—Kinorhyncha—Desmoscolecidae—Chaetosomatidae—Enoplidae. This view revives the long-defunct theories of Bütschli, which there was no purpose in resuscitating, and is explained by the slight acquaintance of both authors with the true free-living nematodes; transitional forms were unknown to them. Rhabdogaster is no doubt a less specialized form of the same group.

Thus three genera are related here:

1) Rhabdogaster Metshnikov 1867: Zeit. Wiss. Zool. 17, p. 542 (nomen praeocc. in dipteris: Loew 1857, gen. renominandus); Steiner: Zool. Jahrb. Syst. 39, p. 574.[**]
2) Tristicochaeta Panceri 1876: Rendiconti Acc. Sci. Fis. -mat. Napoli 7; Chaetosoma ex. p. Schepotieff; Chaetosoma Steiner 1916: Zool. Jahrb. Syst. 39, p. 561, nec Claparède 1863.[†]
3) Draconema Cobb 1913, see p. 190.

---

[*] In Chaetosoma (Tristicochaeta) primitivum Steiner this is not observed.

[**] Rh. cygnoides: Metshnikov 1867: Zeit. Wiss. Zool. 17, p. 542, Table 31, Figures 9—11; Schepotieff 1907: Z. Anz 31, p. 154; 1908: Zool. Jahrb. Syst. 26, p. 393, Table 26; Nematodes p. 59, Table 11. Steiner 1916: Zool. Jahrb. Syst. 39, p. 575, Table 26, d—Figure 17a. Salerno (M), Ischia (Panceri), Heligoland, Canary Islands (Greeff); Bergen 250 m. Naples on stones covered by a thin layer of algae, Rovigno, Brindisi on algae (Schneider); Naples, Kiel Firth, White Sea strait on algae (Steiner).

[†] Three species: (1) Tr. inarimense Panceri 1876: Rendic. Acc. Sci. Fis. -Mat. Napoli 7. ? Ch. tristicochaeta Schepotieff 1907: Zool. Anz. 31, p. 159, Figure 24; 1908: Zool. Jahrb. Syst. 26, p. 406, Table 27, Figure 7, 14d; Table 28, Figure 5; Nematodes p. 67, Table 12, 13, Ischia (P.); Bergen, Naples, common on stones. (2) Chaetosoma longirostrum Schepotieff 1908: Zool. Anz. 31, p. 159, Figure 25; Zool. Jahrb. Syst. 26, p. 406, Table 27, Figures 8, 14e; Table 28, Figures 1, 2, 6—15; Nematodes p. 67, Tables 12, 13. Bergen, Naples, common on stones. (3) Chaetosoma primitivum Steiner 1916: Zool. Jahrb. Syst. 39, p. 564, Table 25, d—Figure 14a. White sea strait, on algae. The first two species are related here on the basis of Shchepot'ev's work, so that the synonymy given here is doubtful.

1 (4). Large, stout, slightly curved bristles anterior to anus.
2 (3). Head markedly separated from neck. Two bulbs on esophagus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Draconema** Cobb
3 (2). Head slightly swollen, so that neck is hardly marked. One bulb . . . . . . . . . . . . . . . . . . . . . . . . . . . **Tristicochaeta** Panceri
4 (1). Comparatively slender bristles curved into hooks anterior to anus . . . . . . . . . . . . . . . . . . . . . . . **Rhabdogaster** Metshnikov

### Genus DRACONEMA Cobb 1913

Chaetosoma Claparède 1863: Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Tiere. Leipzig p. 88 (nom. praeocc. in Colept.: Dejean, Westwood 1851).
264 Ch. Panceri 1876: Rendiconti Acc. Sci. Fis.-matem. Napoli 7 (the work was not available to me).
Ch. ex. p. Schepotieff 1908: Zool. Jahrb. Syst. 26, p. 401; Nematodes etc., p. 62.
Draconema Cobb 1913: Journ. Washington Acad. Sci. 3, p. 145.
Dr. (nec Chaetosoma) Steiner 1916: Zool. Jahrb. Syst. 39, p. 561.

Type species: Dr. ophiocephalum (Claparède 1863)*

These are small worms with a very characteristically shaped body. The swelling corresponding to the esophageal region is sometimes barrel-shaped and sometimes lemon-shaped (see Figures 55a, b, 56). It is followed by a slender neck from which it is usually sharply demarcated. The posterior swelling, as in other nematodes, corresponds to the genital organs and is particularly marked in females. The **cuticle** is annulated, the annules in the middle of the anterior swelling being far coarser than the others; anterior to these there is an area on which the annules disappear entirely, and another nonannulated area occurs at the end of the tail. The entire surface of the body is covered by many long bristles, which gave rise to the former name of the genus. The bristles are especially numerous on the head, where in addition to those on the dorsal side there are some pairs of specialized clawlike bristles (the "occipital [adhesive] bristles" of Steiner). Other specialized bristles very characteristic for this genus are located in two, three, or four rows on the ventral surface anterior to the anus; where three rows are present, the bristles of the central row are about twice larger than those of the lateral rows. These bristles are developed uniformly in both sexes. Panceri isolated species with three rows of bristles in a special genus Tristicochaeta, but this difference alone is insufficient for the 265 establishment of a new genus, as Shchepot'ev pointed out, and its maintenance is based on other features (p. 191). In many species there are fewer of these bristles and their number increases with age.

In front of the anterior part of the head, there is a small movable area which can probably be withdrawn and protruded with the closing and opening of the mouth. An elevation—the rostrum in Shchepot'ev's terminology—is located at its center and contains the oral aperture.* It is beset with six small bristles that are probably homologous with the labial or anterior row of cephalic bristles of other nematodes. The six "anterior cephalic fibers" of Shchepot'ev, located between the lateral organ and anterior annule, apparently vary in number in different species. I cannot concur with Shchepot'ev, who describes "six large triangular teeth" in the cavity of the vestibule. In my opinion he simply paid inadequate attention to his preparations and took the folds of the cuticle inside the rostrum for teeth. These folds may be stretched when the mouth is distended. The esophagus is furnished with two distinct expansions between which the nerve ring is located. Mechnikov, Barrois, and Claparède drew two swellings in their species, but Shchepot'ev oddly described only one swelling for all Chaetosoma, and drew it for Ch. ophiocephalum Claparède also. It is evident from Steiner's paper that Shchepot'ev here committed a serious error which arose from his omitting to examine any living animals and, judging from the drawings, to prepare any cleared whole mounts. Because of this, quite mistaken information is given about the nerve ring also, which I will not repeat.

266 The lateral organs are located on the sides of the head. These are canals in the cuticle, recurved sometimes in the shape of a horseshoe and sometimes spiral. Shchepot'ev, having seen and drawn them repeatedly, describes their structure wrongly ("two external annular thickenings") and completely misunderstands their significance. The cervical gland is apparently located at the beginning of the neck. The intestine is well developed. These worms are polymyarian.

The **female genital organs** consist of paired, reflexed ovaries and a spacious, thick-walled uterus. The eggs are small, according to Shchepot'ev. The **testes** are paired; the spicules are slender, curved, with small gubernacula. The tail is elongate and conoid.

The relationships have been described above.

Genus Chaetosoma was described for the first time by Claparède (1863), and later another species of the genus was described by Mechnikov (1867); this author united it with Rhabdogaster, which he had described for the first time, in a special group "Nematoda reptantia," while the remaining free-living nematodes were isolated as "Nematoda natantia." Subsequently several species were described (Barrois 1875, Levinsen 1881), but only in 1908 did Shchepot'ev begin to study them again. However, his superficial observations and inadequate preparations seriously call into question the value of his descriptions. He united Chaetosoma with Rhabdogaster into the single group Nematochaetae, upon which he conferred the rank of family. Cobb (1913) described a new species of Chaetosoma as Draconema cephalatum n.g., n.sp., but this species was not so different from Claparède's type as to merit isolation as a separate genus. Nevertheless, the name was retained, as Chaetosoma is a nomen praeoccupatum. Steiner (1916) suggests maintaining Cobb's designation for species with a double bulb and calling only species with a simple bulb Chaetosoma, thereby leaving in genus Chaetosoma

---

* Draconema is taken merely as a nomen novum for Chaetosoma Claparède, and therefore the type species for the genus must be that selected by Claparède.

* Steiner evidently misunderstood Shchepot'ev, as he states that the latter designates the esophageal region as the head, and all the anterior smooth portion (the head) as the rostrum.

only his Ch. primitivum and two other species and transferring all the remainder, including the type species, to the new genus: this is inadmissible according to the rules of nomenclature. Therefore, if we 267 retain Draconema for the first group, we must restore Tristicochaeta Panceri for Chaetosoma Steiner nec Claparède. Steiner includes in his work a critique of Shchepot'ev's paper, and in many respects his observations coincide with mine. For the reasons elaborated above I take this group only as a subfamily: Chaetosomatini.

The genus is divided into three groups.*

α. Species with four rows of bristles.

1) Dr. cephalatum Cobb 1913, see p. 193.

β. Species with three rows of bristles.

2) Ch. groenlandicum Levinsen 1881: Vid. Medd. Naturh. För. Kjöbenhavn 1881, p. 132. Greenland.
3) Dr. ponticum n.sp., see p. 195.

1 (2). Not more than ten bristles in each row. . . . . **Dr. ponticum** n. sp.
2 (1). 22—26 bristles . . . . . . . . . . . . . . . **Dr. groenlandicum** (Levinsen)

γ. Species with two rows of bristles.

4) Chaetosoma ophiocephalum Claparède 1863: Beobacht. über Anatomie etc. p. 88, Table 18, Figures 2, 3; ? Shchepot'ev 1908: Zool. Anz. 31, p. 157; Zool. Jahrb. Syst. 26, p. 405, Table 27, Figures 3, 4, 14a; Table 28, Figures 16—18; Nematodes p. 66, Tables 12, 13. St. Vaast (Claparède); Bergen, rarely on stones (Schneider).
5) Ch. claparedi Metshnikov 1866: Zeit. Wiss. Zool. 17, p. 539, Table 31, Figures 1—8; ? Shchepot'ev 1908: Z. Anz. 31, p. 157, Figure 22; Zool. Jahrb. Syst. 26, p. 405, Table 27, Figures 1, 2, 14b; Table 28, Figures 4, 20. Nematodes p. 66, Tables 12, 13, Salerno (Mechnikov). Bergen, Naples, very common, particularly on small sponges (Schneider).
6) Ch. macrocephalum Schepotieff 1908: Z. Anz. 31, p. 158, Table 23, Zool. Jahrb. Syst. 26, p. 406, Table 27, Figures 5, 6, 14c; Nematodes p. 66, Table 12. Bergen, common on the coast; Naples, very common on stones.
7) Ch. armatum Barrois 1874: Revue Sci. Nat. Montpellier 3, p. 514, Table 9, Figures 3—5. Roscoff.

1 (2). 22—24 bristles in ventral row. . . . **Dr. ophiocephalum** Claparède
2 (1). Not more than 15.
3 (4). Head flattened dorsoventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Dr. macrocephalum** Schepotieff
4 (3). Head round.
5 (6). Stout supplementary bristles on tail . . . . **Dr. armatum** Barrois
6 (5). These absent . . . . . . . . . . . . . . . . . **Dr. claparedi** Metshnikov

55. **Draconema cephalatum** Cobb 1913
(Table 8, Figure 55)

Journ. Washington Acad. Sci. 3, p. 145, Figures.
Steiner 1916: Zool. Jahrb. Syst. 39, p. 567, Table 24, 13a—d,
Table 25, Figures 13e—i. 268

$$\text{♂}\ \frac{\begin{array}{ccccc} - & 5.0 & 9.2 & 22 & 92.0 \end{array}}{\begin{array}{ccccc} 1.7 & 5.8 & 2.5 & 5.4 & 2.5 \end{array}}\ 1800$$

$$\alpha = 18;\ \beta = 11;\ \gamma = 12^1/_2.$$

$$\text{♀}\ \frac{\begin{array}{ccccccc} - & 5.8 & 10.6 & 31.5 & 52.8 & 69 & 91.5 \end{array}}{\begin{array}{ccccccc} 1.6 & 5.2 & 3.0 & & 8.9 & & 1.8 \end{array}}\ 1420$$

$$\alpha = 11;\ \beta = 9^1/_2;\ \gamma = 11.$$

The dimensions are of the anterior end of ♂ (compressed); ♀ was lost after the drawing was made.

| ♂ | Anterior bristles | End of oral region | Beginning of annules | Nerve ring (end of annules) | End of esophagus |
|---|---|---|---|---|---|
| Length | — | 6 | 32 | 80 | 160 |
| Width | 16 | 35 | 76 | 103 | 49 |

The **body** has the form characteristic for Draconema. In the female, it swells more in the middle than in the esophageal region, in the male somewhat less. The diameter at the anus is small, five times less than the maximum diameter in the female, more than twice less in the male. The neck is approximately twice narrower than the esophageal swelling, which is barrel-shaped. The **cuticle** is sharply annulated; the annules in general run regularly, but some may be incomplete and wedged out by the two neighboring annules (see Figure 55c). Anteriorly, 8—10 rows of annules are very markedly thickened, and are clearly observed at first glance (Figures 55a, b, c). Posteriorly, in front of the anus, the annules are smaller on the dorsal side than on the ventral. At midbody on the lateral field, the annules curve somewhat posteriorly, producing a slightly S-shaped figure. Anteriorly, the thickness of the cuticle opposite the labial annules is about 4$\mu$, and the intervals between the annules is 2.7$\mu$; at midbody these measurements are 2.7$\mu$ and 1.5$\mu$, while posteriorly, they attain 3.5$\mu$. The annules on the anterior end of the body in front of the labial annules are hardly noticeable (Figure 55c), while posteriorly they cease 40$\mu$ from the end. Numerous bristles are disposed in four longitudinal subventral rows along the entire body. The bristles are very long (40—50$\mu$), particularly in the esophageal region (up to 65$\mu$), but short on the tail. Between the rows there are some 269 additional irregularly placed bristles. Apart from the occipital bristles (see below), the most conspicuous rows are of specialized bristles, lying preanally. There are four such rows here, as distinct from all other forms of Draconema, in which there are only two or three.

---

* Extreme care is necessary when dealing with the species described by Shchepot'ev: he apparently united different species under one name, and different individuals of the same species are described as separate species.

The overall distance that they occupy is almost twice the length of the tail. The anterior bristles of both the internal and external rows are larger in the male (55 μ in the outer row, 45 μ in the inner), and posteriorly they are smaller (45 and 27 μ). In the external rows in the male, I counted 16 bristles (of which four on the left and two on the right were usual pointed bristles). There were 18–20 bristles in the inner rows. These are differentiated from the others (Figure 55e) by their somewhat stouter bases and their less marked tapering to the end. At the end the bristles are truncated and a special cavity is observed in the cut end. They usually curve posteriorly.*

The **head** is truncated; anteriorly, it has a specialized area demarcated by a wavy line with a softer cuticle, which may probably be drawn in. On the most anterior part, there are six bristles which are homologous either with the labial papillae or with the six anterior oral bristles of other nematodes (s. c. —Figure 55c). It is impossible to determine from the mass of bristles of the anterior end of the body those that are homologous with the other bristles. The lateral organ is an incomplete spiral in the form of a horseshoe. It is located in the middle of the smooth anterior space (o. l. —Figure 55c) and is 19 μ long. Over the dorsal side there is a fringe of six pairs of thick clawlike bristles 35 μ long, disposed in two rows—three pairs in the anterior and three in the posterior: these are the occipital bristles of Steiner** (set. —Figure 55c). The posterior row lies almost at the boundary of the annules. The entire anterior part
270 of the body, including the coarsely annulated portion, is densely beset with bristles of various lengths. Close inspection reveals that they lie in the form of four irregular subventral rows on each side; there are also bristles apart from these rows.

The mouth located at the end of the oral elevation is narrow; its lumen is constricted, as Shchepot'ev indicates (1908, Table 13, Figure 6 of the Russian edition), by six folds extending within the cavity of the vestibule. When the mouth opens these folds probably stretch out. An oral cavity is not isolated. Steiner doubtfully notes the presence of a small tooth of which I saw no sign; nor could I see the chitinized processes around the mouth.† The **esophagus** is divided by a constriction (25 μ thick) into two approximately equal parts (about 45 μ thick). Some retractor muscles are attached to the anterior swelling. Anteriorly and posteriorly (cardia of Cobb and Steiner), it narrows greatly (13 μ anteriorly and 17 μ posteriorly). The constriction is encircled by the **nerve ring.** Steiner describes esophageal glands. The small **cervical gland** is located in the cervical region not far behind the end of the esophagus. Posterior to it there is another small cell, as in the other forms of Chromadoridae (Cobb, Steiner). The **intestine** is straight and consists of large cells. The hindgut is fairly long, joining the midgut at the level of the most posterior enlarged bristles. The lateral fields are very broad, while the musculature is weak; the species is polymyarian.

---

* For the various interpretations of the significance of these and the occipital bristles and of the glands connected to them see the general part.

** It is hardly possible to regard these as homologous with the cephalic bristles, as Steiner thinks (p. 565).

† "Chitinapophysen im Gewebe rings dem Mundeingang" p. 570.

---

The **ovaries** (ov. —Figure 55b) are quite large, reflexed,* and paired. The **uterus** is saccular with a continuous lumen, and thick walls. The vagina traverses $^2/_7$ of the body width internally. There were no ripe eggs.

There are two short **testes**—one facing anteriorly, and the other posteriorly. Both discharge into a common reservoir, to which the vas
271 deferens is attached (see Figure 55a). The spicules are 80 μ long, slender and curved with an irregular manubrium at the base. The gubernacula are small (27 μ long), paired, and adjacent to the ends of the spicules (see Figure 55d).

The **tail** is regularly conoid and of the same form as in the majority of Spilophorini, with a portion devoid of annules at the end. Three caudal glands lie in tandem in the caudal cavity. The caudal pore opens at the end of a short tube, whose boundary is observed within the tail as a special annular elevation, while externally it is quite inconspicuous (Figure 55d).

The proportions at the posterior end of the male are: length of tail 3.2; length of nonannulated portion 0.9; width at end of annules 0.33; length of spicules 1.8; gubernaculum 0.6; distance from anus to posterior large bristle 1.8; length of row of bristles 4.2.

Only two specimens of this species were found: male in coquina at 27 sajenes, Georgievskii Monastery 7.12; female—algae on sand, Kruglaya Bay 6.12.

The species is apparently cosmopolitan: Cobb found it near red algae in various parts of the world, primarily on the coast of Jamaica. Steiner obtained it from Naples, Kiel, algae from the White Sea strait, and the Guinean coast of Africa. Steiner's description reached me only at the time of proofreading (I was also unable to obtain Cobb's work); I originally considered this species new and called it Chaetosoma quadriseris n. sp.

### 56. **Draconema ponticum** n. sp.

(Table 8, Figure 56)

$$\text{young}\ ♀\ \frac{\begin{array}{ccccc}—&6.0&12&50&90\end{array}}{\begin{array}{ccccc}1.8&6.2&3.1&4.8&2.6\end{array}}\ 1050$$

$$\alpha=21;\ \beta=8^1/_8;\ \gamma=10.$$

| Dimensions | End of oral disk | Beginning of annules | End of annules and nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 5 | 38 | 65 | 127 |
| Width | 11 | 20 | 65 | 32 |

272

The maximum width of the anterior barrel-shaped expansion is twice greater than the width of the neck, whence the **body** expands to the middle $1^1/_2$ times and tapers less than twofold to the anus. The **cuticle** is annulated, as in the preceding species, but the large annules of the anterior portion are not so well developed (see Figures 55c and 56) and are somewhat more regular. These annules are 2.5 μ wide, and the thickness of the cuticle is also 2.5 μ; on the remainder of the body the

---

* Steiner's observation that they are straight seems definitely wrong to me.

annules are 1.2—1.3 μ wide for a cuticular thickness of 1.5 μ. These annules also are slightly S-shaped laterally. The bristles are disposed in 4 subventral rows and on the anterior expansion in 8 or 10 irregular rows; they are numerous and 27—37μ long. The specialized bristles on the end of the body are of the same structure as in the foregoing species, lying in three rows with six bristles 43—51μ long in the outer rows and nine bristles 30μ long in the inner.

The **rostrum** is small and beset with six bristles as in the preceding species. The lateral cephalic bristles number four only, measuring 27μ. Two anterior are set nearer the midline, while the posterior are shifted more laterally. The anterior part of the head is apparently quite devoid of annules but the cuticle on it is rough. The lateral organ is far thinner than in the foregoing species; its enclosed end is bent under the basal part (see Figure 56), so that a completely enclosed spiral is produced. The lateral organ is 12μ long.

The **oral cavity** is inconspicuous. The **esophagus** is of the same structure as in the foregoing species. The diameter of both swellings is 35μ, the narrow portion between them is 22μ, the posterior part (cardia) is 14μ. The **nerve ring** lies nearer to the anterior swelling. The **cervical gland** apparently lies at the very beginning of the narrow portion. The **genital organs** are hardly developed. The **tail** is exactly as in the foregoing species. The proportions at the posterior end are: length of tail
273 2.6; width at end 4.2; length of smooth portion 1.5.

Only one immature female was found in coquina (27 sajenes) at Georgievskii Monastery.

This species is easily differentiated by the small number of bristles in each row from the other forms of Draconema so far described which have three rows of bristles.

## III. Family *DESMOSCOLECIDAE*

These are aberrant marine nematodes with fusiform, sometimes very short bodies and well developed cuticular annules, in several species consisting of some glandular secretion covered with adhering foreign bodies. Some are very small—Trichoderma minutum Steiner is less than 100μ long. The ovaries are apparently straight. This group is linked with the Monhysteridae through Eudesmoscolex. There are four genera. Three species of Desmoscolex found by Reinhard in Odessa are marked in bold type.

1) Desmoscolex Claparède 1863: Beobacht. üb. Anat. u. Entw.-Gesch. wirbelloser Tiere p. 89; Mechnikov 1865: Zeit. Wiss. Zool. 17; Greeff 1869: Arch. Naturg. 35, Abt. 1; Panceri 1876: Atti Accad. Sci. fis.-matem. Napoli 7; Reinhard 1883: Z. Anz. 3; Shchepot'ev 1907: Zool. Anz. 31, p. 135; 1908 (1): Zeit. Wiss. Zool. 90, p. 179; (2): Nematodes, etc. St. Petersburg, p. 37, (the number of figures on the tables in the two forgoing papers is the same); Steiner 1916: Zool. Anz. 47, p. 323; Southern 1914: Proc. R. Irish Acad. 31, pt. 54, p. 61.

Species: (1) D. adelphus Greeff 1869: loc. cit., p. 113; Shchepot'ev 1907: p. 143; 1908 (1): p. 191, Table 8, Figures 17—19; (2); p. 45, Table 6. Bergen, Heligoland. (2) D. adriaticus Shchepotieff 1907: p. 139, Figure 5; 1908 (1): p. 188, Table 8, Figure 24; Table 9, Figures 1, 2; (2): p. 43, Tables 6, 7. Bergen, Rovigno, Brindisi, Naples. (3) D. annulatus Shchepotieff 1907: p. 138, Figure 3; 1908 (1): p. 187, Table 8, Figures 8, 9; (2): p. 42, Table 6, Naples. (4) D. bergensis Shchepotieff 1907: p. 142, Figure 8; 1908 (1): p. 191, Table 8, Figures 29—31; (2): p. 45, Table 6. Bergen. (5) D. chaetogaster Greeff 1869: p. 114, Table 6, Figures 11, 12; Shchepot'ev 1907: p. 140, Figure 6, 1908 (1): p. 189, Table 8, Figures 25—28; (2): p. 43, Table 6. Naples, Heligoland. (6) D. elongatus Panceri 1876: Shchepot'ev 1907: p. 141; 1908 (1): p. 190, Table 8, Figures 15, 16; (2): p. 44, Table 6. Naples. (7) **D. greeffi** Reinhard 1881: p. 591; Shchepot'ev 1907: p. 132; 1908 (1): p. 191, Table 8, Figures 21—23; (2): p. 44, Table 6. Naples, Odessa. (8) D. lanuginosus Panceri 1876; Shchepot'ev 1907. p. 140; 1908 (1): p. 189, Table 8, Figures 6, 7; (2): p. 43, Table 6. Naples, Ischia. (9) D. maximus Shchepotieff 1907; p. 141, Figure 7; 1908 (1): p. 190, Table 8, Figure 20; (2): p. 44, Table 6. Naples, in algae. (10) **D. medius** Reinhard 1881: p. 592; Shchepot'ev 1907: p. 141, 1908 (1): p. 190, Table 8, Figures 32, 33; (2): p. 44, Table 6. Naples, Odessa. (11) D. minor Schepotieff 1907: p. 139, Figure 4; 1908 (1) p. 187, Table 8, Figures 13, 14; (2): p. 42, Table 6. Bergen. (12) **D. minutus** Claparède 1863: p. 89, Table 18, Figures 4—7; Mechnikov 1865: Z. Wiss. Zool. 15, p. 461, Table 35, Figure 12; Greeff 1869: p. 100, Table 6, Figures 1—7; Shchepot'ev 1907: p. 137, Figures 1, 2; 1908 (1): p. 178, Table 8, Figures 1, 2; Table 9, Figures 3—25; Table 10, Figures 3—5, 7; (2): p. 41, Tables 6—8. Southern 1914, p. 62. Bergen, Heligoland, St. Vaast, west coast of Ireland, sand with coquina, 24 sajenes; Naples, Brindisi, Odessa. (13) D. nematoides Greeff 1869: p. 112, Table 6, Figure 8; Shchepot'ev 1907: p. 141; 1908 (1): p. 189, Table 8, Figures 3—5; Table 9, Figures 2, 6, 8—21; (2): p. 44, Tables 6, 8; Southern 1914 1914, p. 62. Naples, Heligoland, Bergen, west coast of Ireland, sand with coquina, 24 sajenes. (14) D. norvegicus Schepotieff 1907: p. 143, Figure 9; 1908 (1): p. 191, Table 8, Figures 10—12; (2): p. 45, Table 6. Bergen. (15) D. profundus Schepotieff 1907: p. 143; 1908 (1): p. 192, Table 8, Figures 34—37; (2): p. 45, Table 6. Bergen from a depth of 400 m. (16) D. hupferi Steiner 1916: p. 325, Figure 1. Senegal—Goré, 32 m; Togo—Porto Seguro, 13m. (17) D. rudolphi Steiner 1916: p. 326, Figure 2; Gold Coast [now Ghana]—Prampram, 9 m. (18) D. prampramensis Steiner 1916: p. 329, Figure 4, from the same place. (19) D. platycricus Steiner 1916: p. 331, Figure 5; from the same place. (20) D. michaelseni Steiner 1916: p. 332, Figure 6; S.W. Africa—Lüderitz Bay, 0—10 m. (21) D. lissus Steiner 1916: p. 333, Figure 7; Cameroons, Victoria, on a wharf. (22) D. nanus Steiner 1916: p. 334,

Figure 8; Gold Coast, Prampram, 9 m. (23) D. leptus Steiner 1916: p. 335, Figure 9, from the same place. (24) D. conurus Steiner 1916: p. 336, Figure 10, from the same place; v. togoënsis Steiner 1916: p. 337, Figure 11; Togo, Porto Seguro, 13m.

The larvae of some forms of Desmoscolex were found by Mechnikov in plankton around Odessa (Tr. I s"ezda Rus. Est. 1869, otd. Zool. [Proceedings of the First Conference of Russian Natural Scientists, 1869, Zoological Section], p. 269).

2) Tricoma Cobb 1893: Proc. Linn. Soc. N. S. W. p. 389; 1912: Journ. Washington Acad. Sci. 2, p. 480; Steiner 1916: Zool. Anz. 47, p. 324.

Species: (1) Tr. cincta Cobb 1893: p. 390. Naples, Heligoland (after Bresslau). (2) Tr. major Cobb 1912: p. 484. Jamaica, on rocks and in algae. (3) Tr. similis Cobb 1912: p. 483. New Guinea. (4) Tr. africana Steiner 1916: p. 338, Figure 18; Gold Coast.—Prampram, 9 m; (5) Tr. glutinosa Steiner 1916: p. 339, Figure 13; from the same place. (6) Tr. robusta Steiner 1916: p. 340; from the same place. (7) Tr. crenata Steiner 1916: p. 341; from the same place. (8) Tr. tubichaeta Steiner 1916: p. 342; Figure 14; from the same place. (9) Tr. intermedia Steiner 1916: p. 342, Figure 15; from the same place. (10) Tr. tenuis Steiner 1916: p. 344; Figure 16; from the same place, with stony bottom. (11) Tr. gracilis Steiner 1916: p. 344, Figure 17, ditto. (12) Tr. crassicoma Steiner 1916: p. 345, Figure 18; ditto. (13) Tr. cobbi Steiner 1916: p. 346, Figure 19; Togo, Porto Seguro, 13 m. According to Steiner here also are related three species described as Desmoscolex from the west coast of Ireland, sand with coquina, 24 sajenes: (14) D. brevirostris Southern 1914: Proc. Roy. Irish. Acad. 31; pt. 54, p. 63, Table 11, Figures 30A-D. (15) D. longirostris Southern 1914: p. 62, Table 11, Figures 29A-D. (16) D. polydesmus Southern 1914: p. 64, Table 11, Figures 31A—C. In addition, there are probably related here several species presented above as Desmoscolex.

3) Eudesmoscolex Steiner 1916: Zool. Jahrb. Syst. 39, p. 579; Zool. Anz. 47, p. 324.

One species: Eu. oligochaetus Steiner 1916: loc. cit., p. 580,
275 Table 25, Figures 15a-c; White Sea strait, in algae.

Probably also belonging here are:

4) Trichoderma Greeff 1869: Arch. Naturg. 35 (1), p. 115; Panceri 1876: Atti Acad. Sci. Fis.-mat Napoli 7; Shchepot'ev 1907: Zool. Anz. 31, p. 153; 1908: Zool. Jahrb. Syst. 26, p. 385; Nematodes, etc.: p. 56. Steiner 1916: Zool. Anz. 47, p. 324 (nom. praeocc: Stephens 1839: in Coleopt.; Swains 1839 in piscis gen. renominandus.

Species: (1) Tr. oxycaudatum Greeff 1869: p. 115, Table 6, Figures 9, 10; Panceri 1876; ? Shchepot'ev 1907: p. 153; Figures 17, 18; 1908 (1): p. 385, Table 25; (2): p. 56, Table 10; Heligoland (Greeff); Bergen—Heligoland, 200—250 m (Schneider); Salerno (Mechnikov), Ischia, Naples, $1^1/_2$ m, Rovigno (Schneider); (2) Tr. minutum Steiner 1916: p. 347, Figure 20; Togo, Porto Seguro, 13 m; (3) Tr. loxum Steiner 1916: p. 348, from the same place and from the Gold Coast—Prampram, 8—9 m with var. heterophallum Steiner 1916 together with the foregoing in Togo; (4) Tr. macrotrichum Steiner 1916: p. 349, Figure 22, Gold Coast.

For Richtersia Steiner see the Appendix.

1 (4). Supplementary (secretory) annules of cuticle present.
2 (3). Annules uneven: some larger, remainder smaller . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Desmoscolex** Claparède
3 (2). Annules all uniform . . . . . . . . . . . . . . . . . . . . . **Tricoma** Cobb
4 (1). Such annules absent.
5 (6). Body fairly long with few bristles . . . **Eudesmoscolex** Claparède
6 (5). Body short, all hairy . . . . . . . . . . . . . . . . **Trichoderma** Greeff

## IV. Family *MONHYSTERIDAE*

A large number of large and small free-living nematodes are incorporated here. The large members of this family may be very highly specialized (Sphaerolaimini, Siphonolaimini), while the small ones have a reduced character; for example, the intestine in many representatives of Monhystera consists of only two rows of cells.

The lateral organs in the simplest case are elliptical and shifted anteriorly (Paramonhystera Steiner). The next stage of advancement is circular lateral organs with thin walls, characteristic for many genera; from here, more complex forms of lateral organ are derived. The ovaries are always straight. The tail is usually not pointed.

I relate here six subfamilies; the division is made chiefly according
276 to the structure of the lateral organ and requires further elaboration.

1) Monhysterini (an entire range of genera: Monhystera, Linhomoeus, Desmolaimus, Terschellingia, Theristus, Cobbia, etc., p. 200.
2) Sphaerolaimini (Sphaerolaimus), p. 223.
3) Siphonolaimini (Siphonolaimus, Solenolaimus) p. 229.
4) Axonolaimini (Axonolaimus, Araeolaimoides, and two new genera), p. 230.
5) Comesomini (Comesoma, Sabatieria, Parasabatieria) p. 239.
6) Diplopeltini (Diplopeltis, Acmaeolaimus n.g.), p. 247.

1 (6). Lateral organs circular or elliptical.
2 (5). Oral cavity immovable.
3 (4). Oral cavity of fairly simple structure; large, small or completely absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 1. **Monhysterini**
4 (3). Oral cavity very large, complex, layer of labial rods attached to it anteriorly . . . . . . . . . . . . . . . . . . . . . . . . 2. **Sphaerolaimini**
5 (2). Oral cavity narrow, long, protrusible, functioning as a thorny spine. Intestine often black . . . . . . . . 3. **Siphonolaimini**

6 (1). Lateral organs of more complex form: spiral or concealed spiral.
7 (10). Lateral organs thin-walled.
8 (9). Lateral organs spiral with very few turns, sometimes less than one, or in the form of complex tube. . . . . . . . . . . 4. **Axonolaimini**
9 (8). Lateral organs spiral with several turns . . . . . . 5. **Comesomini**
10 (7). Lateral organs in form of thick cuticular plates, inside of which lies spirally curved tube. . . . . . . . . . . . . . 6. **Diplopeltini**

## 1. Subfamily **Monhysterini**

A fairly varied set of forms characterized by circular or elliptical lateral organs* and **straight ovaries** are incorporated here. The remaining features are not constant: the cuticle is smooth or annulated; the cephalic bristles are in one or two circlets, the esophagus is with a bulb or straight and narrow. The uterus is usually two-chambered; the spicules are of various structure; the gubernaculum sometimes has paired posterior
277 processes.

Here I incorporate many genera which in future will possibly be formed into several subfamilies.

1) Paramonhystera Steiner 1916, see p. 202.
2) Penzancia de Man 1889, see p. 205.
3) Theristus Bastian 1865 — Theristus — Tachyhodites ex. p.: Trans. Linn. Soc. 25, pp. 155, 156; Monhystera ex. p. Bütschli 1874: Abh. Senck. Ges. 9, p. 24; Monhystera subg. Theristus de Man 1889: Mém. Soc. Zool. France 2, p. 7.**
278 4) Cobbia de Man 1907, see p. 207.
5) Desmolaimus de Man 1880, 1884: Nemat. Niederl. Fauna, p. 50. Freshwater and brackish water genus.*
6) Monhystera Bastian 1865, see p. 210.
7) Araeolaimus de Man 1888: Mém. Soc. Zool. France 1, p. 14.**
8) Linhomoeus Bastian 1865, see p. 213.
9) Metalinhomoeus de Man 1907, see p. 217.
10) Terschellingia de Man 1888, see p. 219.
11) Prosphaerolaimus n.g., see p. 220.
12) ? Disconema n.g., see p. 221.

Here also apparently are:

279 13) ? Aegialoalaimus de Man 1907: Mém. Soc. Zool. France 20, p. 35.†

Chromagaster steinolaima Steiner 1916: Zool. Jahrb. Syst. 39, p. 632, Table 32, Figures 35a—c; algae from White Sea strait, also apparently similar to the last-named genus.

---

* In Araeolaimus de Man they are spiral, but I retain this genus here as it has little in common with Comesomini.

** There are numerous species here:
A. Species with gubernaculum provided with posterior processes:
(1) Monhystera setosa Bütschli 1874: Abh. Senck. Ges. 9, p. 29, Tables 5, 6, Figure 11; de Man 1888: Mém. Soc. Zool. France 1, p. 9, Table 1, Figure 5; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 11, Figure 3 nec Hofmänner et Menzel 1914; on the coasts of Kiel Firth, also in fresh water (Bütschli); mud on stones in a canal on Walcheren Island (de Man); Tvärminne, mud from the bay, (G. Schneider). (2) Th. pseudosetosus nom. nov. M. setosa Hofmänner 1913 (nec Bütschli 1874): Z. Anz. 42, p. 413, Figures 1—4; R. Suisse Zool. 21, p. 613, Table 15, Figures 4, 5; M. dubia Steiner Arch Hydrobiol. Planktonk. 8, p. 451, Figures 1—3. Hofmänner et Menzel 1915 (nec Bütschli 1873): Revue Suisse Zool. 23, p. 130. Stefanski 1914: Recherches Ném. Léman, p. 22; freshwater species from Swiss lakes; Rhone, Inn, (in mud); in Lake Geneva — on the coast among algae, in sandy mud, 40 m; in mud, 300 m (Stefanski). (3) M. setosissima Cobb 1894: Proc. Linn. Soc. N. S. W. 8, p. 405; Port Jackson N. S. W., mud and sand, not common. (4) M. gracillima Cobb 1894: loc. cit., p. 406, from the same place. (5) Tachyhodites natans Bastian 1865: Trans. Linn. Soc. 25, p. 155, Table 13, Figures 182—184; Falmouth. (6) ? Th. acer Bastian 1865: Trans. Linn. Soc. 25, p. 156, Table 13, Figures 187, 188; M. (Th.) acris de Man 1889: Mém. Soc. Zool. France 2, p. 182, Table 5, Figure 1. Common on the coast of the North Sea (Walcheren I), English Channel, west coast of Ireland — under stones on the coast, among Spirorbis, adult individuals in September (Southern). (7) ? M. elongata Bütschli 1874: Abh. Senck. Ges. 9, p. 26, Table 2, Figure 9. Fine sand on the coast; Kiel, Sylt.

(Continued from previous page.)
B. Species lacking processes on the gubernaculum.
(8) M. oxycerca de Man 1888: Mém. Soc. Zool. France 1, p. 10, Table 1, Figure 6; M. (Penzancia) o. 1889: ibid. 2, p. 7 Walcheren Island, mud on stones in seawater canal. (9) M. lata Cobb 1894: Proc. Linn. Soc. N. S. W. 8, p. 404. Sand, Port Jackson N. S. W. Common. (10) M. (Theristus) normandica de Man 1890: Mém. Soc. Zool. France 3, p. 69, Table 3, Figure 1. Coasts of Normandy and Calvados, very common; west coast of Ireland, 2—4 sajenes, mature in August (Southern). (11) M. mas-papillatus Cobb 1891: Proc. Linn. Soc. N. S. W. 5, p. 463. Sand at low tide, Aden. (12) M. polychaeta Steiner 1915: Zool. Jahrb. Syst. 38, p. 224, Table 22, Figures 1—3; very similar to M. pilosa Cobb — Sumatra, Sabang, diatom mud. (13) M. agilis de Man 1880, 1884: Nem. Niederl. Fauna, p. 43, Table 4, Figure 15; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 430. Terrestrial and freshwater species: Holland, all year round t., p.; Norway, Bygdøy (de Man); Austria, Lake Lunzersee in mud, 20 m, brooks, ponds (Micoletzky. (14) ? M. labiata Daday 1904: Zool. Jahrb. Syst. 19, p. 480, Table 27, Figures 1—3. Turkestan, Koi-Sary. Possibly belongs to another genus.
C. Species with males unknown.
(15) Th. arcticus (Steiner 1916) Monhystera lata Cobb var. arctica: Zool. Jahrb. Syst. 39, p. 641, Table 33, Figures 39a — c; White Sea strait in algae (16) M. horrida Steiner 1916: loc. cit., p. 643, Table 33, Figures 40a-c; from the same place. Both species probably belong to the foregoing group, similar to Th. polychaetus Steiner. (17) M. australis Cobb 1894: Proc. Linn. Soc. N. S. W. 8, p. 408. Sand at the tidemark at Port Jackson N. S. W. (18) M. gracilis de Man 1878: Tijd. Nederl. Dierk. Vereen. 3, p. 105, Table 8, Figure 11; Rouville 1904: CR. Ass. Franç. Avanc. Sci., p. 792. Naples (de Man), Sète (Rouville).

* Two species: (1) D. zeelandicus de Man 1880, 1884: loc. cit., p. 51, Table 6, Figure 23; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27 No. 7, p. 9, Figure 9. In brackish earth in Holland (de Man); Tvärminne Bay — Gulf of Finland — in mud (G. Schneider). (2) D. balatonicus Daday 1894, 1897: Zool. Jahrb. Syst. 10, p. 102, Table 11, Figures 14, 15. Balaton Lake in Hungary. This species is probably related to another genus (de Man, Mém. Soc. Zool. France 20, p. 81).

** Four species: (1) A. bioculatus (de Man 1878) Spira b.: Tijd. Nederl. Dierk. Ver. 3, p. 107, Table 8, Figure 13. Naples. (2) A. elegans de Man 1888: Mém. Soc. Zool. France 1, p. 16, Table 1, Figure 9. Coast of Holland. (3) A. dolichoposthius Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr 1, p. 123. A. elegans Steiner 1916: Zool. Jahrb. Syst. 39, p. 634, Table 17, Figures 38a, b; Table 33, Figures 38c — f. Murmansk: Ekaterininskaya Harbor, Lake Mogil'noe, White Sea strait, on algae. (4) Spira mediterranea de Man 1878 (loc. cit., p. 108, Table 9, Figure 14), subsequently related by him to this genus, also probably does not belong here; similarly (5) A. cobbi Steiner 1916: loc. cit., p. 637, Table 17, Figures 36a, b; Table 32, Figures 36c — e. White Sea strait, on algae.

† One species: Ae. elegans de Man 1907: loc. cit., p. 35, Table 1, Figure 2. On the coast of Yerseke (Holland).

1 (10). Oral cavity broad, in form of wide cone extending to anterior portion of esophagus.
2 (9). Anterior part not embraced by esophagus, narrow, ringlike.
3 (4). Lateral organs large, transverse-elliptical with very indistinct outline . . . . . . . . . . . . . . . . . . . . . . . . **Paramonhystera** Steiner
4 (3). Lateral organs circular.
5 (8). Oral cavity not toothed.
6 (7). Spicules long and thin, gubernaculum without posterior processes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Penzancia** de Man
7 (6). Spicules stout, usually short, gubernaculum usually with posterior processes . . . . . . . . . . . . . . . . . . **Theristus** Bastian
8 (5). Oral cavity toothed . . . . . . . . . . . . . . . . . . . . . . **Cobbia** de Man
9 (2). Anterior part not embraced by esophagus in form of long prism . . . . . . . . . . . . . . . . . . . . . . **Prismatolaimus** de Man
10 (1). Oral cavity narrow; either very short, or entirely absent.
11 (12). Oral cavity narrow and long; thickening observed in tube of esophagus. . . . . . . . . . . . . . . . . . . . . . . . . **Araeolaimus** de Man
12 (11). Oral cavity short or entirely absent; no thickening.
13 (14). Lateral organs longitudinally oval. . . . . . . . . . . **Disconema** n. g.
14 (13). Lateral organs circular.
15 (18). Oral cavity cup-shaped, sharply outlined posteriorly.
16 (17). Bulb absent, ten cephalic bristles . . . . . . . . **Linhomoeus** Bastian
17 (16). Bulb present, four cephalic bristles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Metalinhomoeus** de Man
18 (15). Oral cavity of other structure or entirely absent.
19 (22). Bulb present.
20 (21). Oral cavity distinct, with cuticular annules around it . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Desmolaimus** de Man
21 (20). Oral cavity indistinct, may also be entirely absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Terschellingia** de Man
22 (19). Bulb absent (present in some species wrongly related to Monhystera).
23 (24). Oral cavity conical, embraced by esophagus. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Monhystera** Bastian
24 (23). Oral cavity in form of anterior extension of esophagus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Prosphaerolaimus** n. g.

## Genus PARAMONHYSTERA Steiner 1916

Monhystera subg. Paramonhystera Steiner 1916: Zool. Jahrb. Syst. 39, p. 639.

280 Type species: P. megacephala Steiner 1916

These are medium-sized nematodes with annulated cuticle. The head has six lips, six labial and ten cephalic bristles, the latter in one row. The lateral organ disposed near the anterior margins of the head is **very large,** transversely oval, rarely almost circular. Its outlines are indistinct. The oral cavity is conical with a cuticular ring to which the esophagus is attached (as in Theristus, Penzancia, Cobbia). The esophagus is straight. The single ovary is anterior and straight. The spicules are short, slightly curved (in P. elliptica n. sp.).

The genus is similar to the genera mentioned above in the structure of the cuticle and the oral cavity, but differs from them sharply in the primitive structure of the lateral organ.

There are three species:

1) P. elliptica n. sp., see below.
2) P. setosa n. sp., see p. 204.
3) P. megacephala Steiner 1916: Z. Jahrb. Syst. 39, p. 639, Table 32, Figures 37a—f. White Sea strait, in algae.

1 (4). Lateral organs distinctly transversely oval.
2 (3). Only one circlet of four long bristles behind lateral organ. Latter shifted very close to anterior margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. elliptica** n. sp.
3 (2). Three circlets of bristles down to nerve ring. Lateral organ shifted somewhat posteriorly . . . . . . . . . . . . . . **P. setosa** n. sp.
4 (1). Lateral organs almost round . . . . . . . . . **P. megacephala** Steiner

### 57. **Paramonhystera elliptica** n. sp.

(Table 9, Figure 59)

$$♂\;\frac{—\quad 8.0\quad 19.3\quad 35.61^{*}\quad 55^{**}\quad 91.8}{1.5\quad 2.6\quad 3.2\qquad (3.7)\qquad 1.8}\;2100.$$

$$\alpha=27;\; \beta=4{,}1;\; \gamma=12.$$

$$♀\;\frac{—\quad 7.3\quad 18.3\quad 60^{\dagger}\quad 73\quad 91.7}{1.4\quad 2.5\quad 2.8\qquad 3.1\qquad 2.0}\;2800$$

$$\alpha=32;\; \beta=4.4;\; \gamma=12.$$

281

| Dimensions adult ♀ | Cephalic bristles | Posterior border of lateral organ | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | — | 22 | 30 | 215 | 550 |
| Width | 32 | 40 | 44 | 65 | 85 |

The **body** tapers very slightly to the beginning of the esophagus, by $^1/_3$ to the anus. From the end of the esophagus it tapers twofold anteriorly. The **cuticle** is thin, 2 $\mu$, distinctly annulated, especially in the inner layer. The annules are deeper and more distinct at the middle of the body. The subcuticular layer is full of numerous granules that give the worms a dark appearance. Some slender bristles lie on the subventral lines.

The **head** is truncated. Six distinct semicircular lips, 6 $\mu$ long, seal the mouth. The base of each of them is beset with a protruding labial papilla. The ten cephalic bristles, 17 $\mu$ long, lie in a plain circlet posterior to the

---

* Beginning of testis.
** Beginning of vas deferens.
† Beginning of uterus.

papillae. The sublateral bristles are considerably smaller, but better developed in the male. The lateral organ is very large, elliptical, extended transversely, and has a thin and smooth cuticular lining. The subcuticle is light and lacks granules. The borders are very thin and hardly conspicuous. In the middle posteriorly, there is a protruding papilla on which a nerve bundle terminates in several bristles (a—Figures 59a, b). Some long supplementary cephalic bristles about $20\mu$ long (half the body width) lie behind the lateral organ.

The oral cavity has the form of a broad funnel attached to a weakly developed cuticular ring. Anteriorly, the funnel is closed by the cephalic arch and lips; posteriorly, its thick lining continues directly into the tube of the esophagus. The subventral sectors of the esophagus are inserted somewhat more deeply into the funnel than the dorsal. The length of the oral cavity is: anterior chamber $8\mu$, posterior $20\mu$; width $25\mu$. The **esophagus** is straight, not very wide ($35-45\mu$, about 53% of the body width posteriorly). The nerve ring encircles the esophagus at its anterior
282 third. The narrow cervical gland is located posterior to the esophagus.

The **female genital tract** is single and anterior. The ovary is straight and short. The uterus has thin walls and contains five small round eggs $70\mu$ in diameter. Their shape varies somewhat according to their position in the uterus. There is a second, short, rudimentary uterus. The vagina obliquely traverses 0.6 of the body width.

There are apparently two short testes. The vas deferens is very long. The **spicules** are short, slightly curved, with an enlargement before the end (Figure 59d); their length is $54\mu$. The gubernaculum is in the form of a small thickening behind the spicules

The tail is conoid, short, slightly tapering to the end. The proportions are: length in female 4, in male 3.5; width at end 0.2; spicules 1.4.

Many specimens of this species were found in deep sand of Peschanaya Bay 1, 6, 7.12; algae on it 6.12, female; oyster banks 6.12.

Several specimens of another species very similar to this one, but of smaller size (the adult female is only $1{,}400\mu$), were found in mussels under the station 6.12; I have not yet described it because of insufficient material.

### 58. **Paramonhystera setosa** n. sp.

(Table 9, Figure 60)

$$\text{young ♀}\ \frac{\text{—}\quad 10.0\quad 17.0\quad ?\quad 71.2\quad 91.8}{1.4\quad 2.9\quad 3.3\quad 4.0^{*}\quad 3.5\quad 2.4}\ 2630$$

$$\alpha=25;\ \beta=5^1/_2;\ \gamma=12.$$

| Young ♀ | Cephalic bristles | Papilla of lateral organ | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 15 | about 25 | 160 | 410 |
| Width | 30 | 37 | | 65 | 85 |

---

* Thickest part.

283 These are short, stout nematodes. The widest part is opposite the uterus anterior to the vulva. In the female the body tapers to the end almost twofold, and to the beginning of the esophagus only very slightly. From this point anteriorly, it tapers $2^1/_2$ times. The **cuticle** is thin ($1^1/_2\mu$) and annulated, the annules being located on its inner surface and $2\mu$ apart. Long and slender bristles are dispersed over the entire body in the sublateral and submedian lines. Anterior to the nerve ring there are three circlets of very long bristles. The most anterior of these is the most developed, the posterior the least.

The **head** is somewhat more rounded than in P. elliptica. The lips are well developed, as in the latter species ($5\mu$ long). The labial papillae are converted into short, stout bristles. The ten short cephalic bristles are $13\mu$ long ($^1/_3$ of the head width) and arranged in a plain circlet. The sublateral bristles are shorter ($8\mu$) and thinner. Some extraneous bristles, two short subdorsal on each side, are present in this circlet. The lateral organ is somewhat smaller than in the forgoing species, both relatively and absolutely ($10\mu$ long, $26\mu$ wide) and is shifted more posteriorly. The sensory capsule is very large ($30\times17\mu$). Its papilla is located on the posterior margin of the lateral organ, which is devoid of bristles, unlike the preceding species.

The oral cavity is constructed as in the forgoing species, but its walls in the posterior part are somewhat thinner and it is narrower and longer. Its dimensions are: length of anterior part $6\mu$, of posterior part $19\mu$; width $19\mu$. The esophagus is straight, gradually widening from $34\mu$ anteriorly to $42\mu$ posteriorly (half the body width). The nerve ring is posterior to its middle.

The female genital tract was not fully developed. The vulva is removed far posteriorly.

The **tail** (Figure 60b) is fairly short, conoid in its anterior half, rounded at the end. Its length is $3.5\mu$, width at the end $0.22\mu$.

Two specimens of this species were found in Zostera 5.12.

## 284 Genus PENZANCIA de Man 1889

Theristus ex p. Bastian 1865.
Monhystera subg. Penzancia de Man 1889 ex. p.: Mém. Soc. Zool. France 2, p. 7.

Type species: P. velox (Bastian 1865) de Man 1889

These are nematodes of medium size with an annulated cuticle. On the head in front of the oral cavity a light portion projects. The labial papillae are converted into short bristles; the cephalic bristles are long, in a plain circlet. The lateral organs are circular. The oral cavity is spacious, stiffened in the middle by a chitinized ring, to which the esophagus is attached. Anterior to this ring, in the region of the light lips, the walls are thin; posteriorly, the cavity gradually narrows conically, becoming transformed into the esophageal tube. The esophagus is wide, without a bulb. The female genital tract is single and anterior; the ovary is straight.

The spicules are very long and slender, with adjacent gubernaculum. The tail is long.

This genus forms with genera Paramonhystera Steiner, Theristus (Bastian) de Man, and Cobbia de Man a compact group of originally marine nematodes formerly incorporated in genus Monhystera. The long, slender spicules differentiate it from these three genera, while all four genera are easily differentiated from the other species of Monhystera s. lat. by their fairly coarsely annulated cuticle and by the characteristically wide oral cavity with its chitinized ring.

I enumerate here only two species:

1) P. velox (Bastian 1865) Theristus v.: Trans. Linn. Soc. 25, p. 157, Table 13, Figures 189–191; Monhystera v.: Bütschli 1874: Abh. Senck. Ges. 9, p. 26, Table 2, Figure 6; Monhystera (P.) v. de Man 1889: Mém. Soc. Zool. France 2, p. 7, M. v. Steiner 1916: Zool. Jahrb. Syst. 39, p. 645, Table 17, Figures 42a, e; Table 34, Figures 42b, d, f. Falmouth, in algae at low tide (Bastian). Libava, sand 5–20 f. (Grimm); Kiel in sand and algae on the coast (Bütschli); Penzance in algae (de Man); White Sea strait on algae (Steiner).
2) P. euxina n. sp., see below.

285
1 (2). Lateral organ $^1/_6$ of body width, $1^1/_2$ head lengths from anterior end . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. velox** (Bastian)
2 (1). Lateral organ larger than $^1/_4$ of head width, less than one head length from anterior end . . . . . . . . . . . . . . . . . . **P. euxina** n. sp.

59. **Penzancia euxina** n. sp.
(Table 9, Figure 61)

$$\text{♂}\ \frac{—\quad 5.9\quad 14.1\quad 20\quad 34\quad 92.3}{0.9\quad 1.6\quad 1.9\quad 2.1\quad 1.4}\ 2300$$

$$\alpha=52;\ \beta=7;\ \gamma=13.$$

$$\text{♀}\ \frac{—\quad 5.5\quad 14.4\quad 54\quad 69\quad 91.5}{1.0\quad 1.7\quad 1.9\quad 2.2\quad 1.5}\ 2800$$

$$\alpha=45;\ \beta=7;\ \gamma=12.$$

| Dimensions ♀ | Cephalic bristles | Lateral organ | Cervical pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 5 | 20 | 150 | 170 | 390 |
| Width | 26 | 35 | | 50 | 55 |

The **body** is fairly stout, tapering to the anus by $^1/_3$ , to the beginning of the esophagus only very slightly, and hence anteriorly twofold. The **cuticle** is quite thick (about $1^1/_2\mu$), annulated externally; the intervals between the annules are also $1^1/_2\mu$. The bristles are quite numerous, denser subventrally.

The **head** (Figure 61a) is sharply truncated; its regularity is broken by six anteriorly projecting elevations upon which the short labial papillae are set. Behind these lies a circlet of ten long and slender bristles. The submedian bristles are shorter (only $14\mu$), while the remaining six are $16\mu$ long. The lateral organ is circular, with a thin bottom; it is $9\mu$ in diameter in the female ($^1/_4$ of the head width). In the male it is somewhat larger ($12\mu$, or about $^1/_3$ of the head width). Anterior to the lateral organ lies a rather irregular, clearly marked cephalic line.

The **oral aperture** is closed by six lamellar lips. The oral cavity in general consists of two chambers. The anterior is free and narrows anteriorly, its walls becoming thinner. The posterior chamber is surrounded by the esophagus and tapers conically posteriorly, gradually 286 becoming transformed into the esophageal tube. The regularity of its form is somewhat broken by the intrusion of the esophageal musculature into it opposite each sector. At the boundary between the two chambers lies a thick ring to which the esophageal musculature attaches anteriorly. The dimensions of the oral cavity are: length of anterior chamber $8\mu$, of posterior chamber $16\mu$, width $22\mu$. The esophagus is stout, of even thickness over its entire extent ($27-30\mu$, 60–65% of the body width). The nerve ring is very thin. The small cervical gland lies behind the end of the esophagus; it is long and narrow, measuring $40\times 80\mu$. The cervical pore lies not far behind the nerve ring. The intestine consists of two or four rows of cells.

The **female genital tract** is single; the ovary is single and straight. The uterus is very long, containing 2–4 eggs measuring $70\times 40-45\mu$. Judging from the dimensions, larger ones may also be located there. The vagina is thin-walled, obliquely traversing half the body width. Two short testes, in the form of pendants, are set on a large seminal vesicle; the posterior testis is shorter. The spicules (Figures 61d, e) are long ($70\mu$), thin, evenly curved. Their curvature may be greater or lesser. The thin gubernaculum (about $30\mu$ long) encircles their ends

The **tail** (Figures 61c, d) is quite long and thick at the end. In the female it is longer and tapers more evenly to the end, while in the male it tapers to the middle whereupon a portion of even diameter follows. The proportions are: length of tail in male 3.7, in female 5.5; width at end 0.22–0.25; spicules about 2; gubernaculum 9.

Two females and one male of this species were found in dirty sand from Grafskii Wharf 1.12; immature females in Kruglaya Bay 1.12.

## Genus COBBIA de Man 1907

Mém. Soc. Zool. France 20, p. 47.

Type species: C. trefusiaeformis de Man 1907

287 This genus is very similar to Penzancia, more especially to Theristus, but is differentiated from them by the structure of the oral cavity. Here are located two or three **teeth, bearing the apertures of the esophageal glands.**

The cuticle is annulated, the bristles long. The female genital tract is single and anterior. The spicules are short and stout; the gubernaculum has no posterior processes. All three known species are marine.

1) C. trefusiaeformis de Man 1907: Mém. Soc. Zool. France 20, p. 47, Table 1, Figure 7. Jerseke (Holland).
2) C. triodonta n.sp., see below.
3) C. sabulicola n.sp., see p. 209.
Here also is possibly related Monhystera demani Rouville 1903 (CR. Ass. Franç. Avanc. Sci. 1904, p. 792 from Sète.

1 (4). Three teeth.
2 (3). Lateral organ $^1/_3$ of head width . . . . . **C. trefusiaeformis** de Man
3 (2). Lateral organ $^1/_5$ of head width . . . . . . . . . . . **C. triodonta** n. sp.
4 (1). Two subventral teeth. . . . . . . . . . . . . . . . . . . **C. sabulicola** n. sp.

### 60. **Cobbia triodonta** n.sp.
(Table 9, Figure 62)

$$\text{♀}\ \frac{—\quad 6.0\quad 16.3\quad 45^{*}\quad 60^{\dagger}\quad 86}{1.2\quad 1.7\quad 1.7\quad 2.3^{**}\quad 2.1^{\dagger}\quad 1.4}\ 2940$$

$$\alpha=43;\ \beta=6;\ \gamma=7.$$

$$\text{♂}\ \frac{—\quad 5.8\quad 16.5\quad —\quad 86.0}{1.2\quad 1.8\quad 1.9\quad 1.9\quad 1.6}\ 2750$$

$$\alpha=54;\ \beta=6;\ \gamma=8^1/_3.$$

| Dimensions ♀ | Labial bristles | Cephalic bristles | End of oral cavity | Lateral organ | Nerve ring | Cervical pore | End of esophagus |
|---|---|---|---|---|---|---|---|
| Length | – | 12 | 23 | 46 | 145 | 150 | 405 |
| Width | 27 | 30 | 40 | 43 | 43 | – | 43 |

The **body** is quite slender, of very even width. In the female, it is widest opposite the uterus, while it is thinner at the vulva. The body in the female tapers to the anus $1^1/_2$ times, only slightly in the male. In the 288 female, it tapers $1^1/_2$ times to the beginning of the esophagus; it hardly tapers in the male. From this point, it tapers $1^1/_2$ times more. The **cuticle** is thin, annulated, $1^1/_2\mu$; externally, the annules are $3\mu$ apart, internally, they are twice as frequent. The bristles are very few, if present at all.

The **head** is truncated with rounded margins. The oral aperture is closed by six wide lips that are rounded at the end, exactly as in Oncholaimini (Figure 61c). Each lip is about $6\mu$ long. The ten cephalic bristles are disposed in a plain circlet, the sublateral bristles being somewhat shorter (24 and $19\mu$) and correspondingly thinner (see Figure 61c). The lateral organ is shifted far posteriorly (see Figure 61a); it is circular with thin walls; a curved funnel bearing nerves opens at its middle.

The general form of the **oral cavity** is funnel-shaped; anteriorly, there is a ring not embraced by the esophagus. This ring is thicker opposite the sectors of the esophagus and thinner opposite its angles. Only inconspicuous processes of the walls of the capsule extend anterior to it (see Figures 61b: a, opposite sector, b, opposite angle). Inside the oral cavity on each of the three sectors there rises an elevation so large in this species that it may be designated a tooth. All three teeth (see Figures 61a, b, c) are located at the same height, but the dorsal is less developed (Figure 61b). A duct of the esophageal glands opens on each tooth (gl. oes. —Figure 61b). Posteriorly, the oral cavity is imperceptibly transformed into the esophageal tube. The latter is well developed, muscular, evenly expanding from $20\mu$ anteriorly to $27\mu$ posteriorly (63 % of the body width). The nerve ring encircles its anterior third. The cervical pore lies just posterior to the nerve ring.

The **ovary** is single, anterior, and straight; the uterus has thin walls. The eggs measure $125\times 45\mu$ with a thick shell. The vagina is oblique, with several large glands near it.

The **spicules** (Figure 61g) are short ($40\mu$) and stout. Their base is 289 slightly swollen. The gubernaculum covers their ends.

The **tail** is very long, conically tapering to the posterior third, whence follows a thin filiform part. The proportions are: length of tail in male 8, in female 9; width at end 0.1; spicules 1.0.

One female and a young male were found in Zostera from the Chernaya River 5.12.

### 61. **Cobbia sabulicola** n. sp.
(Table 9, Figure 63)

$$\text{♀}\ \frac{—\quad 8.5\quad 25\quad 52^{*}\quad 68\quad 87}{1.2\quad 2.2\quad 2.9\quad 3.0^{*}\quad 2.9\quad 1.9}\ 1900$$

$$\alpha=33,\ \beta=4,\ \gamma=7-8.$$

| Dimensions ♀ | Cephalic bristles | End of oral cavity | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 20 | 50 | 175 | 445 |
| Width | 27 | 32 | 35 | 45 | 55 |

The **body** tapers by $^1/_3$ to the anus, hardly to the beginning of the esophagus, from here to the anterior end $2^1/_2$ times. The **cuticle** is thin ($2\mu$) and annulated; the annules are observed externally and internally and are $3\mu$ apart. Some long and thin bristles are set in the sublateral lines.

The **head** is truncated. All that part of the head lying anterior to the oral cavity is transparent, in the form of a dome with an uneven surface. The labial bristles are set on this dome anteriorly. I could not determine if true lips were present, but they probably are. There are ten cephalic bristles; the sublaterals are somewhat smaller and set posteriorly to the submedians (16 and $12\mu$), and are shorter than the width of the head. A supplementary cephalic bristle is set immediately posterior to the lateral, so that a circlet of 12 bristles is formed. The lateral organ is

---

* Beginning of genital tracts
** Maximum width
† Vulva and corresponding width

* Length and width at beginning of uterus.

shifted far posteriorly, is circular with thin walls, and large ($13\mu$, or more than $^{1}/_{3}$ of the body width).

290 The oral cavity is conical. Anteriorly, it has no walls of its own, but is bordered by the thin cuticle of the dome. This is followed by a thick cuticular ring adjacent to the outer cuticle, with special elevations under it, composing a kind of cephalic capsule. Its larger posterior chamber is conical, with small elevations on the subventral sectors on which the esophageal glands open. The length of the anterior chamber is $6\mu$, the posterior $14\mu$; the maximum width is $16\mu$. The esophagus is very long but not stout, hardly thickening at its posterior end. Its thickness anteriorly is $20\mu$, posteriorly $24\mu$ (0.4 of the body width).

The ovary is single, anterior, and straight; the uterus in my specimens is small.

The **tail** is very long, conically narrowing to the extreme tip. The proportions are: length 6.5; width at end 0.12.

Several females were found in sand from Kruglaya Bay 1.12.

## Genus **MONHYSTERA** Bastian 1865

Trans. Linn. Soc. 25, p. 97; Bütschli 1873; N. Acta 26, No. 5, p. 58; 1874 ex p.: Abh. Senck. Ges. 9, p. 24; de Man ex p. 1876: Tijd. Nederl. Dierk. Ver. 2, p. 174; 1878: ibid. 3, p. 104; 1884: Nemat. Niederl. Fauna, p. 35; 1888: Mém. Soc. Zool. France 1, p. 4; Cobb 1888: Jen. Zeitschr. Naturwiss. 23, p. 71; Jägerskiöld 1909: Süsswasserfauna Deutschlands, Heft 16, p. 10; Hofmänner 1913. Revue Suisse Zool. 21, p. 608; Menzel 1914: Arch. Naturgesch. 80A, Heft 3, p. 43.

I did not encounter this genus in the Black Sea. For convenience, I compile a separate list of the published data on the many species of this genus. It is predominantly a freshwater genus, but there are many marine species also. The type species must be considered Monhystera stagnalis Bastian 1865.

Genera Theristus and Penzancia having been removed, the following species, characterized by a **small oral cavity and weakly developed lips**, are incorporated here.

A. Marine species: (1) M. ambigua Bastian 1865: Trans. Linn. Soc. 25, p. 99, Table 9, Figures 14, 15; M. ambiguoides Bütschli 1874: Abh. Senck. Ges. 9, p. 27, Table 3, Figure 4; M. a. de Man 1888: Mém. Soc. Zool. France 1, p. 7, Table 1, Figure 4; Falmouth, sand at low tide (Bastian); Kiel, algae on the coast (Bütschli); Walcheren, mud on stones 291 in canal (de Man). (2) M. barentsi Steiner 1916: Zool. Jahrb. Syst. 39, p. 648, Table 34, Figure 14a–c. White Sea strait, algae. (3) M. bipunctata G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 15, Figure 5. Mud from the bottom of Tvärminne Bay. (4) M. brevicollis Cobb 1894: Proc. Linn. Soc. N. S. W. 8, p. 403, sand at low tide, Port Jackson N. S. W. (5) M. diplops Cobb 1894: loc. cit., p. 401, Figure 8; algae and sand at the same place. (6) M. disjuncta Bastian 1865: Trans. Linn. Soc. 25, p. 98, Table 9, Figures 12, 13. Sand at low tide, Falmouth. (7) M. leptosoma de Man 1893: Mém. Soc. Zool. France 6, p. 83, Table 5, Figure 2. Falmouth, on rocks in algae, in September. (8) M. ocellata Bütschli 1874: Abh. Senck. Ges. 9, p. 29, Tables 2, 3, Figure 10; de Man 1888: Mém. Soc. Zool. France 1, p. 6, Table 1, Figure 2; Kiel, on the coast (Bütschli); Walcheren, mud on stones (de Man). (9) M. parva (Bastian 1865) Tachyhodites p.: Trans. Linn. Soc. 25, p. 156, Table 13, Figures 185, 186; M. p. de Man 1888: Mém. Soc. Zool. France 1, p. 7, Table 1, Figure 3. Falmouth, Walcheren, on the coast. (10) M. socialis Bütschli 1874: loc. cit., p. 28, Table 2, Figure 8; common in brackish water near Kiel (Bütschli); near Copenhagen, common on the coast in algae (Ditlevsen). (11) M. stenosoma de Man 1907: Mém. Soc. Zool. France 20, p. 36, Table 1, Figure 3; Jerseke (Holland); (12) M. trabeculosa G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 13, Figure 4. Mud from the bottom of Tvärminne Bay. (13) M. uniformis Cobb 1914: Nem. Shackleton Exp. Antarctic Seas (quoted from Steiner).

B. **Freshwater species**: (14) M. alpina nom. nov.; M. demani Hofmänner et Menzel 1914: Zool. Anz. 44, p. 81, Figures 1, 2; 1915: Revue Suisse Zool. 23, p. 122; Menzel 1914: Arch. Naturg. 80A, Heft 3, p. 44. Switzerland p. (15) M. crasissima Ditlevsen 1911: Vidensk. Medd. naturh. Fören. Kjöbenhavn 63, p. 219, Table 3, Figures 14, 15, 22. p. Denmark. (16) M. dispar Bastian 1865: Trans. Linn. Soc. 25, p. 97, Table 9, Figures 1, 2; de Man 1884: Nem. Niederl. Fauna, p. 41, Table 3, Figure 12; 1907: Ann. biol. lac. 2, p. 11; Jägerskiöld 1900: Süsswasserfauna Deut., Heft 16, p. 12; Hofmänner 1913: Revue Suisse Zool. 21, p. 612; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 422, Table 10, Figure 3; Stefanski 1914: Recherches Ném. Léman, p. 18, Table 1, Figures 3a, b; 1916: Zool. Anz. 46, p. 377; Syn.: M. crassa Bütschli 1873: N. Acta 26, No. 5, p. 63; Daday 1897: Zool. Jahrb. Syst. 10, p. 97; Jägerskiöld 1909: loc. cit., p. 13. In fresh water and earth. Russia—Obersee near Revel [Tallin], Finland p. (G. Schneider); Denmark, Germany, Holland, England, France, Switzerland, Austria (Lunz, Salzburg, Eastern Alps, Chernovtsy), Holland; Tunis. (17) M. filiformis Bastian 1865: Trans. Linn. Soc. 25, p. 98, Table 9, Figures 7, 8; Bütschli 1873: N. Acta 26, No. 5, p. 63; de Man 1884: Nemat. Niederl. Fauna, p. 41, Table 3, Figure 13; 1885: Tijd. Nederl. Dierk. Ver. (2) 1, p. 19; Jägerskiöld 1909: Süsswf. Deut., p. 14; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 426, Table 10, Figure 4. Stefanski 1914: Recherches Ném. Léman p. 21; 1916: Zool. Anz. 46, p. 378. Syn.: M. rustica Bütschli 1873: loc. cit., p. 63; Cobb 1893: Macleay Memorial Volume, p. 30; Agric. Gaz. N. S. W. 4, p. 822, Figure 40. In fresh water and earth: Russia (Novaya Zemlya, Finland, Moscow), Germany, Holland, England, France, Austria, Switzerland, Australia (N. S. Wales, Fiji). (18) M. fülleborni Daday 1910: Zoologica 59, p. 44, Table 2, Figures 10–12. Africa, Lake Nyassa. (19) M. helvetica Steiner 1914: Arch. Hydrobiol. Planktonk. 9, p. 421. Switzerland p. (20) M. impetuosa Cobb 1906: Rep. on the Work of the Exper. Stat. of the Hawaiian Sugar Planters' Assoc. Divis. Pathol. Physiol. Bull. No. 6, p. 186. Hawaiian Islands t. (21) M. insignis Cobb 1893: Agric. Gaz. N. S. W. 4, p. 823, N. S. Wales t. (22) M. longicaudata Bastian 1865: Trans. Linn. Soc. 25, p. 98, Table 9, Figures 5, 6. England, p., t. (23) M. macrura de Man 1880;

292 1884: Nemat. Niederl. Fauna, p. 39, Table 3, Figure 9; Hofmänner et Menzel 1915: Revue Suisse Zool. 23, p. 127. Russia (Moscow), Germany, Holland, France, Switzerland, Tunis, p. t. (24) M. microphthalma de Man 1880: Nemat. Niederl. Fauna, p. 38, Table 2, Figure 8; Daday 1897: Zool. Jahrb. Syst. 10, p. 99; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 10, Figure 2. Brackish water species: Holland, Gulf of Finland; (?) Hungary. (25) M. paludicola de Man 1881; 1884: Nem. Niederl. Fauna, p. 37, Table 2, Figure 7; 1885: Tijd. Nederl. Dierk. Ver. (2) 1, p. 18; Daday 1897: Zool. Jahrb. Syst. 10, p. 98; 1905: Zoologica 44, p. 51, Table 3, Figures 2—4; Jägerskiöld 1909: Süsswasserfauna Deut., Heft 16, p. 11; Hofmänner et Menzel 1913: Revue Suisse Zool. 21, p. 609, Table 15, Figure 1; 1915, ibid. 23, p. 123; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 415. Stefanski 1914: Recherches Ném. Léman p. 17. Russia (Finland, Moscow, Bologoe), Austria, Hungary, Holland, Switzerland, South America (Paraguay). (26) M. stagnalis Bastian 1865: Trans. Linn. Soc. 25, p. 97, Table 9, Figures 9—11; Bütschli 1873: N. Acta 26, No. 5, p. 61, Table 20, Figure 22; Linstow 1876: Arch. Naturg. 42, p. 12, Table 2, Figure 31 (M. ocellata); Oerley 1881: Termész. Füz. 6; Daday 1897: Zool. Jahrb. Syst. 10, p. 96; Jägerskiöld 1909: Süsswf. D., Heft 16, p. 10; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 410, Table 15, Figure 15. Austria (Eastern Alps, Lunz, Chernovtsy); Switzerland, Russia (Bologoe); England, Germany, Hungary. (27) M. papuana Daday 1899: Termész. Füz. 24, p. 4, Table 1, Figures 19, 20 p. New Guinea. (28) M. pratensis Cobb 1893: Agric. Gaz. N. S. W. 4, p. 823, N. S. Wales. (29) M. propinqua Daday 1905: Zoologica 44, p. 52, Table 2, Figures 10—12. Paraguay p. (30) M. pseudobulbosa Daday 1897: Zool. Jahrb. Syst. 10, p. 98, Table 13, Figures 3—5. Hungary. (31) M. rivularis Bastian 1865: Trans. Linn. Soc. 25, p. 97, Table 9, Figures 3, 4. England, p, t. (32) M. simplex de Man 1880; 1884: Nemat. Niederl. Fauna, p. 43, Table 4, Figure 14. Russia (Moscow), Holland, England, Austria, Germany, Switzerland, France, Norway. (33) M. similis Bütschli 1873: N. Acta 26, No. 5, p. 62, Table 5, Figure 30; de Man 1884: Nemat. Niederl. Fauna, p. 40, Table 3, Figure 11; Daday 1897: Zool. Jahrb. Syst. 10, p. 97; 1908: Math. naturw. Ber. Ungarn 26, p. 283; Jägerskiöld 1909: Süsswf. D. Heft. 16, p. 13; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 420. Stefanski 1914: Recherches Ném. Léman p. 20. Switzerland, Austria, France, Germany, Holland, Hungary, Poland, Finland, Denmark, Mongolia, Africa (Lake Nyassa). (34) M. subrustica Cobb 1906: Rep. Work Exper. Stat. Hawaiian Sugar Planters' Assoc. Divis. Pathol. Physiol. Bull. No. 6, p. 185. Hawaiian Islands t. (35) M. tatrica Daday 1897: Zool. Jahrb. Syst. 10, p. 96, Table 13, Figures 6, 7. Hungary. (36) M. villosa Bütschli 1873: N. Acta 26, No. 5, p. 64, Tables 5, 6, Figure 28; de Man 1885: Tijd. Nederl. Dierk. Ver. (2) 1, p. 10; Menzel 1914: Arch. Naturg. 80A, Heft 3, p. 45; Stefanski 1914: Recherches Ném. Léman p. 21; Steiner 1916: Zool. Anz. 47, p. 63, Figures 6a—c; Syn.: M. australis Cobb 1893: Agric. Gaz. N. S. W. 4, p. 824, p, t. Holland, Germany, Switzerland, Hungary, Novaya Zemlya, Australia. (37) M. vulgaris de Man 1880; 1884: Nemat. Niederl. Fauna, p. 39, Table 3, Figure 10; 1885: Tijd. Nederl. Dierk. Ver. (2) 1, p. 19; 1907: Ann. Soc. Zool. malacol. Belgique 41, p. 158; Jägerskiöld 1909: Süsswf. D., Heft 16, p. 12; Micoletzky 1914: Zool. Jahrb. Syst. 36, p. 417, Table 9, Figure 2; Hofmänner 1914: Zool. Anz. 44, p. 91; 1915: Revue Suisse Zool. 23, p. 125, Table 4, Figure 3. Stefanski 1914: Recherches Ném. Léman p. 19. Russia (Moscow, Novaya Zemlya), Germany, Holland, France, Switzerland, Austria, Tunis.

293 Apart from these, Monhystera includes species that should be in other genera, or should have new genera established for them:

A. **Marine species:** (1) M. anechma Southern 1914: Proc. Roy. Irish. Ac. 31, pt. 54, p. 13, Table 3, Figures 7a-f. Western Ireland, sand with coquina, 24 sajenes. (2) M. cephalophora de Man 1878: Tijd. Nederl. Dierk. Ver. 3, p. 106, Table 7, Figure 12. Naples. (3) M. demani Rouville 1903; 1905: CR. Ass. Franç. Avanc. Sci. p. 792; Sète, canal de Bourdigues.

B. **Freshwater and terrestrial species:** (4) M. annulifera Daday 1905: Zoologica 44, p. 52, Table 2, Figures 15—17. Paraguay p. (5) M. bulbifera de Man 1880; 1884: Nemat. Niederl. Fauna p. 44, Table 4, Figure 16. Holland, Switzerland, Ireland. (6) M. carcinicola Baylis 1915: Ann. Mag. Nat. Hist. (8) 16, p. 418, Figures 4—6. In the branchial cavity of terrestrial crabs from Jamaica. (7) M. crasissides Micoletzky 1913; 1914: Zool. Jahrb. Syst. 36, p. 424, Table 15, Figures 16a-c. Austria. (8) M. dintheriana de Man 1885: Tijd. Nederl. Dierk. Ver. (2) 1, p. 2, Table 1, Figure 1. Holland t. (9) M. dubia Bütschli 1873: N. Acta 26, No. 5, p. 65, Table 21, Figure 26. Daday 1897: Zool. Jahrb. Syst. 10, p. 95, Table 11, Figure 9; G. Schneider 1906: Acta Soc F. Fl. Fenn. 27, No7, p. 12; Jägerskiöld 1909: Süsswf. Deut., Heft 16, p. 14; (nec Steiner 1913: Hofmänner 1913, 1914, 1915). Germany, Hungary, Gulf of Finland. I definitely oppose Hofmänner's inference on the identity of this species with the marine Theristus setosus Bütschli 1874. Bütschli 1873, p. 60, 66 clearly mentions that the "Seitenkreischen" are spiral, comparing them even with those of Comesoma. Furthermore, all authors describe the lateral organs of Th. setosus as distinctly circular. (10) M. longicauda Daday 1899: Termész. Füzetek 24, p. 5, Table 2, Figures 3, 4. New Guinea p. (11) M. wilsoni Baylis 1915: Ann. Mag. Nat. Hist. (8) 16, p. 415, Figures 1—3. In branchial cavity of terrestrial crabs from Jamaica.

## Genus LINHOMOEUS Bastian 1865

Trans. Linn. Soc. 25, p. 154.
Bütschli 1874: Abh. Senck. Ges. 9, p. 31.
De Man 1889; Mém. Soc. Zool. France 2, p. 207.

Type species: L. hirsutus Bastian 1865

The body is frequently filiform, sometimes of quite considerable size. The cuticle is thin, with a slight annulation. The epidermal fields are very wide and restrict the muscles, which are so weakly developed that

Bütschli (1874, p. 31) considers them to be meromyarian. My specimens
294 were too poorly preserved for anything to be seen in them. There are six labial papillae, ten cephalic bristles **disposed in one circlet. The lateral organs are circular, with a very thick bottom,** and are therefore very conspicuous. **The oral cavity is quite considerable,** tapers anteriorly, the broad and flat posterior wall joining the esophagus, which gradually expands posteriorly, not forming a bulb. The ovaries are frequently paired, more rarely unpaired, and straight. The spicules are arched. **The gubernaculum has two posterior processes.** The tail is of various form; in the majority it is long and conoid, but may be also thick and blunt. This is one of the features by which the subgenera are differentiated. In females, there is an histolytic breakdown of the tail, resulting in a short blunt tail being formed of the long conoid one. It is thus necessary to be particularly careful when distinguishing subgenera.

This genus was first described by Bastian (1865), then in more detail by Bütschli (1874) and de Man (1889). Later, de Man (1907) proposed a very convenient subdivision into subgenera, which I also follow.

The similarity of Linhomoeus to Siphonolaimini should be noted: there is the same softness of coating, the strongly developed lateral fields, the rounded head, and the histolysis of the tail in females.

1st subgenus: Eulinhomoeus de Man 1907: Mém. Soc. Zool. France 20, p. 74: oral cavity with denticles along margins of aperture of esophagus. Tail cylindrical. One species, consequently type species of the subgenus:

1) L. (Eul.) elongatus Bastian 1865: Trans. Linn. Soc. 25, p. 155, Table 12, Figures 180, 181; de Man 1889: Mém. Soc. Zool. France 2, p. 207, Table 7, Figure 11; Steiner 1916: Zool. Jahrb. Syst. 39, p. 592, Table 31, Figure 34. Falmouth in algae. (Bastian), Vlissingen, St. Vaast (de Man); Kola Gulf (Savel'ev). White Sea strait in algae (Steiner).

2nd subgenus: Linhomoeus s. str. de Man 1907. Mém. Soc. Zool. France, 20, p. 74: oral cavity without denticles. Tail cylindrical. Type subgenus: L. hirsutus Bastian 1865.

2) L. hirsutus Bastian 1865: Trans. Linn. Soc. 25, p. 154, Table 12, Figures 178, 179; Bütschli 1874: Abh. Senck. Ges. 9, p. 31, Table 3, Figure 15. Falmouth (Bastian), Oyster bank near Sylt (Bütschli).

295

3) L. obtusicaudatus de Man 1889: Mém. Soc. Zool. France 2, p. 6. Penzance, rare.

1 (2). Female genital tract double . . . . . . . . . . . . . **L. hirsutus** Bastian
2 (1). Female genital tract single . . . . . . . . . **L. obtusicaudatus** de Man

3rd subgenus: Paralinhomoeus de Man. Oral cavity without denticles. Tail pointed.* Type subgenus: L. (P.) Lepturus de Man 1907.

4) L. (P.). Lepturus de Man 1907: Mém. Soc. Zool. France 20, p. 74, Table 4, Figure 15. Not very common. Veere, Jerseke, Falmouth (de Man), Kola Gulf (Savel'ev).

5) L. (P.) filiformis n. sp., see p. 215.

6) L. (P.) ostraearum n. sp., see p. 216.

7) L. (P.) tenuicaudatus Bütschli 1874: Abh. Senck. Ges. 9, p. 32, Table 3, Figure 16. Sand at 10 sajenes. Kiel Firth, together with Paroncholaimus vulgaris Bastian.

8) L. (P.) linurus Saveljev 1912: Trav. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 120. Kola Gulf, Ekaterininskaya Harbor — mud with stones at 30—40 m.

9) L. (P.) attenuatus de Man 1907: Mém. Soc. Zool. France 20, p. 78. Very common. Jerseke.

10) L. (? P.) mirabilis Bütschli 1874: Abh. Senck. Ges. 9, p. 33, Table 4, Figure 17. Kiel Firth, sand at 10 sajenes with Paroncholaimus vulgaris Bastian.

1 (12). One female gonopore.
2 (11). Head width about $1/2 - 1/3$ of width at end of esophagus.
3 (10). Tail not very long, shorter or just longer than esophagus.
4 (9). Body thin, $1^1/_2 - 2\,\%$ .
5 (8). Four long and six short cephalic bristles.
6 (7). Lateral organ small — about $1/4$ of the corresponding body width . . . . . . . . . . . . . . . . . . . . . . . . . . **L. lepturus** de Man
7 (6). Lateral organ almost half body width. . . . . . **L. filiformis** n. sp.
8 (5). All ten cephalic bristles short . . . . . . . . . **L. ostraearum** n. sp.
9 (4). Body thick, about 3 % . . . . . . . . . . . **L. tenuicaudatus** Bütschli
10 (3). Tail very long, almost twice longer than esophagus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **L. linurus** Saveljev
11 (2). Head width equal to $1/3$ of body width at beginning of intestine . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **L. attenuatus** de Man
12 (1). Two female gonopores. . . . . . . . . . . . . . **L. mirabilis** Bütschli

296

### 62. **Linhomoeus (Paralinhomoeus) filiformis** n. sp.

(Table 9, Figure 57)

$$\text{♂}\ \frac{-\quad 4.1\quad 8.0\quad ?\quad 91.0}{1.0\quad 1.3\quad 1.3\quad 1.7\quad 1.6}\ 1890$$

$$\alpha = 58;\ \beta = 12^1/_2;\ \gamma = 11.$$

| Dimensions ♂ | End of oral cavity | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 6 | 25 | 75 | 145 |
| Width | 18 | 22 | 25 | 27 |

The **body** is filiform, of very even thickness, tapering anteriorly very little. The **cuticle** is $1^1/_2\,\mu$ thick, annulated; the outer annules are $1^1/_2\,\mu$ apart, the inner approximately twice as frequent. The bristles are short and few.

The **head** (Figure 57a) is rounded. Around the oral aperture there is an elevation, near which are apparently six labial papillae. The cephalic bristles are composed of four large submedians $11\,\mu$ long and six small bristles $2\,\mu$ long. The lateral organ is large ($10\,\mu$), almost half

---

* The possibility of histolysis of the tail in females should be noted. I suspect such an occurrence in L. mirabilis Bütschli, and therefore relate it to this subgenus.

the width of the head. The vestibule is 3$\mu$ long, located between the inwardly turned margins of the cuticle of the head. The oral cavity is very distinct, with thick walls 3$\mu$ deep, 11$\mu$ wide. A small dorsal tooth is apparently present. The esophagus expands from 14–15$\mu$ anteriorly (60% of the body width) to 22$\mu$ posteriorly (80%).

The **spicules** (Figure 57b) are of the usual structure for Linhomoeus, curved and gradually tapering to the end (30$\mu$ long). The gubernaculum with two posterior processes is 25$\mu$ long. The **tail** (Figure 57b) is conoid, gradually becoming pointed posteriorly, with a small portion of uniform width at the end. The proportions are: length of tail 5.5; width at end 0.1; spicules 1.1; gubernaculum 0.9.

One male of this species was found in Zostera from the Chernaya 297 River 5.12.

The large lateral organ clearly differentiates this species from L. ostraearum n.sp. and L. lepturus de Man.

### 63. **Linhomoeus (Paralinhomoeus) ostraearum** n.sp.
(Table 9, Figure 58)

$$\text{♂}\ \frac{\begin{array}{cccccc} - & 3.9 & 7.4 & 33 & 61 & 93.3 \end{array}}{\begin{array}{cccccc} 1.2 & 1.7 & 1.9 & 1.7 & & 1.6 \end{array}}\ 4200\text{—}4350.$$

$$\alpha = 52\text{—}55;\ \beta = 13^1/_2\text{—}15;\ \gamma = 15\text{—}15^1/_2.$$

I was unable to obtain adult females.

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 7 | 15 | 28 | 165 | 280 |
| Width | 29 | – | 51 | 73 | 81 |

The **body** is filiform, of very even thickness, almost uniform from the anus to the anterior end. Anteriorly, the body is quite evenly rounded. The cuticle is thin (1–$1^1/_2$$\mu$ thick); the inner layer is weakly annulated with annules 0.8–0.9 wide. A few short bristles are present all over the body.

The **head** (Figure 58a) is rounded, devoid of lips; the oral aperture is encircled by a small elevation. The small labial papillae are located around the mouth itself. These are followed by a circlet of ten short, normally disposed cephalic bristles 5$\mu$ long. The lateral organs are large (15$\mu$ –$^1/_3$ of the body width) circular pits, lined with very thick cuticle, which makes them very conspicuous. The margins on the ventral side are undercut, which is possibly a sign of their former spirality (see Figure 58a).

The **oral cavity** is clearly demarcated and its anterior chamber **is** not embraced by the esophagus. Its bottom is at the same time the anterior surface of the esophagus, while anteriorly, it is partially closed by the inner cuticular layer bending inwards (Figure 58a). Its lateral walls are 298 thicker than the bottom. The length of the vestibule is 6$\mu$, its width is 3$\mu$; the oral cavity proper is 16$\mu$ wide and 9$\mu$ deep. The **esophagus** is very muscular, thickened posteriorly, but does not form a bulb. It gradually expands posteriorly from 32$\mu$ anteriorly to 45$\mu$ at the nerve ring (60% of the body width) and up to 60$\mu$ posteriorly (about 70%). I could not distinguish a cervical gland. The excretory pore lies immediately opposite the nerve ring at the end of the median third of the esophagus. The lateral fields consist of very large cells, some of which are similar to the glands of Fiacra: the musculature is greatly reduced and weakly developed. The cells of the intestine are large.

I did not have any adult females. In the males, the **testis** is apparently single. The vas deferens follows it with dark granules in the epithelium.

The **spicules** (Figure 58d) are evenly curved, about 70$\mu$ long. In the basal part their general form is trihedral: there is one thick ray on the dorsal side and two thinner rays on the ventral; at the base this regularity is broken by the formation of a knob, observed only within the body of the spicule. The end is pointed. The gubernaculum is a very complex structure. Two posterior processes are first noted (a – Figure 58d). The direct continuation of these is a piece that covers the spicules laterally (b – Figure 58d) and a widening between the spicules (c – Figure 58d). In addition, anterior to the spicules there is a small portion of the gubernaculum that may be protruded from the anal pore together with the spicules. The length of the gubernaculum from the anterior part to the end of the processes is 35$\mu$.

The **tail** in the male (Figure 58c) is conoid in the anterior half and of even width in the posterior. In still immature females that in all other features are exactly similar to the males there is histolysis of the tail, so that it appears shortened (Figure 58b), without any sign of the terminal tubes of the glands, and with irregular oblique cells inside. In very young 299 females the tail is still pointed. Such a phenomenon was described by Zur Strassen (1904) in Solenolaimus (his Anthraconema). The proportions (male) are: length of tail 4; width at end 0.1; spicules 1.1; gubernaculum 0.5.

Several males, females, and juveniles were found in oyster banks 6.12.

Among the species described, the closest relative of the Black Sea form is L. (P.) lepturus de Man from the coasts of Holland, which is differentiated, however, by its shorter bristles.

## Genus METALINHOMOEUS de Man 1907

Mém. Soc. Zool. France 20, p. 81.

Type species: M. typicus de Man 1907

This genus was isolated by de Man from Linhomoeus because of its bulb. Instead of ten cephalic bristles, this genus has only four. The remaining features coincide.

1) M. typicus de Man 1907: Mém. Soc. Zool. France 20, p. 82, Tables 3, 4, Figure 16.
2) M. zosterae n. sp., see p. 218.
The two species are easily distinguished by the condition of the oral cavity, which in M. typicus is entirely embraced by the esophagus, while in M. zosterae it is partially free.

### 64. **Metalinhomoeus zosterae** n. sp.
(Table 9, Figure 64)

$$\text{♀}\ \begin{array}{ccccccc} — & 3.5 & 5.2 & 52 & 57.5 & 62.5 & 94.0 \\ \hline 0.7 & 1.0 & 1.2 & & 1.2 & & 0.9 \end{array}\ 3200$$

$$\alpha = 83\text{—}90;\ \beta = 18\text{—}19;\ \gamma = 17.$$

| Dimensions ♀ | End of oral cavity | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 7 | 16 | 84 | 125 |
| Width | 15 | 20 | 25 | 30 |

The **body** is filiform, very slightly tapering to the anus and end of the esophagus. On the extension of the esophagus the anterior tapering also
300 is very slight, particularly if we consider that the most anterior measurement is made at the rounded off anterior end. The **cuticle** is finely annulated, its annules $1^1/_2\mu$ apart, its thickness $1-1^1/_2\,\mu$. Bristles are not observed.

The head is rounded. Around the mouth (Figure 64a) there are minute elevations, but I cannot state unequivocally that these are labial papillae. Only four fairly long ($7\mu$) submedian cephalic bristles are noted. The lateral organ, as in Linhomoeus, is a circular, clearly pronounced hollow with thick walls $8\mu$ in diameter (0.4 of the body diameter). The vestibule is a narrow passage in the thick cuticle surrounding it (Figure 64a). The oral cavity follows like a truncated pyramid, with its narrow end attached to the cuticle of the lips and its broad end supported by the esophagus. Its width is $8\mu$, its depth $5\mu$. Its walls are thicker opposite the sectors of the **esophagus**, which is $10-12\mu$ thick in its anterior part (about 50% of the body thickness); posteriorly, it thickens into a longitudinal true bulb about $60\mu$ long and $25\mu$ wide (85% of the body width). The **cervical gland** is located immediately behind its end and the cervical pore is opposite the nerve ring.

The **ovaries** are paired and straight; the uterus is small, and the vagina expands from within the gonopore as a tube; it is thick, and $10\mu$ long.

The **spicules** (Figure 64) are small, $22\mu$, curved almost to form a right angle. Here, as in Linhomoeus, histolysis creating a secondary shortening is observed in the tail. The proportions are: length of tail of female 6, of male 4; width at end 0.2 – 0.3; spicules 0.7; gubernaculum 0.7.

Several females of the species were found in Zostera 5.12.

The different form of the oral cavity clearly distinguishes this species
301 from M. typicus de Man.

Another species of Metalinhomoeus was found in oyster banks 6.12. I do not describe it here because of the inadequacy of the material.

## Genus TERSCHELLINGIA de Man 1888

Mém. Soc. Zool. France 1, p. 11.

Type species: T. communis de Man 1888

These are small nematodes. The cuticle is smooth or finely annulated. On the head there are six short labial bristles (inside the vestibule), four cephalic bristles, and a circular lateral organ with thick walls. **The oral cavity is very small or absent. The esophagus is short and has a bulb. The female genital apparatus is paired.** The ovaries are straight, the uterus is two-chambered. The spicules (not known in all) are short and curved. The gubernaculum has two posterior processes. **The tail is very long with a filiform portion.**

This genus was somewhat incompletely characterized by de Man as Monhystera provided with a bulb; the features emphasized here are also characteristic for the genus. De Man did not attribute to them such significance originally. This is a close relative of genera Linhomoeus and Metalinhomoeus.

There are five species:

1) T. communis de Man 1888: Mém. Soc. Zool. France 1, p. 12, Table 1, Figure 7. On the coast of Holland; ? Sète (Rouville).
2) T. pontica n.sp., see below.
3) T. longicaudata de Man 1907: Mém. Soc. Zool. France 20, p. 39, Table 1, Figure 4. Veere, Jerseke (Holland).
4) T. exilis Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 392. Sand at low tide. Port Jackson N. S. W.
5) T. (?) filiformis de Man 1907: Mém. Soc. Zool. France 20, p. 41, Table 1, Figure 5. Veere, Jerseke (Holland); may belong to another genus.

Monhystera bulbifera de Man 1880 and M. bulbosa Grimm 1876 (see p. 170) do not belong to this genus.

1 (4, 5, 6). $\alpha = 30$; lateral organ lies its own width from anterior end.
2 (3). Filiform portion accounts for half length of tail; lateral
302 organ $^1/_4$ of head width . . . . . . . . . . . . **T. communis** de Man
3 (2). Filiform portion accounts for $^2/_3$ of length of tail; lateral organ greater than $^1/_3$ of width of head . . . . **T. pontica** n. sp.
4 (1, 5, 6). $\alpha = 45$ . . . . . . . . . . . . . . . . . . . . . **T. longicaudata** de Man
5 (1, 4, 6). $\alpha = 70$ . . . . . . . . . . . . . . . . . . . . . . . . . **T. exilis** Cobb
6 (1, 4, 5). $\alpha = 150$ . . . . . . . . . . . . . . . . . . . . . . . **T. filiformis** de Man

### 65. **Terschellingia pontica** n.sp.
(Table 9, Figure 65)

$$\text{♀}\ \begin{array}{ccccccccc} — & 4.2 & 8.7 & 24 & 33 & 43 & 51 & 61 & 80 \\ \hline 1.1 & 2.0 & 2.3 & & & 3.3 & & & 2.1 \end{array}\ 1400$$

$$\alpha = 30;\ \beta = 11^1/_2;\ \gamma = 5.$$

| Dimensions ♀ | Cephalic bristles | Middle of lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 3 | 9 | 60 | 110 |
| Width | 14 | 19 | 26 | 85 |

The **body** is approximately uniform over one third, tapers to the anus and end of the esophagus. Hence, it tapers twofold anteriorly. The **cuticle** is thick (in relation to the size of the nematode), $1^{1}/_{2}\,\mu$, and smooth. Very few bristles are observed on the body.

The **head** (Figures 65a, c) is rounded, only slightly flattened anteriorly. Lips are absent, the six small labial bristles are apparently located inside the vestibule. There are four cephalic bristles ($2^{1}/_{2}\,\mu$), possibly six more very small bristles. The four supplementary submedian cephalic bristles are located posteriorly to these, opposite the anterior margin of the lateral organ. There are one or two bristles even posterior to the lateral organ. The latter is circular, with very thick walls $8^{1}/_{2}\,\mu$ in diameter, somewhat more than $^{1}/_{3}$ of the head width, reminiscent of the lateral organ of *Linhomoeus*.

The **vestibule** is small, formed of an inward fold of the cuticle of the head. The oral cavity is absent and the esophageal tube is attached directly to the vestibule. The **esophagus** (Figure 65c) is rounded anteriorly, $12\,\mu$ wide, posteriorly expanding to a bulb $28\,\mu$ wide, or $^{4}/_{5}$ of the diameter
303 of the body. The small cervical gland is located behind the end of the esophagus. I did not see the cervical pore. The ovary is straight, but the extreme end of it is apparently reflexed. The uterus has two chambers; the eggs are large, elongate, $100 \times 40\,\mu$. The vagina has fairly thick walls and is $^{2}/_{5}$ of the body diameter.

The **tail** (Figure 65b) tapers conically in the anterior $^{1}/_{3}$, the posterior $^{2}/_{3}$ are filiform, and only the tip is slightly thickened. The caudal glands are accommodated within the tail. The proportions are: length of tail 10.5; width at end 0.09 (about $3\,\mu$).

One adult female of this species was found in *Zostera* from the North Side 11.12.

This species is very similar to T. *communis* de Man, but the filiform portion of the tail takes up only half of its length, and the lateral organ is only $^{1}/_{4}$ of the head width and is shifted more anteriorly.

## Genus PROSPHAEROLAIMUS n. g.

These are stout nematodes with a finely annulated cuticle. On the head are six lips, two rows of six papillae and four bristles. Besides the true bristles are many supplementary cephalic bristles. The lateral organ is circular and well developed. **The oral cavity is almost absent.** The **very strongly developed esophagus** is reminiscent of *Sphaerolaimus*. The ovary is straight. The tail is long, conoid, and rounded at the end.

It is possible that *Sphaerolaimus* were forms developed from nematodes such as these by further specialization.

The sole species is:

### 66. **Prosphaerolaimus eurypharynx** n. g., n. sp.
(Table 9, Figure 66)

$$\text{♀}\ \frac{\begin{array}{ccccccc} — & 6.0 & 9.8 & 40.5 & 48.5 & 53.0 & 84.5 \end{array}}{\begin{array}{ccccccc} 1.4 & 3.1 & 3.1 & & 3.5 & & 2.6 \end{array}}\ 2300$$

$$\alpha = 30;\ \beta = 10;\ \gamma = 6^{1}/_{2}.$$

304

| Dimensions ♀ | Anterior end | Cephalic bristles | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | – | 9 | 11 | 114 | 190 |
| Width | 9 | 25 | 36 | 56 | 56 |

The **body** is stout, of uniform width from the nerve ring almost to the anus, tapering only slightly. The tapering is sharply expressed to the anterior end, so that the diameter of the body at the cephalic bristles is equal to half the diameter at the beginning of the intestine. The **cuticle** is $2\,\mu$ thick, very finely annulated, with a large number of long, slender bristles set all along it.

The **head** is rounded. The oral cavity is closed by thick lips, apparently six in number (lab.—Figure 66a). Each lip projects internally as a broad cuticular expansion. A labial papilla is set behind each lip, and fairly large cephalic papillae are set behind them as well as four cephalic bristles $10\,\mu$ long or 0.4 of the head width. An entire row of supplementary cephalic bristles of various length is disposed behind them. Some of these are longer than the cephalic. The lateral organ is well developed, circular, with some thickenings within; its diameter is $12\,\mu$.

The oral cavity is small, with a small dorsal tooth.

The **esophagus** is stout; anteriorly, its diameter is about $30\,\mu$, posteriorly, it expands gradually to $70\,\mu$ ($^{2}/_{3}$ of the body width), but a bulb is not formed. The nerve ring is located at the end of its central third. The cervical pore is located immediately in front of the nerve ring. The intestine is wide, consisting of many rows of cells.

The **ovaries** are short and straight. The uterus is undivided. The vagina lies obliquely, but would be 0.4 of the body width if it were straight.

The **tail** (Figure 66b) is very long, tapers sharply to its middle, while the second half is thin, the end slightly swollen. The proportions are: length 6; width at end 0.11.

One female was found in *Zostera* from the Chernaya River 5.12.

305

## Genus DISCONEMA n.g.

Type species: D. *alaima* n. sp.

These are filiform worms with a finely annulated cuticle. Lips are absent; there are six labial papillae, and ten cephalic bristles in a plain circlet. The **massive lateral organ** has signs of a concealed spiral. **There**

**is no oral cavity.** The esophagus has an indistinct bulb. The female genital organs are paired, the ovaries are straight. The tail is quite short.

I approximate this species to Monhysterini (the Linhomoeus – Terschellingia group), since the lateral organ is apparently a modification of the circular type possessed by this group.

The sole species is:

67. **Disconema alaima** n.sp.
(Tables 10, 11, Figure 74)

$$\text{♀}\ \frac{\begin{array}{ccccccc} — & 2.4 & 6.0 & 40 & 45 & 50.5 & 96.0 \end{array}}{\begin{array}{ccccccc} 0.6 & 1.3 & 1.3 & & 1.4 & & 1.0 \end{array}}\ 3620$$

$$\alpha=72;\ \beta=17;\ \gamma=25.$$

| Dimensions ♀ | Cephalic bristles | Lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 8 | 27 (front) | 85 | 210 |
| Width | 16 | 30 (middle) | 38 | 39 |

The **body** is very long, filiform, of even width. The anterior tapering occurs chiefly ($2^1/_2$ times) in the preneural region, while posteriorly ($1^1/_2$ times) it is in the immediately preanal part. The **cuticle** is thin, about $2\mu$; the inner layer is annulated with annules about $1\mu$ wide.

The head is pointed (Figure 74a), with the extreme end rounded. Around the margins of the mouth there are six very small labial papillae, behind which ten cephalic bristles are disposed in a single circlet. They are $11\mu$ long, except for the sublaterals, which are $5\mu$. The lateral organ is very
306 large ($35\times14\mu$) (the width is about half the body diameter), elliptical, with thick walls and an elevated middle. In the deeper portion (Figure 74b), some signs of spirality are observed: notches abutting obliquely on the middle of the disk are noted. On the head, the margins of the epidermal cells are well marked. The entire part anterior to the cephalic bristles is apparently formed from one row of six cells. Behind the cephalic bristles there are also six cells in a second row. A third row is adjacent to the lateral organ (see Figure 74a).

An oral cavity is lacking and the esophagus joins the oral aperture directly and anteriorly is rounded. Posteriorly, the esophagus expands into an indistinct bulb (Figure 74c). Its thickness anteriorly is $12\mu$, opposite the nerve ring it is $16\mu$, and posteriorly, $30\mu$ ($^3/_4$ of the body width). The nerve ring lies behind the middle of the esophagus. The intestine consists of cuboid cells that leave only a narrow lumen.

The ovaries are paired and straight. The vagina is short, about $^1/_5$ of the body width.

The tail is conoid with a thickened end. It is $4\mu$ long, and its width at the end is $0.5\mu$.

A few individuals of this species were found in sand of Kruglaya Bay 5.12, 6.12, 7.13.

## 2. Subfamily **Sphaerolaimini**

This subfamily is differentiated from the other Monhysteridae by its large and complex oral capsule. The circular lateral organs and straight, unpaired ovaries clearly indicate their true relationship. The structure of the esophagus is to a certain extent like that of Enoplus, Cyatholaimus and Linhomoeus, but it is readily distinguished from the last two by the even distribution of the muscular and plasmatic elements.

There is one genus, which should probably be subdivided (de Man):

307 ### Genus SPHAEROLAIMUS Bastian 1865

Trans. Linn. Soc. 25, p. 157.
De Man 1884: Nemat. Niederl. Fauna, p. 71.
De Man 1908: Mém. Soc. Zool. France 20, p. 54.

Type species: Sph. hirsutus Bastian 1865

These are medium-sized nematodes with a stout body. The cuticle is weakly annulated (in some species a smooth cuticle is described). Six lips are present with labial papillae (rarely bristles) at the base of each. Ten short cephalic bristles (rarely papillae) lie behind them. The supplementary cephalic bristles are much longer than the main ones. They often lie in eight bundles. The lateral organ is circular, larger in the male. The oral cavity is spacious with thick walls. Its anterior chamber (the vestibule proper) consists of a cone of specialized rods. The second chamber is a thick, chitinized ring of varying width, not embraced by the esophagus. Its anterior part is closely pressed to the cuticle. The posterior, enclosed part is conical, sometimes subdivided into two secondary parts. The esophagus is very muscular. There is only one anterior ovary, which is straight. The tail at first sharply tapers conically, but its posterior half is of even thickness. The spicules are curved, sometimes long. The gubernaculum is small.

This genus was described originally by Bastian and is a very compact group, although fairly varied morphologically. De Man (1908) suggested that for this reason it should be divided further into several genera. Bastian himself noted that the genus was characteristic for mud. I also found the Black Sea species in mud or in oyster banks, in very muddy facies. The majority of other authors also found their worms in mud.

Altogether nine species have been described:

1) Sph. hirsutus Bastian 1865: Trans. Linn. Soc. 25, p. 157, Table 13, Figures 192–194; ? Bütschli 1874: Abh. Senck. Ges. 9, p. 43, Table 7, Figure 32; de Man 1907: Mém. Soc. Zool.
308 France 20, p. 55, Tables 2, 3, Figure 9. Mud from the harbor, Falmouth (Bastian); coast of Kiel Firth (Bütschli); coasts of Holland (de Man); west coast of Ireland, mud from depth of

7 sajenes, adult in May (Southern). The species described by Bütschli may be another form.

2) Sph. brevicollis Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 119. Ekaterininskaya Harbor — mud at low tide; Lake Mogil'noe.
3) Sph. ostreae n. sp., see below.
4) Sph. macrocirculus n. sp., see p. 226.
5) Sph. balticus G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 35, Figure 16. It is possible, judging from the smooth cuticle, that this species should be isolated in another genus (de Man);
6) Sph. dispar n. sp., see p. 227.
7) Sph. gracilis de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 179, Table 12, Figure 47; 1884: Nem. Niederl. Fauna, p. 72, Table 10, Figure 41. Earth with brackish water, Holland. Should possibly be isolated in a separate genus (de Man).
8) Sph. hirticollis Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 393. Sand at low tide, Port Jackson N. S. W. Possibly another genus (de Man).

1 (10). Oral capsule adjacent to cuticle over a large extent.
2 (9). Walls of oral capsule not very thick.
3 (4). Cephalic bristles in form of papillae . . . . **Sph. hirsutus** Bastian
4 (3). True cephalic bristles.
5 (8). Supplementary cephalic bristles in eight regular groups.
6 (7). Spicules with velum along entire internal margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Sph. brevicollis** Saveljev
7 (6). Velum only at end of spicule. . . . . . . . . . . . **Sph. ostreae** n. sp.
8 (5). Supplementary cephalic bristles lie in irregular groups . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Sph. macrocirculus** n. sp.
9 (2). Walls of oral cavity very thick, so that its lumen is less than double thickness of walls . . . . . . . . . **Sph. balticus** G. Schneider
10 (1). Oral capsule only a narrow ring adjacent to cuticle.
10 (13). Spicules short.
11 (12). Walls of oral capsule thin. . . . . . . . . . . . . **Sph. gracilis** de Man
12 (11). Walls thick . . . . . . . . . . . . . . . . . . . . . . . . . . **Sph. dispar** n. sp.
13 (10). Spicules long . . . . . . . . . . . . . . . . . . . . . **Sph. hirticollis** Cobb

### 68. **Sphaerolaimus ostreae** n. sp.
(Table 10, Figure 67)

$$\male\ \frac{2.5 \quad 9.2 \quad 22 \quad - \quad 88}{1.4 \quad 3.7 \quad 4.0 \quad 4.0 \quad 3.0}\ 1620$$

$$\alpha = 25;\ \beta = 4^1/_2;\ \gamma = 8^1/_2.$$

| Dimensions ♂ | Beginning and end of external part of oral cavity | | End of oral capsule | Nerve ring | Excretory pore | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 11 | 26 | 37 | 150 | 200 | 340 |
| Width | 22 | 32 | 38 | 55 | – | 60 |

309 The **body** is stout, of even width almost from the nerve ring to the posterior part. It tapers to the anus by $^1/_4$, while from the end of the esophagus to the anterior end of the cephalic capsule it tapers almost threefold. The **cuticle** is fairly thick ($2^1/_2\,\mu$), the annules on its inner surface are $1.2\,\mu$ apart. Bristles, apart from anteriorly and posteriorly, are not observed in this species.

The **head** (Figure 67a) in general appears pointed and similar to that of the following species. Anteriorly, there are six thick lips $6\,\mu$ long, folded when at rest. The base of each lip is beset with a labial papilla, behind which lies a circlet of ten short bristles, the four submedians being somewhat longer than the rest ($4\,\mu$ and $3\,\mu$). The supplementary cephalic bristles are very long, up to $27\,\mu$; here they are sparse, and **are disposed in 8 groups of 3 — 4 bristles opposite the anterior part of the oral capsule.** Four of the groups lie submedially and four sublaterally. The lateral organ is large, circular ($11\,\mu$, or $^1/_3$ of the corresponding body width), disposed near the posterior margin of the anterior chamber of the oral capsule.

In general outline, the oral capsule is constructed as in the following species, but differences exist. First, it is somewhat longer, and the cone of rods (vestibule) is also longer. The main anterior part adjacent to the cuticle anteriorly bears eight excavations and posteriorly four appendages in a single line above and below each lateral organ. This part is pierced by pores and canals, which create a spongy appearance. The entire posterior part, the inner layer, and the wide strip along the posterior margin are devoid of these pores. Here, no such contrast is observed in the density of the pores as in the following species, but nevertheless, there are at least two sublateral tongues with a greater density of pores (a — Figure 67a); the areas between these have fewer pores. A discontinuous thickening runs along the posterior margin of the anterior part of the cavity, and separate grooves lie on its surface (b — Figure 67a). In the 310 posterior part of the oral capsule, opposite the sectors of the esophagus, thickenings extend to the internal angles of the esophageal tube (c — Figure 67a), and between the sectors such thickenings extend to the external angles (d — Figure 67a).

The **esophagus** is stout, expanding from $27\,\mu$ anteriorly to $38\,\mu$ posteriorly, occupying 55 — 65 % of the body thickness. The **nerve ring** lies somewhat anterior to its middle. The **cervical pore** is located behind the nerve ring. The end of the cervical glands is attached to it directly, not forming a special tube. I could not find the beginning of the gland. The narrow intestine consists of few rows of large cells.

I could not distinguish the internal genital organs. The **spicules**, in contrast to the preceding species, are short ($70\,\mu$ long), and taper to both ends. The walls at both ends are thickened, so that the lumen is narrow. Inside the spicules, a longitudinal thickening of its wall is noted. The gubernaculum is very small and is adjacent to the spicules ventrally (gub. — Figure 67c). There are some slender and short bristles lying anterior and posterior to the anus. Apparently three papillae lie preanally.

The **tail** as usual in Sphaerolaimus tapers gradually in its anterior three-quarters; the posterior part is thin, somewhat thickened at the tip, where there are several small bristles. The proportions are: length of tail 3.8; width at end 0.2; spicules 1.4.

Only one male was found in oyster banks 6.12. Our species differs from Sph. macrocirculus n.sp. in (1) the short spicules; (2) underdeveloped gubernaculum; (3) thickenings on the end of the tail; (4) even distribution of the supplementary cephalic bristles.

### 69. **Sphaerolaimus macrocirculus** n.sp.

(Table 10, Figure 68)

$$♂\ \frac{1.3 \quad 13.3 \quad 30.7 \quad - \quad 84.0}{2.3^{*} \quad 5.3 \quad 5.3 \quad 5.5 \quad 4.5}\ 1850$$

$$\alpha=18;\ \beta=3^{1}/_{3};\ \gamma=6.$$

311

| Dimensions ♂ | End of lips | Front of oral capsule | Back of oral cavity | End of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | 6 | 14 | 43 | 60 | 210 | 440 |
| Width | 15 | 32 | 48 | 55 | 72 | 74 |

The **body** is very plump, tapering to the anus only slightly (to 0.8), hardly to the nerve ring. From this point, the body tapers gradually anteriorly (see dimensions), chiefly opposite the oral cavity. The **cuticle** is about $2^{1}/_{4}\mu$ thick and at first appears smooth. There is, however, very fine annulation on its inner layer, the annules being about $1\mu$ apart. Fairly numerous bristles are observed over the entire body, sometimes quite long, some reaching $20\mu$.

The **head** generally appears pointed when the lips are folded (Figure 68a). The entrance to the oral cavity is closed by six lips which are tightly folded when at rest. The lips are quite thick, thicker at the base, as is well seen in profile (Figure 68a). A ring of six labial papillae follows the lips, one at the base of each, while posterior to this there is a circlet of ten very slender cephalic bristles. The submedian bristles are larger ($12\mu$), while the remaining six are somewhat shorter, only $9\mu$. All the region of the oral cavity is beset with numerous bristles of various lengths (up to $20\mu$), disposed without particular regularity.

The lateral organ is circular, about $17\mu$ in diameter, or $^{1}/_{3}$ of the body width, located in a hollow in the oral capsule, here adjacent to the cuticle.

The internal structure of the head is very complex. The first part of the **oral capsule** consists of a truncated cone of chitinized rods (actually the vestibule), with its apex anteriorly (a – Figure 68a). The rods anteriorly are thinner and more densely packed than posteriorly. They are adjacent to the cuticle, which at that point is greatly thickened. The
312 second chamber is the oral capsule proper. The anterior part is closely adjacent to the cuticle, and plays the part here of the absent cephalic capsule. Anteriorly, there are eight excavations between which are eight lobes: four submedian, two median, and two lateral (e – Figure 68a). The posterior margin of this part is quite regular and forms only two processes on each side encircling the lateral organs (b – Figure 68a). In this species the processes are fairly long. The internal structure of this part is notable. It is a spongy mass, entirely pierced through by separate pores (in the drawing this is not depicted entirely satisfactorily); these pores are denser anteriorly, while posteriorly they descend in six tongues, two median and four subventral (see Figure 68a). Between these tongues the pores are considerably more sparse. The parts free of pores are the internal plate of the oral capsule adjacent to the oral cavity, a portion of the posterior border of the anterior chamber, and all the internal posterior chamber. Posteriorly, the oral capsule is reduced to three tongues in each sector, reaching the internal angles of the esophageal lumen (c – Figure 68c), while between the sectors it terminates more anteriorly, forming an irregular expansion at the margin (d – Figure 68a). The dimensions are: overall length from lips to back $60\mu$, the lips accounting for $6\mu$, the rod cone $8\mu$, the anterior chamber $29\mu$, the posterior $17\mu$; the width of the cone anteriorly $29\mu$, posteriorly $41\mu$, of the posterior chamber anteriorly $30\mu$; the thickness of the walls: anterior chamber $4-7\mu$, posterior $2-3^{1}/_{2}\mu$.

The esophagus is muscular, as in Enoplini and Cyatholaimini. It expands from $70\mu$ anteriorly to $95\mu$ posteriorly (60 – 70% of the body width). The nerve ring encircles it at the middle. The cardia was not very well developed. The intestine is narrow, consisting of rows of large cells filled with dark granules. There is a distinct internal cuticle.

There are two testes at the ends of a spacious seminal vesicle. The vas deferens consists of large cells in two columns.

313 The spicules (Figures 68b, c) are long, $150\mu$. They taper before the base, after which there is a funnel. The widest part of the spicule follows; it then gradually narrows to the end. A complex ray forming a second enlargement of the spicule lies not far from the end on the ventral side. The end of the spicule is blunt, curving slightly to form a hook ventrally. The gubernaculum (Figure 68c) is small ($35\mu$), adjacent dorsally to the spicules. It forms a round process at the base (a – Figure 68c); the end (b – Figure 68c) is extended into a small process, and laterally it covers the ends of the spicules. Anterior to the anus there is a row of eight accessory papillae. They are weakly developed and do not bear bristles.

The tail (Figure 68b) in its basal half tapers only slightly, the main tapering being in the third quarter, while the posterior quarter is thin and of even diameter. The proportions (male) are: length of tail 3.5; width at end 0.14; spicules 3.0; gubernaculum 0.7; distance from anus to anterior papilla 7.0.

There was only one male, probably immature; mussel mud, Kacha River 8.13.

### 70. **Sphaerolaimus dispar** n.sp.

(Table 10, Figure 69)

$$♂\ \frac{3.7 \quad 8.7 \quad 22.5 \quad 38.3^{*} \quad 86.7}{2.2 \quad 4.3 \quad 4.7 \quad 4.8 \quad 3.7}\ 1620$$

$$\alpha=21;\ \beta=4^{1}/_{2};\ \gamma=8.$$

$$♀\ \frac{3.5 \quad 9.6 \quad 22.6 \quad 42 \quad 62.6 \quad 89.3}{2.3 \quad 5.3 \quad 5.6 \quad \quad 5.6 \quad 3.0}\ 2400$$

$$\alpha=18;\ \beta=4^{1}/_{2};\ \gamma=9.$$

---

* Anterior margin of oral cavity.

* Beginning of genital apparatus.

| Dimensions ♂ | Cephalic bristles | Beginning of ring of oral capsule | Border of middle and posterior chambers of oral capsule | Back of oral cavity | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|
| Length | – | 11 | 35 | 62 | 140 | 365 |
| Width | 22 | 38 | 57 | 60 | 70 | 73 |
| ♀ | | | | | | |
| Length | – | 14 | 40 | 70 | 205 | 510 |
| Width | 25 | 45 | 67 | 78 | 110 | 115 |

314 The **body** is thick, tapering to the anus less than twofold, more markedly in the female. At the beginning of the esophagus the body hardly tapers; anteriorly, it tapers sharply, more so opposite the oral capsule, about half at its ring, and about $^1/_4$ at the anterior end of the rod cone. The **cuticle** is quite clearly annulated, the annules being observed on both its inner and outer layers, more markedly on the inner. The distance between the annules is $2^1/_4\,\mu$, the thickness of the cuticle is $3\,\mu$. The long ($30\,\mu$) and slender bristles are observed in large numbers all over the body.

The **head** is generally conoid, somewhat unevenly truncated at the end (Figures 69a, b). Six short labial bristles are set upon the six short, thin lips: the bristles here are converted into papillae (s. lab. — Figure 69b). Behind them, opposite the posterior part of the vestibule, is a circlet of ten cephalic bristles (s. c — Figure 69b). Their length is $5\,\mu$, although the four sublaterals are rather shorter. Posterior to these is a mass of supplementary cephalic bristles. Some of them lying more towards the conical part of the oral cavity are short ($5\,\mu$), while opposite the ring of the oral capsule and further posteriorly they lie without any regularity of length (up to $22\,\mu$) and are numerous. The lateral organ is of very varying size in the male and female. It is circular with thick walls In the male its diameter is $16\,\mu$, $^1/_3$ of the corresponding width of the body; in the female it is only $8\,\mu$, or $^1/_8$ of the corresponding width.

Sexual dimorphism exists in the oral capsule also: in the female the capsule is far more massive (see Figures 69a, b). A small vestibule is located in front of the capsule; its width is $15\,\mu$ in the female, $11\,\mu$ in the male, its depth is $4\,\mu$ (vest.— Figure 69b). This is followed by the cone of rods, as in the other forms of Sphaerolaimus (a — Figure 69b). In the female the rods are packed tightly together and meet the oral capsule more posteriorly. They are rounded at the base, while in the male they are irregular. In addition, there is in the female a considerably larger
315 space between these and the cuticle than in the male (b — Figure 69b, compare Figure 69a). The length of the separate rods in the male is $11\,\mu$, in the female $14\,\mu$; the cone in the male is $9\,\mu$, in the female $12\,\mu$. The cone is contiguous with the end of the oral capsule, and is constructed somewhat differently than in other forms of Sphaerolaimus where the anterior part of the ring is adjacent to the cuticle over a large area and has a specialized structure. Here, it is quite homogeneous and is only a narrow ring (c — Figure 69b). This part bears six excavations on the anterior margin: two lateral and four submedian. There are six broad plates between the excavations attached to the cuticle (one of these is seen laterally in Figure 69b, two in Figure 69a). A narrow belt succeeds this ring, not encircled by the esophagus, more narrow in the female. The total width of the belt is $10-12\,\mu$, while the thickness of the walls is about $5-6\,\mu$. Behind this are the two parts of the oral capsule that are embraced. Both these are conical, with curved walls; the posterior is a more pointed cone (d, e — Figure 69b). Apparently, both chambers consist of large number of separate plates, but I could not distinguish this satisfactorily. The oral cavity in young individuals is somewhat different: the rods in front of the cone are sparse, thicker, and shorter. The walls of the belt are thinner, and longitudinally striated (see Figure 69f).

The **esophagus** is very stout, without a bulb. Its thickness is $45-50\,\mu$ in the male, $50-55\,\mu$ in the female, or 65 – 70 % of the body width. The nerve ring encircles it anterior to its middle. The intestine consists of large dark cells and is lined throughout with a thick cuticle (see Figure 69c). The hindgut is quite long and voluminous: its cuticle is a direct continuation of the external cuticle. At its end the midgut has a complex valve (a — Figure 69c). The small cervical gland is located behind the end of the esophagus, and its pore is rather anterior to the nerve ring.

The ovary is single and anterior, straight and very long. The uterus is quite short. The vagina is oblique with powerful musculature, half the body width. I did not detect the internal male genital organs. Some
316 accumulation of small cells probably related to them is located not far posterior to the end of the esophagus. The vas deferens is long, extending into the anterior half of the body.

The **spicules** (Figure 69e) are short ($65\,\mu$), curved, the end slightly so. Before the end there is a small velum. The gubernaculum is small ($24\,\mu$), with a small process rising vertically.

The **tail** (Figures 69c, d) is conoid in the anterior two-thirds, while the posterior third is of even width and there is no thickening at the end. There is a bundle of bristles at the extreme tip. The proportions are: length of tail in male and female 3.5 – 3.7; width at end 0.08 – 0.09; spicules 1.1; gubernaculum 0.4.

About a dozen females and three males of this species were found in mussel mud from Kacha River 8. 13.

This species is so greatly differentiated by its narrow cephalic ring from the other forms of Sphaerolaimus that it may constitute a special genus.

## 3. Subfamily **Siphonolaimini**

Representatives of this highly organized subfamily are not encountered in the Black Sea. They are characterized by outstretched ovaries and circular lateral organs, which confirm their place among Monhysteridae. This subfamily is differentiated from the others of this group by the narrow oral cavity, which may be extended anteriorly and probably functions as a piercing organ. The high organization of the nervous system (Zur Strassen) is interesting. The nerve cells are accumulated in true ganglia, which does not occur in the other free-living nematodes. The black intestine and the histolysis of the tail in adult females are characteristic. Linhomoeus may be cited as a probable relative of this group (see p. 214); if this is confirmed, then Linhomoeus will constitute a whole with Siphonolaimini. There are two genera: genus Anthraconema Zur Strassen 1904 corresponds to them both.

317 1) Siphonolaimus de Man 1893: Mém. Soc. Zool. France 6, p. 99; Chromagaster Cobb 1893: Proc. Linn. Soc. N.S.W. 8, p. 416. Species: 1) S. niger de Man 1893: loc. cit., p. 100, Table 6, Figure 8. Falmouth, Walcheren. 2) Chromagaster nigricans Cobb 1893: loc. cit., p. 416. Naples, sand. 3) Chr. purpurea Cobb 1893: loc. cit., p. 417, Figure 12. Port Adelaide, South Australia. 4) Anthraconema sagax Zur Strassen 1904: Zool. Jahrb. Suppl. 7, p. 301. Naples, oxeas sand; found by me in Villefranche in a hole under the municipal sewage system.

2) Solenolaimus Cobb 1893: loc. cit., p. 419. Species: 1) S. obtusus Cobb 1893: loc. cit., p. 419, Figure 13. Naples, sand. 2) Anthraconema weissmani Zur Strassen 1904: loc. cit., p. 301. The same place. The two species may be identical.

Chromagaster stenolaima Steiner 1916; Zool. Jahrb. Syst. 39, p. 632, Table 32, Figures 35a-c. White Sea strait, in algae. This species in any case belongs to neither the one nor the other genus and consequently not to Chromagaster Cobb, which coincides fully with Siphonolaimus de Man. The fact that Cobb and Steiner did not find a movable spine is easily explained by its absence: there is a protrusible oral cavity, but no spine (see Zur Strassen and the general part).

## 4. Subfamily **Axonolaimini**

These are nematodes of medium size, rarely small. The cuticle is smooth or very finely annulated. The cephalic bristles are in one or two rows. **The lateral organs are in the form of a spiral, incomplete or with one small turn,** frequently very large, oval. The esophagus is most often without a bulb. The ovaries are straight. The spicules, where known, are short. The gubernaculum is frequently with two dorsal processes.

I relate here the following genera:

1) Axonolaimus de Man 1889, see p. 231.
2) Conolaimus n.g., see p. 235.
3) Araeolaimoides de Man 1893, see p. 236.
4) Sphaerocephalum n.g., see p. 238.

The last genus is included here only provisionally.

1 (6). Esophagus quite straight, slender.
2 (5). Oral cavity large.
3 (4). Lateral organs oval (in general outline), opposite posterior chamber of oral cavity. . . . . . . . . . . . . . . **Axonolaimus** de Man
4 (3). Lateral organs circular, opposite anterior chamber of oral cavity . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Conolaimus** n. g.
318 5 (2). No oral cavity . . . . . . . . . . . . . . . . . . . **Araeolaimoides** de Man
6 (1). Esophagus clearly expanded posteriorly. Lateral organs in general outline circular, small. . . . . . . . **Sphaerocephalum** n. g.

### Genus AXONOLAIMUS de Man 1889

Mém. Soc. Zool. France 2, p. 3.

Type species: Ax. spinosus (Bütschli 1874) de Man 1889

These are quite large worms with a smooth cuticle. On the head are six labial papillae and four large cephalic bristles, and probably an additional row of cephalic papillae. **The lateral organs are large, in the form of an elongated tube folded into two, oval in general. The oral cavity is in the form of two trihedral pyramids joined by their bases.** The anterior pyramid is truncated and shorter than the posterior, which is entire. The apex of the posterior pyramid is directed posteriorly and embraced by the esophagus, which is slender, without a bulb. The ovaries are straight, the uterus is two-chambered. The testes are paired. The spicules are short and arched; the gubernaculum has two posterior processes.

This genus was established by de Man for Anoplostoma spinosum Bütschli, as this species is definitely quite different from Anoplostoma, which are related to an entirely different group. I consider it necessary to isolate in another genus —Conolaimus n. g. (p. 235)—the species which have small lateral organs that are circular in general outline. Thus, only three species are related to genus Axonolaimus:

1) Ax. spinosus (Bütschli 1874); Anoplostoma sp.: Abh. Senck. Ges. 9, p. 37, Table 5, Figure 20; de Man 1888: Mém. Soc. Zool. France 1, p. 19, Table 2, Figure 11; Axonolaimus sp.: de Man 1889: Mém. 2, p. 3; G. Schneider 1906: Acta Soc. F. Fl. Fenn. 27, No. 7, p. 39, Figure 18. Kola Gulf, Lake Mogil'noe (Savel'ev); North Sea; Walcheren, mud on stones of the canal (de Man); Baltic Sea: Kiel Firth, sand on coast (Bütschli), mud from Tvärminne Bay (G. Schneider).
2) Ax. ponticus n.sp., see p. 233.
3) Ax. setosus n.sp., see p. 231.

319 1 (2). Very many long bristles on tail of male and bulge in middle. Cephalic bristles longer than head width. Two bends of lateral organ tightly folded. . . . . . . . . . . . . . . . . . . **A. setosus** n. sp.
2 (1). On tail of male bristles few and short, bulge absent. Cephalic bristles shorter than head width.
3 (4). Two bends of lateral organ tightly folded. Anterior chamber of oral cavity $^1/_4$ of its overall length. . . . . . **A. spinosus** (Bütschli)
4 (3). Two bends not tightly folded. Anterior chamber of oral cavity $^1/_3$ of its overall length . . . . . . . . . . . . . . . . **A. ponticus** n. sp.

### 71. **Axonolaimus setosus** n.sp.

(Table 10, Figure 70)

$$\text{♂}\ \frac{0.6 \quad 5.6 \quad 8.5 \quad 19.5 \quad 57^{*} \quad 93.5}{0.5 \quad 1.2 \quad 1.3 \qquad 1.4 \qquad 1.3}\ 3600$$

$$\alpha = 72;\ \beta = 12;\ \gamma = 15.$$

---

* Beginning of vas deferens.

$$\text{♀}\ \frac{0.8 \quad 5.5 \quad 8.3 \quad 22.5 \quad 44 \quad 50.5 \quad 58 \quad 71 \quad 92.8}{0.6 \quad 1.0 \quad 1.1 \qquad\qquad\qquad 1.3 \qquad\qquad\qquad 1.1}\ 4100$$

$$\alpha=75;\ \beta=12;\ \gamma=14.$$

| Dimensions | Cephalic bristles | End of oral cavity | Cervical pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| ♂ | | | | | |
| Length | 7 | 27 | 160 | 175 | 265 |
| Width | 17 | 22 | – | 43 | 50 |
| ♀ | | | | | |
| Length | 7 | 30 | 195 | 215 | 320 |
| Width | 15 | 23 | – | 48 | 51 |

The **body** is filiform, hardly tapering to the anus and end of the esophagus, whence anteriorly it tapers approximately twofold. The **cuticle** is smooth, two-layered, both layers being of uniform thickness; its total thickness is about 2 μ, anteriorly it increases up to 3 μ. There are four rows of submedian bristles running along the entire body which are larger anteriorly.

The **head** (Figure 70a) is pointed, but rounded anteriorly. Between the six well-marked labial papillae lying in special pits there are six low mounds, almost completely closing the entrance to the oral cavity. 320 The four long cephalic bristles are 17 – 20 μ long, somewhat more than the head width. Between them in the same circlet there are six hardly conspicuous cephalic papillae (not drawn in the figure). The lateral organ is large, elongate, in the form of a tube folded in two, the inner walls tightly pressed to each other. One of its ends is open and here enter its nerves; the other end is bluntly rounded. Its dimensions are 17 × 6 μ.

The oral cavity is wide, consisting of two chambers in the form of pyramids, joined by the bases. The anterior pyramid (vestibule) is truncated, the posterior is pointed. The walls of both chambers are smooth without any ornamentation whatsoever. The length of the anterior chamber is 7 μ, of the posterior 22 – 23 μ, the maximum width is 10 μ. The esophagus is slender, from 12 – 14 μ anteriorly, expanding to 30 – 35 μ posteriorly (more than half the body width). Posteriorly, it is ovally closed.

The nerve ring is located somewhat anterior to the posterior third of the esophagus. The cervical gland is narrow, located at $^2/_3$ the length of the esophagus behind its end, is 40 μ long, and 5 μ wide. Its pore is located not far anterior to the nerve ring. Two large (35 × 40 μ), probably phagocytic cells lie on the ventral line, one exactly behind the cervical gland and the other at the beginning of the genital tract.

The ovaries are straight. Their syncytial end is curved around the intestine, sometimes posterior to it. This is succeeded by a portion of two rows of small cells. The cells then grow larger and are disposed in one row, and the last two cells are filled with dark vitelline granules. On the boundary of the ovary with the uterus there is a conelike valve directed into the uterus, evidently to prevent the reverse movement of the eggs. The walls of the uterus consist of large round cells; there were no mature eggs in it. The vagina divides at its origin into two branches diverging to midbody. Several large glands are located around them.

There are two testes, the posterior by far the shorter; both join the 321 seminal vesicle, which gives rise to the vas deferens directly. Its basal part is clothed in epithelium that is as yet irregular, while the characteristic structure in the form of a pile of coins begins only at some distance further; only a short posterior section is invested with musculature and represents the ejaculatory duct. The spicules (Figure 70b) are greatly curved; the manubrium is directed obliquely upwards. The end is extended in the form of a process. The spicules are wider at the base than at the end and special thickenings are observed in the walls. Their length is 70 μ. The gubernaculum is complex with two posterior processes united at the base, which covers the ends of the spicules. Its length is 40 μ.

The **tail** of the female (Figure 70c) is of the same form as in the male, sometimes even longer, but lacks the characteristic swelling in the middle: there are only a few long and slender bristles on it. In the male, the terminal filiform part of the tail is longer and the middle bears a pronounced swelling on the ventral side. The bristles are distributed in four rows — two subdorsal and two subventral. Special groups of bristles lie on the ventral side between the subventral rows, one postanally, the other on the ventral swelling. A group of short bristles lies at the beginning of the slender part. Some bristles lie at the end of the tail. In the female, there is a large anal gland behind the anus.

The proportions are: length of tail in male 5.0, in female 5.5 – 6.0; width at end 0.2; spicules 1.2; gubernaculum 0.7.

This species is encountered together with Ax. ponticus, but less frequently, chiefly in deep sand of Peschanaya Bay: 1.12, young; 6.12, adult females and males; algae on sand from the same place 6.12 (more than A. ponticus); one female was found in sand from Georgievskii Monastery, some juveniles in coquina from the same place. Apart from these, single specimens were found in Cystoseira from Shmit Bay 7.12 and in phyllophores 6.12.

The males of this species are easily distinguished from Ax. ponticus by the shorter and wider spicules, their short manubrium, the swelling in 322 the middle of the tail, and its bristle armature. The females, on the other hand, are far more difficult to distinguish; they have a more extended tail with a longer filiform part and longer caudal bristles. The only obvious distinguishing feature is the form of the lateral organ.

### 72. **Axonolaimus ponticus** n. sp.

(Table 19, Figure 71)

$$\text{♂}\ \frac{0.8 \quad 6.0 \quad 9.5 \quad 21^{*} \quad 39^{**} \quad 52^{\dagger} \quad 53.5^{\dagger\dagger} \quad 57.5^{\ddagger} \quad 92.3}{0.4 \quad 1.3 \quad 1.3 \qquad\qquad\qquad (1.5) \qquad\qquad\qquad 1.4}\ 3640$$

$$\alpha=67;\ \beta=10^1/_2;\ \gamma=13.$$

$$\text{♀}\ \frac{0.7 \quad 5.8 \quad 8.8 \quad 17 \quad 46.5 \quad 54 \quad 59.5 \quad 82 \quad 92.3}{0.5 \quad 1.2 \quad 1.4 \qquad\qquad\qquad 1.6 \qquad\qquad\qquad 1.2}\ 4000$$

$$\alpha=63;\ \beta=11^1/_2;\ \gamma=13.$$

---

* Beginning of genital tract.

** Beginning of seminal vesicle.

† Beginning of base of vas deferens and posterior testis.

†† End of posterior testis.

‡ Beginning of vas deferens proper.

| Dimensions ♂ | Cephalic bristles | End of oral cavity | Cervical pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 27 | 165 | 200 | 315 |
| Width | 15 | 24 | – | 43 | 43 |
| ♀ | | | | | |
| Length | 7 | 27 | 180 | 215 | 330 |
| Width | 17 | 23 | – | 43 | 50 |

This species is very similar to Ax. setosus, and therefore I shall give detailed information only about the differentiating features.

The dimensions and proportions are the same, but the female is somewhat stouter. The cuticle is similar. The bristles in this species are shorter and there are fewer of them; this is particularly noticed on the posterior end of the male.

The **head** is in general of similar structure (Figure 71a). The labial papillae and their excavations are here far more developed, while the cephalic bristles are shorter, only 12$\mu$, or about $^3/_4$ of the head width. The lateral organs are 13×5$\mu$, which is shorter, and their tube is narrower, so that its two bends are not closely pressed together as in Ax. setosus
323 but somewhat separated (see Figures 70a and 71a).

The structure of the oral cavity, and esophagus, glands, and internal genital organs are as in Ax. setosus.

The eggs are 100×40$\mu$, small compared with the size of the worm. Sharp differences are observed in the posterior end, chiefly in the male (Figure 71b). The **spicules** are considerably narrower than in Ax. setosus and more slightly curved. Their length is 65$\mu$. The manubrium is far longer and there is not such a narrow end. The gubernaculum is shorter (28$\mu$) and of more irregular form; its walls are thicker, its end is sometimes recurved downwards. The bristles on the tail are numerous, both in the submedial lines and between them; they are considerably shorter than in Ax. setosus. In front of the anus and around it there is a group of longer bristles, but they are correspondingly shorter. Finally, differences are observed in the form of the **tail:** in both sexes, it gradually tapers to the extreme tip and only a small portion at the end is of even width (see Figures 70b, c and 71b, c). Furthermore, the tail of the male is completely devoid of the swelling in the middle that is characteristic for Ax. setosus. The proportions are: length of tail in male 4.2–4.5; in female 4.5–5.5; width at end 0.14; spicules 1.3; gubernaculum 0.7.

This species is together with Ax. setosus n.sp. one of the most numerous inhabitants of oxeas sand from Kruglaya Bay: 1,5, 6.12; Georgievskii Monastery, sand, 9 sajenes, many specimens, but more immature; 18 sajenes, 2 juveniles. In addition, one female in Zostera from the Chernaya River 5.12; and many juveniles in deposits on Potamogeton from Streletskaya Bay, S. Zernov 3.10.

The differences from Ax. setosus n. sp. are given above.

---

## Genus CONOLAIMUS n.g.

Axonolaimus ex. p. auct.

Type species: C. angustilaimus n. sp.

324 In general structure—the disposition of the bristles, structure of the oral cavity, genital organs—this genus is very similar to Axonolaimus. The differences consist in the **lateral organs being shifted quite anteriorly** and positioned opposite the anterior chamber of the oral cavity. They also have a flask-shaped form, but are not **folded** as in Axonolaimus but **curved,** and therefore their outer contour is not **oval** but **round.**

Apart from my new species, there are three more species related here, all described as Axonolaimus.

1) C. limalis (Saveljev 1912): Tr. Soc. Imp. Natur. St. Pétersbourg 43, livr. 1, p. 118. Ekaterininskaya Harbor, muddy sand, some meters.
2) C. angustilaimus n.sp., see below.
3) C. filiformis (de Man 1889): Mém. Soc. Zool. France 2, p. 3. Penzance (English Channel). In algae on the coast of Clare Island (west coast of Ireland), mature in May and July (Southern).
4) C. impar (Saveljev 1912: loc.cit., p. 119. Coastal zone of Ekaterininskaya Harbor. The two last species are incompletely described and are difficult to distinguish.

1 (4). Species of medium thickness ($\alpha = 35-50$).
2 (3). Oral cavity almost $^1/_4$ of esophagus; $\alpha = 35$ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **C. limalis** Saveljev
3 (2). Oral cavity $^1/_6$ of esophagus; $\alpha = 50$ . . . . **C. angustilaimus** n. sp.
4 (1). Species slender ($\alpha = 80-100$).
5 (6). Tail conoid; gubernaculum less than $^2/_3$ of spicules; $\alpha = 80-90$. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **C. filiformis** de Man
6 (5). Tail with filiform termination; gubernaculum $^2/_3$ of spicules; $\alpha = 95-100$. . . . . . . . . . . . . . . . . . . . . . . . . **C. impar** Saveljev

### 73. **Conolaimus angustilaimus** n. sp.
(Table 10, Figure 72)

$$♀\ \frac{1.1\quad 4.4\quad 6.7\quad 38\quad 48\quad 53\quad 60\quad 70\quad 96.0}{0.7\quad 1.3\quad 1.4\qquad\qquad 20\qquad\qquad 1.3}\ 2430$$

$$\alpha = 50;\ \beta = 15;\ \gamma = 25.$$

| Dimensions ♀ | Middle and end of oral cavity | | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | 11 | 27 | 103 | 160 |
| Width | 16 | 23 | 32 | 36 |

The **body** is slender, filiform, tapering by $^1/_3$ from the middle to the anus and beginning of the esophagus. From this point, it tapers anteriorly more than twofold. 325

The **cuticle** is thin ($1-1^1/_2\mu$) and smooth. The bristles are up to $6\mu$ long and lie along the sublateral lines.

The **head** is generally rounded. True lips are absent. The circlet of six projecting labial papillae lies around the oral aperture, alternating with projecting rays of the vestibule. The four cephalic bristles are $18\mu$ long, somewhat more than the head diameter; not far from them small submedian bristles are observed; I did not observe laterals. The lateral organ is small, $8\mu$ in diameter (half the head width), in the form of an open spiral. It lies quite anteriorly, opposite the cephalic bristles and the anterior chamber of the oral cavity. Supplementary cephalic bristles lie in a circlet of four bristles behind the main ones and in a pair behind each lateral organ.

The **oral cavity** consists of two cones joined by their bases. The anterior cone (vestibule) is smaller ($9\mu$) with thickenings on its walls, probably six in number, which extend as pointed anterior margins out of the oral aperture and play the part of lips, closing the entrance to the oral cavity. The posterior part is $18\mu$ long, with thick walls, not bearing any specialized structures. The maximum width of the oral cavity is $8^1/_2\,\mu$. The **esophagus** is very short and slender (half the body width, $20\mu$ at the posterior end and $15\mu$ in the middle). The nerve ring encircles the posterior third. Some large cells are observed inside the body: these are probably phagocytes. The first is behind the end of the esophagus, the second at the beginning of the ovary, the third between them.

The ovaries are paired and straight, but their extreme tip is reflexed. The uterus is two-chambered with thick walls. The vagina is $^2/_7$ of the body width, the ovejector diverges from it exactly laterally.

The **tail** is short, conoid, blunt at the end.

The proportions are: length of tail 3; width at end 0.17.

Only one female of this species was found in oyster banks 6.12.

326

## Genus ARAEOLAIMOIDES de Man 1893

Mém. Soc. Zool. France 6, p. 86, Table 5, Figure 4.

Type species: A. microphthalmus de Man 1893

These are small nematodes with a greatly narrowed anterior end and an annulated cuticle. Labial papillae are observed on the slender head. Four cephalic bristles lie behind these and there are also supplementary cephalic bristles. The lateral organ is flask-shaped, bent double. The oral cavity is absent; the esophagus is very narrow. Eyes with lens are present. The ovaries are straight. The spicules are short; the tail is pointed at the end.

I relate this genus to Axonolaimini because of the structure of the lateral organs. However, the distribution of the cephalic bristles in A. zosterae n. sp. and the pointed tail are very reminiscent of Diplopeltis.

De Man, whom I consider the author of this genus, states: "La création d'un nouveau genre Araeolaimoides est peut-être justifiée." It is impossible not to agree with this, but de Man puts this name in parentheses, calling his species Araeolaimus (Araeolaimoides) microphthalmus n.sp.*

This species is easily distinguished from that described below by the lateral bristles in front of the lateral organs: in A. zosterae n.sp. there are only sublaterals.

### 74. Araeolaimoides zosterae n. sp.

(Table 10, Figure 73)

$$\text{♂}\ \frac{-\quad 9.0\quad 12.6\quad 27\quad 44.5\quad 55\quad 89}{0.5\quad 1.8\quad 1.9\qquad 2.4\qquad 1.9}\ 1850$$

$$\alpha=42;\ \beta=8;\ \gamma=9.$$

| Dimensions ♂ | Anterior end | Cephalic bristles | Lateral organ | Cervical pore | Eyes | Nerve ring | End of esophagus |
|---|---|---|---|---|---|---|---|
| Length | – | – | 14 | 25 | 60 | 125 | 170 |
| Width | 2½ | 6½ | 10 | – | 18 | 25 | 26 |

327 The **body** tapers slightly (by $^1/_5$) to the anus and end of the esophagus; anteriorly, it is sharply pointed, and at the cephalic bristles it is $^1/_4$ of the width at the beginning of the esophagus; all this tapering occurs in the portion anterior to the nerve ring. The **cuticle** is thin (about $1\mu$) and very finely annulated, the annules separated by $0.8\mu$. Fairly numerous bristles about $5\mu$ long are set along the sublateral lines.

The **head** is pointed and very characteristic because of the bristles. The oral aperture is encircled by an elevation of thickened cuticle beset with small labial papillae. I did not see six cephalic papillae, which probably are nevertheless present. The four cephalic bristles are stout, but only $5\mu$ long, shorter than the succeeding supplementary bristles. The latter are set in pairs behind each cephalic bristle. The dorsals are longer (about $17\mu$), the ventrals being only $14\mu$. Apart from these, two shorter and thinner bristles lie dorsal to the lateral organ. For the whole length of the esophagus there are along the sublateral lines separate groups of 2–3 short bristles. The lateral organs of the Axonolaimus type are in the form of a curved tube. The closed end is wider (see Figure 73a), the open longer, located dorsally. They are $5\mu$ long.

The oral cavity is absent. The esophagus is very narrow, $4\mu$ anteriorly, $6\mu$ posteriorly (rather more than $^1/_4$ of the body width). Two small eyes are located more posteriorly (Figure 73b). They have small crystals and contain a small, cuplike accumulation of pigment. The nerve ring is broad. The elongate ($25\times 8\mu$) cervical gland lies posterior to the end of the esophagus, and its pore is removed far anteriorly and is located not far posterior to the lateral organ.

---

* Mém. Soc. Zool. France 6, p. 86, Table 5, Figure 4 — quite common in September and October among algae and in mud covering the rocks at Trefusis near Falmouth (English Channel). Araeolaimus cobbi Steiner 1916 is apparently not related here; see Appendix.

The two testes are joined to the wide seminal vesicle, from which the vas deferens originates, consisting of one row of cuboid cells. The **spicules** (Figures 73c, d) are curved, broad, widest in the middle, with an additional thickening inside; the manubrium tapers and the end is 328 extended into a long point; the spicules are $32\mu$ long. The gubernaculum is short, curving away from the spicules, not completely covering their ends (Figure 73d). It is $16\mu$ long. There are no specialized papillae.

The **tail** is long, slightly tapering to a point at the end. The caudal glands are accommodated within it; their tube is quite long. The proportions are: length of tail 6; width at end 0.3; spicules 1.3; gubernaculum 0.05.

One male of this species was found in Zostera on the north side 5. 12.

## Genus SPHAEROCEPHALUM n.g.

Type species: Sph. crassicauda n. sp.

These are worms of medium size, thin, with a finely annulated cuticle. On the head there are six small papillae, ten long and slender cephalic bristles, and supplementary cephalic bristles. **The lateral organ is in the form of a spiral with one small turn,** whose ends are one on top of the other. The beginning and end of the esophagus are swollen, but a true bulb is absent. The ovary is single, anterior, and straight, but the uterine branches are paired. **The tail is very stout,** with a terminal tube in the form of a caudal appendage.

I place this genus in Axonolaimini because of the form of the lateral organ. The similarity should also be noted with some forms of Chromadoridae, such as Laxus Cobb or Chromaspira m., where there are also slender flexible bristles on the head and a similar lateral organ. Some species now related to genus Araeolaimus de Man should possibly be transferred here.

The sole species is:

### 75. Sphaerocephalum crassicauda n. sp.

(Table 11, Figure 75)

$$\text{♀}\ \frac{-}{1.0}\ \frac{4.3 \quad 8.8 \quad 40 \quad 48 \quad 58 \quad 96.8}{1.6 \quad 1.6 \qquad 1.7 \qquad 1.1}\ 2750$$

$$\alpha = 6;\ \beta = 11^1/_2;\ \gamma = 30.$$

| Dimensions ♀ | Cephalic bristles | Lateral organ | Cervical pore | Nerve ring | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 30 | 95 | 125 | 255 |
| Width | 25 | 35 | – | 40 | 43 |

329 The **body** is of very even thickness and hardly tapers ($1^1/_2$ times) anteriorly and to the anus. The cuticle is very thin (about $1\mu$) and annulated; the annules are very small ($0.5-0.6\mu$). There are many long, slender bristles, particularly anteriorly.

The **head** is rounded and devoid of lips. The labial papillae are very small, lying somewhat removed from the margins of the mouth. They are followed by ten long and slender cephalic bristles $17\mu$ long ($^3/_4$ of the body width). The sublaterals are far shorter, only $5\mu$. These bristles are concealed among the supplementary cephalic bristles, which are longer and fairly numerous. The lateral organs are circular, $8\mu$ ($^1/_5$ of the body width), but more careful examination indicates that they are spiral with one small turn.

The vestibule is absent, the very small oral cavity opening directly to the outside (see Figure 75b); the latter is very small, only $4\mu$ long, but it possesses distinct walls; an expansion is observed at the anterior end of the esophagus also. In one of my specimens this expansion was very notable, but this may have been an artificial manifestation. The **esophagus** tapers from $25\mu$ anteriorly to $20\mu$ in the middle (half the body width), while posteriorly, it expands once more to $35\mu$ (0.7 of the body width). However, a true bulb is not formed (Figure 75a). The nerve ring lies half way along the esophagus. The intestine consists of large cells. The large cervical gland lies immediately behind the end of the esophagus and displaces laterally the wall of the intestine, which forms a curve. The cervical pore lies anterior to the nerve ring. The ovary is large and straight, single and anterior, but a posterior branch of the uterus is present, forming a common cavity with the anterior branch. There were 6 eggs in the uterus, measuring $115 \times 40\mu$. The vagina is inconspicuous, $^1/_4$ of the body width.

The **tail** (Figure 75c) is long, very stout, only very slightly tapering to the end, the extreme tip expanded and rounded, and the tube protruding from that point. The proportions are: length of tail $4.5-5.5$; width 330 at end 0.7.

One female of the species was found in deep Cystoseira 6.12, another in mussels 6.12.

## 5. Subfamily Comesomini

These are small or medium-sized nematodes with a finely annulated or smooth cuticle. The head is separated by a small constriction and has a characteristic form; on it are two circlets of papillae (6 labial and 6 cephalic) and four bristles. **The lateral organ is distinctly spiral.** The oral cavity is small, the esophagus straight and slender. The ovaries are paired and straight. There are three genera here, differentiated only by the males.

1) Comesoma Bastian 1865, see p. 240.
2) Sabatieria Rouville 1903; 1905: Comptes-rendus de l'Ass. Franç.

pour l'Avancement des Sciences 1904, p. 794: de Man 1908: Mém. Soc. Zool. France 20, p. 63.*

3) Parasabatieria de Man 1907, see p. 244.

It is quite possible that Monhystera dubia Bütschli 1873 will prove to be a member of this subfamily (see p. 213).

1 (2). Spicules long, gubernaculum without posterior processes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Comesoma** Bastian
2 (1). Spicules short, gubernaculum with posterior processes.
3 (4). Preanal papillae present in male . . . . . . . **Parasabatieria** de Man
4 (3). Such papillae absent . . . . . . . . . . . . . . . . . . . **Sabatieria** Rouville

## Genus COMESOMA Bastian 1865

Trans. Linn. Soc. 25, p. 158.
Bütschli 1874: Abh. Senck. Ges. 9, p. 30.
De Man 1890: Mém. Soc. Zool. France 3, p. 171.

331 Type species: C. vulgare Bastian 1865 (de Man 1890)

The head is narrow, separated from the neck by an annular depression. The cuticle has annules and on the boundary of the inner and outer layers punctations which in turn may be distributed in rows, creating a secondary annulation. There are six labial papillae, in typical species six cephalic papillae and four long and stout bristles. **The lateral organ is large and spiral. The oral cavity is small, open anteriorly,** with a small tooth; the aperture may be closed by lips. The esophagus is slender, without a bulb. The ovaries are straight, the uterus two-chambered. **The spicules are long,** considerably longer than the diameter at the anus. There are usually supplementary bristles in the male. The tail is long, conoid and swollen at the end.

This characteristic species was established by Bastian and redescribed by Bütschli, who quite rightly compared it to Monhystera (1874, p. 31), and by de Man. Rouville (1903) isolated species provided with short spicules and gubernaculum with posterior processes into a separate genus, Sabatieria. The members of this genus that are provided with a preanal row of papillae in the male were isolated by de Man (1907) as Parasabatieria. The latter genus incorporated also C. heterura Cobb. Dubious species are: C. similis Cobb with six long cephalic bristles and C. dubia n. sp., the structure of whose oral cavity is still inadequately clarified.

There are six known species:

1) C. vulgare Bastian 1865: Trans. Linn. Soc. 25, p. 158, Table 13, Figures 195—197; de Man 1890: Mém. Soc. Zool. France 3, p. 172, Table 3, Figure 3. Falmouth (de Man, Bastian), Sète (Rouville).
2) C. stenocephalum n. sp., see p. 241.
3) C. jubata Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 389. Sand at low tide, Port Jackson N. S. W.
4) C. profundi Bastian 1865: Trans. Linn. Soc. 25, p. 159, Table 13, Figures 198—200; Bütschli 1874: Abh. Senck. Ges. 9, p. 31, Table 3, Figure 14. Mud from a depth of 20 sajenes, Falmouth (Bastian); mud from 13 sajenes, Kiel, oyster bank, Sylt (Bütschli).
5) C. (?) dubia n. sp., see p. 343.
6) C. (?) similis Cobb 1898: Proc. Linn. Soc. N. S. W. 23, p. 387. Sand at low tide, Port Jackson N. S. W.

332 1 (8). On head four cephalic bristles and two rows of six papillae (cephalic and labial).
2 (5). Supplementary cephalic bristles (only in adults).
3 (4). Punctations on cuticle at midbody in regular rows. 3—6 supplementary cephalic bristles for each main bristle. Head $^2/_5$ of width at end of esophagus . . . . . . . . . . **C. vulgare** Bastian
4 (3). Punctations on cuticle of midbody disposed irregularly. Supplementary bristles numbering 2—3 for each main bristle. Head $^1/_3$ of width at end of esophagus. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **C. stenocephalum** n. sp.
5 (2). Supplementary cephalic bristles absent.
6 (7). Cephalic bristles longer than head width. . . . . . . **C. jubata** Cobb
7 (6). Twice shorter . . . . . . . . . . . . . . . . . . . . . **C. profundi** Bastian
8 (1). Two rows of cephalic bristles: six in anterior, four in posterior row.
9 (12). Anterior bristles shorter than posterior.
10 (11). Lateral organ stands one head width from anterior margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **C. profundi** Bastian
11 (10). Only half a head width distant . . . . . . . . . . . . . **C.** (?) **dubia** n. sp.
12 (9). Posterior bristles shorter than anterior . . . . **C.** (?) **similis** Cobb

### 76. **Comesoma stenocephalum** n. sp.

(Table 11, Figure 76)

$$\text{immature } ♀ \; \frac{—\quad 4.5\quad 7.3\quad 46.7\quad 48.7\quad 58.3\quad 93.0}{0.4\quad 1.3\quad 1.4\qquad\quad 2.0\qquad\quad 1.3}\; 4600$$

$$\alpha = 50;\ \beta = 14;\ \gamma = 14.$$

$$♂ \; \frac{—\quad 3.9\quad 7.0\quad 38^{*}\quad 46^{**}\quad 55^{\dagger}\quad 73^{\dagger\dagger}\quad 93.0}{0.5\quad 1.3\quad 1.5\qquad\qquad 1.8\qquad\qquad 1.3}\; 4600$$

$$\alpha = 55;\ \beta = 14;\ \gamma = 14.$$

* Beginning of anterior testis.
** End of anterior testis.
† End of posterior testis.
†† Boundary of vas deferens and ejaculatory duct.

---

* Here are four species: (1) S. tenuicaudata (Bastian 1865) Spira t.: Trans. Linn. Soc. 25, p. 160, Table 13, Figures 207—209; S. t.: de Man 1908: Mém. Soc. Zool. France 20, p. 62, Table 3, Figure 10; Falmouth, sand at low tide (Bastian); Veere, Yerseke—Holland, very common (de Man). (2) S. oxycephala (Bütschli 1874) Spilophora o.: Abh. Senck. Ges. 9, p. 47, Table 7, Figure 28. Kiel Firth in sand, several sajenes, with Onch. vulgaris. (3) S. cettensis Rouville 1905: loc. cit., p. 794. Sète, canal de Bourdigues. (4) S. praedatrix de Man 1907: Mém. Soc. Zool. France 20, p. 63, Table 3, Figure 11 Jerseke (Holland). (5) S. celtica Southern 1914: Proc. Roy. Irish. Ac. 31, pt. 54, p. 25, Table 3, Figure 8 A—D. Clew Bay (west coast of Ireland) sand and coquina from 24 sajenes in May. (6) S. longiseta Steiner 1916: Zool. Jahr. Syst. 39, p. 593, Table 28, Figures 22a-d. White Sea strait, in algae. (7) S. antarctica Cobb 1914: Nem. Shackleton Exp. p. 14; Cape Royds, Ross Island, Antarctic Ocean.

| Dimensions ♀ (immature) | Cephalic bristles | Lateral organ | Nerve ring | Cervical pore | End of esophagus |
|---|---|---|---|---|---|
| Length | 8 | 14 | 205 | 215 | 330 |
| Width | 27 | 27 | 65 | – | 70 |
| ♂ | | | | | |
| Length | 9 | 17 | 170 | 195 | 305 |
| Width | 24 | 25 | 57 | – | 65 |

333 The **body** tapers slightly but noticeably to the anus and end of the esophagus. The tapering is very marked within the limits of the esophageal region, twofold, which is greater than in the other species. The **cuticle** is fairly thick, about $2.5\mu$. Two layers are distinguished in it: the outer, which is quite thin and smooth, and the inner, which accounts for more than half the overall thickness. A row of punctations $0.8\mu$ apart is observed on the outer surface of the inner layer. At midbody any regularity in their arrangement is difficult to ascertain. Anteriorly, the rows have fewer punctations, are $1\mu$ apart, and are more regular (Figure 76a). The inner surface of this layer is also striated, the hardly visible annules standing $2\mu$ apart. I did not note any bristles apart from the anterior and posterior groups described below.

The **head** is truncated, tapering quite sharply to the cephalic bristles. Six very small labial papillae are set around the oral aperture; behind these are six considerably larger cephalic papillae, and four long cephalic bristles $22\mu$ long and as wide as the head. Behind these there are still more supplementary cephalic bristles. Dorsally these bristles are far more freely distributed than ventrally, where they are densely grouped. Their number is not constant. In young individuals they are absent entirely, while in the old ones there are two or three for each cephalic bristle The lateral organ is large—$16\mu$ in the male, or $^2/_3$ of the head width, and $12\mu$ in the female, or somewhat less than half the head width.

The entrance to the oral cavity is $10\mu$ in diameter, and closed only by inconspicuous lips. The **oral cavity,** in the form of a flat-bottomed cup with its opening anteriorly, has a thick bottom and is $8\mu$ deep. A tooth arises from the bottom in the dorsal sector. The oral cavity may be widthdrawn deeper than shown in the figure. The **esophagus** is thin and straight. It gradually expands from $17-19\mu$ anteriorly to $35-40\mu$ posteriorly, all the time occupying 55% of the body thickness. The **nerve ring** encircles it at the end of the second third. The cervical gland is
334 located behind the end of the esophagus; its stout duct runs anteriorly and opens somewhat posterior to the nerve ring. There are many large glands in the fairly wide lateral fields.

The **ovary** is straight, greatly outstretched, as is its syncytial portion also. The **uterus** is double; in my specimens it contained no eggs. There are two testes at whose end is a large seminal vesicle to which the long vas deferens is joined. The sperm are oval and $3\mu$ long. The spicules are long (Figure 76c), $165\mu$, their initial part is straight, the end blunt, somewhat expanding on the ventral side (Figure 76d). The gubernaculum is very small, $40\mu$ long, covering the end of the spicules in the middle and laterally (Figure 76d). Posteriorly, there is a thin plate joining its two halves (gub. m. —Figure 76d); laterally, the lateral plates have a complex configuration, their outer ends abutting against the cuticle (gub. l. — Figure 76d). Anterior and posterior to the anus, down to the narrow portion of the tail, there are ten pairs of short subventral bristles of various lengths, the posterior somewhat shorter and the anterior sparse.

The **tail** (Figures 76b, c) is even, first tapering more slightly to the posterior third, which is slender, with a swelling at the tip. The proportions are: length of tail in male and female 5; narrow posterior portion 1.4; width at end 0.2; spicules 2.4; length of posterior row of bristles 3.5; of anterior row 3.5.

This species is quite common in the Black Sea and is characteristic for oxeas sand: Kruglaya Bay 5.12, 6.12; algae on it 6.12, many immature females; saccocirrous sand from the same place 7.12, young male and female; phyllophores 6.12, young female with rudimentary anterior ovary, but complete uterus.

This species is easily distinguished from C. vulgare Bastian (1) in there being not more than three supplementary cephalic bristles in each bundle, while in C. vulgare there are 4—5; (2) in the far narrower head in our species; (3) in the lack of regular rows of punctations on the cuticle as in the northern species.

### 335 77. Comesoma (?) dubia n.sp.

(Table 11, Figure 77)

$$♂\ \frac{-\quad 5.6\quad 8.7\quad -\quad 92.3}{0.6\quad 1.6\quad 1.8\quad 2.1\quad 1.8}\,2800$$

$$\alpha=49;\ \beta=11^1/_2;\ \gamma=14$$

| Dimensions ♂ | Cephalic bristles | Lateral organ | Nerve ring | Cervical pore | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 9 | 150 | 175 | 250 |
| Width | 16 | 17 | 50 | – | 55 |

The **body** is filiform, of even width from the anus to the end of the esophagus, whence anteriorly it tapers three times, mainly in the preneural region. The cuticle is thin ($1.5\mu$); the annules on it at the middle are hardly conspicuous ($0.6\mu$). Anteriorly, the punctations are more noticeable and are joined in distinct annules $0.8\mu$ from each other. I found bristles only in the anterior part of the body.

The **head** (Figure 77a) tapers greatly and is truncated anteriorly. Three lips close the entrance to the oral cavity. Six distinct small labial papillae are present. There are ten cephalic bristles, the anterior six shorter, ($6\mu$, about $^1/_3$ of the head width), and the posterior four longer ($17\mu$, equal to the head width). The lateral organs are spiral with two small turns. From both a secretion had emerged in the form of a long congealed chord. Their diameter is $9\mu$, or half the head width. The walls of the **oral cavity** are hardly thickened; the cavity is quite deep, $7\mu$ from the lips, but almost all is occupied by the organs projecting into it. On the dorsal side there is a chitinized tooth $4\mu$ long (den. —Figure 77a); two elevations rise in the subventral sectors also (a—Figure 77a), ending in chitinized tips. The **esophagus** is slender, straight, without a bulb, gradually thickening posteriorly (from 15 to $25\mu$), being constantly (apart from at the anterior end) less than half the head width. The cardia is located posteriorly and is

19$\mu$ long. I could not detect the cervical gland. Its pore lies not far
336 posterior to the nerve ring.

The **spicules** (Figures 77b, c) are long (175$\mu$); a long thick velum extends internally from the trunk. The base is expanded, pointed at the end. The gubernaculum consists of two parts: one thin (gub. — Figure 77c), adjacent to the spicules, the other thicker, in the form of a specialized hollow body joined to the ends of the spicules. The cuticle behind the anus is greatly thickened and this piece is attached to it. The entire length is about 40$\mu$.

The **tail** is quite evenly conoid, somewhat swollen at the end. The pore pierces the terminal thickening of the cuticle. The proportions (male) are: length of tail 4; width at end 0.2; spicules 3.5; gubernaculum 0.8.

One male of this species was found in Zostera from the Chernaya River 5.12; another male was found in Zostera from the north side 11.12.

If the structure of the oral cavity as I have described it is confirmed by more material, this species will be related to a new genus.

One more species of Comesoma which so far I have not described was found in oyster banks 6.12 as a female and two juveniles. There were no supplementary cephalic bristles upon it, and the punctations were disposed in annules.

## Genus PARASABATIERIA de Man 1907

Mém. Soc. Zool. France 20, p. 66.

Type species: P. vulgaris de Man 1907

These are small and medium-sized nematodes; the cephalic end, genital organs, and tail are exactly as in Comesoma. The differences are confined to the spicules, which are short and curved, and the gubernaculum, which is provided with two processes directed posteriorly. Anterior to the anus is a row of preanal median papillae, a differentiating feature from Sabatieria Rouville. The following five species are related here:

1) P. kolaënsis Saveljev 1912: Tr. Soc. Nat. St. Pétersbourg 43, livr. 1, p. 123. Ekaterininskaya Harbor — mud at low tide.
337 2) P. heterura (Cobb) 1898: Comesoma h.: Proc. Linn. Soc. N.S.W. 23, p. 386; 4 — 5 sajenes. Port Jackson N. S. W.
3) P. vulgaris de Man 1907: Mém. Soc. Zool. France 20, p. 66, Tables 1, 3, 4, Figure 12. Coast of Yerseke Island (Holland).
4) P. clavicauda n. sp., see p. 245.
5) P. abyssalis n. sp., see p. 246.

1 (2). Length 4 mm; cephalic bristles $^1/_4$ of diameter of head; spicules $^3/_5$ of tail; 38 — 40 preanal papillae in male . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. kolaënsis** Saveljev
2 (1). Length not more than 3 mm; bristles about half head diameter; spicules less than half tail; not more than 15 papillae.
3 (6). Medium size (2.2 — 2.8 mm).
4 (5). 15 preanal papillae in male . . . . . . . . . . . . . **P. heterura** Cobb
5 (4). 7 — 9 papillae, lateral organs slightly smaller than half head diameter . . . . . . . . . . . . . . . . . . . . . . . . . **P. vulgaris** de Man
6 (3). Small species, $1^1/_2$ — 2 mm; lateral organ considerably larger than half head width; spicules $^1/_3$ of tail.
7 (8). Lateral organs $^2/_3$ of head. Tail characteristically swollen at end, so that no slender portion of even diameter is formed. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. clavicauda** n. sp.
8 (7). Lateral organs $^5/_6$ of head; tail has portion of even diameter; 10 preanal papillae . . . . . . . . . . . . . . . . . . . **P. abyssalis** n. sp.

### 78. **Parasabatieria clavicauda** n. sp.

(Table 11, Figure 78)

$$♂\ \frac{\begin{array}{ccccc} — & 6.6 & 12.3 & — & 91.1 \end{array}}{\begin{array}{ccccc} 0.9 & 2.2 & 2.3 & 3.0 & 2.6 \end{array}}\ 1270$$

$\alpha=33;\ \beta=8;\ \gamma=11.$

$$♀\ \frac{\begin{array}{ccccccc} — & 5.3 & 10.8 & 43 & 49 & 59 & 91.5 \end{array}}{\begin{array}{ccccccc} 0.8 & 2.3 & 2.6 & & 3.3 & & 1.8 \end{array}}\ 1620$$

$\alpha=30;\ \beta=9;\ \gamma=12.$

| Dimensions ♂ | Cephalic bristles | Lateral organ | Nerve ring | Cervical pore | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 8 | 75 | 95 | 150 |
| Width | 10 | 12 | 27 | — | 30 |
| ♀ | | | | | |
| Length | 6 | 8 | 95 | ? | 175 |
| Width | 12 | 13 | 33 | — | 37 |

The **body** expands markedly in the middle; in the male it tapers slightly
338 to the anus, and in the female almost twofold. It tapers by $^1/_4$ to the beginning of the esophagus and from here anteriorly the tapering is very great, up to three times in adults. The **cuticle** is 1$\mu$ thick, punctations are very weakly observed on it, but arranged in transverse rows 0.8$\mu$ apart.

The **head** is rounded, bearing six labial and six cephalic papillae and four cephalic bristles which reach the posterior margin of the lateral organ; they are 7$\mu$ long, somewhat more than half the head width. The lateral organ is large, spiral, with $2^1/_4$ turns. Its width is 8$\mu$, or $^2/_3$ of the head width.

I was unable to distinguish any lips closing the entrance to the oral cavity, but they nevertheless are probably present. The oral cavity is small, open anteriorly, as in the other forms of Parasabatieria. A part of it is apparently not embraced by the esophagus. Its depth is about $2^1/_2\mu$. The esophagus anteriorly occupies a fairly considerable part of the width of the body, opposite the nerve ring it is about half (15$\mu$), and posteriorly about 70% of the body width, expanding up to 25$\mu$. The posterior end of the esophagus has a small bulb in its internal structure of 30$\mu$ length. There is a fairly considerable cardia. The intestine consists of a few rows of large cells. The cervical pore is located behind the nerve ring.

The ovary is straight, of the usual type. The uterus is two-chambered. The vagina traverses internally $^{2}/_{5}$ of the body width.

The spicules (Figure 78c) have thin walls and probably are triangular in cross section, one of the angles directed internally. The spicule generally is of very even diameter, although its upper plane is narrow in the middle and expands to both ends. At the base, a longitudinal stiffening is observed within the spicule, considerably more greatly developed than in P. abyssalis m. Near the apex internal stiffenings are also noted. The spicules are 43 μ long. The gubernaculum, as in the other species, consists of a median piece connecting the spicules, two
339 lateral pieces covering their ends, and two posterior processes directed obliquely upwards. The structure of the median piece is quite complex: in profile, separate folds of a chitinized substance are observed attached by their origins to the posterior processes (a—Figure 78c). In front of the anus there are 8 papillae, the anterior and not the posterior being closer together, as opposed to P. abyssalis m.

The **tail** is shorter than in the following species, with hardly any portion of even diameter at its end, so that the terminal swelling is almost directly attached to the coniform part, which gives rise to the name of the species. The proportions are: length of tail of female 4.5, of male 3.5; width at end of female 0.3, of male 0.25; spicules 1.3; gubernaculum 1.2; distance from anus to anterior papilla 5.

One male of this species was found in Zostera on the north side 11.12, many females in mud from the Chernaya River 6.12.

The species differs from the following by the greater swelling at the end of the tail and by the different form of the spicules. P. vulgaris de Man is larger and its lateral organs are somewhat smaller.

### 79. **Parasabatieria abyssalis** n. sp.
(Table 11, Figure 79)

$$♂\ \frac{—\quad 7.5\quad 13.5\quad 37^{*}\quad 90.5}{0.8\quad 2.4\quad 2.7\quad 3.0\quad 2.3}\ 1650$$

$$\alpha=33;\ \beta=7^{1}/_{2};\ \gamma=10^{1}/_{2}.$$

$$♀\ \frac{—\quad 8.0\quad 15.3\quad 41\quad 89.0}{1.0\quad 2.7\quad 3.3\quad 4.0\quad 3.0}\ 1500$$

$$\alpha=25;\ \beta=6^{1}/_{2};\ \gamma=9.$$

| Dimensions<br>♂ | Cephalic bristles | Lateral organ | Nerve ring | Cervical pore | End of esophagus |
|---|---|---|---|---|---|
| Length | 6 | 11 | 110 | 120 | 210 |
| Width | 10 | 14 | 40 | – | 45 |
| ♀ | | | | | |
| Length | 5 | 12 | 115 | 135 | 230 |
| Width | 12 | 15 | 43 | – | 50 |

---

* Beginning of genital tract.

340 The **body** tapers from the middle to the anus by $^{1}/_{4}$ and to the end of the esophagus somewhat less. From here anteriorly it tapers more than $^{1}/_{3}$. The **cuticle** is thin, 1.5 μ, similar in structure to Comesoma. There are two layers in it: the outer is smooth and the inner bears punctations externally. These are irregular, not forming annules; in the middle they are smaller, anteriorly larger. On its internal surface this layer bears narrow annules 0.5—0.7 μ apart. The bristles are few.

The **head** (Figure 79a) is rounded and bears two rows of papillae, six labial and six cephalic; behind them there are four short cephalic bristles (6 μ, about half the head width). The lateral organ is spiral, with $3^{1}/_{2}$ turns; in both sexes it is of uniform width (10—11 μ), very large, occupying about $^{5}/_{6}$ of the head width. Because of this, in Figure 79a its lateral bends appear pressed together. Three (?) high lips completely close the entrance to the oral cavity, which is small but distinct, appearing as a cup-shaped depression, 4 μ deep, in the anterior end of the esophagus. The esophagus gradually expands posteriorly and forms there an oval bulb, distinguished only by its inner structure; externally, it is hardly differentiated. Anteriorly, the esophagus is 11—13 μ wide, and posteriorly it reaches 30 μ (60—70% of the body thickness). The **cervical gland** is large, more than half the diameter of the body, 90×30 μ, its posterior end in line with the esophagus posterior to it. The cervical pore is a small pit in the cuticle, behind which there is a coniform chitinized canal joining the duct of the gland.

The ovary is straight. The uterus is two-chambered, small, possibly becoming larger in older females. The vagina traverses $^{1}/_{3}$ of the body width.

There are two testes; the sperm are oval, 3 μ long. The spicules (Figure 79d) are flat, short (40 μ), slightly curved. The end is pointed, but the base is widened with a specialized thickening inside. The gubernaculum is furnished with two posterior processes; its anterior part covers the
341 ends of the spicules. An unpaired piece located between the spicules joins the two halves. The overall length of the gubernaculum is about 27 μ. In the male there are supplementary bristles; one preanal pair and 3—4 postanal pairs (see Figure 79c). There is a row of preanal median papillae; the four posterior lie closely adjacent, while the six anterior are more spaced out.

The **tail** tapers gradually to the middle of its length. From this point to the end it is almost of even width, slightly swollen at the end. The proportions are: length of tail of male 5.3, of female 3.5—4; width at end 0.2—0.3; spicules 1.1; gubernaculum 0.8.

This species is encountered in mussels (Kacha 8.13, many) and phaseolin mud (Georgievskii Monastery 7.13, a few males and females).

The huge lateral organs easily differentiate it from all the other described species of this genus.

## 6. Subfamily **Diplopeltini**

The cuticle is finely annulated. There are two circlets of six papillae and four cephalic bristles on the head. Sometimes there are supplementary cephalic bristles. **The lateral organ is large, in the form of a thick plate, with a spiral contained within.** The ovaries are straight, the tail pointed.

The characteristic lateral organs differentiate this subfamily, but the structure of the esophagus and genital organs is as in the majority of other forms of Monhysteridae. The pointed tail and distribution of the bristles anteriorly in Araeolaimoides zosterae m. are reminiscent of representatives of this subfamily. However, they can by no means be united with Diplopeltis (Southern). Genus Disconema m. (p. 221) is also similar.

The two genera are:

1) Diplopeltis Cobb 1905: lateral organs oval, oral cavity very narrow, see p. 248.
2) Acmaeolaimus n. g., lateral organs circular, oral cavity quite considerable, see p. 250.

342

## Genus DIPLOPELTIS Cobb 1905

Discophora Villot 1875: Arch. Zool. Exp. (1) 4, p. 463 (nom. praeocc. in Lepidopteris: Boisduval 1807).
Dipeltis Cobb 1891: Proc. Linn. Soc. N. S. W. 6, p. 147, (nom. praeocc.).
Diplopeltis Cobb 1905 in Stiles and Hassal p. 100 – renominatio.
Dipeltis Southern 1914: Proc. Roy. Irish. Acad. 31, pt. 54, p. 15.

Type species: D. cirrhatus (Eberth 1863)*

These are small and medium-sized nematodes with a smooth or very finely annulated cuticle. The head is greatly truncated, bears four submedian cephalic bristles, behind which, in the majority of species, there follow rows of supplementary cephalic bristles. The lateral organs are very large, in the form of thick plates with an incomplete spiral contained within. The oral cavity and esophagus are inconspicuous. The ovaries are straight. The spicules are short and curved. The tail is pointed.

The first species of this genus was described as Enoplus cirrhatus n. sp. by Eberth (1863). However, Bastian noted as early as 1865 that this species did not belong to genus Enoplus as conceived by Dujardin (1845), but he refrained from describing a new genus as he had no material available. Villot (1875), however, having found E. cirrhatus near Roscoff, established for it the new genus Discophora. This designation, as a nomen praeoccupatum, had to give way to the later Dipeltis, created by Cobb, who did not know of Villot's work. This name was subsequently replaced by Cobb himself for the same reason. Later authors disregarded the latter name.

There are five or six species:

1) D. cirrhatus (Eberth 1863) Enoplus c.: Untersuch. üb. Nematoden, p. 34, Table 2, Figures 20–22; Table 4, Figure 17; Table 5, Figure 4. Discophora c.: Villot 1875: Arch. Z. Exp. (1) 4, p. 463, Table 11, Figure 10; Dipeltis c.: Cobb 1891: Proc. Linn. Soc. N. S. W. 6, p. 156. Nice, Roscoff.
343 2) D. typicus Cobb 1891: Proc. Linn. Soc. N. S. W. 6, p. 157, Figure 9; var.: Southern 1914: Proc. Roy. Irish. Acad. 31, pt. 54, p. 15, Table 2, Figures 4-f. "Coral bank, Secca della Gajola." Bay of Naples 35 m (Cobb); among tubes of Spirorbis under stones on the west coast of Ireland in September (Southern); Southern considers that these two species are probably synonyms. His species is somewhat differentiated from Cobb's and may coincide with that of Eberth and Villot.
3) D. eberthi n. sp., see below.
4) D. minor Cobb 1891: Proc. Linn. Soc. N. S. W. 6, p. 156. Sand in Ceylon, March.
5) D. incisus Southern 1914: Proc. Roy. Irish. Acad. 31, pt. 54, p. 17, Table 2, Figure 5A-E; from a depth of 24 sajenes in Clew Bay (west coast of Ireland), coquina and sand from Polygordius.
6) D. barentsi Steiner 1916: Zool. Jahrb. Syst. 39, p. 628, Table 31, Figures 33a-c. White Sea strait, in algae. This species has a large oral cavity and is probably related to another genus.

1 (10). Oral cavity absent or very small.
2 (7). Behind four cephalic bristles runs whole row of supplementary bristles.
3 (4). This row is twice longer than lateral organ ................................................ **D. cirrhatus** (Eberth)
4 (3). This row is twice (or slightly more) longer than lateral organ.
5 (6). Lateral organ regular, disk-shaped; bristles set evenly in all the rows ................................ **D. typicus** Cobb
6 (5). Lateral organ posteriorly has irregular outline; anterior bristles dense, hardly extending beyond end of lateral organ; posterior stand in line with it ................ **D. eberthi** n. sp.
7 (2). Bristles absent.
8 (9). Lateral organs evenly rounded ................ **D. minor** Cobb
9 (8). Lateral organs incised anteriorly and laterally............................................... **D. incisus** Southern
10 (1). Oral cavity free, quite large ............ **D. barentsi** Steiner

80. **Diplopeltis eberthi** n. sp.
(Table 11, Figure 80)

$$\text{♀}\;\frac{\begin{array}{ccccccc} - & 4.0 & 5.7 & 42 & 49.5 & 55 & 94.6 \end{array}}{\begin{array}{ccccccc} 0.4 & 1.4 & 1.8 & & 2.5 & & 1.4 \end{array}}\;3650$$

$$\alpha = 40;\; \beta = 17.5;\; \gamma = 18.$$

---

* Eberths's form must be taken as the type species, as it was the type of the genus established by Villot. Cobb's names, however, should be considered only as nomina nova. Cobb's type was D. typicus.

| Dimensions ♀ | Anterior bristles | End of lateral organ | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | — | 30 | 170 | 240 |
| Width | 15 | 32 | 57 | 68 |

The **body** in the female tapers quite greatly, almost to half, from the 344 middle to the anus, more slightly to the end of the esophagus, whence to the anterior end it tapers $4^1/_2$ times. The **cuticle** is completely smooth, two-layered, the outer layer taking up about $^1/_3$ of the thickness, which is about 3.5$\mu$. Only the anterior bristles are present.

The **head** (Figure 80) is somewhat truncated anteriorly. There are papillae upon it probably in two circlets: the labial and cephalic papillae. There are four cephalic bristles 14$\mu$ long, hardly less than the head width. Four sublateral rows of nine bristles each follow, the posterior bristles being removed far from the anterior ones, which are set in a row. Each row contains ten bristles if the cephalic bristles are included. The lateral organ consists of a large oval plate, extended longitudinally, measuring 26×18$\mu$, or about 0.6 of the diameter of the head at the middle. Posteriorly, the plate is incised and has an irregular outline; here, canals enter the organ but soon reach an orifice of irregular form (a—Figure 80); the thick bundle of nerves of the lateral organ terminates at the bottom of the orifice (b—Figure 80). Anteriorly from the orifice there runs an enclosed horseshoe-shaped canal (c—Figure 80). The lateral organ is reminiscent to a certain extent of the lateral organs of Metachromadora, described above. The difference is, however, that there the canals are open. Some distance posteriorly to it, a small, curved, cuticular body lies internally (d—Figure 80). This is probably the lens of an eye whose pigment is dissolved.

The oral cavity is inconspicuous; there may be a small tooth (see Figure 80). The esophagus is very narrow; it expands from 13$\mu$ anteriorly to 22$\mu$ ($^1/_3$ of the body width) posteriorly. The intestine is narrow and consists of large elongated cells. The nerve ring encircles the esophagus over its posterior third. The cervical gland is very large, measuring 130×40$\mu$, located more than one length of the esophagus posterior to its end. The cervical pore is shifted far anteriorly and lies opposite the anterior end of the lateral organ (p. ex.—Figure 80). The terminal duct of the gland forms a swelling before the end (gl. ex. — Figure 80). A long, 345 slender, terminal tube runs from this swelling to the pore (e—Figure 80).

The **ovaries** are paired and straight; the uterus is undivided. Ripe eggs measure 50×40$\mu$. The vagina is short, $^1/_5$ of the body diameter.

The **tail** is quite long, with a terminal tube, and therefore appears pointed as in Chromadoridae. The proportions are: length 3.4; width at end 0.2.

Only one female of this species was found in sand of Peschanaya Bay 7.12.

## Genus ACMAEOLAIMUS n.g.

The cuticle is thick and finely annulated. On the head are two circlets of six papillae and four stout cephalic bristles. The lateral organ is in the form of a thick plate with a spiral concealed within. The oral cavity is in the form of an open cup; its dorsal ray has a thickening which extends posteriorly. The tail is conoid. The internal structure is not known.

This genus is so characteristic that I have decided to describe it from inadequate material. The lateral organs are very similar to those of Diplopeltis, so that I combine this new genus with it in the same group. The oral cavity is reminiscent of Comesoma. The dorsal thickening in it is partly reminiscent of Camacolaimus and Acanthopharynx, but this is only a superficial similarity.

There is one species:

### 81. **Acmaeolaimus diplopeltoides** n.sp.
(Table 11, Figure 81)

$$♀\ \frac{0.6 \quad ? \quad 3.5 \quad 59 \quad 96.7}{0.6 \quad ? \quad 1.1 \quad 1.9 \quad 1.4}\ 3360$$

$$\alpha=47;\ \beta=33;\ \gamma=33.$$

| Dimensions ♀ | Front | Cephalic bristles | Nerve ring | End of esophagus |
|---|---|---|---|---|
| Length | — | 12 | ? | 100 |
| Width | 12 | 21 | ? | 30 |

The **body** is quite slender, weakly tapering posteriorly and to the end 346 of the esophagus, whence anteriorly it tapers $2^1/_2$ times. The **cuticle** is thick ($2^1/_4\ \mu$), finely annulated, the annules being 1.4$\mu$ apart. I did not see bristles.

The **head** (Figure 81) is pointed and truncated. Six small labial papillae are set along the margins of the mouth, followed by four very conspicuous cephalic bristles 14$\mu$ long. There is a very marked lateral organ which is circular, 10$\mu$ wide, or half the head width. This, as in Diplopeltis, is a thick plate, with a spiral concealed inside. The **oral cavity** is cup-shaped, very similar to that of Comesoma, 4$\mu$ deep. Anteriorly, no structures close the entrance; a large thickening of cuticle which continues behind it also runs along the entire dorsal ray (see Figure 81). The overall length of this thickening is 22$\mu$. The esophagus is apparently slender and short. Apart from this, I can say nothing about the internal organization because the one specimen I had was poorly preserved.

The tail is stout, the end pointed, as in Diplopeltis. The proportions are: length of tail 2.5.

One female was found in oxeas sand of Georgievskii Monastery 7.13.

## V. Family *ANGUILLULIDAE*
(Rhabditidae Oerley)

This family has hardly any marine representatives and is mentioned here only for the sake of completeness.

As noted in the introduction, here belong several forms bearing a larval character, with signs of higher organization. Many of them are

meromyarian. Two esophageal expansions and a cervical gland in the form of two lateral vessels are characteristic for many of them, as for the parasitic nematodes. Some forms undoubtedly very similar to this family are indeed parasites. Many other parasites have larvae reminiscent of Rhabditis. It has already been suggested that these forms are neotenic larvae of parasites, so that this family is more closely connected with
347 the parasites than with the true free-living nematodes.

However, some parallels are observed with the freshwater representatives of Enoplidae-Dorylaimini (the formation of a spine, longitudinal striation of the cuticle, etc.). There may also be more similar relationships here.

A. Genera with oral cavity without spine. Polymyarian with weakly expressed reduction. All these groups—especially 11—17—are genera associated to a certain degree with Monhysteridae.

1) Plectus Bastian 1865: Trans. Linn. Soc. 25, p. 118, Bütschli 1873: N. Acta 26, No. 5, p. 83; de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 145; 1884: Nemat. Nied. F., p. 104; Jägerskiöld 1909: Süsswasserf. Deutsch., Heft 16, p. 22; Hofmänner 1913: Revue Suisse Zool. 21, p. 622; Menzel 1914: Arch. Naturg. 80A, Heft 3, p. 56. About 35 species.
2) Haliplectus Cobb 1913: Journ. Washington Acad. Sci. 3, p. 443. Close relatives of Plectus.
3) Wilsonema Cobb 1913: loc. cit., p. 443.
4) Chronogaster Cobb 1913: loc. cit., p. 443.
5) Cylindrolaimus de Man 1880; 1884: loc. cit., p. 83; Cobb 1916: Journ. Parasitol. 2, p. 199; 9 species.
6) Teratocephalus de Man 1876: loc. cit., p. 137; 1884: loc. cit., 101; Jägerskiöld 1909: loc. cit., p. 21; Menzel 1914: loc. cit., p. 55; 5 species.
7) ? Mitrephoros Linstow 1877: Arch. Naturg. 43, p. 2; Jägerskiöld 1909: loc. cit., p. 46; one species (? syn. praec.).
8) ? Leptolaimus de Man 1876: loc. cit., p. 169; 1884: loc. cit., p. 81; one species.
9) ? Anonchus Cobb 1913: loc. cit. p. 444: one species.
10) ? Pseudobathylaimus nom. nov. pro Bathylaimus Daday 1905: Zoologica 44, p. 60; Hofmänner 1914: Zool. Anz. 44, p. 83; 1915: Revue Suisse Zool. 23, p. 62 (praeocc.: Cobb 1893).
11) ? Aphanolaimus de Man 1880; 1884: loc. cit., p. 35; Jägerskiöld 1909: loc. cit., p. 7; 9 species.
12) ? Pseudochromadora Daday 1899: Term. Füz. 24, p. 7; one species.
13) ? Halaphanolaimus Southern 1914: Proc. Roy. Irish. Acad. 31, pt. 54, p. 11; marine genus; one species: H. pellucidus Southern 1914: p. 11, Table 1, Figures 2A—F; Clew Bay, west coast of Ireland: sand and coquina with Polygordius from a depth of 24 sajenes.
14) ? Cricolaimus Southern 1914: ibid., p. 20; one species: Cr. elongatus Southern 1914: p. 21, Table 2, Figures 6A—G; sand on the coast in September.
15) ? Dagda Southern 1914: ibid., p. 29; one species: D. bipapillata Southern 1914: p. 30, Table 4, Figures 10A—G. The same place in March.
16) ? Diodontolaimus Southern 1914: ibid., p. 31; one species: D. sabulosus Southern 1914: p. 31, Table 4, Figures 11A—F. In sand and under Zostera, in the same place in March.
17) ? Aplectus Cobb 1914: Nem. Shackleton Exp. p. 12; one species: A. antarcticus Cobb 1914: Antarctic Ocean near Ross Island, 30—50 sajenes.

B. Genera without spine, simple organization, meromyarian, or at any rate with simplified musculature.

348

1) Rhabditis Dujardin 1845: Histoire Nat. des Helm., p. 239; Bastian 1865: Trans. Linn. Soc. 25, p. 128; Bütschli 1873: N. Acta 26, No. 5, p. 95; de Man 1876: Tijd. Nederl. Dierk. Ver. 2, p. 153; 1884: Nemat. Niederl. F., p. 118; Oerley 1886: Die Rhabditiden, p. 24; Jägerskiöld 1909: Süsswf. Deut., Heft 16, p. 26; Hofmänner 1913: R. Suisse Zool. 21, p. 626; Pelodera—Leptodera A. Schneider 1866: Monogr. d. Nematoden, p. 159. One marine species: Rh. marina Bastian 1865: loc. cit., p. 129, Table 10, Figures 60—62; Ditlevsen 1911: Vid. Medd. Naturh. Fören. Kjöbenhavn 63, p. 240, Table 2, Figures 1—5, 7. Steiner 1916: Zool. Jahrb. Syst. 39, p. 518, Table 18, Figures 1a—g. In the sea on the coasts of England and Denmark (in decaying seaweed). In the White Sea strait in algae; and about 60 freshwater and terrestrial species.
2) Anguillula Ehrenberg 1838; Bastian 1865: loc. cit, p. 110; Bütschli 1873: loc. cit., p. 78; Jägerskiöld 1909: loc. cit., p. 26; de Man 1910: Zool. Jahrb. Syst. 29, p. 362; 4 species.
3) Cephalobus Bastian 1865: loc. cit., p. 124; Bütschli 1873: loc. cit., p. 77; de Man 1876: loc. cit., p. 139, 1884: loc. cit., p. 89; Oerley 1886: loc. cit., p. 38; Cobb 1893: Agric. Gaz. N. S. W. 4, p. 829; Jägerskiöld 1909: loc. cit., p. 19; Hofmänner 1913: loc. cit., p. 621; Menzel 1914: loc. cit., p. 54. More than 30 species.
4) Rhabditolaimus Fuchs 1915: Zool. Jahrb. Syst. 38, p. 191; 2 species.
5) Diploscapter Cobb 1913: Journ. Washington Acad. Sci. 3, p. 442.
6) Macrolaimus Maupas 1900: Arch. Zool. Exp. (3) 8, p. 578; one species.
7) Gymnolaimus Cobb 1913: Loc. cit., p. 443. Single species: G. exilis (Cobb 1893): Macleay Memor. Vol. p. 40, Table 2.
8) Diplogasteroides de Man 1912: Zool. Jahrb. Suppl. 15, Bd. I, p. 439; one species.
9) Demaniella Steiner 1914: Arch. Hydrobiol. Planktonk. 9, p. 427; one species.
10) Diplogaster M. Schultze 1859; Carus Icones Zootomicae, Table 8, Figure 1; Bastian 1865 p. 116; Claus 1869: Zeit. Wiss. Zool. 12, p. 355; Bütschli 1873: loc. cit., p. 119; 1874: Abh. Senck. Ges. 9, p. 22; 1876: Zeit. Wiss. Zool. 26, p. 367; de Man 1876: loc. cit., p. 158; 1884: loc. cit., p. 84; Oerley 1886: loc. cit., p. 40; Cobb 1893: Macleay Memorial Volume, p. 15; Jägerskiöld 1909:

loc. cit., p. 28; Potts 1910: Quart. Journ. Micr. Sci. 55, p. 437; Hofmänner 1913: loc. cit., p. 629; 35 species.

11) ? Macroposthonia de Man 1880; 1884: loc. cit., 124; one species.

12) Bunonema Jägerskiöld 1905: Zool. Anz. 28, p. 557; Menzel 1914: loc. cit., p. 74; Hofmänner and Menzel 1915: Revue Suisse. Zool. 23, p. 178; Cobb 1915; Stefanski 1914: Ném. du Léman. p. 36; 7 species.

13) ? Craspedonema Richters 1908: Ber. Senck. Ges., p. 24; Steiner 1916: Z. Anz. 46, p. 332; one species, related to the preceding.

C. Species with a spine in oral cavity (subfamily Tylenchini Marcinowski 1908: Arb. Kais. Biol. Anst. 7, p. 57).

1) Neonchus Cobb 1893: Agric. Gaz. N. S.W. 4, p. 819. One species. A strange genus, reminiscent in its tooth of Chromadoridae, in its lateral organs of Plectus. It can hardly be common with Mononchus as Cobb thinks. 349

2) Isonchus Cobb 1913: Journ. Washington Acad. Sci. 3, p. 439.

3) Tylopharynx de Man 1876, p. 116; 1884, p. 131. One species.

4) Aphelenchus Bastian 1865 p. 126; Bütschli 1873 p. 45; 1876 p. 364; de Man 1876 p. 135; 1884 p. 136; Cobb 1893: Macleay Memor. Vol. p. 53; Jägerskiöld 1909, p. 45; Hofmänner 1913, p. 646. About 30 species.

5) Tylenchorhynchus Cobb 1913, p. 438.

6) ? Nemonchus Cobb 1913, p. 438.

7) Eutylenchus Cobb 1913, p. 437.

8) Dolichodorus Cobb 1914: Trans. Amer. Micr. Soc. 33, p. 92; one species.

9) Tylenchus Bastian 1965: loc. cit., p. 125; Bütschli 1873: loc. cit., p. 31; de Man 1876: loc. cit., p. 124; 1884: loc. cit., p. 140; Cobb 1893: Agric. Gaz. N. S. W. 4, p. 812; Macleay Memor. Vol. p. 47; Jägerskiöld 1909: loc. cit., p. 43; Hofmänner 1913: loc. cit., p. 645; Menzel 1914: loc. cit., p. 61. About 50 species. One species in the sea: T. fucicola de Man 1892: Festschr. Leuckart, p. 121, Table 16; in galls on fuchus in England.

10) Tylenchulus Cobb 1913: Journ. Washington Acad. Sci. 3, p. 288; Journ. Agric. Research 2, p. 217; one species.

11) Heterodera Müller 1883; Strubell 1888: Zoologica 2; Meloidogyne Göldi 1889: Zool. Jahrb. Syst. 4, p. 262; Arch. Mus. Nac. Rio de Janeiro 8, p. 68; 2 species.

12) Atylenchus Cobb 1913: loc. cit., p. 437; one species.

13) Hoplolaimus Daday 1905: Zoologica 44, p. 62; Menzel 1917: Revue Suisse Zool. 25, p. 153; Iota Cobb 1913, p. 437; Criconema Hofmänner and Menzel 1914: Zool. Anz., p. 88; 1915: Revue Suisse Zool. 23, p. 207; Menzel 1914: loc. cit., p. 76. Micoletzky 1917: Zool. Jahrb. Syst. 40, p. 576; Ogma Southern 1914: Proc. Roy. Irish. Acad. 31, pt. 54, p. 65. The last author considers this species a representative of a special family Ogmidae, for which there can hardly be any real basis; this is probably simply an aberrant relative of Tylenchus. The synonymy is after Menzel (1917). It is possible that the name Iota Cobb = Ogma Southern is maintained for species with a more complex cuticle (see R. p. 370). Ten species.

350

## GENERA WHOSE SYSTEMATIC POSITION IS NOT CLEAR

Here belong in part insufficiently studied genera, in part those belonging to original types to which I shall not allocate a place until the system is revised. I do not include here the undefined genera of old authors, for which I refer the reader to Bastian. The appendices and corrections at the end of the book should also be consulted.

1) Odontophora Bütschli 1874 with large lips anteriorly represents the original type. One species: O. marina Bütschli 1874: Abh. Senck. Ges. 9, p. 49, Table 3, Figure 13. Oyster banks, Sylt.

2) Fimbrilla Cobb 1905 in Stiles and Hassal p. 107, pro Fimbria Cobb 1893 (praeocc.). One species: F. tenuis Cobb 1893: Proc. Linn. Soc. N. S.W. 8, p. 420; from seaweed, Ceylon, inadequately described.

3) Diplolaimus Linstow 1876: Arch. Naturg. 42, p. 16. What this genus is will probably remain locked with the author forever. It is possible that in genus Bunonema Jägerskiöld we have something similar.

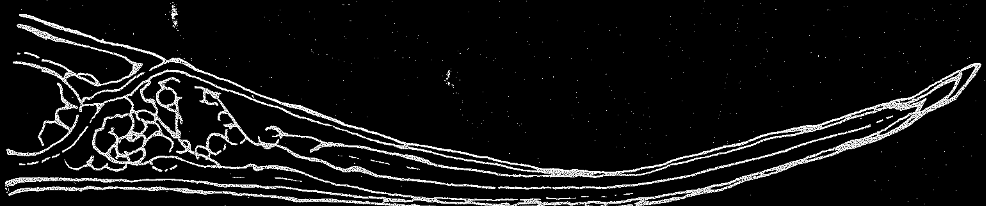
4) Anthonema Cobb 1906: Report of Work of the Experimental Station of the Hawaiian Sugar Planters' Association. Divis. Pathol. Physiol. Bull. No. 5, p. 117. In earth. I have not succeeded in obtaining the description.

Free-Living Marine Nematodes

I. N. Filip'ev

# Free-Living Marine Nematodes of the Sevastopol Area

## Issue 2



TRANSLATED FROM RUSSIAN

ISRAEL PROGRAM FOR SCIENTIFIC TRANSLATIONS

TRUDY OSOBOI ZOOLOGICHESKOI LABORATORII I SEVASTOPOL'SKOI
BIOLOGICHESKOI STANTSII ROSSIISKOI AKADEMII NAUK

Transactions of the Zoological Laboratory and the Sevastopol Biological Station
of the Russian Academy of Sciences

Series II No. 4

## I.N. Filip'ev

# FREE-LIVING MARINE NEMATODES OF THE SEVASTOPOL AREA

(Svobodnozhivushchiya morskiya nematody okrestnostei Sevastopolya)

Issue II

(Read at the meeting of the Department of Physics and Mathematics
on 26 November, 1914)

Rossiiskaya Gosudarstvennaya Akademicheskaya Tipografiya
Petrograd 1921

Translated from Russian

Israel Program for Scientific Translations
Jerusalem 1970

IPST Cat. No. 5458

Translated by M. Raveh

Printed in Jerusalem by Keter Press
Binding: Wiener Bindery Ltd., Jerusalem

---

# Table of Contents

## TRANSALTOR'S NOTE

This book is published in two parts, called Issue I and Issue II.
Issue I was prefaced by the following note:

"In his descriptions of the species the author of this book refers to and makes great use of drawings. Unfortunately, the part of the book containing the drawings of the species was not available at the time of translation, so that the translator has been obliged to rely largely on his imagination, which for the description of complicated organs and their disposition may not always have been adequate.

The references to the drawings have nevertheless been retained in the translation so that the reader who acquires a copy of the original Russian book will have no difficulty in relating the written description to the drawings. To this end, the Russian page numbers have been reproduced in the left-hand margin of the translation.

The Russian original contains sections on the general comparative morphology of free-living and parasitic nematodes, as well as Appendices. These also were not available for translation."

Throughout Issue I (Part I, IPST Cat. No. 1921, TT 67–51338) reference has been made to tables which in effect are plates. To avoid confusion, the term table has been retained throughout Part II.

Page numbers in the text refer to English pages of Part II, unless Part I is specifically mentioned. Page numbers in the index are covered by the note on p. 200

---

## *COMPARATIVE MORPHOLOGY*

353 In this part I have attempted to collect the information found in numerous papers on the structure, development and biology of nematodes. In presenting the material, I have not separated my observations from the published data. The examination of free-living nematodes has been made almost exclusively on whole mounts, and authors who studied living forms (Bütschli, 1873; de Man, 1886) have probably obtained better results than authors who used sections, which are not suitable for the study of these small animals. Only incomplete descriptions exist for the majority of nematodes, so that it is necessary to use data obtained with larger parasitic nematodes for the purpose of clarification. A comparison with parasitic forms and information on corresponding organs are given at the end of each section, as the establishment of a system is the main purpose of this work.

It is possible that there will be reservations about the need for this part, which is not directly connected with the preceding part. However, this work will save considerable labor and may be of use not only to specialists.

In the designation of the parts of the body of nematodes the example of the majority of authors has been followed (particularly Cobb and Stewart), who classify them according to the intestinal canal. Counting from the anterior to the posterior end, there are the following parts: the pharyngeal
354 part (next to the buccal cavity), the esophageal part, divided into a preneural and postneural part anterior and posterior to the nerve ring, the intestinal part, and the tail (posterior to the anus).

## I. SIZE, SHAPE AND METHODS OF MEASUREMENT

### 1. SIZE

Free-living nematodes are small, particularly in comparison with parasitic nematodes, such as Ascaris megalocephala (30 × 1 cm) or Eustronylus gigas (up to 1 m). The largest free-living nematodes are only 50 mm long and 0.25 mm thick ("Leptosomatum" australe Linstow). Species of Deontostoma, Fiacra and Cylicolaimus are 20–30 mm long. However, most species are shorter than 5 mm, some of them only 0.5 mm or even less. Thus, according to Shchepot'ev, Trichoderma is only 100 μ long and Tr. minutum Steiner, 1916, only 82 μ, being the smallest of all known nematodes. Their average size is about 2.5–3 mm.

Marine nematodes are thus of maximum and minimum size. Freshwater forms are generally much smaller, and only a few are larger (Dorylaimus, Mononchus), while there are several dozen large marine species. The average size is 1–2 mm, and very small species, less than 1 mm long, are numerous.

Only the Anguillulidae and Desmoscolecidae contain exclusively small forms, 2–3 mm in the Anguillulidae. The other families contain large and small forms. The majority of Enoplidae are large forms, such as all Leptosomatini (the largest of all free-living nematodes) and the Enoplini. Among the other subfamilies, large forms are also not rare: Paroncholaimus among the Oncholaimini, many species of Dorylaimus. However, small forms are also numerous: Anticomini, many species of Oncholaimini among marine nematodes, and a large number of Dorylaimini and freshwater forms related to them. Chromadoridae are usually small, there are larger forms only among the Cyatholaimini, while Chromadorini, Spilipherini and Draconematini are usually very small, about 1 mm. The 355 Monhysteridae are also usually small, but they include large forms such as the Siphonolaimini (up to 23 mm), Sphaerolaimus, which are thick and short, Linhomoeus, which are long and thin; there are medium-sized nematodes only in a few other genera.

## 2 SHAPE

### A. General Shape of the Body

In general, nematodes are very slender forms, round in cross section. Only the posterior part of males is sometimes flattened dorso-ventrally by the action of the bursal musculature.

The longest forms are usually very thin, e.g., the Leptosomatini: the ratio of length to width ($\alpha$ according to de Man, see below) in this subfamily is about 100, sometimes slightly less; in the smallest forms (Trichoderma, Richtersia) $\alpha = 10$ or even less (7.3 in R. collaris Steiner). A value of $\alpha = 30$ usually indicates a thick nematode, values of $\alpha = 50$ to 100 indicate a thin or very thin form. Thickness is a less variable factor than length in genera or subfamilies. For example, there are numerous forms of varying length in the genus Monhystera. The shortest forms (0.8–1.5 mm) are thick, while the long forms, such as M. leptosoma de Man (3.25 mm), are among the thinnest nematodes ($\alpha = 140$).

In the Black Sea fauna, thin forms are, for example, Eurystoma assimile de Man ($\alpha = 100$); the longest is Oxystoma filiforme Fil. ($\alpha = 115$–$130$). Thick nematodes are Enoplus euxinus Fil. ($\alpha = 30$–$35$), Sphaerolaimus ($\alpha = 30$), Halichoanolaimus ($\alpha = 25$–$35$), Cyatholaimus demani Fil. Long nematodes are Linhomoeus (L. elongatus Bast. ($\alpha = 125$–$130$, length 10 mm)), Siphonolaimus, Terschellingia filiformis de Man, Dorylaimus tenuis Ditlevsen, Laxus Cobb, Nuada leptosoma Southern ($\alpha = 217$).

The majority of forms mentioned above are of more or less uniform 356 width over their whole length. For example, Enoplus, Halichoanolaimus and Sphaerolaimus are thick; Linhomoeus, Siphonolaimus, Terschellingia and Eurystoma are thin; Enoploides amphioxi Fil. and Cobbia triodonta Fil. are of average thickness. However, there are numerous examples of the opposite. The smallest and thickest nematodes mentioned above, Trichoderma, Richtersia and Desmoscolex, have a fusiform body and are pointed anteriorly and posteriorly. A similar form is common in small Chromadoridae (Sphilophorella, Chromadorina) and among small species of other families (Anoplostoma, Araeolaimoides, Cephalobus). Other forms taper sharply at the cephalic end, but the anus is still situated in the thick part of the body. Such a shape is characteristic for Leptosomatini, Paroncholaimus, Enchelidiidae and Oxystoma. An extreme example is Symplocostoma; the width of the head of S. longicolle Bast. is a fifth or sixth of the width of the body at the base of the esophagus. The flexibility of the anterior end is connected with this. Symplocostoma can coil its anterior end in a serpentine manner in any direction.

The anal diameter may be different in both sexes; it is always thicker in the male. This is due to the fact that the copulatory apparatus and its musculature are situated at the posterior end of the male. This is particularly marked in forms with a long body and a strong copulatory apparatus. In some of these forms (Deontostoma, Cylicolaimus) the body near the anus of the male becomes swollen, so that the short tail is clavate.

A rare form is Pelagonema obtusicauda Fil., which is swollen in the middle, with a thin esophageal section.

There is a very characteristic shape among the Draconematini, which is clearly marked in Draconema cephalatum Cobb (Table 8, 357 Figure 55a, b). The whole esophageal part is swollen, slolioform. There is a short, thinner section, the rostrum anteriorly. Behind the esophageal part is a thin neck, and there is a second swelling in the region of the genital organs. In some species of Tristicochaeta (e.g., in Tr. primitivum Steiner) this shape is not well marked, but Tr. longirostrum Schepotieff has a very long neck. This shape is not as rare among nematodes as stated by authors who dealt only with this group; there are transitional forms among the Spilipherini. Such a form is Metachromadora macroutera Fil. among the Black Sea nematodes (Table 7, Figure 42i and formula on p. 157, Part I*). Steiner describes another transitional form, Desmodora poseidoni St.** There is thus a tendency in several groups of Spilipherini towards the body shape of Draconema.

Finally, there is the shape of the plant parasite Heterodera. The mature female is dolioform, quite different from other nematodes; the vulva is displaced posteriorly. Other plant parasites, e.g., Tylenchus tritici (Bauer) and Tylenchulus Cobb, are transitional.

### B. Tail

The boundary of the tail is the anus, which is rarely situated on an elevation (Monoposthia, Desmoscolex, males of Oncholaimus of the dujardini group).

The shape of the tail also varies markedly.

Some genera and species have a short, rounded tail (Leptosomatum and related genera, Table 1, Figures 1c, 2b, 3d; Paroncholaimus, Table 3, Figure 18e, f); Oncholaimus brevicaudatus n. sp. – one of

---

* [See note on p. VI.]

** A similar shape has been described by Southern for D. sanguinea (1914, p. 27).

the very short-tailed forms (Table 4, Figure 23b, c). Thick, long tails are rare, e. g., in Sphaerocephalum crassicauda Fil. (Table 11, Figure 75c) and in some species of Linhomoeus (Bütschli, 1874). Moderately long, conical tails are characteristic for numerous species of Chromadoridae (Table 5, Figure 37c; Table 6, Figure 41c; Table 7, 358 Figures 42f, i, 44c, d, etc.). The tail of species of Viscosia is long and tapers only slightly posteriorly (Table 4, Figure 20b, c, Table 5, Figure 21b). Many species of Halichoanolaimus have a tail which tapers conically at the base, while the posterior part forms a thin filament which may be curled around objects (Table 6, Figure 39e, g). Such a tail was described by Cobb (1893) for the related genus Demonema. The same shape, but less marked, is present in Adoncholaimus.

Finally, an entire group may have a very long tail which becomes gradually pointed and thin towards the end, e. g., Cyatholaimus of the group longicaudatus de Man (p. 138, Part I) and most freshwater Dorylaimini. The genus Dorylaimus contains, together with long-tailed forms, many short-tailed forms; there are also species in which the female is long-tailed and the male short-tailed. This proves that a short tail is of secondary origin. The young of both sexes are long-tailed like the females, and the tail becomes short only after the last molt.* This tail can therefore not be compared with the primarily short tail of the Leptosomatini; the resemblance is purely coincidental. Several long-tailed marine forms have been described by de Man: Terschellingia longicaudata, 1907 (tail one-quarter of total length), Trefusia longicauda, 1893, and Cobbia trefusiaeformis, 1907.

The tail is frequently swollen at the end. In most Enoplidae and Monhysteridae with a short tail (Tables 2–5, 9–11) this swelling is situated at the tip of the tail. It is well marked in some species of Oxystoma (Table 2, Figure 8c). A club is present in Acoma borealis Steiner, 1916.

On the other hand, in Chromadoridae and Diplopeltini the tail is pointed and ends with the excretory duct of the caudal glands (Table 5, Figures 37c, 38b; Table 6, Figures 36c, 38b, 41c; Table 7, Figure 42f, h). The terminal swelling in these forms (if present) forms the greater part of the tail, leaving space for a tube, "caudal sucker" of Bastian (Table 7, Figure 44c). Special structures in place of this tube are present only in Spira and Chromaspira (Table 7, Figures 45b, 46b, 47c).

Finally, there are forms with pointed tails which do not end with an excretory duct. Such forms are Spilophorella (Table 8, Figure 54c), where the caudal pore is not situated at the tip of the tail, and the long-tailed Dorylaimini (Ironus, Syringolaimus, many species of Dorylaimus), in which the caudal glands are apparently absent. Desmoscolex also has a pointed tail (the "terminal spine" of Shchepot'ev). Sharp tails without a pore at the end are also present in the majority of Anguillulidae (Cephalobus, Rhabditis, Anguillula). A characteristic tail has been described for Cephalobus aculeatus Daday, 1905: it tapers gradually to the posterior third, and then forms a sharp point. Steiner (1914) described a type of palmate outgrowth at the end of the tail of Aphelenchus penardi.

---

* Linstow, 1876, Table 1, Figure 19; Ditlevsen, 1911, Table 4, p. 28; Hofmänner and Menzel, 1915, p. 225; Micoletzky, 1914, p. 518; Linstow, 1885, p. 235.

An interesting development has taken place in the Siphonolaimini and Linhomoeus. A type of cell appears in the cavity of the long tail and 359 histolysis takes place, so that a short, rounded tail is formed from the long, pointed or round one.* This has been described in detail by Zur Strassen (1904) for Solenolaimus. I observed this phenomenon in Linhomoeus (Table 9, Figure 58b) and in Metalinhomoeus. Bütschli gives very clear pictures of this phenomenon (1874, Table 4, Figure 17a, b).

The tail of the female is usually longer, particularly as regards the width at the anus (see my paper, 1916, Table 4), as already recorded by Marion (1870, p. 39). The tail of the male is often curved ventrally. This sometimes makes it possible to distinguish immature males with undeveloped genital organs (see Table 3, Figure 18e, f – Paroncholaimus zernovi Fil. and Thoracostoma denticaudatum Schneider, Filip'ev, 1916). A sharp sexual dimorphism is present in some species of Dorylaimus (see above).

I do not follow Cobb in suggesting a provisional terminology for different shapes of the tail, but use only descriptive terms. I suggest a new term only for a filamentous end of the tail of uniform width – caudal flagellum.

## 3. SYSTEMATIC IMPORTANCE OF SIZE AND VARIATION OF SPECIES

All authors give measurements and ratios of various parts of the body in their descriptions and consider them of systematic importance; but, only Cobb stresses the absolute importance of measurements for systematics.

However, it is necessary to be very careful. The body of nematodes, despite its dense cuticle, is very contractile. This is shown by the folds of the esophagus in fixed nematodes: the body has contracted but the 360 esophagus has not. Through tetanization of Ascaris, Goldschmidt** obtained a contraction of up to $^2/_3$. Furthermore, the body proportions of young specimens do not correspond to the proportions of the adults. The tail and esophagus of young specimens are markedly longer in relation to total body length. This becomes evident if the formulae of individuals of different size of Paroncholaimus zernovi or Enoplus euxinus are compared (pp. 57, 78, Part I; see also my description of Thoracostoma denticaudatum Schn., 1916, p. 89).

If the actual measurements are expressed by these relative sizes, it appears that the middle part of the nematode grows more rapidly than the esophageal part and the tail. The esophageal part and the tail hardly grow after the last molt, but the middle part grows markedly. Consequently, the relative width of the body also changes, becoming smaller in adult nematodes.*** The width is also influenced by another factor – the development of the genital organs, which causes the width of the body in the middle to increase markedly in size, particularly in the female (e. g., Figure 42i, female, and Figure 42k, part of male Metachromadora macroutera).

---

* This explains de Man's observation: queue de longueur variable' (1890, p. 208).

** 1904, p. 77; see also Southern, 1914, p. 4 and Micoletzky, 1914.

*** Cf. Oerley (1886, p. 99), Hofmänner (1913, p. 632).

Other factors are the life conditions of the species: Trilobus gracilis Bast. and Ironus ignavus Bast. have different shapes according to their habitat and varying relative measurements, particularly of the tail.[*] The plant parasites and saprophages of the Anguillulidae vary in the same way, as was noted by Pérez (1866). According to Johnson (1913), Rh. pellio is twice as long and thicker on decomposing earthworms than in the artificial media which he used.[**]

There are sometimes marked variations even among nematodes caught 361 at the same time. Although this had been known for a long time, only taxonomists who dealt with a large number of individuals of one or a few species paid attention to this phenomenon. These variations were recently studied by Micoletzky (1914, p. 381; 1917), who examined a large number of specimens of several species statistically and gave several graphs. The absolute length and width varies by a factor of 2, the relative width and length of the esophagus 1.6 and of the tail 1.9, and the number of preanal papillae in the male 1.4–2; the position of the vulva is more constant, varying only by a factor of 1.2. This variation is probably exaggerated, as the author apparently also measured not fully mature individuals.

No statistical examination of marine nematodes has been made until now. However, if only fully adult individuals are examined, the proportions will probably be more constant than those given by Micoletzky. The variations should not be greater than a factor of 1.2–1.3 times and sometimes even less. The different size of individuals from different localities must also be taken into account. Thus, Paroncholaimus zernovi Fil. and Enoplus euxinus Fil. are larger at Georgievskii Monastery than at Sevastopol.[***] The posterior end of Eurystoma assimile de Man proved to be particularly variable.[†] I initially considered these variants to be different species, until I found all transitions between the extreme forms in a large amount of material.

Nematodes may also grow considerably in the adult stage. Thus, according to Hagmeier,[††] adult males of Mermis brevis are 4 to 20 mm 362 long and females 8–35 mm long. Such a large variation is apparently not found in free-living forms. However, adult Thoracostoma denticaudatum Schn. may be 8–14 mm long. As the width is almost constant, such different lengths give very different relative figures.

## 4. FORMULAE

Bütschli and Bastian recorded the ratio of the length of esophagus and tail to total length. De Man added the ratio of total length to maximum width, calling the ratio $\alpha$, the ratio of body length to esophagus length ($\beta$), and the ratio of body length to tail length ($\gamma$). These symbols are simple, but the great disadvantage is that they are reciprocal values.

This disadvantage is avoided in the decimal formula of Cobb, which I have used with some modifications.

The dimensions of the different parts of the body are expressed in % of its total length. The length of the various parts is written above and the corresponding width below.

Formula of female

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Buccal cavity, if well developed | Nerve ring | End of esophagus | Beginning of anterior ovary | Beginning of anterior uterus | Female gonopore | End of posterior uterus | End of posterior ovary | Anus | Total length in μ |
| Width at cephalic bristles | Corresponding width | Corresponding width | | | Maximum width | | | Corresponding width | |

Formula of male

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Buccal cavity, if well developed | Nerve ring | End of esophagus | Beginning of anterior testis | Beginning of vas deferens | End of posterior testis | Anus | Total length in μ |
| Width at cephalic bristles | Corresponding width | Corresponding width | | Maximum width | | Corresponding width | |

363 If some other measurements are introduced, or if the formula is changed, mention is always made in a footnote.

This formula is convenient because it provides direct proportions and makes it possible to recognize the shape of the nematode immediately.[*]

However, there is an important objection to this formula: it takes as unity the total length of the body, and this varies markedly with age. A more constant value should have been taken as unity, e.g., the length of the esophagus or the width of the body at the base.

The large number of measurements and calculations necessary are inconvenient. Only Micoletzky uses the formula apart from its author. Other authors disregard it. Steiner[**] even stated that he did not want to waste time on calculations. Cobb (1902) suggests that drawings or

---

[*] See Hofmänner, 1913; Stefanski, 1914, 1917; Brakenhoff, 1914. De Man (1884, p. 168) also described some markedly varying forms.

[**] Extensive data on Anguillulidae are found in Ritzema-Bos (1887–1888, Tylenchus dipsaci (Kühn)); Marcinowski (1908–1909, numerous species); Schwartz (1911, Aphelenchus olesistus R. Bos). For saprozoites see also Maupas (1901) and Conte (1900).

[***] See pp. 57, 78, Part I.

[†] p. 113, Part I.

[††] 1912, p. 544.

[*] I do not use the symbols originally proposed by Cobb or those in his latest study (1913). They may be confused by the printer and result in incomprehensibility rather than brevity. Cobb states: "The author who is guided by his own convenience rather than the reader's will hardly meet with general approval." However, he only uses these symbols in two publications (1913 and 1914a), but not in the other study of the same year (1914b).

[**] 1916, p. 516.

photographs be given and the measurements made from these, but this would take more time than using an ocular micrometer. To simplify calculations a graph or a logarithmic slide-rule may be used.

In addition to the formula, two further measurements are used:

1) Absolute length of the anterior end of the body of male and female.
2) Relative length of the posterior end of the body of both sexes.

364 The anal diameter is taken as unity, giving length of tail and thickness at the end, length of spicules and gubernaculum, and distance of accessory genital papillae of male from anus.

### 5. COLOR

The color of nematodes depends on the color of the internal organs, mainly of the intestine, as the cuticle is usually transparent. Only in some clearly annulated species does the thick cuticle influence the color. Such species are Euchromadora, Desmodora and Desmoscolex. In some species of Cyatholaimus and Terschellingia the cuticle is brown.

## II. STRUCTURE OF THE BODY

The body of nematodes consists of an external tube, which consists of the dermal, muscular and nervous system ("skin-muscle-nerve system" of Rauther*) and the internal organs, intestine and genital organs. Between them lie some cells of doubtful function which will be discussed after the epidermis.

### 1. SKIN-MUSCLE-NERVE LAYER

This term of Rauther's is applied to the whole body wall of the nematode – the epidermis and cuticle, the underlying longitudinal musculature and the nervous system, which is situated in the epidermis and in the deeper layers. This is usually termed the dermal-muscular sac in other helminths. Rauther only added the prefix "nervous."

### A. Body Wall

The epidermis consists of a single-layer epithelium, which is clearly 365 cellular in free-living nematodes. The external layer of the epithelium forms the cuticle, which extends into the openings of the body, mouth, anus, vulva and cervical (excretory) pore, lines the esophagus, hindgut and vagina, and forms a cuticular ampulla near the cervical pore. Nematodes undergo molts and shed the cuticle during development; both the external and the lining of the organs mentioned.

---

* 1906 – Haut-Nerven-Muskelsystem.

#### a. Cuticle

The cuticle of free-living nematodes is of varying structure, sometimes simple and smooth, sometimes complex, annulated or with punctations, etc. It is always of compound structure: it always consists of at least two layers. These layers are clearly recognizable in sections and are divided into secondary layers which react differently to stains (Jägerskiöld, 1901; Türk, 1903; de Man, 1904). However, it never attains the complexity found in the large parasitic forms – Ascaris (Bömmel, 1895; Toldt, 1903; Goldschmidt, 1904) or Lecanocephalus (Hamann, 1895).

The cuticle is highly resistant to various reagents, particularly in some larval stages of Anguillulidae. They may survive for many days in toxic liquids and fixatives. Stains penetrate the cuticle with difficulty. Some authors (Cobb, 1898, p. 42) therefore believe that respiration does not take place through the cuticle but only through the pores (p. 14). There 366 seems to be an insufficient basis for this suggestion, as the cuticle of true free-living nematodes is much more easily penetrated by reagents. The body of these nematodes is in a state of active metabolism with the outside like that of the majority of other aquatic, particularly marine, animals, while Rhabditis and related genera are tightly enclosed in their sheath, and external exchange is reduced to a minimum.

The swelling of the thick cuticle of many Enoplidae (Leptosomatini, etc.) by the action of some reagents, e. g., acetic acid, should be noted. This should be considered when the thickness of the cuticle is measured.

Pérez (1866) noted the great elasticity of the cuticle of free-living nematodes. This becomes evident when the nematodes are killed with weak fixatives. They coil energetically at first and stretch when they die, assuming the shape characteristic for the species. Thus, Enoplus extends into a straight rod, while Paroncholaimus remains slightly coiled. If Paroncholaimus is rolled under the cover glass, constrictions, almost knots, are formed in many places. When the cover glass is removed and water added, the cuticle extends the body again.

The cuticle of some species of Viscosia and Oncholaimellus is sticky. Bastian, Bütschli and de Man (1890) recorded the adhesion of foreign particles to the cuticle. The cuticle of these forms is not wettable with water, and when they come to the surface they remain on it. This is also characteristic for many other nematodes which do not have a sticky cuticle – Spilophorella, Simplocostoma, Ironus and Dorylaimus.* This property may be used when material is collected (p. 3, Part I).

367 The cuticle of free-living nematodes is either smooth or annulated with varying complexity, and aberrant forms of cuticle are also observed, which will be discussed at the end. There is a smooth cuticle in the great majority of Enoplidae, and there are transitions to an annulated cuticle

---

* Ditlevsen, 1911.

only among the Enoplini. There are some very finely annulated species[*] in Dorylaimus and Mononchus while D. annulatus Daday, 1905, is more coarsely annulated. But even among forms which have been considered to have a smooth cuticle, such as Leptosomatum, a very fine annulation can be made out under high magnification on the anterior part of the body.[**] Entirely smooth forms are also formed among Monhysteridae and Anguillulidae, but these are much smaller. All Chromadoridae have a more or less complex cuticle.

Care should be taken not to confuse with true annulation the folds of the cuticle which are often also present in smooth forms in the preanal part of the male when the body is strongly bent.[***]

**Smooth cuticle.** Its thickness varies greatly, depending mainly on the size of the nematode. Large forms have a thicker cuticle, for example, Leptosomatini (cf. all figures in Table 1[†]) and also Dorylaimini, particularly marine species. But in Enoplus and Oncholaimini, the cuticle, although still thick, is relatively much thinner (cf. Table 2, Figures 10, 11; Table 3, Figure 18a, e, f; Table 4, Figure 20). The cuticle is very thin in small or thin nematodes, e.g., 0.5 $\mu$ in Eurystoma; it is also thin in smooth Monhysteridae; de Man (1907) gives 1 $\mu$ for Monhystera stenosoma. Examples of species with a thin, smooth (or very finely 368 annulated) and soft cuticle are Linhomoeus (see pp. 215, 216, Part I) and Siphonolaimini.[††] This makes them very suitable for anatomical-histological examination. The genus Nuada Southern,[†††] with a relatively thick cuticle, is an example of the opposite.

Secondary specializations of the smooth cuticle are layers of obliquely crossing fibers in the anterior end of the body which are apparently present in all Enoplini[‡] and Leptosomatini, some species of Oncholaimini and Dorylaimus. This layer is replaced by an entirely smooth layer near the cephalic line, as noted by Bütschli (1874). These fibers were observed for the first time by Eberth in Enoplus.[‡‡] Such crossing fibers are also often present in parasites (Bastian, 1866, p. 549; Goldschmidt, 1901).

Other specializations are the longitudinal stripes in many freshwater Dorylaimini (Dorylaimus and others[‡‡‡]) and particularly in many species of Anguillulidae. Bastian (1865) warned against confusion of these cuticular structures with the apparent longitudinal striation caused by the underlying muscles which are visible through the cuticle.

Other specializations are rows of lines on the sides of the tail of Halalaimus gracilis de Man (1888, p. 2).

---

[*] Dorylaimus – Linstow, 1879, p. 163; Cobb, 1888; de Man, 1906, p. 168, 1907, p. 26; Mononchus – de Man, 1904, p. 5; Micoletzky, 1914, p. 482; Hofmänner and Menzel, 1915, p. 148.

[**] De Man, 1893; Steiner, 1916; Filip'ev, 1916. De Man (1904, p. 36) describes a very fine annulation also in Deontostoma antarcticum (Linst.) (width of annuli 0.6 $\mu$).

[***] See Bütschli, 1876, p. 379.

[†] 8–9 $\mu$ in Fiacra strasseni Türk, 1903; 10 $\mu$ in Deontostoma arcticum Sav. (Filip'ev, 1916), see also pp. 66, 68, 70, 76; 7–12 $\mu$ in different parts of the body in Thoracostoma setosum Linst. (de Man, 1904); and up to 15 $\mu$ in "Leptosomatum" australe Linstow, 1907, and Fiacra acuticaudata Jägerskiöld, 1901.

[††] De Man, 1893, p. 99; Cobb, 1893, p. 416; Zur Strassen, 1904.

[†††] 1914, p. 10.

[‡] De Man, 1904, p. 21, denies the existence of this layer in Enoplus michaelseni Linst.

[‡‡] 1863, p. 35, 36.

[‡‡‡] Bütschli, 1876, p. 378; de Man, 1876, p. 111; 1884, p. 8; 1907, p. 26; Daday, 1897, p. 127; Cobb, 1914b, p. 112.

**Annulated cuticle.** As stated above, there are also forms transitional to forms with an annulated cuticle in groups with a smooth cuticle. These annulations are present only on the external layer of the cuticle and either only anteriorly (Leptosomatini) or throughout the entire length (Dorylaimini). Other transitional forms among Enoplidae are the Enoplini. De Man noted punctations in the intermediate layer of the cuticle in Enoplus and Triodontolaimus. These punctations sometimes form regular transverse rows. In Enoploides and Enoplolaimus the punctations also form rows, but there is in addition a fine annulation on the external layer of the cuticle (de Man, 1893 and 1904; Savel'ev, 1912).

A cuticle of similar structure is also present in other groups, e.g., among Cyatholaimini: Halichoanolaimus and Dignathonema have only an internal annulation, caused by arrangement of the granules of the intermediate layer and in rows by the slight corrugation of the internal surface of the cuticle (Table 6, Figure 39a). Cyatholaimus shows a higher degree of specialization. Thus, there are three layers of annulation in C. demani Fil.: 1) flat external annules, 2) rows of punctations in pairs on one external annulus and 3) annules on the internal surface corresponding to the rows of punctations. C. punctatus Bast. has one row of punctations on an annulus laterally and dorsally and 3 rows ventrally (de Man, 1890). A similar structure of the cuticle, but without the external annules, is present in the Comesomini (see p. 242, Part I and Table 11, Figure 76a). There is a simpler annulation in other Monhysteridae.

369 The most complex cuticular structure is present in the other three tribes of Chromadoridae – Spilipherini, Chromadorini and Draconematini. The whole or almost the whole cuticle is annulated, the annules usually being very distinct, sometimes chitinized, hard and brittle (Euchromadora, Desmodora, Monoposthia). The cuticle is sometimes so thick that the living animal is gray and hardly transparent (Euchromadora, Monoposthia, Desmodora). The head, without annules, is immediately recognizable in these forms.

The annules may be smooth or may bear various cuticular structures and serrations. There are forms with relatively little marked annulation which could have been placed in the preceding groups – Spira, Chromaspira, Onyx (Table 6, Figure 41a). Other genera, such as Desmodora,[*] Chromadoropsis,[**] Metachromadora, Monoposthia and Draconematini, have sharply marked smooth annules which consist of thickened cuticle; the intervals between them are formed of a less dense cuticle. The annules run around the entire body, sometimes disappearing. The front of the head and end of the tail are always without annules. In the Acanthopharyngini (Desmodora and Draconematini, Table 8, Figures 55c, 56) a larger part anteriorly is without annules. It is covered with a thick, dense cuticle forming a kind of cephalic capsule (see below). In Desm. bullata Steiner, 1916, the cuticle of this part is swollen and forms a thickening. In Metachromadora, Onyx and Chromadoropsis this part is covered with annules, but these are smaller and arranged differently from the posterior annules (Table 6, Figure 41a; Table 7, Figures 42b, c, d, 43; cf. also pp. 154, 157; Part I).

---

[*] See de Man, 1889; Steiner, 1916.

[**] See de Man, 1907.

There is greater variety in the structure of the cuticle in the other Chromadoridae. A common character is that the annules are not simple, as in the preceding group, but bear punctations or elongate, small structures (Euchromadora, Rhabdotoderma Marion, many marine forms*). The punctations are sometimes present around the entire body (Chromadorina obtusa Fil.) and are sometimes interrupted on the dorsal or ventral side. In Chromadora hyalocephala Steiner, the punctations form a narrow stripe on the sides, while the greater part of the dorsal and ventral surface is without punctation. In Euchromadora and some other forms** several anterior annules are fused, so that there are small smooth areas in the four submedian lines and four fields of punctations are present. The ventral and dorsal fields soon become less marked posteriorly and are absent in the esophageal part of the body.***

These punctations at the sides may not be distinguishable from the others or they may be markedly larger. There may be 2, 3 or 4 rows of such punctations (Table 8, Figures 50a, c, 51, 52a–c, 54a). In Euchromadora there are characteristic alar structures at the sides of each annulus (Eberth, 1863). The punctations may be situated either on the
370 annules (e.g., Chromadorella mytilicola Fil., Table 8, Figure 53b) or between them (e.g., Chromadorina obtusa Fil., Table 7, Figure 44b), or they may form serrated margins on the annules (e.g., anteriorly in Chromadora sabulicola Fil., Chr. poecilosomoides Fil., Chr. mytilicola Fil., Table 8, Figures 51a, 52a–c, 53a). These punctations are sometimes like pores and have been described as such, but this is not correct.†

The cuticle is of different stucture anteriorly in almost all Chromadoridae; it is more or less thickened in the preneural part of the body, but still in the region of annulation. The thickening is sometimes accompanied by a band of coarser annules. This is best marked in Draconema (Table 8, Figures 55c, 56) and less clearly marked in Metachromadora, Euchromadora, Desmodora†† and most other Chromadoridae.

There are interesting relationships in the Desmoscolecidae. In the simplest case there is an undulate cuticle, which cannot be called strictly annulated (Eudesmoscolex Steiner†††). In true Desmoscolex and Tricoma very distinct annules are present on the surface. These, however, do not belong to the cuticle but are a secretion in which foreign particles are contained—sand grains, diatoms, etc. (Shchepot'ev, 1908; Steiner, 1916).

In the genera Trichoderma Greeff and Richtersia Steiner, numerous short bristles are situated on the annules of the very thick cuticle. These bristles, in contrast to true bristles which are described below, are solid and not hollow, and are apparently not sensory organs.‡

---

* E.g., Chr. sumatrana Steiner, 1915, Spilophora loricata Steiner, 1916.

** Chromadora poecilosoma de Man, 1893, Spilophora loricata Steiner.

*** See also p. 173, Part I, and de Man, 1886.

† De Man, 1888, Jägerskiöld, 1904 in Hypodontolaimus; G. Schneider, 1906 in Cyatholaimus; de Man, 1893 in Spiliphera.

†† Steiner, 1916, p. 547.

††† "Die Ringelung wird... nur vorgetäuscht durch kreisförmig den Körper umgebende kielartige Erhebungen," p. 579.

‡ Shchepot'ev, 1908; Steiner, 1916a, b.

In the interesting terrestrial genus Hoplolaimus Daday (see p. 254, Part I), the annulated cuticle is covered with 8 rows of scalelike processes which are directed backwards. As Cobb noted,* this structure permits the animal to move only forward in the soil.

The structure of the cuticle of the terrestrial genera Bunonema Jäg. and Craspedonema Richters is characteristic. The ventral surface bears no specialized structures, but large warts cover the dorsal surface, giving the nematode a very peculiar appearance. There are sometimes additional specialized structures between them, whose function is not known.**

**Lateral ridge** (Seitenmembran, membrane latérale of authors, cuticular wings of Cobb) [lateral alae]. This term designates the lateral ridge of
371 the cuticle along the body. It usually begins near the end of the esophagus and extends to the anus, sometimes even further.

This structure is particularly common among Anguillulidae and Monhysteridae and is also present in many species of Chromadoridae. In the latter group the ridge is either simple (Metachromadora) or combined with punctations (p. 12). There are sometimes special structures serving as supports (Spilophora loricata, Chromadora craspedota Steiner, 1916). Enoplidae generally have no lateral ridge, but Jägerskiöld (1916) found a special intermediate layer in Thoracostoma acuticaudatum in the cuticle along the lateral fields, possibly a remnant of the lateral ridge. Such a layer has been described for Ascaris spiculigera Rud., but related forms, such as Asc. mystax Rud. and others, have a true lateral ridge (Jägerskiöld, 1894; Bömmel, 1895).

There are smooth annules in Monoposthia de Man. Each annulus forms backwards-directed processes in several places. These processes form longitudinal ridges along the whole or almost the whole body. De Man (1890) found 19 such ridges in the male and 20 in the female of M. rostata Bast. (Table 7, Figure 48). There are only 6 ridges in M. mielki Steiner, 1916. The individual plates of hard cuticle on the ridges are articulated, which gives the body great flexibility (Steiner). Similar structures have been described for Desmodora sanguinea Southern.***

The bursa, also a fold of the cuticle, is described in the chapter on the male genitalia.

Opinions on the importance of the cuticle for systematics of nematodes differ sharply. Bastian (1865) and Marion (1870) placed annulated and smooth genera at different ends of their systems. Bastian considers the longitudinal rows of punctations of Chromadora as the difference between Chromadora and Spilophora.† On the other hand, Bütschli (1873, 1874) and de Man (1884, 1888, 1889) include annulated and smooth forms in the same genus, e.g., in the genera Monhystera and Tripyla. Tripyla probably contains only annulated forms. The genus Monhystera in the form accepted until now is not admissible: the annulated subgenera established by de Man have to be distinguished from true Monhystera. However, this is only a special case, in which the decisive

---

* 1914, p. 479; see also 1914b.

** Cf. Richters, 1905; Jägerskiöld, 1905; Stefanski, 1914; Hofmänner and Menzel, 1915; Steiner, 1914, 1916; Cobb (1915) believes that the processes are situated not on the dorsal or ventral side but on the right side. The structure is thus markedly asymmetrical.

*** 1914, p. 27.

† "Longitudinal rows of dots," p. 165.

element is not the structure of the cuticle but other characters (see pp. 205, 210, Part I).

372 Another group with a cuticle of varying structure is Chromadorini and Spilipherini. De Man separated Desmodora by this character, but gave no further description. For example, Chromadoropsis vivipara de Man, 1907, with smooth annules was originally described as a species of Chromadora. Steiner (1916) was doubtful about this character. I have described above the structure of the cuticle as a generic character of Euchromadora* and have defined the genus Chromadora as Chromadorini with one tooth and with a specially differentiated cuticle on the lateral lines. This analysis could not be made more general for lack of material. If we remember how completely genera like Monoposthia, Onyx and Metachromadora are characterized by their cuticle, we come to the following conclusion: the structure of the cuticle is as good a character for the definition of genera as other characters, and species which differ markedly in the structure of the cuticle should not be placed in the same genus. Marked variation of the cuticle in any group requires the establishment of a large number of genera.

### b. Bristles and papillae

Bristles (setae) and papillae are appendages with a sensory function. Papillae or other structures combined with glands should be distinguished by special terms (see below, some genital appendages of males). The bristles and papillae themselves, however, should be considered as modifications of the same organ (cf. also p. 21**).

373 This concept is simple and not new, but it was not accepted immediately. Bastian (1865, 1866) considered the papillae as pores and compared them with the pores of Echinodermata, which is noted here only as a curiosity. Bütschli (1873) rejected this view and considered the pores of Bastian as simple papillae. However, such pores are often mentioned by various authors.*** The cuticle above a "pore" is much thinner and has no opening.

A canal which is directed not perpendicularly but obliquely to the surface of the cuticle sometimes shows a thickening above a sensory organ, a hair or a papilla (Phanoderma, Table 1, Figure 5a †).

Bristles and papillae are found in varying numbers on the body. Large forms with a thick cuticle have more bristles and papillae, smaller forms less. The anterior part of the body, the posterior end of the male and the region of the female gonopore are particularly well provided with bristles. They are much less numerous on other parts of the body.

Forms with particularly numerous bristles or papillae are Paroncholaimus papilliferus Fil., "Leptosomatum" australe Linst. and Thoracostoma setosum Linst., according to de Man (1904). All these species are large.

---

* The character of de Man – inequality of spicules – has proven to be only a specific character.

** "Borsten und Papillen können also, als verschiedene Ausbildungen desselben Organs auftreten" (Rauther, 1909, p. 538).

*** De Man, 1878, p. 103; Oerley, 1886, p. 14; Brakenhoff, 1914, p. 277.

† Marion (1870) described such a structure as in Thorac. setigerum "cellule nucléolée" (Table L, Figure 1, 1a, p. 13).

The bristles often form 4 submedian rows along the body in small species of Chromadoridae and Monhystera. This is also the case in Draconematini (Barrois, 1875). The bristles of the different rows sometimes form regular crowns. Cobb (1898) considers this as relicts of metamerism. The bristles of Paroncholaimus zernovi Fil. are distributed over the entire body, but are very scanty opposite the muscle fields, with the largest number present on the epidermal fields, particularly on the lateral fields (see below).

Although bristles are present in many species, they are present only anteriorly and posteriorly in the male, the other parts of the body being almost entirely without bristles, e. g., in Metoncholaimus demani Zur Strassen. Its closest relative in the genus, M. pristiurus Zur Str., has a much better developed armature of bristles.

374 The bristles and papillae of the anterior end will be discussed below. We mention here only that the entire preneural part of the body is usually abundantly provided with bristles. They are either irregularly distributed all over this part (Paronch. zernovi Fil., Table 3, Figure 18a, also in the particularly hairy species mentioned above) or concentrated on the lateral surface (most species of Leptosomatini, Table 1, Figures 1a, b, 2a), or they form definite groups (Leptosomatides euxina Fil., Table 1, Figure 3a; Anticoma, p. 45, Part I, Table 2, Figure 6a, s. cerv.; Thoracostoma denticaudatum Schn.*). The term proposed by Cobb – cervical bristles (setae cervicales**) – is generally accepted.

The bristles always contain a canal, which extends through their entire length (as distinct from the solid spines of Richtersia). Drops are sometimes noted at the end of the bristle. Bütschli (1874) considered this as proof that the bristles are connected with glands. However, Cobb (1898, p. 26) stated that this occurs after death, which seems more likely. The bristles are always movably attached to the cuticle; they differ in this respect from spines and papillae.

Bristles may be long and flexible, not very pointed at the end. Such bristles are present in the genera Prosphaerolaimus (Table 9, Figure 66a), Onyx (Table 6, Figure 41a) and Laxus, according to Cobb. Quatrefages (1846) noted these bristles and established for these nematodes the new genus Hemipsilus. Sphaerolaimus may be considered as transitional to the next category, with fine, straight bristles (Table 10, Figures 67a, 68a, 69a, b). The most common form of bristle is a more or less long, pointed cone truncate at the end. An example with long bristles of this type is Paramonhystera (Table 9, Figures 59a, 60a) and many species of Theristus (see pp. 200, 201, 202, Part I). Species with short bristles are Leptosomatum punctatum Eberth (Table 1, Figure 2a) and Paroncholaimus zernovi Fil. (Table 3, Figure 18a, b, c, m, n).

375 Papillae are present in very many species; some species of the same genus may have short bristles, others papillae.

Thus, Leptosomatum bacillatum Eberth (Table 1, Figure 1a, b) and Paroncholaimus papilliferus Fil. have papillae, while the species mentioned above have short bristles. Among the genera in which species with papillae predominate we mention Leptosomatum, Halichoanolaimus (Table 5, Figure 38a; Table 6, Figure 39a, b), Adoncholaimus,*** Solenolaimus† and almost all species of Dorylaimini.

---

* See Filip'ev, 1916.

** The cervical papilla of Ascaris is apparently a homologous structure (see Hesse, 1892; Goldschmidt, 1903).

*** Cf. de Man, 1886, 1889.

† Cobb, 1894, p. 419.

The peculiar spines and hooks on the cuticle of Oncholaimus armatus Daday, 1901, cannot be included in the above categories of bristles.

The bristles of Draconematini are also interesting. In Rhabdogaster there are thick bristles curved into a hook. In the male they form two rows along the entire ventral surface, in females only in front of the vulva.[*] The bristles of Draconema[**] form two, three[***] or four rows on the ventral surface in front of the anus, so densely that Chaparède, who described Draconema (Chaetosoma), called them fins.[†] The bristles are slightly S-shaped. The base is slightly thickened into a bulb and the end forms a small cup (Table 8, Figure 55a, b, d, e). These are certainly modified bristles, as there is sometimes a normal, pointed bristle of the same length in a row of these modified bristles. Their number increases with age; there are only 1–2 pairs in very young worms.[††] There are also several specially differentiated bristles on the head of Draconema. These are much thicker and their base is swollen, but the end is pointed and
376 without a depression. These bristles are apparently actively movable (Mechnikov, 1867). Steiner (1916) believes that these bristles excrete a fluid capable of attaching the anterior part of the body and presents arguments against the sensory function of the bristles: if they were sensory, they would project, would not be curved towards the head, and would be situated around the entire body.[†††] This seems unlikely. A glutinous secretion may be excreted by the anterior and posterior bristles, but they are probably only mechanically attached to the substrate during crawling, as described by Mechnikov and Shchepot'ev (see p. 188, Part I). I do not agree that these bristles are homologous with the cephalic bristles of other nematodes (see p. 21). It seems best to use Steiner's term – occipital bristles (Nackenborsten – setae occipitales).

Complex bristles with a lanceolate end are present also in Desmoscolex (Shchepot'ev, 1908). His observation that muscle fibers are attached to these bristles and that they function as suckers seems doubtful (p. 39, Russian edition). Complex tubular bristles have been described by Steiner (1916b) for various species of Tricoma.

Specialized structures have been described for Acanthopharynx striatopunctatus Marion, 1870 – short tubes with a conical base which are probably modified papillae.[‡] The round pores which are present on the lateral fields in Cyatholaimus are also specialized structures (see p. 141, Part I[‡‡]).

---

[*] Mechnikov, 1867, p. 543; Shchepot'ev, 1908, p. 60; Steiner, 1916, p. 574.

[**] Steiner, 1916, p. 573.

[***] It is interesting that there are about double the number of bristles in the central row in this case than in the lateral rows, an indication of their complex origin.

[†] "Flossen," 1863, p. 88.

[††] Mechnikov, 1867; Shchepot'ev, 1908.

[†††] "Wären die Borsten sensitiver Natur, so wären sie gewiss nicht dem Kopfe zu-, sondern vom Kopfe abgebogen, nicht nur auf die Rückenseite des Kopfes beschränkt, sondern ringsherum angeordnet un bätten kaum ein stumpfes Ende und die Form einer Röhre."

[‡] p. 69, Table K, Figure 3, 3b.

[‡‡] Cobb (1898, p. 401) stated that in C. heterurus there are "two longitudinal rows of circles in the lateral regions, separated by a space equal to one-fourth the width of the body." In another work (1914b) he described them as ' lateral markings" in freshwater species. The round pores of Spilophora tentabunda de Man (1890, p. 177) probably belong here.

---

True bristles are almost never present in parasitic nematodes and the semiparasitic Mermithidae – only papillae. For this reason, Diesing (1861) described some free-living nematodes as Cirrhostomea. The spines
377 and hairs which are present in some genera are usually not true bristles but correspond to the hairs of Trichoderma and related forms (see p. 12). There are probably true movable spines – modified bristles – only in Tropidocerca (Linstow, 1899).

The systematic importance of the development of the bristles is very small and generally of not more than specific value. However, the characteristic bristles of Draconematini characterize the entire tribe.

### c. Structure of the head

The structure of the head is best explained through an example (Table 3, Figure 18b, head of Paroncholaimus zernovi Fil., anteriorly). There is a large mouth opening covered with platelike lips (lab.). Next there is a circle of 6 labial papillae, one at the base of each lip (p. lab.). Outside them project 10 cephalic bristles (o. s. l. is the sensory organ of one of these bristles); two pairs are situated in the submedian position and one on the lateral surface. The lateral organ (0. 1) is situated below the lateral bristles. This structure of the head, modified to some extent, is present in all free-living nematodes, as has been noted by Schneider and Bütschli and definitively established by de Man.[*] However, these appendages are sometimes little marked, which resulted in the description of forms without papillae or bristles (Aegialoalaimus, Alaimus), though they will probably be found after more detailed study.

Schneider's "rule"[**] concerning the triradiate symmetry of the anterior end of the nematode is thus established. We may even speak of a
378 hexamerous symmetry, but there are only three sectors in the esophagus, a dorsal and two subventral sectors.[***] The arrangement of the organs on the head does not completely correspond with a triradiate symmetry, which seems to be only apparent. The same applies to the structure of the esophagus. The true symmetry is nevertheless bilateral. The question therefore remains of whether this rule should be considered as primitive (Rauther, 1909). Its general distribution among free-living and parasitic nematodes suggests that the first view is correct. However, the same triradiate structure appears in very different groups in the animal kingdom and it is hardly possible to suggest, as Rauther does, that this structure is a common heritage of nematodes and, for example, fly larvae. I therefore believe that this is a secondary adaptation which developed independently in a group of nematodes and also developed independently in other groups.

---

[*] See also the diagram of Jägerskiöld (1909).

[**] 1866, p. 237.

[***] De Man (1889) described a ventral and two subdorsal lips for Thalassironus britannicus. This is probably only an incorrect observation or an abnormality, as in Chromadora minor Cobb, where the head, as appears from the lateral fields, is turned 180° with respect to the rest of the body. All proportions therefore appear reversed.

The width of the head varies considerably: sometimes it is as wide as the body – Enoploides amphioxi Fil., Dignathonema (Table 6, Figure 40f), Halichoanolaimus, Cobbia; sometimes it is a little narrower than the body – Enoplus, some species of Oncholaimini, Sphaerolaimus; and sometimes it tapers sharply – Simplocostoma, Enchelidium, Leptosomatini (see also p. 3).

The head is occasionally widened and separated from the rest of the body by a constriction which is sometimes weakly marked, e. g., Enchelidium, Eurystoma, Simplocostoma, Comesomini (cf. Table 4, Figure 29a; Table 5, Figures 29a, 30a; Table 11, Figures 76a, 77a, 78a, 79a) and rarely more marked, e. g., Cephalonema Cobb, 1893, and Microlaimus, according to Steiner (1916, p. 591). The cephalic line often lies in the depth of the constriction, marking the boundary of the cephalic part. However, this line may also be present on heads which are not separated by a constriction, e. g., Enoplus, Viscosia (Table 2, Figures 10a, 11a; Table 4, Figure 20a). It marks here the end of the cephalic carapace and the end of the punctations of the middle layer of the cuticle and the crossed fibers (see p. 10, also de Man, 1896). Such a line is present in Penzancia (Table 9, Figure 61a) and probably also in other genera of this group. It is usually recognizable externally in Oncholaimini, but is marked by the internal structure of the head (see below). It is weakly marked in the Leptosomatini.

379 The head may be either truncate anteriorly, as in Halichoanolaimus, Metachromadora, Spira and others (Table 6, Figures 39a, b, 42a; Table 7, Figure 46a, b), rounded as in Onyx, Chromaspira, Terschellingia, Linhomoeus and Prosphaerolaimus (Table 6, Figure 41b; Table 7, Figure 45b; Table 9, Figures 57a, 58a, 65a, 66a) or, finally, its form may be changed by various tubercles and the lips, examples of which will be given below.

The head is often without annulation, which is present on the body, so that the head appears lighter (see p. 11). In Paramonhystera, Cobbia and related genera, the head is completely transparent, because the walls of the wide vestibule are very thin and attached to the external cuticle, which is without annules (Table 9, Figures 59a, 60a, 63a).

The sharp snout of Draconematini (Table 8, Figures 55c, 56, rostrum of Shchepot'ev) and the "winglike appendages" of Desmoscolecidae* deserve special mention. In Bunonema and Iota there is a characteristic sharply separated "cephalic segment" and the head can move and bend.** Retraction of the head is well known also for all species of Chromadoridae, and is assumed for Tylenchus.***

## 1. Cephalic Appendages and Tubercles

This term designates immovable appendages of the cephalic end, varying in shape and projecting anteriorly, as in Teratocephalus,† some species of Cephalobus,* Diploscapter Cobb,** and other terrestrial genera (de Man, 1884). The median membranes on the head of Wilsonema Cobb, 1913, also belong here, which were established for Plectus auriculatus, P. otophorus and related species.*** All these genera are terrestrial forms (rarely freshwater). In marine forms, true movable lips replace these tubercles. Occasionally, cephalic appendages are also present in parasites; they are sometimes greatly developed and of strange form. There is no room to describe them here.

380 In addition to these specialized projections of the head, there are often less well-defined structures. They are usually called lips, but it seems incorrect to give them the same name as the movable lips, which are described below. We suggest the name "cephalic tubercles" (tuber cephalicus. The "lips" of Leptosomatum (de Man, 1893) and many species of Dorylaimus† belong here, along with the three cephalic projections of Phanoderma (Table 1, Figure 5a–d). The "lips" of many parasites (e. g., Ascaris) also belong here.

## 2. Lips (labia)

I suggest this term only for the movable appendages that close the entrance to the oral cavity. Such lips are relatively rare among nematodes. Their development is usually connected with the formation of a wide buccal capsule. In these forms there are lips in the form of six thin, movable plates.

Such forms are the Oncholaimini (Table 3, Figures 18a, b, 19a††), particularly Viscosia (Table 4, Figure 20a), where parts of the lips extend far posteriorly. The same is present in Halichoanolaimus (Table 6, Figure 39a–c†††), Sphaerolaimus (Table 10, Figures 67a, 68a, 69a, b‡), Cobbia (Table 9, Figure 62c) and probably in other genera of this group as well. Cobb (1893, p. 4) described three lips for Mononchus, with "each lip divided into two parts," i. e., six lips. However, the formation of a wide buccal capsule does not always result in the formation of true lips. Thus, lips are absent in Symplocostoma and Eurystoma and the entrance to the buccal capsule is open wide (Table 5, Figures 29a, 30a).

There are three lips in Enoplini – a dorsal and two subventral lips. In Enoplus these are small movable appendages. There are already specializations in this genus, e. g., in E. maeoticus Fil. The base of 381 the lip consists of thicker cuticle and there are thicker processes along the anterior margin, while the middle is formed by thinner material (1916, Table 5, Figure 10a). The genera Enoploides and Enoplolaimus have very large lips. The lips of Enoploides amphioxi Fil.

---

* Cobb, 1893, p. 482; Shchepot'ev, 1908, p. 40, 57, 63; Steiner, 1916.

** Jägerskiöld, 1905; Steiner, 1914; Hofmänner and Menzel, 1915, p. 210; Stefanski, 1914.

*** Bütschli, 1873, p. 33; also "Symplocostoma" lacustris Daday, 1897, p. 120.

† In this genus the projections are supported by characteristic chitinized parts (Cobb, 1914b, p. 84).

---

* E.g. Cephalobus cilatus Linst.: de Man, 1884, Table 15, Figure 61.

** See Cobb, 1893; Maupas, 1901, p. 537; Cobb, 1913, 1914, p. 476.

*** See de Man, 1884, Table 18, Figures 76a, 77a; Cobb, 1914, p. 462.

† See Bütschli, 1873, p. 22; de Man, 1876, 1884, 1906, p. 168; Daday, 1910, p. 53; Brakenhoff, 1914, p. 301. However, Steiner (1916) described true movable lips for his D. antarcticus.

†† See also de Man, 1886; Rauther, 1907.

††† Peculiar lips which project anteriorly were described by Linstow (1900) for Spilophora punctata, which apparently belongs to this genus.

‡ See also de Man, 1907.

(Table 2, Figure 12a, b) project markedly anteriorly; the middle part is thicker, gradually becoming thinner anteriorly, and the lateral parts are formed by two thin plates. These are cross-striated, such that they seem to consist of separate, densely packed bristles. Such plates, though less well developed, are also present in other species of Enoploides (Table 3, Figures 13a, 14a, 15a). The lips of Enoplolaimus, are well developed and sometimes of complex structure, but plates like the above are not present (Table 3, Figure 16a*). Three movable lips have also been described by Bütschli (1874, p. 49) for the peculiar genus Odontophora. Cobb also described three large lips for the predaceous Selachinema,** with a fringe of bristles in one species, as in Enoploides.

The unusual genus Dignathonema Fil. has only two large subventral lips (Table 6, Figure 40a, b, c), the dorsal lip being reduced. These lips are perhaps transitional to cephalic tubercles.

The labial apparatus of Onyx has a specialized structure. There are 12 labial rods, which project slightly from the mouth in the resting position (Table 6, Figure 41b). They may diverge widely when the mouth is open (Figure 41a). Six of these rods apparently correspond to labial papillae.

True lips are also present in parasitic nematodes in connection with an independent buccal capsule. Cucullanus*** is an example, while the mouth is open wide in Sclerostomidae.†

The majority of forms with lips are thus grouped in well-isolated tribes
382 (Oncholaimini, Enoplini, Sphaerolaimini), while Halichoanolaimus and Dignathonema are included in the Cyatholaimini. This character is thus generic to some extent. It may become necessary to consider the latter two genera as a separate subfamily.

### 3. Labial Crown of Bristles or Papillae

I designate as labial papillae or bristles (papillae s. setae labiales) the first crown of papillae, situated next to the mouth or behind the lips.†† There are always six organs of this type in the crown – one lateral and two submedian pairs.

If lips are present, the papillae are situated immediately behind them (Oncholaimini, Table 3, Figure 18a, b) or on them (Halichoanolaimus, Table 6, Figure 39c). In species with three high lips, like the Enoplini, the papillae are situated in single pairs on each lip (Table 2, Figure 10a). In Dignathonema (Table 6, Figure 40a–c) the apical (lateral) papilla (p. l. l.) is present in the form of a short, thick bristle, while the others are shorter (Figure 40c, p. l. sd., p. l. sv.). It is interesting that, in spite of the reduction of the dorsal lip, its papillae are not displaced to the lateral

---

* See also de Man, 1893, 1904; Savel'ev, 1912.

** 1914, pp. 484, 486.

*** Cf. A. Schneider, 1866, Table 5, Figure 4.

† Cf. Looss, 1905, Table 1.

†† This name is preferable to the "mouth papillae" ("Mundpapillen") of Hagmeier, as they are not necessarily situated on the margin of the mouth.

lips. The papillae are sometimes situated inside the vestibule (Metachromadora, Table 7, Figure 42d).

Labial organs in the form of bristles are present in Enoploides and Enoplolaimus (Table 2, Figure 12a, c; Table 3, Figures 13a, 14, 15a, 16a). It is important to note that these are not true bristles, as they are immovable appendages of the cuticle. However, in some species of Spilipherini, Chromadorini, Cobbia and Theristus, there are true movable labial bristles, but they are always short. In most nematodes, however, the labial crown is developed in the form of papillae, which sometimes do not project above the surface. Their weak development or concealed position is the reason that they have sometimes been overlooked.

383 The labial papillae are also present in parasites, e. g., in Mermithidae (Rauther, 1909; Hagmeier). The labial and cephalic crowns of Mermithidae are fused into a common structure, but the internal structure makes it possible to recognize them. According to Schneider, they are also present in many other parasites (1866, p. 235). Goldschmidt (1908) did not find them in Ascaris.

### 4. Cephalic Crown of Bristles or Papillae

This crown (setae s. papillae cephalicae*) consists of 10 bristles or papillae arranged in six groups. The four submedian groups consist of two bristles each, and there is one bristle on each side. Only these 10 bristles are constant in all free-living nematodes and should be called true cephalic bristles. If there are more bristles, the others are designated as supplementary cephalic bristles (setae subcephalicae**).

The cephalic crown may consist of true bristles and papillae, with the latter sometimes even situated in pits (Leptosomatum, Table 1, Figure 1a, b). Examples of hairy or hairless forms and bristles of various shapes have been given above (p. 15). We only mention that the cephalic bristles are very constant. All the bristles on the body are sometimes reduced, but they are always present on the head. The cephalic bristles clearly prove the homology of bristles and papillae (Bütschli, 1873; Rauther, 1909).

There are also cases in which the supplementary cephalic bristles are better developed than the true cephalic bristles and take over their function. This is the case in the family Monhysteridae in the group Theristus–Cobbia, and also in Sphaerolaimus, where the cephalic crown some-
384 times consists of papillae and the role of the cephalic bristles is taken over by the supplementary cephalic bristles (see following section).

The cephalic crown is not a single morphological structure. There are only rarely 10 uniform bristles, e. g., in Paroncholaimus (Table 3, Figure 18b). Four of them – the sublaterals – are usually longer than the other six (Table 2, Figures 10a, 12b; Table 3, Figure 13a; Table 5, Figure 34).

The cephalic crown is sometimes divided in two – an anterior group of 6 shorter bristles and a posterior group of 4 longer bristles.*** They

---

* The term "cephalic setae" was already used by Bastian.

** Cobb, 1893, p. 405, also noted "true cephalic hairs" in his "Monhystera setosissima."

*** The opposite is rarely observed – 6 long and 4 short bristles, e.g., in Cyatholaimus punctatus de Man, 1890, p. 182; Selachinema Cobb, 1914, p. 486.

may be situated either close together, as in Onyx (Table 6, Figure 14a), Anoplostoma (Table 2, Figure 7a) or far apart, as in Oxystoma (Table 2, Figure 8a[*]).

In most species of Spilipherini, Chromadorini and Acanthopharyngini and many species of Monhysteridae, the anterior crown consists of papillae, while the posterior crown consists of 4 bristles, as noted by Bütschli (1873, p. 14). This is also the case in the Desmoscolecidae, where there are 4 stout, hornlike bristles.[**] In these forms we should distinguish not two but three crowns (cf. Table 7, Figure 42d): 1) 6 labial papillae (pap. labiales); 2) 6 cephalic papillae (pap. cephalicae) or anterior cephalic bristles (setae ceph. anteriores); 3) 4 cephalic bristles (setae ceph.) or posterior cephalic bristles (seta ceph. posteriores). This was already noted by de Man (1886), but he did not stress its importance.[***]

However, there are apparently cases where one or the other of the crowns is absent. Thus, in Enchelidium and Symplocostoma 385 I found only 6 cephalic bristles (Table 4, Figure 28a; Table 5, Figures 31a, 32b). De Man described the same phenomenon (1888). On the other hand, in many small species of Chromadorini I found and others described only one circle of papillae and 4 bristles. We should remember, however, that both are small forms and very delicate structures, so that inaccurate observations are always possible. In addition, my observations are not definitive, as my Enchelidium and Symplocostoma material was not in good condition. The labial papillae of Chromadorini may be concealed in the vestibule and thus be overlooked.[†] I also found only 6 bristles on the rostrum of Draconema, the labial or anterior cephalic bristles (Table 8, Figure 55c).

Only Jägerskiöld (1901) doubted the sensory function of these bristles, but after the work of Zur Strassen (1904) and my own notes (1912) no doubt should remain

In parasites – Mermithidae (Rauther, 1906, 1909; Hagmeier, 1912) and Ascaris (Goldschmidt, 1903, 1908) – the same arrangement of the cephalic papillae has been described and there is also proof of their sensory function.

The development of the cephalic crown in the form of bristles or papillae should not be considered very important. The differences between these species and others are sometimes so small that this character certainly has not more than specific value. For example, Leptosomatum punctatum Eb. (Table 1, Figure 2) has bristles and other species of the genus have papillae. Viscosia glabra Bast. has papillae and other species of Viscosia have bristles.

The division of the crown into two is a different matter. In the Chroma- 386 doridae, I would even like to give this character subfamily rank. However, it is possible that this division is exceptional, and regrouping may be necessary on the basis of other characters. In my opinion, however, it is quite inadmissible to include species with 4 and 10 bristles in the same genus, as was done by Micoletzky (1914) and avoided by Cobb (1913).

## 5. Supplementary Cephalic Bristles (setae subcephalicae)

This term designates bristles adjacent to the cephalic bristles but not belonging to the main group of 10 bristles. Two categories of these bristles should be distinguished.

Bristles of the first category are situated immediately behind the true cephalic bristles, belonging to the lateral and submedian lines. They apparently increase the number of true cephalic bristles. Such bristles are common in the Monhysteridae. The bristles which follow the lateral bristles in the group Theristus primarily belong here, e.g., in Cobbia sabulicola Fil. (Table 9, Figure 63a). Thus, 12 cephalic bristles are present instead of 10, or even more.[*] The groups of bristles behind the main cephalic bristles in Comesoma also belong here (Table 11, Figure 76a[**]). Their number varies both with age and in different individuals of the same species. In the genera Diplopeltis (Table 11, Figure 80[***]), Araeolaimoides (Table 10, Figure 73a[†]) and others, the 4 main cephalic bristles are followed by 4 longitudinal rows of supplementary cephalic bristles.

Bristles of the second category are also found in Monhysteridae. In many species of Sphaerolaimus (Table 10, Figure 63a) there are 8 groups of numerous long bristles. These have the function of the main cephalic bristles, which are only weakly developed in this species.[††] In other species of Sphaerolaimus, these bristles are not arranged in definite groups. A similar arrangement is present in some species of Theristus.[†††] Such bristles may be called post-cephalic bristles (setae postcephalicae).

For the cervical bristles, see above, p. 15.

## 387 6. Lateral Organ

The lateral organs (organa lateralia, amphidisci[‡]) are depressions of various forms on the lateral parts of the head. This organ is sometimes

---

[*] Also in Trefusia de Man (1893); Holalaimus (1888).

[**] See Cobb, 1894, 1913; Shchepot'ev, 1908; Steiner, 1916.

[***] This arrangement is so regular that we are justified in doubting the correctness of the observations of Micoletzky, 1914, p. 495, who described 10 papillae and 4 bristles in Ethmolaimus alpinus. There should be 6 labial and 6 cephalic papillae – 12 altogether.

[†] The data of de Man (1907) concerning 6 cephalic bristles in Cobbia trefusiaeformis seem doubtful. There are always 10 bristles in the Black Sea species.

---

[*] Th. normandicus dM., Th. setosus Bt. – 12, Th. acer Bast. – 14–3 lateral (de Man, 1890).

[**] Known to Bastian (1865, p. 158) and de Man (1890).

[***] Cf. also Eberth, 1883, p. 35; Cobb, 1891.

[†] Cf. also de Man, 1893, p. 87.

[††] Cf. also de Man, 1907, p. 57.

[†††] Cf. Steiner, 1915, p. 225, Th. polychaetus; 1916, p. 643, Th. horridus, Cobb, 1914, p. 18, Th. pilosus.

[‡] "Amphids" of Cobb (1913).

displaced close to the anterior margin (many species of Chromadoridae, Table 6, Figure 36a; Table 7, Figures 42b, c, 46a, 47c) and sometimes displaced far posteriorly (Oxystomina, Table 2, Figures 8a, 9a; Tripyloides, Table 6, Figure 35a; Anoplostoma, several species of Monhysteridae). The same position of the organ ventral to the lateral bristles is a characteristic for the majority of Enoplidae (e. g., Table 3, Figure 18b), but is not constant. It is displaced dorsally in Eurystomina. The cephalic line is usually situated behind the opening of the lateral organ (Table 2, Figures 10a, 11a), but in Eurystomina it is situated at both sides of its slit (Table 5, Figure 29a).

The function of the lateral organs is certainly sensory, as a strong nerve always leads to them (Zur Strassen, 1904; Filip'ev, 1912). The "glands" described by de Man and others, and also the "muscle fibers" of Türk (1903), are clearly nerves and companion cells. A similar nerve is apparently the "canal" connected in Plectus parietinus to the lateral organ, whose lateral processes bear papillae.* There seems to be no doubt about their sensory function (de Man, 1886; Cobb, 1898). De Man considered them to be the pores of glands. He stated as proof that a mucous secretion sometimes exudes from the opening.** It is possible that the cavity of the lateral organ is filled with a mucous mass*** which exudes from the opening after death, but this does not disprove their sensory function. There does
388 not seem to be any reason to ascribe an auditory function to the lateral organs, as was done by Marion (1870) and Bütschli (1873). The latter afterwards (1874) changed his interpretation and considered them to be modified papillae. Zur Strassen's suggestion that these organs have an olfactory function is more likely.

The lateral organs are of varying structure in free-living nematodes. There are three basic types: pocket-shaped (cyathiform), spiral and circular lateral organs. The latter two may be modifications of the same basic shape. Other shapes may be reduced to these three. The same applies to the six different shapes of lateral organ described by Cobb (1914, p. 482).

1) Pocket-shaped lateral organ.† This type is characteristic for the family Enoplidae.†† The lateral organ consists of a depression in the cuticle, whose posterior part is covered and whose anterior part is open to the outside.††† A papilla projects into the cavity from the back, containing the nerve ending of the lateral organ (Table 3, Figure 18c; Table 4, Figure 20a—o. o. l). Organs of this type are usually small, sometimes

---

* Cobb, 1898, p. 44.

** Cf., e. g., de Man, 1888, Table 2, p. 8.

*** Steiner, 1916, p. 612.

† The comparison with a pocket was suggested by Cobb, who described "two oblique lateral pockets" in Onch. orientalis (1890, p. 458).

†† Only Trypiloides (see p. 129, Part I) has a spiral lateral organ. For Enoplolaimus, see p. 71, p. 25 of this book.

††† The description of the lateral organs of Dorylaimus and related forms as "slitlike" (Cobb, 1913) is inaccurate. A sentence of Hofmänner is mistaken: "Les espèces des genres Dorylaimus et Trilobus en sont toujours dépourvues" (1913, p. 598). Another error is an observation of Steiner (1915, p. 227), who did not find the fine outlines of the cavity of the lateral organ in Leptosomatum sabangense.

minute (Enoploides, Table 2, Figure 12c). It is fairly large only in some species of Oncholaimini. The organ is usually oval, rarely round (Viscosia) or greatly extended (Oxystomina, Halalaimus), and sometimes transversely oval (Enchelidium, Eurystomina, Table 4, Figure 25b; Table 5, Figure 29a*). The pocket is covered by a tongue extending from its posterior margin and curved towards the outside.**

389 The pore may be very small (Leptosomatini, Table 1). In typical cases it occupies only a third of the length of the organ (Enoplus, Paroncholaimus, Table 2, Figure 10a; Table 3, Figure 18c). In Viscosia there is a large, round lateral organ and almost its entire anterior half is open (Table 4, Figure 20a). The posterior pocket of Oxystomina is very small, the lateral organ is greatly extended longitudinally and most of its anterior part is open (Table 2, Figures 8a, 9a). The lateral organ of Halalaimus is even more marked in this respect (de Man, 1888).

The lateral organ of Thalassoalaimus is a modification of this type. There is a narrow but very long curved slit which continues into a narrow, deep pocket.***

This type of lateral organ is weakly marked. Bastian (1865) and Bütschli (1873, 1876) described "cervical slits," "Seitenpapillen" and "lateral openings" in Dorylaimus, Trilobus, etc., but the first exact description was given by de Man (1886). He recognized it as a true lateral organ and connected it with the other types.

If the observations of de Man (1893, 1904) and Savel'ev (1912) are correct, Enoplolaimus has a characteristic form of lateral organ — projecting bulb with a cavity anterior to the lateral bristle. If this structure is confirmed, it would be an exception in free-living nematodes. However, Enoploides closely resembles Enoplolaimus in head structure, the latter having a lateral organ of normal structure situated, as in other nematodes, behind the lateral bristles (Table 2, Figure 12c). The structure described for Enoplolaimus as the lateral organ is probably not this but a homologue of the "lateral slit" of Enoplus (see p. 29). The true lateral organ is probably the same as in Enoploides, but was overlooked because of its small size.

390 2) **Spiral lateral organs** are present in Chromadoridae and Monhysteridae. Tripyloides, which belongs in all other characters to the Enoplidae, also has a spiral lateral organ. However, it is not external, as in most other genera, but invaginated and communicates with the environment only through a small opening. The last turn of the spiral is curved to the outside. In Tr. vulgaris de Man, 1886, the spiral is apparently more or less regular, which is not the case in the Black Sea species Tr. demani Fil. (Table 6, Figure 35a). Its structure is thus not known. This is probably only a secondary modification of the cyathiform lateral organ which is typical for Enoplidae. There is also a tendency to form a spiral in other species of this family, e. g., in Oxystoma clavicauda Fil. (Table 2, Figure 8a) the pocket is slightly asymmetrical and its end is curved.

---

* De Man (1907) described for Eur. terricola transversely oval lateral organs without a pocket, dorsal to the lateral bristles.

** See also de Man, 1888, pp. 13, 25.

*** See de Man, 1893; Steiner, 1916, p. 649.

Typical spiral lateral organs are always open (Table 6, Figure 40b; Table 7, Figure 42c, d); only the posterior part of the external turn is covered and the papilla of the lateral organ opens here (e.g., Table 6, Figure 39a). The outer turn of the spiral, in which the nerve ends, is usually on the dorsal side, so that a right-hand spiral turns to the left and a left-hand spiral to the right, as recorded by Cobb (1898, pp. 19, 44). It is not known whether this rule is constant, but the reverse relationships also exist. Lateral organs of this type are immediately recognizable in many species and were described by Bastian (1865, 1866, "lateral markings"), Bütschli (1873, 1874) and Marion (1870).

The best-developed spirals, with sometimes up to five turns, are found among Cyatholaimini (Table 5, Figures 37a, 38a; Table 6, Figures 39a, 40a) and also in several species of Desmodora and Comesoma (Table 11, Figure 76a*). The smallest number of turns is present in Spilipherini (Table 6, Figure 41a; Table 7, Figure 44b) and also in other species of Comesomini (Table 11, Figures 78a, 79a**). There is sometimes only a single turn (Chromaspira, Table 7, Figure 45a).

391 The lateral organs of Spira (Table 7, Figures 46a, 47b) are also a typical spiral with one turn. The walls of the external and internal margins are thickened, but the part at which the ends of the spiral are adjacent has thin walls; the lateral organ therefore appears to be round with an incised margin, as described by de Man (1890) and Cobb (1898, p. 391). However, Cobb noted that its internal tubercle is a small spiral.

A modification of the spiral lateral organ is present in Axonolaimus and Araeolaimoides. There is the same tube as in the spiral organ, a loop rather than a spiral (Table 10, Figures 70a, 71a, 73a). In Conolaimus there is an almost typical spiral (Table 10, Figure 72).

There is another modification in the Draconematini. The spiral is small and forms a curved canal inside the thick cuticle of the head (Table 8, Figures 55c, 56). It sometimes forms a full spiral and sometimes a horseshoe-shaped loop. Shchepot'ev (1908, p. 63) described them as "two external ringlike thickenings" without understanding their function. According to his drawings, they may project in other forms.

There is a special modification in Metachromadora and to a lesser extent in some species of Desmodora (Table 7, Figures 42b–e, 43). The walls of the lateral organ are very thick, so that a plate is formed in which an open spiral with one small turn is situated.

Lateral organs of this structure, but still more specialized, are found in the Diplopeltini (Table 11, Figures 80, 81). The spiral is enclosed in a thick plate. There is an opening at the base of the spiral in Diplopeltis, which continues into a blind, curved pocket.***

The lateral organs of the Acanthopharyngini are apparently also modifications
392 of this type; thus, in Acontiolaimus (Table 6, Figure 36a) the organ is a spiral but its membrane is very thick, so that its structure is not clear.†

---

* See also de Man, 1890.

** See de Man, 1907; Steiner, 1916.

*** Cf. Eberth, 1863; Villot, 1876; Cobb, 1891.

† See also de Man, 1890 – Camacolaimus; Steiner, 1916 – Dermatolaimus.

3) Circular lateral organs are characteristic for Monhysteridae. This type was also known to Bastian, who called them "circular depressions." Three categories of such organs should be distinguished:

1. Lateral organs with a thick wall, as in the genera of the group Theristus–Cobbia (Table 9, Figures 61a, b, 62a, 63), Sphaerolaimus (Table 10, Figures 67a, 68a, 69a, b) and Monhystera (s. str.). These organs are always without a central spot; they are sometimes situated far from the anterior margin of the head. The papilla of the sensory bulb is situated symmetrically in the middle.* Sometimes platelike appendages are present near them (possibly consisting of hardened secretion**). This type of circular organ is apparently of independent origin. Its most primitive stage is found in Paramonhystera (Table 9, Figures 59a, b, 60a). There is a weakly demarcated, wide, smooth depression in the middle of the annulated cuticle of the head. The papilla of the sensory organ opens symmetrically near the posterior margin. In P. elliptica Fil. this papilla bears a group of short bristles, indicating the complex origin of the lateral organ.

2. Another type of circular lateral organ is the thick-walled amphidisc of Linhomoeus, Terschellingia and related genera (see Table 9, Figures 57a, 58a, 64a, 65a, 66a), and also of the Siphonolaimini.*** They are deep pits lined with thick chitin, often with a central spot. There is also an oblique slit on the posterior margin of the organ on the dorsal side (Table 9, Figures 58a, 65a, c). This slit is probably a rudiment of the
393 spiral structure of the organ, so that this form of lateral organ may be of secondary origin.† These pits are also sometimes filled with secretion.††

3. The lateral organs of Monoposthia (Table 7, Figure 48) and Tripyla are also related to the circular organs. They are shallow pits with a modified cuticle, extended longitudinally in Monoposthia and laterally in Tripyla. It is unlikely that they have anything in common with the circular lateral organs described above.

A secondary modification of this form is the oval lateral organ of Disconema (Table 10, Figure 74a, b). There is a flat elevation in the middle, and it is incised posteriorly and dorsally, as in Linhomoeus, etc. The large lateral organs of the freshwater genus Aphanolaimus probably belong here. They are deep round pits, and there is a vesicle of thin cuticle (or mucous material) at its bottom.†††

The lateral organs of Chromadorini are transverse slits at the anterior margin of the head. They are rarely well marked, sometimes not recognizable. There is a complete reduction of the lateral organs in some cases (Table 8, Figure 50a, o. 1; Figures 51a, 52a, 53a, 54a).‡

---

* See also Steiner, 1916, p. 646.

** See de Man, 1884, Table 4, Figure 14b.

*** See Zur Strassen, 1904.

† The lateral organs of Ethmolaimus, Microlaimus and others apparently belong here. Hofmänner and Menzel (1915) drew a spiral for Ethmolaimus. See Steiner, 1916, p. 591, Cobb, 1914a, for Microlaimus.

†† "Bei Sphaerolaimus hirsutus Bast. . . schien sich von dem Boden der Grube ein dieselbe fast ausfüllender blasser Körper bis über den Rand zu erheben." (Bütschli, 1874, p. 6). The fibers of the lateral organ of Linhomoeus are apparently a foreign substance.

††† See de Man, 1884, pp. 8, 34; Hofmänner and Menzel, 1915, p. 121.

‡ See also de Man, 1886, p. 71; 1890, p. 198; 1893, p. 98, Cobb, 1914a.

**Aberrant forms of lateral organs.** Shchepot'ev (1908) and Steiner (1916) described small vesicular lateral organs in Desmoscolex, which have not been described in other nematodes.

There are probably other forms of lateral organs in Anguillulidae which cannot be included in the categories described above. Thus, the lateral organ of Plectus is a deep pit with a thick anterior and thin posterior margin, so that a "stirrup form" (Cobb*) is obtained. Bastian considered 394 these lateral organs to be openings of the canals of the excretory system. The lateral papillae of Diplogaster are also a form of lateral organ.**

There are 4 large chitinized circles on the head in the genus Pseudochromadora.*** The two lateral circles are probably the lateral organs, the two median circles are some specialized structures.

Lateral organs are also present in parasitic nematodes. Hagmeier (1912) described and drew the lateral organs of various species of Mermithidae. As in Enoplidae, the organ is cyathiform, with an internal cavity directed obliquely posteriorly. Its sensory bulb ends in several hairs which project into the cavity. It is sometimes very large (Mermis tenuis Hgm., p. 541) and of complex structure (M. nigrescens Duj., p. 568), though it is sometimes small and papilliform. According to Rauther (1906), true lateral organs are absent in Mermis albicans, but instead of adjoining the lateral group of papillae there is a characteristic "discoidal ending" of several nerve fibers which is homologous with the lateral organs.† The resemblance to Enoplidae is clear if we assume a direct relation of these parasites with the Dorylaimini, as was done by Steiner (1917).

The cervical papillae of Ascaris (Bütschli, 1874) and Ichthyonema (Jägerskiöld, 1901††) were considered as homologous with the lateral organs, but this is apparently not correct. According to Goldschmidt (1903), these papillae are of simple structure, while the lateral organ is always connected with a large fascicle of nerves. The dorsolateral papilla of Ascaris is such an organ (Goldschmidt, 1903; Hesse, 1893). This organ, and not the cervical papillae, as stated by Zur Strassen (1904), should be considered as the homologue of the lateral organ. The lateral organ of Ascaris and Mermis is thus displaced to the dorsal side in contrast to its position in the majority of free-living nematodes (Rauther, 1909).

The shape of the lateral organ is an important systematic character. Thus, the cyathiform lateral organ is characteristic for almost the entire family Enoplidae. This form is not present in the other families, but the spiral and circular organs in various modifications are common. In the Chromadoridae, at least in the marine forms,††† circular organs have never been formed, but they are common in the Monhysteridae. Spiral lateral organs are characteristic for both families. Too great an emphasis on 395 this character may produce groups based on a single character (for example, my subfamilies of Monhysteridae), but these groups usually have proven to be homologous. In any case, we should never place species with different lateral organs in the same genus, as has often been done.*

### 7. The Cephalic Slit of Enoplus (fissura cephalica)

This genus has a characteristic organ situated ventrally near the lateral bristle. It is a deep fissure with the entire outline anteriorly but not closed posteriorly (Table 2, Figure 10a, fiss. ceph.). This is obviously a sensory organ. De Man (1886) found it for the first time in En. communis Bast. I found it in En. euxinus Fil. and En. crassus Fil. (1916). It is probably also present in other species, but it is absent in E. brevis Bast., according to de Man. I did not find it in other species of Enoplus which I examined. Rauther (1907, p. 723) believed that this is the external opening of the lateral esophageal glands (see below), which seems unlikely. Southern** noted a triangular pit, probably homologous to the cephalic slit, in Fiacra longisetosa.

### 8. Internal Structure of the Head

The head down to the cephalic line consists of 10 epidermal cells in Paroncholaimus zernovi Fil. Six of these cells form an anterior row, four a posterior row.*** The anterior row forms the lips, and the labial papillae are situated on them; the posterior row is interrupted by the 396 cephalic papillae and the lateral organ. The posterior margin of the posterior row of 4 cells marks the cephalic line. The division of the cuticle into two layers corresponds to this line. The outer layer is the outer covering of the head; the inner layer above the anterior row of cells is separated from the outer layer and attached separately to the buccal capsule, not reaching its external margin (Table 3, Figures 18a–a, 19a; Table 4, Figures 23a, 26a, 27a). Between these two layers there is an annular space around the mouth. This cephalic pocket was described and drawn in the first descriptions of Oncholaimini, but only Stewart (1906) considered it to be a special structure.† The inner layer is rarely slightly chitinized in Oncholaimini (e. g., Table 4, Figure 27a) and it begins further posteriorly than the cephalic pocket in these cases.

This division of the cuticle is also present in other Enoplidae with a wide buccal capsule, e. g., in Symplocostoma and Eurystoma

---

* See de Man, 1884, Tables 16–18.

** See Bütschli, 1876, p. 370, Table 23, Figure 5a, b; Cobb, 1914b. He also described a characteristic dorsal organ resembling the lateral organ in males of this genus.

*** Daday, 1901, p. 7.

† "Scheibenförmige Nervenendigungen" (p. 47), Hagmeier, p. 558.

†† Cf. Jägerskiöld, 1894, p. 493.

††† They are apparently present in some freshwater forms.

* E. g., Micoletzky (1914, 1915); Daday (1897, 1905, 1910).

** 1914, p. 36.

*** Goldschmidt (1903) described modified epidermal cells at the anterior end of Ascaris: 6 "Kolbenzellen" anteriorly and 4 "Faserzellen" posteriorly. There are 9 'Arcadenzellen" behind them. Although the cells end at the nerve ring, they are adjacent to the cuticle only anteriorly.

† Cephalic pockets filled with a granular substance often accompany the development of a thick-walled oral capsule. Looss (1905, p. 75) described a similar structure in Ancylostoma, but its buccal capsule obviously developed independently of that of Oncholaimini.

(Table 5, Figures 29a, 30a, 31a, 32b, 34a). In Enchelidium (Table 4, Figure 28a, b), there is no large buccal capsule but a structure of this type is present as in Diplopeltis incisus Southern (1914, p. 17).

Oncholaimini do not require an external hardening of the head, as their mouth organs are not movable; the buccal capsule strengthens it sufficiently. But if the mouth organs are movable, hardening becomes necessary. The superficial cephalic capsule (capsula cephalica superficialis) fulfills this purpose in Enoplini.

We have noted above (p. 10) that the cuticle changes anterior to the
397 cephalic line — the layer of crossing fibers and the punctations of its middle layer disappear.* The cuticle also becomes thinner and its internal layer becomes harder.** This is sometimes clearly marked (Table 3, Figure 13a) and sometimes weakly marked (Table 2, Figures 10a, 12a, b). This type of cephalic capsule was described specifically by Savel'ev (1912).

The superficial cephalic capsule of Phanoderma belongs here. This is the thickened middle layer of the cuticle, which is striated longitudinally (cf. Table 1, Figure 5a–d; the striation is well delineated in Figure 4a).

**The internal cephalic capsule** (capsula cephalica interna) provides the anterior point of attachment of the esophagus. It is usually directly attached to its chitinized lining and is a well-defined morphological structure.*** There is a pocket between it and the external cuticle anteriorly which is homologous with the pocket of Oncholaimini described above (Table 1, Figure 3b).

Some genera of Leptosomatini have a weakly developed cephalic capsule; it is sometimes almost not differentiated (Leptosomatum, Table 1, Figures 1a, b, 2a†) in others it is weakly developed but clearly marked (Leptosomatides, Table 1, Figure 3a, b); finally, in the genera Fiacra, Deontostoma and Thoracostoma it is well marked and usually
398 yellow, so that it is easily recognized. In most species of Fiacra and also in Cyclicolaimus it has the form of a narrow ring (Jägerskiöld, 1901; Türk, 1903).

In other species of Fiacra and in the two other genera, 6 posteriorly directed processes are present on the posterior margin of the capsule — 2 median and 4 sublateral. The cephalic bristles and lateral organs are situated in the indentations between them. The lobes of the cephalic capsule are sometimes expanded, so that there are only narrow slits posteriorly, between them; they are sometimes perforated and small chitinized bodies are sometimes present at their posterior margin.†† All these characters are suitable for specific differentiation (de Man, 1888, 1893, 1904; Filip'ev, 1916). The labial papillae are situated on the cephalic capsule and not in the indentations, so that the nerves penetrate the capsule through canals.

The same structure is present in Phanoderma (Table 1, Figure 5b–p. lab.), Halichoanolaimus and Dignathonema (Table 6, Figure 39c–p. lab., n. p. lab., 40c–p. l. sd., p. l. sv.); similar structures are the small vaults above the labial papillae in Paroncholaimus (Table 3, Figure 18b).

The cephalic capsule either forms a truncate cone anteriorly (Thoracostoma) or is bluntly truncate (Deontostoma). There is a hollow, immovable tooth on the ventral side in Thoracostoma (Filip'ev, 1916). The internal structure is also very complex; there are processes which are directed forwards and inwards into the tissue of the esophagus. An anterior dorsal process at the dorsal wall of the esophagus is particularly constant.

A chitinized band develops in Deontostoma arcticum Sav. inside the external layer of cuticle, forming a narrow secondary cephalic capsule (Filip'ev, 1916).

The cephalic capsule of Phanoderma is reinforced by three anteriorly directed processes. These processes are hollow (see Table 1, Figure 5a–d and p. 39, Part I). This capsule is directly connected to the
399 superficial capsule. It should thus be considered only as part of the superficial cephalic capsule and does not correspond to that of other species of Leptosomatini, which isolates Phanoderma.

Finally, in Enoplini there is a homologue of the internal cephalic capsule in addition to the superficial capsule; this is a ring which surrounds the mouth organs and to which the jaws and the esophagus are attached, as in Leptosomatini. This interpretation of the ring is confirmed by sections, which show that it separates an anterior pocket filled with granular material, as in Leptosomatini and Oncholaimini (see Rauther's drawing, 1907, p. 720). It is usually narrower near the jaws, but becomes wider between them; sometimes characteristic plates are present here, sometimes only the ring is present (see c. ceph. — Table 2, Figures 10a, 11a, 12a, b; Table 3, Figures 13a, 14, 15a, 16a).

Similar conditions produce similar structures, e. g., a cuticular ring around the anterior part of the oral capsule is also present in a different group, Halichoanolaimus (Table 4, Figure 38a). Such a ring is also present in Dignathonema (Table 6, Figure 40b). There is a thick external cephalic carapace in Desmodora and Draconematini (p. 11).

The superficial cephalic capsule around the entire head should therefore be distinguished from the internal capsule in its anterior part. The layer of the cuticle which forms the bottom of the cephalic pocket in Oncholaimini and the maxillary ring in Enoplini are homologous. All these organs are modifications of the inner layer of the cuticle. A true (internal) cephalic capsule has not been formed outside the family Enoplidae. Various forms are found in well-defined groups. For example, genera of Leptosomatini have a cephalic capsule. However, its shape varies even in related forms; it thus shows better the relationship of different groups than characters for differentiation.

---

* However, in some cases the cephalic capsule bears punctations (Enoplolaimus acantholaimus Saveljev, 1912).

** Cf. Rauther, 1907, drawing on p. 720.

*** "Capsule céphalique," "Kopfkapsel" of the authors, "Kopfkrause" of A. Schneider (1866). Jägerskiöld (1901, p. 7) states that the cephalic capsule supports the cephalic bristles. This seems unlikely. The opinion of Steiner (1915, p. 227) that the esophagus of Leptosomatum sabangense is not attached to the cephalic capsule but that muscles are attached to it which draw the esophagus forward is apparently an error.

† "Charpente chitineuse" of de Man (1893, p. 102). "Eine niedrige Stufe der Kopfkapsel" (Steiner, 1916, p. 613).

†† I found such small bodies in young specimens of Th. denticaudatum (Schn.). They were absent in old specimens, apparently having merged with the margin.

### 400 9. Sexual and Age Dimorphism in the Development of the Cephalic Organs

Sexual dimorphism is marked both in the development of the cephalic bristles and of the lateral organs. Thus, de Man (1890) noted that the cephalic bristles in the male are longer than in the female of Oncholaimellus calvadosicus.

The lateral organs are also often larger in the male, e.g., in Onyx (p. 154, Part I), Oxystomina clavicauda Fil. (p. 50, Part I), they are twice as large in Viscosia cobbi Fil. (p. 86, Part I). The difference is particularly great in Sphaerolaimus dispar Fil. (Table 10, Figure 69a, b). It is very striking, as the lateral organs are large. The band of the oral capsule is also narrower in the female and changes with growth.

Other authors recorded dimorphism of the lateral organs in Diplogaster rivalis (Leyding) (de Man, 1884, p. 84), Ethmolaimus revaliensis G. Schneider (1906, p. 683), Oxystomina elongata Büt. (de Man, 1907, p. 44) and Sphaerolaimus hirsutus Bast. (ibid., p. 59); a different position of the lateral organ in young individuals has also been recorded.

Changes with age are also known among Anguillulidae. Thus, the larvae and males of Heterodera have a chitinized hood on the head which is apparently used to pass between hard particles of soil (Strubell, 1888). Such a hood is also present in larvae of Plectus. De Man (1904) considered them to belong to a different subgenus, but Micoletzky (1914) proved that they are only stages of development.

Finally, in males of Diplogaster trichuris Cobb there is a dorsal papilla which resembles the lateral organ in structure (Cobb, 1914a).

## d. Epidermis

### 1. Epithelium and Longitudinal Fields

The epidermis of free-living nematodes is a single-layer epithelium with distinct cell boundaries. The so-called longitudinal fields are only local thickenings of the epithelium.

Retzius (1906) stained the cell boundaries in free-living nematodes by silver impregnation. The cells proved to be arranged in longitudinal rows. In Enoplidae there are 8 of these rows: 2 narrow median rows, 2 narrow
401 lateral rows and 4 wide rows between them. Irregularity has rarely been observed in these rows — 2 cells instead of one, etc. I was able (1912) to confirm these data. It should be noted that silver stains the boundaries not only in the epithelium but very distinctly in the cuticle. This supports the view of Zur Strassen (1896, 1904) that almost the entire epithelium takes part in the formation of the cuticle. However, this is not true for all forms. Almost complete absence of epidermis has been recorded for Fiacra and Cylicolaimus,* while in Paroncholaimus, Adoncholaimus and Enoplus a thick plasmatic layer remains under the musculature.**

---

* Jägerskiöld, 1901; Türk, 1903; also Solenolaimus – Zur Strassen, 1904.

** De Man, 1886; Jammes, 1895; Stewart, 1906; Rauther, 1907, unpublished data.

The bristles take part independently in the mosaic of the epidermis. They are usually situated at the boundaries of the cellular zones, but if they are situated on the zone itself there is a characteristic groove to the bristle from the boundary.

The "longitudinal lines" or "fields" are local inflations of the epithelium which project into the body cavity and divide the musculature into parts. In Paroncholaimus (see my note, 1912) there are 8 such "fields": two median fields formed by the middle part of the median rows of cells*; two lateral fields each formed by 3 rows of cells by the narrow lateral and part of the wide submedian rows, the other part of the cells of this row extending as a wide but thin process under the musculature; 4 submedian lines are formed on the boundary of the median and submedian rows of cells, from parts of both. They are always situated nearer to the median fields. The submedian fields are not constant and may be absent in many species.**
402 The cells are arranged differently anteriorly, which will be described elsewhere. The median lines are more markedly developed anteriorly. The inflation of the epidermis on the ventral line of the tail has been called "pulvillus postanalis" by Looss.

There are well-developed longitudinal fields in Spira***; they have also been recorded in Rhabdogaster,† several species of Chromadora,†† Linhomoeus,††† Theristus‡ and Siphonolaimus.‡‡ Tripyloides has wide submedian fields.‡‡‡

Three rows of cells in the lateral fields have been described for Fiacra strasseni Türk (1903), but in some parts of the body their number increases to five. The cells of the middle row differ histologically from those of the 2 lateral rows; they absorb fat from fat cells in the body cavity. De Man★ also described 3 – 4 rows of cells in the middle of the body of Enoplus michaelseni Linst. and 5—6 rows in Thoracostoma setosum Linst. The increase of the number of cells in the epidermis is related to their increase in other organs. I observed this in Paroncholaimus papilliferus Fil.★★

The shape of the cells of the epidermis varies; cells of the submedian rows are more wide than long, the cells of the narrow lateral rows in Paroncholaimus are square, in others they may be extended longitudinally and irregularly distributed, e.g., in Leptosomatides euxina Fil.

---

* The nuclei in the dorsal and ventral lines have also been described by de Man (1886) and Türk (1903).

** De Man (1886, 1904); Jägerskiöld (1901); Türk (1903); Stewart (1906). Also recorded for parasites. Nuclei in the submedian lines have only been described by Hagmeier (1912, p. 535) for Mermis terricola at the anterior end; these are apparently special structures.

*** De Man, 1890, pp 174, 175.

† Shchepot'ev, 1908, p. 61.

†† Steiner, 1916, p. 539.

††† Bütschli, 1874, p. 31; de Man, 1890, p. 207.

‡ De Man, 1890, p. 182.

‡‡ De Man, 1893, p. 99.

‡‡‡ De Man, 1886.

★ 1904, pp. 21, 26.

★★ 1916, p. 112, Table 5, Figure 13a, b.

The epidermis is usually granular, and its granules are stained vitally with methylene blue; the nuclei are also sometimes stained and after death the boundaries of the cells (Paroncholaimus, Golovin, 1901; Rauther, 1907; Filip'ev, 1912). The epidermis of Anguillulidae is packed with globules of fat (?).[*]

403 There are specialized structures in Metoncholaimus eberthi Fil.; the cells of the lateral fields are very large, vesicular, so that there seems to be internal segmentation in some places (Table 4, Figure 27b). The same structure is also present in Oncholaimus megastoma Eberth[**] and Monhystera trabeculosa G. Schneider.[***] The cell structure in Disconema is very distinct anteriorly (Table 10, Figure 74a, b).

Quatrefages (1846), Bastian (1865, 1866) and Schneider (1866) already distinguished longitudinal fields in free-living nematodes. However, Marion described an uninterrupted muscle layer.[†] In one case, he described cells of the lateral fields underlying the musculature. He probably considered the thick cuticle of Thoracostoma as musculature (Bütschli, 1874).

All authors who studied free-living nematodes recognized the lateral fields as processes of the epidermis. In the past, the lateral fields of parasitic nematodes were believed to be mesodermal (Zur Strassen, 1896), but after the work of Martini (1903—1909) this view was rejected. In parasites, and many adult Anguillulidae[††] among the free-living nematodes, the cells of the epidermis form a syncytium and the nuclei break up amitotically into many small parts (Martini, 1909). The middle row of cells of the lateral field is more constant and remains defined. Goldschmidt (1903) therefore suggested that it is a special mesodermal formation in the remaining ectodermal "subcuticle." However, he later (1906) rejected this view. For details the reader is referred to Martini (1909[†††]).

During the development of a large number of parasites and their larvae
404 there are only 5 rows of cells of epidermis — (originally 6) lateral, as in free-living nematodes, and submedian. The difference is that the flat processes of the cells of the upper rows do not end at the submedian lines but cross them and the dorsal line and reach the adjacent lateral line. The entire cover of the upper half of the body thus consists of one row of cells, whose nuclei are situated alternately on the right and left. Nuclei are present only anteriorly in the dorsal line (Martini, 1906—1909).

If these are compared with the 8 rows of cells of Enoplidae, we find a marked difference from the parasites (probably also from Anguillulidae[‡]). This is possibly one of the characters which distinguish these groups sharply from true free-living nematodes.

---

[*] Pérez, 1866, p. 291; de Man, 1910, p. 366.

[**] 1863, p. 26, Table 1, Figure 20.

[***] 1906, p. 13.

[†] ..."une couche musculaire ininterrompue."

[††] See Chatin, 1891, 1897.

[†††] Stewart (1906, p. 107) believed that in Paroncholaimus vulgaris "the submedian lines are not epidermal, but are merely mesodermal partitions between groups of muscle-cells." This is incomprehensible.

[‡] However, Nasonov (1897, p. 7) described a similar 8 rows in the genital region of the female of Oxyuris flagellum.

## 2. Dermal Glands

The dermal glands of nematodes are always unicellular. Knowledge of their histology makes the few reports of multicellular glands doubtful. The authors probably observed other structures.

There are several categories of dermal glands in free-living nematodes which were partly defined by Jägerskiöld (1901), who described the glands of nematodes in general. These are (1) glands of the lateral field, (2) cephalic, (3) cervical, (4) vaginal, (5) preanal glands of the male, (6) anal, (7) paired, (8) true caudal glands. We shall discuss only categories 1, 2, 3, 7 and 8; the others are discussed with the corresponding organs.

### a. Glands of the lateral fields

These are large cells with dark, coarsely granulate content in the lateral
405 fields of several species of Leptosomatini. A narrow duct connects them with the body wall, and there is usually a thin bristle in their opening. They are more numerous near the female gonopore and are sometimes present only in this region.

Bastian recorded them for the first time (1865, p. 146) for Thoracostoma figuratum. Marion observed them (1870, pp. 46—47) in Th. zolae, de Man (1893) also in Th. figuratum. Jägerskiöld studied them in detail (1901) after finding them in Cylicolaimus magnus Villot and Fiacra acuticaudata Jäg. Türk (1903) found them in related species, de Man (1904, pp. 26, 37) in Thoracostoma setosum Linst. and Deontostoma antarcticum Linst., Steiner (1916, p. 616) in Leptosomatides steineri Fil. (Leptosomatum gracile Steiner nec Bast.). I have not found ducts in these cells in the closely related L. euxina Fil., so that these are possibly not glands but phagocytic cells. The cells described on the ventral line in Leptosomatum sabangense Steiner (1915, p. 229) probably have the same function. Steiner probably considered neighboring papillae as their ducts.

Marion considered these cells as adhesive. Jägerskiöld believed that they have an excretory function, which they assume instead of the lost cervical glands in these forms. Zur Strassen (1904) interpreted them as supporting cells of the nerve endings (see below) because such cells are always associated with a bristle in Solenolaimus and a nerve is connected with them. There is usually a bristle in Leptosomatini near the opening of the gland, and Jägerskiöld (pp. 67—68) admits that it is difficult to distinguish their pores from papillae. However, Zur Strassen's interpretation is probably incorrect. These cells closely resemble glands of other animals (nucleus pressed to the wall, etc.). The presence of a nerve in the gland is very common. On the other hand, the "glands" of the lateral fields of Paroncholaimus vulgaris Bast., described by Stewart (1906, p. 111, Table 7, Figure 7), are probably such supporting cells.

In addition to Solenolaimus, such glands have been recorded in Aphanolaimus (Micoletzky, 1914, p. 398). The granular cells of Plectus and Pseudobathylaimus also possibly belong to this category (see Bütschli, 1873; de Man 1886; Daday, 1905, p. 61; Brakenhof, 406 1914, p. 291; Hofmänner and Menzel, 1915). These cells are not connected directly with the outside in Cyatholaimus. However, they are apparently true dermal glands in Comesoma.

Steiner[*] described glands in connection with the ventral bristles in Draconema. I was also able to distinguish large granular cells connected with them. The question remains whether these are glands or supporting cells. As for the "glandular tissue" he described (p. 571) around the esophagus, there are some nerve and muscle cells, but glands are apparently not present. Four characteristic glands were recorded by de Man[**] around the nerve ring in Camacolaimus.

Jägerskiöld (1901) and Golovin (1902) suggested that originally an entire row of dermal cells were excretory, but that their function was taken over by a few cells. Micoletzky (1914, p. 398) agrees with this view with regard to the glands of Aphanolaimus.

### b. Cephalic glands (glandulae cephalicae)

I propose this term for the pair of lateral glands described by Stefanski (1917) for Rhabditis. They are oval cells with a narrow duct opening in line with the lateral cephalic papillae. They became stained in his experiments, so that they are probably excretory.

The glands which have been described anterior to the nerve ring – two for Leptosomatum[***] and six for Adoncholaimus[†] – are apparently not glands but accompanying cells of the cephalic nerves similar to those described by Zur Strassen (1904) for Solenolaimus and Siphonolaimus, and are not to be compared with the cephalic glands of Cheiracanthus[††] or the cervical glands of Ancylostoma,[†††] which have homologues only in the Rhabditidae.

### 407 c. Cervical gland

This gland is usually a large cell or group of cells in the anterior part of the body and has an anterior duct which opens by a pore on the ventral surface. It is very common not only in free-living nematodes but also among parasitic forms, and species without this gland should be regarded as exceptions. As its excretory function has not been proven I suggest the neutral term "cervical gland" (glandula cervicalis). This term is more suitable than "ventral gland," which is commonly used and which is not always exact. Its pore should be called the "cervical pore" (porus cervicalis) rather than "excretory" or "ventral" pore (porus excretorius s. ventralis). Cobb (1913) suggested the term "renette," which is not likely to be accepted.

---

[*] 1916, pp. 571, 572.

[**] 1889, p. 185.

[***] Bastian, 1865, pp. 144–145.

[†] De Man, 1886, p. 19.

[††] See Linstow, 1893.

[†††] See Looss, 1905.

---

The gland is always light-colored and filled with a shiny secretion like the secretion of the caudal glands. In Paroncholaimus the plasma becomes strongly stained with hematoxylin. Basophile granules have also been noted by Stewart (1906). We should distinguish: the body of the gland, the duct, the ampulla and the cuticular excretory duct.

The cervical gland is usually situated at the beginning of the midgut, rarely at the posterior part of the esophagus (Leptosomatum, Phanoderma, Enoplus). It is usually situated near the ventral line, but sometimes curves laterally and is adjacent to the lateral line (Anticoma, Paroncholaimus zernovi Fil., according to Golovin). In Par. vulgaris Bast., according to Stewart, the gland is also displaced – to the right in the male, to the left in the female. In Solenolaimus, according to Zur Strassen (1904), it is situated sometimes at the right and sometimes at the left side.

The majority of authors believe that the function of the gland is excretory. 408 Only Golovin (1902) and Rauther (1909) attempted to answer the question experimentally in free-living nematodes. Golovin fed Paroncholaimus zernovi Fil. and Anticoma pontica Fil. on sodium carminate and ammonium and indigo-sodium sulphate. The stains were deposited in the cervical gland and also in the caudal paired and true glands. If the nematodes were kept for a long time in neutral red and methylene blue, various other tissues were stained at first, then the nematodes were also stained, and the stain accumulated in the phagocytic cells (see below) and in the glands mentioned. In both cases the end parts of the glands were particularly strongly stained. On the other hand, in the experiments of Rauther (1907, 1909) neither the caudal nor the cervical glands became stained, but the stain (indigo, etc.) was deposited in the esophageal glands, so that he thought they are a true excretory apparatus, while the cervical gland is only a mucous gland, possibly for the attachment of sand grains in forms living in tubes (see below). Similar results were obtained by G. Schneider (1906[*]). When I stained the nervous system with methylene blue, the cervical and caudal glands never became stained, but the esophageal glands sometimes did. The excretion of the dyes is not important. Every gland excretes something and takes up some material from the organism. The fact that a cell takes up material from the organism, including stains introduced artificially, does not prove an excretory function. Golovin's observations should perhaps be interpreted in this way, as his results were not decisive.

The question which seemed to be solved after the experiments of Golovin thus remains open and requires further research. The facts given by 409 Golovin cannot be considered as disproved, as all different observations are more or less accidental and cannot be compared with his systematic study.[**]

---

[*] See p. 6; in one case the end of the cervical gland was stained (p. 32).

[**] I received Stefanski's study (1917) in autumn 1917. Stains were absorbed only through the openings in the cuticle, mainly through the mouth, which is reasonable as the author was dealing with Rhabditis. The stains accumulated first in the cuticula (Dorylaimus) and the phagocytic cells, and were excreted by the esophagus, the paired caudal and the special cephalic glands (see pp. 36, 41).

We shall now discuss the form of the cervical gland in free-living nematodes. We must distinguish: 1) glands of the piriform type with a slender duct and a more or less distinctly thickened body; 2) glands of the tubular type with a wide duct which gradually become thicker posteriorly. Both types were observed by Eberth (1863) and Bastian (1865), but only Golovin (1902, p. 87) distinguished them clearly.

Glands with a wide duct are characteristic for almost all Enoplidae while the second type is common among species of Chromadoridae and Monhysteridae. The glands of Anguillulidae belong to a special type (see below). In the Chromadoridae, the body of the gland is usually fusiform and tapers at both ends. This is rare in Monhysteridae, but it is present, for example, in Penzancia euxina Fil.

The gland is very large in Pelagonema obtusicauda Fil. (see p. 84, Part I), Paroncholaimus papilliferus Fil. (1916, p. 111) and Anticoma arctica Steiner (1916, p. 657). The lumen of the intestine in these forms is very narrow opposite the gland because of its pressure.

There is an interesting shape of the cervical gland in Enoplus communis Bast., i. e., it is H-shaped (de Man, 1886). A similar gland is present in Anticoma acuminata Eb. according to Cobb (1890).

A second, smaller gland has been described behind the main gland in Chromadoridae*; it is similar in structure, so that the cervical gland apparently consists of two cells. Steiner recently confirmed this (1916, pp. 533, 543, 571, 607). He described even three cells in one species – 2 small cells anteriorly and posteriorly to a large cell. I can confirm this observation, but the relationship of these cells, and whether the second cell is a gland, is not known.

The Desmoscolecidae also seem to have two cervical glands (Cobb, 1912, Tricoma; Steiner, 1916, Desm. rudolphi, p. 327). Shchepot'ev described two large glands which sometimes have posterior processes and a characteristic duct which is directed not anteriorly, as is usual, but
410 posteriorly. Each gland contains several nuclei and chromophilic bodies. This requires confirmation.

Cobb (1915) described 3 glands near the esophagus in Tylenchus similis. He connects them with the esophagus, but they may also be part of the excretory apparatus.

The position of the cervical pore** varies markedly; it is normally situated anterior or posterior to the nerve ring, i. e., opposite the middle of the esophagus, but it may also be markedly displaced anteriorly.*** The gland forms a widening towards the end of the duct – the ampulla, which is not always clearly developed (cf. Table 1, Figure 5a).

Thus, in Anticoma pontica Fil. the pore is situated almost opposite the lateral organs (Table 2, Figure 6a, por. excr.), but in other species of Anticoma it may have a normal position. It is markedly displaced anteriorly in Symplocostoma (Table 5, Figure 32b) and Phanoderma (Table 1, Figure 52). It is situated more posteriorly in Oncholaimini and Leptosomatum. The extreme case is Diplopeltis (Table 11, Figure 80, p. ex.). Here it is situated in front of the lateral organ.

The gland is not directly connected with the pore by its duct, but by a more or less long chitinized tube. This tube probably develops inside a special cell of the epidermis. It is particularly long in Diplopeltis (Table 11, Figure 80, g. ex. end of plasmatic part of gland).

The cervical gland of Anguillulidae differs sharply from the simple glands of true free-living nematodes. It resembles that of the majority of parasites. A short chitinized canal passes from the gland to the cervical pore. There is a duct inside the gland which is sometimes also chitinized and greatly convoluted.* The gland has two processes to the lateral lines, which are forked into anterior and posterior branches which extend in the
411 lateral fields almost to the end of the body.** The loss of the anterior branches or of one canal is a modification.

In addition, large glands, independent of the lateral canals and situated next to the cervical pore, have been described.*** These glands probably correspond to the "cervical" glands of Strongylidae, which are also situated near the cervical pore.† The term "subcervical glands" (glandulae subcervicales) may be suggested to distinguish them from the true cervical gland (lateral canals).

Marion's observations (1870) on two vessels along the entire length of the body, which open at the posterior end, cannot be accepted. Bütschli (1874) already considered them as erroneous. He apparently considered the cervical gland, the caudal glands and the lateral fields as one structure.

There are several forms in which the cervical gland is apparently absent, such as Fiacra and Cylicolaimus, studied by Jägerskiöld (1901) and Türk (1903). Thoracostoma has also been described as having no cervical gland; Steiner†† thought they are absent in Leptosomatides steineri Fil. (Leptosomatum gracile St. nec. Bast.). I found (1916) a cervical pore in Deontostoma papillatum Linst., but the gland itself is apparently absent; de Man (1893) recorded the same for Thor. figuratum Bast. This suggests that the gland may disappear

---

* De Man, 1888, p. 43 – Hypodontolaimus; Cobb, 1893, p. 397. He thought they were sympathetic nerve cells in Chromadora minor.

** Steiner (1915) recorded two ventral pores in Chromadora macrolaimoides, but it proved impossible to establish their relationship (p. 236).

*** Cobb (1913, 1914) described a marked posterior position of the cervical pore in Tylenchulus semipenetrans, where it is closer to the anus than to the end of the esophagus.

* The genus Plectus Bastian obtained its name because of this character. See also de Man, 1884, p. 105; 1907, p. 20.

** Bastian (1865, p. 118; 1866, p. 599) considered some other structures – lateral ridges – as vessels, as he described their opening on the lateral organs (Bütschli, 1873). Later authors observed true vessels: Schneider (1866, pp. 164, 218); Pérez (1866, p. 186): Ce tube légèrement flexueux parait occuper à peu près toute la longueur du corps.... il flotte librement dans la cavité viscerale"; Bütschli (1873, pp. 15, 34, 79, 86, 108, 112, 117); the canals are sometimes very distinct; 1876, p. 372; Ganin, (1877, p. 169); Oerley (1886, p. 15); Strubell (1888, p. 17) recorded a left canal in Heterodera; Hallez (1900, p. 604); Maupas (1901, pp. 481, 508, 524, 542, 558, 565, 574, 580); Golovin (1902, p. 73); de Man (1909, pp. 362, 385); Fuchs (1915, p. 156).

*** Bütschli, 1873, l. c.; 1874, p. 14; de Man, 1884, p. 105; Cobb, 1893, p. 812; Maupas, Golovin, Fuchs, l. c.

† In detail in Looss (1905, pp. 39, 105); also Augstein (1894, p. 296).

†† 1916, p. 615.

412 with age. Thus, according to Stewart,[*] there is no cervical gland in adult females of Paronch. vulgaris Bast. The disappearance of the cervical gland in this group should apparently be considered as secondary. Its function may have been taken over by other dermal glands described above (Jägerskiöld, 1901).

It is also thought to be absent in: Trefusia de Man, 1893, p. 86; Enoplolaimus ibid., p. 119 (I was also unable to find them; Savel'ev (1912) does not mention them); Dolicholaimus de Man, 1888, p. 32; Dorylaimus de Man, 1884, p. 155; Hofmänner, 1913, p. 600; Bütschli, 1874, p. 19 (however, it should be noted that de Man draws a similar structure in one species (p. 181, Table 30, Figure 126c; cf. also Cobb, 1893, p. 809)); Trilobus Hofm., l. c.; Tripyloides de Man, 1886; Tripyla Hofm., l. c., de Man, 1884, p. 45; Desmodora de Man, 1888, p. 9; Steiner, 1916, p. 545 ff.; Spira de Man, 1890, p. 174; Monhystera and Theristus de Man, 1888, p. 8 (in another work he recognized it only in one species, Monh. ambigua Bast.); Aphanolaimus, Micoletzky, 1914, p. 398. There is also a strong development of other dermal glands in the last genus. However, these records refer only to the species which the authors examined. The glands are often present in other species of the same genera or in related genera.

The structures present in Anguillulidae are also typical for parasitic nematodes. The "lateral canals" of nematodes have been known since Cloquet (1824). Some parts sometimes do not attain full development: the anterior canals may be absent or the posterior canal may be present only on one side. These canals usually consist of a single cell, with a nucleus anteriorly and very long processes posteriorly. Two cells form only the excretory duct of Ascaris (Goldschmidt, 1906). It develops from a single cell. Golovin[**] observed in Ascaris and Cobb (1891) in Oxyuris that this cell is less branched in young individuals.

A special "excretory tissue" is apparently differentiated in parasites in connection with the development of a canal in the lateral fields, while the
413 canals act only as efferent ducts (Jägerskiöld, 1894; Goldschmidt, 1906). However, Martini[***] stated that there are no good reasons to consider these differentiated parts of the cells of the lateral fields as a special "tissue." Cobb[†] found uric acid in this tissue in larger quantity than in other parts of the body of Ascaris.

However, there is also a true cervical gland instead of the lateral canals in parasites, for example, in Angiostomum nigrovenosum,[††] a modified form in Ascaris spiculigera and A. osculata. There are even forms with two such glands.[†††] Many species of Mermithidae also have a true cervical gland, sometimes even two.[‡]

---

[*] 1906, p. 110.

[**] 1902, p. 21.

[***] 1909, p. 602.

[†] 1898, p. 37 ff.

[††] Golovin, 1902, p. 66.

[†††] Heterakis papillosa according to Golovin (1902, p. 61), Sclerostomum equinum according to Bastian (1866, p. 585).

[‡] Pseudomermis zykovi, de Man, 1903, in Zykow, p. 549; Mermis brevis, Hagmeier, 1912, p. 548. The gland is easily stained with vital stains in this form.

---

Jägerskiöld (1894, 1901), Nasonov (1899), Golovin (1902), Stewart (1906) and Rauther (1909) agree that the unicellularity and homology of the "lateral canals" of parasitic nematodes with the cervical gland must be recognized.[*] The same view is found in Bastian,[**] and was formulated more clearly by Bütschli.[***] However, none of the authors considered these formations as simple cells.

We thus consider the cervical gland and the lateral canals as simple cuticular glands[†] and we distinguish, with Golovin, the following categories:

414 1) The true cervical gland of free-living nematodes and a few parasites, without canals inside the body.

2) A massive gland with branched canals inside the body and a large nucleus (Ascaris spiculigera, A. osculata and others).

3) Glands with unbranched intracellular canals – true lateral canals.

a) with anterior and posterior processes (Strongylidae, Anguillulidae);

b) with only posterior processes (typical Ascaris – but Goldschmidt (1906) found the rudiment of an anterior canal in A. lumbricoides);

c) unilateral glands (Asc. ostroumovi Golovin, Heterodera).

It is difficult to use the cervical gland in systematics, as it hardly has been studied in most free-living forms. However, its markedly different form in Anguillulidae is one of the best characters which distinguish this family from true free-living nematodes and relates them to the parasites, particularly to the Strongylidae. The absence of a cervical gland is not an important character and apparently developed independently in several groups, sometimes in connection with the great development of other dermal glands.

### d. Paired caudal glands (glandulae praecaudales)

These glands are present in many species of Anguillulidae and open near the base or in the middle of the tail. They have hardly been studied. Bastian found them in Rhabditis marina (1865, p. 129); de Man in Cephalobus bütschlii (1886, Table 3, Figure 8); Maupas (1901) in various species of Rhabditis, Diplogaster and Cephalobus; Cobb (1914) in Dolichodorus; Golovin in Rh. kovalevskii (1902, p. 72); in his experiments they excreted carmine and he therefore considered them as excretory. Stefanski (1917) obtained similar results with Rh. brevispina. These cells are probably common in species of Rhabditis and its close relatives.

---

[*] Nasonov (1898, p. 15) later rejected his own view (1897) on the multicellularity of the lateral canals of Oxyuris.

[**] 1866, pp. 589–595.

[***] 1874, p. 14.

[†] This view was stated most clearly by Jägerskiöld (1901, p. 77): "Ich finde... dass wir in dieser grossen, beinahe direkt oder durch einen nicht zu langen Gang, dessen Wände alle Kennzeichen der Aussenhaut tragen, an der Haut ausmündenden Zelle in der That eine wahre Hautdrüse vor uns haben."

e. Caudal glands (glandulae caudales)

These glands, 3 in number, are situated in the posterior part of the body and open at the end of the tail in a common caudal pore (porus caudalis). 415 One gland is situated on the ventral side, two on the dorsal side.* The glands resemble the cervical gland, their plasma is homogeneous,** strongly refracts light and seems to be mucous; it also stains intensely with hematoxylin (Jägerskiöld, 1901).

The function of these glands is not entirely clear. It has been established that the secretion of these glands congeals on contact with water, and the nematode may thus become firmly attached to an object.*** This can easily be observed. A nematode is often attached by the posterior end, while its anterior end waves about but does not move from the spot. This is important for collection: even a strong jet of water may not dislodge them from stones or algae.

Bütschli (1874, p. 28) records that Monhystera socialis placed in a vessel wove an entire net between algae and the walls of the vessel. Bastian (1865, p. 81) recorded several species of Chromadora living in sticky tubes in mud. If these were not tubes of some other animal, they evidently are secretions of glands. Cobb (1913) suggests, without any evidence, that Draconema also lives in tubes. This is apparently erroneous. Cf. also Steiner (1916, p. 564).

416 Another possible function of these glands is excretion, as suggested by Bütschli (1874), but without any evidence. Golovin also comes to this conclusion on the basis of the experiments described above. However, these experiments have not been confirmed and the excretory function of these glands can therefore not be considered as established.

Two types of these glands should be distinguished: tubular and piriform.

Glands of the tubular type are present in various Enoplidae. They usually extend far anteriorly beyond the tail. This is especially marked in large forms with a short tail – Thoracostoma, Deontostoma, Fiacra, Leptosomatum and Paroncholaimus, as recorded by Eberth (1863) and Bastian (1865).

Glands of the piriform type are more common and are present in Enoplidae and other families. These glands are rarely situated in front of the anus (thin ducts curve around the anus in Enoplus), but usually inside the tail. The glands are never as well developed in freshwater nematodes as in marine nematodes. A special reservoir has sometimes been described – a widening of the duct in front of the pore (see Table 7, Figure 44c, d; also de Man, 1904; Filip'ev, 1916, pp. 68, 94; and this work, p. 27, Part I).

Marine forms have caudal glands almost without exception, while there are many freshwater forms without caudal glands, e. g., the majority of freshwater Dorylaimini. Only Jägerskiöld described them for females of Dor. crassoides (1908). Other forms without caudal glands are also the majority of Anguillulidae. It has been stated that they are absent in the marine genera Syringolaimus (de Man, 1888) and Acoma borealis (Steiner, 1916, p. 653). The latter case seems doubtful. See also Steiner, 1916, pp. 529, 593.

Some authors connect the absence of caudal glands with the mode of life of the nematodes. Thus, mud dwellers, which do not require attachment, like Dorylaimus and Ironus, and the majority of terrestrial forms, have no caudal glands, while all species living in running water, among plants or in the surf have caudal glands. The attachment is particularly strong in various species of Monhystera.*

The shape of the end of the tail has already been described (p. 3). It must only be remembered that the pore is sometimes not situated on the 417 extreme tip, for example, in Spilophorella (Table 8, Figure 54c) and Thalossoalaimus.** Characteristic bristles are sometimes situated around the pore.

We shall now describe the internal adaptations associated with the pore. The caudal cone belongs here (conus caudalis), a structure characteristic for the majority of Enoplidae and common only in this family (see Table 1, Figure 2c–a; Table 3, Figure 18g–b). This is a blunt cone, usually pressed into the pore and striated longitudinally, to which all three caudal glands are attached. Characteristic folds of cuticle are frequently present around it, which are sometimes chitinized, giving it a more stable position (Table 3, Figure 18 g–a). On the other hand, it sometimes plugs the pore loosely and a passage remains (Table 1, Figure 2c). Finally, particularly if the cuticle at the end of the tail is not thickened, it apparently cannot plug the pore and is situated separately.

This is evidently an adaptation which regulates the exit of secretion from the glands. Golovin considered it as a structure of the cuticle, at the sides of which the pores of the glands are situated. Cobb*** described the cone as a plug, which is forced into the pore by internal pressure and normally closes it tightly. However, if necessary, it may be drawn posteriorly and dorsally by muscles and thus opens the passage for the secretion of the glands. The existence of muscles is doubtful in this explanation. Both explanations consider the cone as a solid structure and assume that the secretion passes at the sides of the cone. Figure 2c, Table 1, seems to support this, as an opening from below is present from the gland directly into the pore, past the cone. The cone is not always tightly situated in the pore in Paroncholaimus zernovi Fil. (Table 3, Figure 18g), as on 418 this drawing, but sometimes projects more posteriorly. Against this explanation we may mention that the glands are always closely attached to the cone. It is sometimes possible to see that the cone is withdrawn from

---

* Such an arrangement has been recorded by Golovin (1902, p. 70) and Türk (1903, p. 307). There are 4 glands in Linhomoeus elongatus, according to Bastian (1865, p. 155) and Steiner (1916, p. 593); the anterior gland is possibly not related to the caudal glands; I can confirm this observation. The same is present, according to Steiner (1916, p. 529), in "Spilophora loricata. Shchepot'ev (1908, pp. 49, 61) found only one caudal gland in Desmoscolex and Rhabdogaster, but this is probably an oversight caused by poor preparations.

** The partitions inside the glands described in Leptosomatides steineri Fil. (Leptosomatum gracile Steiner nec Bast.) are probably due to fixation.

*** Cobb therefore suggests the term 'spinneret' for these glands, and many authors (Schneider, 1866; Bütschli, 1873) call them spinning glands (Spinndrüsen). Carter (1859) even proposed the generic name Urolabes for all free-living nematodes because of this character.

* See Bastian, 1865, p. 553; Cobb, 1898, p. 40; Micoletzky, 1914, pp. 352, 369, 1914a, p. 7.

** De Man, 1907, p. 34.

*** Journ. Parasitol. 2, p. 95: "A needlelike plug, retracting by muscles."

the pore, but the glands remain attached to it. On the other hand, Table 3, Figure 18g, clearly shows that the cone is longitudinally striated and penetrated by pores. I therefore suggest that the secretion of the glands is discharged not together with the cone but through the pores of the cone. This would then be a mechanism similar to the spinning glands of arthropods.

Another adaptation is present in Chromadoridae. In Euchromadora and related genera, e. g., in Spilophora loricata Steiner (1916, p. 529), there are cuticular processes in the terminal tube of the tail forming a compound valve which possibly also regulates the exit of secretion. A cone is never present.

Leydig (1854) discovered these glands. He and Eberth (1863), who observed them later, introduced the term "caudal glands" (Schwanzdrüsen) and observed the discharge of the secretion which serves for attachment.

Bastian (1865) did not consider these structures as glands, but calls them "piriform sacs" or "sucker tubes," whose contraction causes attachment (suction) of the nematode to the substrate. The caudal pore was therefore also called "caudal sucker." In addition to Bastian, only Marion stated an opinion opposed to the view of the adhesive function of these glands.* He erroneously considered them as part of his "tubes excréteurs."

Among parasites, an organ resembling caudal glands has been described only in Paramermis (Kohn). They are apparently never present in endoparasites.

Rauther (1909) suggested that the "pedal" glands of Gastrotricha and Rotatoria are possibly homologous with the caudal glands.

The caudal glands often vary markedly in related forms. We therefore
419 do not consider them as important in systematics. However, some large groups are characterized by different form and structure of these glands.

## B. Cells of the Body Cavity

### a. Phagocytic cells

These cells are round and easily recognized by their granular content, which consists of glistening globules. Golovin described them in detail. He studied the following marine forms: Paroncholaimus zernovi Fil., Eurystomina assimilis de Man, Oncholaimus fuscus Bast., Symplocostoma pontica Fil., Anticoma pontica Fil. and Cyatholaimus demani Fil.

If the nematodes are kept in a solution of stains (sodium carminate, methylene blue, neutral red), these cells become stained rapidly. The globules in the plasma are particularly intensely stained and were therefore called "chromophils." When the staining begins, the cells firmly retain the color, which becomes crystallized in the plasma. The anterior cells are stained first, the posterior cells later. The reaction of the cells is acid, litmus stains them red. Golovin once proved their phagocytic properties directly – the cells in a dissected worm took up India ink directly from the sea water. Vital staining of these cells was first carried out by Shimkevich (1898, 1899), who also recognized them as phagocytic. These data refer to Paroncholaimus zernovi Fil I have confirmed them through my observations. The cells, about 220 in number, are dispersed through the entire body and there is no regular pattern of distribution. These cells are much more numerous in the related northern species Par. vulgaris Bast.

420 There is a similar structure and distribution in other related forms as well; the number of cells in Oncholaimus (?) fuscus Bast. is 150, in Eurystomina assimilis de Man 70. In Symplocostoma ponticum Fil., Golovin recorded a constant number of cells (14) in the esophageal part of the body. The same structure and distribution is present in other species of Oncholaimini (Metoncholaimus demani Z. Str.). They are particularly well developed in Pelagonema obtusicauda Fil. and Paroncholaimus papilliferus Fil. (1916). In Oxystomina filiformis Fil. these cells are very large compared with the width of the worm, sometimes displacing the esophagus to the side (Table 2, Figure 9a). Bütschli (1874, p. 34) and de Man (1907, p. 44) recorded them also in Ox. elongatum Bt. at the lateral lines. We find a similar arrangement in most species of Chromadoridae; Chr. sabulicola Fil. has an especially large number of phagocytic cells. The "cellules à grandes granulations brunes" of Chromadoropsis vivipara de Man (1907, p. 68) probably belong here. These cells are present in Leptosomatides only at the ventral line ("Drüsenzellen" of Steiner) and in Linhomoeus at the lateral fields (Bütschli, 1874, p. 31, L. hirsutus; de Man, 1889, p. 210, L. elongatus Bast.).

Another type of arrangement of these cells is characteristic for the genus Cyatholaimus. They are very numerous and form 8 regular rows, 2 rows near each lateral and median line. The cells also have a granular content, are easily recognized and give a characteristic appearance to the living worm. They have been illustrated in this form by Bastian,* Bütschli** and de Man.*** Similar cells are apparently present in Plectus granulosus Bast. and related species, and also in Pseudobathylaimus.

There is a third type, e. g., in Axonolaimus setosus Fil. There are only two large cells, one behind the cervical gland and the other near the beginning of the uterus. In Conolaimus angustilaimus Fil. there is a third cell between them. The cells situated near the cervical glands in Chromadoridae are possibly such cells.

In Rhabditis and Anguillula, also studied by Golovin, phagocytic cells generally of the first type are fairly numerous and dispersed in
421 different parts of the body. It is interesting that the fluid of the body cavity of these forms has great regenerative properties, as in parasitic nematodes, in contrast to the other free-living nematodes. The cells stain only with a combination of Wasserblau and toluylene red, which was first used by Golovin.††

---

* 1870–2, p. 3.

* 1865, p. 163: "Subcutaneous gland-cells numerous, rounded, granular, giving the animal a peculiar maculated appearance."

** 1874, p. 48.

*** 1889, p. 102.

† See p. 252, Part I.

†† The "numerous floating glands or blood-cells in the cavity of the body,' described by Bastian (1865, p. 129), probably belong here.

These cells are easily recognized and have therefore been known for a long time, but their phagocytic properties were recognized for the first time by Shimkevich (1898, 1899). Bastian[*] considered them as sarcoplasmatic parts of the muscle cells. Jägerskiöld (1901) confused them with nerve cells, distinguishing them only by their granular contents. Stewart[**] considered them to be mesenchymatous elements.

Golovin compared these cells with the large phagocytic organs of parasitic nematodes.[***] However, these are never so numerous, usually only 3–4 in number. They are usually situated in the lateral lines and are also unicellular. The processes with which they are covered are part of the body of the cell. The chromophilic inclusions in these processes resemble those in the phagocytic cells of free-living nematodes.[†]

There is a question about the mesodermal or ectodermal origin of these cells. There are more data supporting the view that they are ectodermal. If we compare these cells with the glands of Thoracostoma, we find that they are very similar. Türk also observed the formation of granules in the cells of the lateral fields. They are apparently in direct connection with the epidermis in Plectus. They should therefore be considered as
422 modified cells of the epidermis and not as masodermal cells. This contradicts the view of Shimkevich, who considered them to be rudiments of the peritoneal epithelium.

### b. Fat cells

I have not observed these formations. De Man (1886) described them in Adoncholaimus fuscus Bast. and Türk (1903) in Fiacra strasseni as branched cells around the midgut filled with fat droplets and not connected with the epidermis. According to Türk, these cells are interlaced and form a whole network around the intestine. Rauther (1907, 1909) observed that methylene blue stains them in Enoplus, Cylicolaimus and Thoracostoma, like phagocytic cells. Shimkevich and Golovin considered them to be homologous with the phagocytic cells of other nematodes; they did not observe them. There is a similar development of phagocytic cells in Strongylus paradoxus, according to Nasonov (1899, p. 15). The question is whether they are the same as the "strandlike organs" which Looss[††] found in Ancylostoma. These formations are possibly part of the nervous system.

---

[*] 1866, p. 582.

[**] 1906, p. 118.

[***] "Büschelförmige Organe." See also Jägerskiöld, 1894, 1898; Nasonov, 1897–1899.

[†] Nasonov originally considered these formations to be multicellular and considered their processes as phagocytes.

[††] 1905, p. 68.

### c. Body cavity and connective tissue

The body cavity (schizocoel) is usually filled to such an extent with phagocytes and nerve cells and processes of the muscle cells that it can hardly be called a cavity.

Thus, Jägerskiöld[*] did not find it at all in Cylicolaimus and only in males of Fiacra. Türk[**] did not find it in related Mediterranean forms; de Man[***] found only narrow slits in Thoracostoma setosum Linst. and only where there were no nerve cells; Stewart[†] also noted its almost complete absence in Paronch. vulgaris Bast.

A homogeneous, intensely staining layer is sometimes described in the body cavity.[††] In Jägerskiöld's view, this is coagulated fluid of the body. The nuclei which Linstow and Stewart found here probably belong to cells which are not directly connected with this substance. Jägerskiöld and
423 Stewart also described fibrils which surround the esophagus and are attached to its wall and to the epidermis. These are probably not connective-tissue fibers as these authors believed, but processes of the muscle cells (see below).

Characteristic crystalloids are sometimes observed in the body cavity around the intestine. I observed these formations in connection with degeneration of the intestine in males of Leptosomatum bacillatum Eb. (see p. 30, Part I). Similar bodies are also present in Leptosomatides euxina Fil. between the end of the esophagus and the genitalia. This is probably fairly common.[†††]

True connective-tissue formations have been described as "isolation tissue" in Ascaris by Goldschmidt (1906). He found a few large cells usually near the nerve ring. A whole system of plates which fill the spaces between the visceral organs belong to them. They have usually been considered as coagulated body fluid (Looss, 1905, p. 67). Thus, the wide "schizocoel" of Ascaris is in fact intracellular lacunae, at least in the anterior part of the body. The stellate cells in the body cavity of Oxyuris, described by Galeb,[‡] are probably the same.

## C. Nervous System

The nervous sytem of nematodes has hardly been studied (except that of
424 Ascaris), especially that of the free-living forms. The authors usually

---

[*] 1901, pp. 11, 42.

[**] 1903, p. 306.

[***] 1904, p. 31.

[†] 1906. p. 113.

[††] "Plasmacylinder, von dem dorsal und ventral zwei Leisten ausstrahlen"... (Linstow 1901) "a dull-pink hyaline ground-work.... with very fine, more intense pink granulation" (Stewart 1906, p. 114); "... eine ganz homogene, bisweilen sich stark färbende Schicht" (Jägerskiöld 1901, p. 14).

[†††] Bütschli (1874, pp. 10, 42) recorded them in Thoracostoma figuratum Bast., Stefanski (1914, p. 48) in Ironus ignavus Bast. The "globules graisseux" in the posterior part of the body in Thalassoalaimus are similar formations (de Man, 1893, p. 82). Fedchenko (1874, p. 8) observed them in Dorylaimus and considered them as blood cells.

[‡] 1878, p. 310 – tissu spongieux.

give no information, except on the position of the nerve ring. Even de Man (1886) in his great monograph does not give any data I intend to study the nervous system in detail and shall therefore delineate the problem only briefly.

The nervous system of nematodes is at a very low stage of development — it is always situated in the epidermis, enclosed in the plasma of its cells.* Only the motor nerves, which are part of the central nervous system, are isolated from the plasma. However, if the cells themselves are not enclosed by special "supporting" and "companion" cells,** their nerves (including the nerve ring) are enclosed. These were discovered by Goldschmidt in Ascaris and are probably modified epidermal cells, so that here too there is a strong connection with the epidermis.

The central, best-developed part of the nervous system is the nerve ring (commissura cephalica of Looss). Its width depends on the width of the esophagus. If it is narrow the ring is wide (Leptosomatini, Symplocostoma, Enchelidium); if it is wide the ring is narrow (Enoplus, Cyatholaimini, Sphaerolaimus). The ring usually surrounds the esophagus in the middle, but it is sometimes markedly displaced anteriorly (Leptosomatini, etc.) If a bulb is present, it is never tightly pressed to it. Eberth*** and Bastian† denied the presence of a nervous system in free-living nematodes and considered the nerve ring as a glandular structure. Marion recognized the nerve ring in nematodes with a smooth cuticle, but he considered it as a different formation in annulated forms, perhaps as the sphincter at the beginning of the midgut.

425 The cells of the central nervous system lie around the nerve ring. There are three main types of these cells:

1) Absence of any structure resembling ganglia; the nerve cells are arranged in a simple layer around the esophagus. This is the type in the majority of free-living forms: Paroncholaimus, see my note (1912), Stewart (1906); Leptosomatini, Jägerskiöld (1901), Türk (1903††).

2) Weakly differentiated ganglia which are in fact only groups of cells. This is the type in Ascaris (Goldschmidt, 1903, 1908, 1909, 1910; Deineka, 1908, 1912), Mermis (Rauther, 1906, Hagmeier, 1912), Ancylostoma (Looss, 1905) and the majority of other parasitic forms.†††

3) Well-differentiated ganglia firmly connected by special "companion" and "supporting" cells. This is the structure in Siphonolaimus and Solenolaimus (Anthraconema Zur Strassen, 1904), but it has not yet been found in other groups.

Six nerves pass anteriorly from the ring to the head organs, always adjacent to the esophagus and not to the epidermis. The internal lining of the esophagus is apparently also of epidermal origin, so that there is no contradiction to the rule concerning the close connection between nerves and epidermis. These nerves innervate the cephalic and labial papillae or bristles and the lateral organs. A strong bundle of muscles with numerous fibers always reaches the lateral organs. The companion cells of these nerves are particularly well developed, e. g., in Solenolaimus and Siphonolaimus, according to Zur Strassen. Similar cells are
426 apparently the 6 "glands" of Adoncholaimus, described by de Man,* and of Leptosomatum and the two lateral "glands" of Bastian** and de Man.***

The posterior nerves in Paroncholaimus extend as follows: ventrally as two roots (radices ventrales profundi) (see Figure A), a large ventral nerve (n. ventralis) extends along the ventral line to the anus. The vulva is passed at one side, or in any case fewer fibers pass at the other side, possibly an indication of its originally asymmetrical position.† The lateral branches of its roots give rise to the subventral nerves (n. subventrales), passing in the corresponding lines.

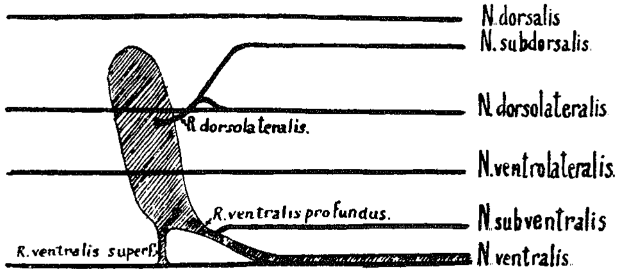


FIGURE A. Relationships of the trunk nerves to the nerve ring in Paroncholaimus zernovi Fil.

The other two roots — the dorsolateral roots (r. dorsolaterales) — each branch into a dorsolateral nerve (n. dorsolaterales in the upper part of the lateral field) and a subdorsal nerve (n. subdorsales in the corresponding field).

Some of the fibers of the ventral nerve do not enter the above roots, but pass to the epidermis anteriorly and have their own third pair of roots (r. ventrales superficiales) from the nerve ring to the ventral line. Some of the fibers also reach these roots and pass to the anterior part of the
427 body. Similar passing fibers are present in the dorsolateral nerve, while the subventral and subdorsal nerves do not have such fibers. Finally, the dorsal nerve (n. dorsalis) and the ventrolateral nerves (n. ventrolaterales) consist only of such fibers and have no direct connection with the ring.

---

* See Stewart, 1906, p. 105; Rauther, 1909, p. 535.

** "Stütz- und Geleitzellen" — Goldschmidt, 1903; 1908; also Zur Strassen, 1904 and Filip'ev, 1912. But Deineka (1908, 1912) considered them as specialized nerve cells in Ascaris.

*** 1863, p. 10.

† 1865, pp. 83, 92; 1866, p. 575.

†† Some authors (Bütschli, 1873, p. 23; 1874, p. 7) do not suspect or even deny the nervous nature of these cells. Thus Jägerskiöld (1901, p. 12) speaks only of an eigentümliches Gewebe," distinguishing in it small and large cells.

††† A similar arrangement has been described by Steiner in "Dipeltis" barentsi (1916, p. 629).

---

* 1886, p. 43, Table 6, Figures 1, 2.

** 1865, p. 145.

*** 1893, p. 106.

† Looss, 1905, p. 138.

The ventral nerve is the largest; there are many cells in the nerve or directly adjacent to it, while the other nerves consist only of fibers.

This arrangement was known in general by Bütschli (1874), Türk (1903) and Stewart (1906), but most details were given for the first time in my note (1912).

The development of the peripheral nervous system corresponds to the development of the bristles. They are particularly numerous in Par. zernovi Fil. Each bristle is innervated by several (up to 5) nerve cells. In my note, I distinguished several types of sensory cells belonging to various bristles. The large accumulation of these cells in the posterior part of the lateral fields in the male induced some authors to speak of anal (Stewart, Jägerskiöld, Voltzenlogel) or bursal (Bütschli, Deineka) ganglia. A special sympathetic nervous system innervates the esophagus (see below).

The motor fibers, which I first described, are situated inside the musculature, at the sides of the body. This observation has so far remained isolated. The "strandlike organs" of Looss[*] are also possibly motor nerves, and not homologues with phagocytic cells, as he thought.

The peripheral nervous sytem of parasitic nematodes, even of such large forms as Ascaris, is much more weakly developed and of simpler structure than in the large free-living forms like Paroncholaimus or Leptosomatini. It is probably even less developed in small reduced forms like Monhystera or Anguillulidae.

428 The central nervous system of parasites also generally follows the above scheme; it differs, however, in details – independent dorsal roots, etc.

It is premature to use the nervous system for systematics, though this may become possible in the future.

Comparison of the nervous system of nematodes with that of other groups of worms is difficult. In any case, it has nothing in common with other "Nemathelminthes" (Gordiacea, Acanthocephali, Brandes, 1899). The only possible points of comparison are in some Platodes – Trematodes (Bütschli, 1895) and Rhabdocoela (Martini, 1913).

## D. Sense Organs

### a. Tango receptors and chemoreceptors

Tango receptors are the bristles and papillae described on pp. 14–23. Their direct connection with nerves, which was observed by almost all authors who studied them in detail, makes their sensory function certain.

The lateral organs are considered as chemoreceptors (p. 23); the large fascicle of nerve fibers connected with them suggests a more complex function. Cobb also considered the labial papillae (see p. 20) as possible chemoreceptors. They also receive fascicles of nerve fibers, which supports this view.

---

[*] 1905, p. 68.

### b. Ocelli

Eyes developed independently in several groups of nematodes. They are always situated in the preneural part of the body, at the sides or on the 429 dorsal surface of the esophagus. Their organization certainly indicates that they are photoreceptors, but they cannot distinguish forms (Cobb). Only Bastian (1865, 1866), did not consider them organs of vision, because of their constant connection with the esophagus, and called them "pseudocelli." There are two main types: 1) eyes closely associated with the esophagus; 2) independent formations near the esophagus.

The first type is widespread among Enoplidae, and all eyes in this family are of this type. The pigment of the eyes, as noted by Bütschli,[*] is always of the same color (red, brown, black[**]) as the pigment of the other parts of the esophagus[***] and does not dissolve in alcohol. The esophagus is sometimes transparent, so that the only pigment present is located in the eyes.

In more complex cases, they consist of a pigment cup with a transparent lens. Such cups are always situated at the sides of the esophagus and project laterally, e. g., the eyes of Leptosomatum (Table 1, Figures 1a, b, 2a), Leptosomatides (Table 1, Figure 3c), Deontostoma, many species of Thoracostoma, Eurystoma (Table 5, Figure 29a[†]) and "Enchelidium" polare Steiner.[††]

The eyes are sometimes situated at different levels, e. g., in Leptosomatides. Their position may vary within the same species. The pigment cup may be irregular (as in all the Black Sea species described) 430 or it may have completely smooth outlines, e. g., in Leptosomatum behringicum Fil.[†††]

Fully differentiated eyes, but without a lens, are found in Phanoderma (Table 1, Figures 4a, 5a, their rectangular shape is characteristic), possibly also in Eurystoma.

The eyes of the following group, to which Thoracostoma caudatum Schn.[‡] belongs, and species with eyes of the genus Enoplus (Table 2, Figure 10a) are less differentiated. The pigment stripes of the esophagus are greatly developed in these forms and form several lateral processes. The anterior processes are more constant, contain a denser pigment and project from the surface of the esophagus: these are also eyes.

There is a characteristic structure of the eyes in Enchelidium (Table 4, Figure 28a, b). A narrow part of the esophagus is adjacent to the oral aperture and then widens. The entire widening is occupied by

---

[*] 1874, p. 13.

[**] Blue eyes have been described only in "Enoplus" coeruleus Eberth (1863, p. 40); the systematic status of this form is not clear, and it possibly belongs to another family. Their color is "violet intense" in Thoracostoma echinodon Marion, according to de Man (1878, p. 104).

[***] This caused Savel'ev to describe a second, less-developed pair of eye spots in Leptosomatum tetrophthalmum; see also Steiner, 1916, p. 612.

[†] Many authors deny the presence of a lens in Eurystoma. It is possibly absent in some species (de Man, 1878, p. 95; 1888, p. 26).

[††] 1916, p. 597.

[†††] 1916, p. 71.

[‡] Cf. Filip'ev, 1916, p. 91, Table 4, Figures 7a, b and de Man, 1888.

an unbroken layer of pigment. Two cuticular bodies which refract light strongly, lateral to the pigment patch, function as lenses.[*] Such an accumulation of pigment in the anterior swelling of the esophagus has been described in Syringolaimus, but it is not constant.[**] Such cuticular bodies are also situated behind the buccal cavity in Symplocostoma (Table 5, c. cut, Figures 30a, 32b, 34a). However, they do not act as lenses, as the pigment spot is situated behind them (cf. Figures 32b, 33a); in other species the pigment spot is situated even further posteriorly. These bodies are possibly homologues of the small denticles of several species of Dorylaimini.

There are still less-differentiated pigment spots in Oncholaimus dujardini de Man and O. attenuatus Duj.[***]

431 Eyes of the second type are found in the other families; they lie near the esophagus but are not connected with it directly. The pigment of these eyes is usually dissolved in alcohol, but is preserved in formalin.

There are true pigment cups with a lens in several species of Monhystera, but the shape of the eyes is not constant and the lens may be absent. The eyes are always displaced dorsally, and their pigment is sometimes fused on the dorsum.[†]

Certain formations with complete outlines of a reniform shape in profile, with or without a lens, are present in Araeolaimus[††] and Araeolaimoides (Table 10, Figure 73b[†††]). The pigment in these forms is usually red or brown and does not dissolve in alcohol. Similar eyes, but with a soluble pigment, are present in Diplopeltis. The lens is illustrated in Table 11, Figure 80–d.[‡]

Finally, undefined accumulations of black,[‡‡] brown,[‡‡‡] red,[★] violet[★★]
432 or green[★★★] color are very common among species of Chromadoridae and Desmoscolecidae. The outline of the eyes of several species of Cyatholaimus are better defined.

---

[*] Cf. also de Man, 1888, p. 13.

[**] Ibid., p. 35.

[***] Bastian, 1865, p. 138; de Man, 1878, p. 94. The four yellow spots of Dorylaimus flavomaculatus Linst. can hardly be considered as eyes: they have too definite an outline on Hofmänner's drawing (1913, pp. 598, 643, Table 16, Figure 17). Pigment has perhaps been deposited in the muscles. See also Micoletzky, 1914, p. 522.

[†] Bastian, 1865, p. 97; Bütschli, 1873, p. 61, 1874, p. 29; Oerley, 1880, p. 147; de Man, 1884, p. 8; Cobb, 1893, p. 401; Hofmänner, 1913, p. 610; Micoletzky, 1914, p. 411; Hofm. and Menzel, 1915, p. 122. Attention should be given to "two bright colorless bodies on the upper surface of the esophagus" of unknown function in Tachyhodites natans Bast. (1865, p. 155).

[††] In Ar. bioculatus dM., yellow-green (1878, p. 107).

[†††] See also de Man, 1893, p. 88.

[‡] See also Cobb, 1891.

[‡‡] Cyatholaimus spirophorus dM., 1878, p. 110; C. demani Fil. (ocellatus dM. nec Bast.) according to dM., 1889, p. 203; C. punctatus dM., 1890, p. 182.

[‡‡‡] Chromadora bioculata M. Sch. according to Bt., 1873, p. 71, dM., 1884, p. 59, Chr. minor Cobb, 1893, p. 396; Chr. nudicapitata Bast. according to dM., 1888, p. 48; Chr. lchberti G. Schneider, 1906, p. 681; Chr. ratzeburgensis Linst. according to dM., 1907, p. 13; Desmoscolex rudolphi and pelophilus Steiner, 1916, p. 327; Tricoma africana etc., p. 338.

[★] Rhabdotoderma morstatti Marion, 1870, p. 32; Chromadora ophrydii Stefanski, 1914, p. 31; Chr. sumatrana, sabangensis Steiner, 1915, Table 23, Figures 12, 18.

[★★] Chromadora oerleyi de Man, 1884, p. 59.

[★★★] Chromadora chlorophthalma dM., 1878, p. 114; Chr. viridis Linst., 1876, p. 14; Cyatholaimus ocellatus Bast., 1865, p. 163 (greenish-brown).

Eyes of free-living nematodes were known to Ehrenberg, who established the genus Enchelidium for forms with eyes.[*] Eyes have been described and illustrated by all authors studying related forms.

Eyes are obviously absent in parasitic nematodes, if Nordmann's record of a parasitic nematode of caddis fly larvae is disregarded.

We described above the difference between the eyes of Enoplidae and the other families. It is difficult to give information on the smaller groups, as eyes are absent in the majority of species. There are sometimes forms with and without eyes in the same genus. Thus, Thoracostoma caecum Savel'ev has no eyes, while other species – Th. echinodon Mar. and Th. figuratum Bast. – have well-developed eyes with a lens. The same is the case in Enoplus and Cyatholaimus. Only the structure of the eye is thus a good generic character, but not its presence or absence.

## E. Musculature

The musculature is a single layer of longitudinal fusiform muscle cells adjacent to the epithelium.[**] These cells are divided by the thickenings of the epidermis (longitudinal fields) into 4 or 6–8 (if submedian fields are present) muscle fields of different width.[***] As only the lateral fields are
433 large, there are, roughly and schematically, two large longitudinal muscles – a dorsal and a ventral. Such a division is common in all free-living nematodes and was described by Eberth (1863), Schneider (1866) and Bastian (1865, 1866), and even earlier for parasites. Only Marion (1870) mentioned an uninterrupted muscle layer. His description, referring to Thoracostoma zolae, confirms Bütschli's suggestion (1874) that he overlooked the true muscles, considering the thick cuticle of this species as muscles.

This arrangement of the muscles makes little variation of movement possible – contraction always takes place only in the dorsoventral plane. For this reason, preserved worms usually lie on the side (Leuckart[†]).

Since the time of A. Schneider, Polymyaria have been distinguished among nematodes, with a large number of cells in each muscle field and Meromyaria with only two rows. The great majority of free-living nematodes are Polymyaria, sometimes with a very large number of cells (large Enoplidae). Meromyaria are found only among Anguillulidae, several species of Rhabditis, Diplogaster, Cephalobus and Anguillula.[††] There is a question only about Linhomoeus (Bütschli[†††]), whose lateral fields are very well developed and packed with musculature. Unfortunately, other authors, including myself, had only poorly preserved

---

[*] 1836, pp. 41, 57.

[**] Their arrangement in a single line induced Rauther (1909, p. 544) to speak of epithelial-muscle cells. However, in coelenterates this name is used for quite different structures, so that this term is quite unsuitable.

[***] Rauther's note (1909, p. 520) on "gleich-grosse Muskelfelder" is completely incorrect.

[†] 1868–76, p. 13.

[††] A good example is Aulolaimoides elegans Micoletzky (1917, p. 518), which has wide muscle cells in the form of an oblique rhomboid, exactly as in Oxyuris.

[†††] 1874, p. 9, see also de Man, 1890, p. 207.

material of this genus, and it was therefore not possible to solve the question. Complete degeneration of the muscles in adult individuals takes place in the plant parasites Heterodera and Tylenchulus.

434 Martini (1903–1909) showed that all nematodes pass a stage of meromyarian larva in which the number of muscle cells is constant. If this stage remains constant, there are adult meromyarian nematodes with a constant number of cells (Martini, 1908b). If the cells multiply, the polymyarian type results. Thus, as noted by Rauther,[*] meromyarity is undoubtedly a larval character, while polymyarity is a character of the adult. It would be an error to consider the larva as the ancestor of a whole number of forms. In my opinion, it is therefore also necessary to consider meromyarian forms not as primitive but as secondary regressive neotenic forms.

In general, the structure of the muscle cells of free-living nematodes resembles that of parasites. There is a fusiform contractile part, usually forming a tube (coelomyaria[**]). This tube is very narrow in many large forms, as the contractile tissue is strongly developed and the sides of the tube are high plates, closely adjacent to each other.[***] The sarcoplasm lies inside the tube. It projects in one or several places and forms swellings, in one of which the nucleus is situated. These swellings are much less developed than in parasites. Attached to them are slender processes to
435 the dorsal or ventral line.[†] Some of these processes are attached to the ectodermal sheath of the esophagus,[††] others are attached to the nerve ring (partly unpublished observations on Paroncholaimus zernovi Fil. and Metonch. pristiurus Z. Str.[†††]).

These processes were at first considered to have an innervating function. Deineka (1908, 1912), on the basis of observations on Ascaris, rejected this view and stated that they probably had a supporting function. Their numbers, both in free-living and parasitic nematodes, make an innervating function unlikely. Their large number was already known to Leydig (1860). Goldschmidt (1910), defending the earlier view, stated that only one process is innervating and the others supporting. In my note (1912, on Paroncholaimus zernovi) I supported Deineka's view in general, rejecting the innervating function of the processes. If the motor nerves which I described should be accepted as such, this view gains further support. However, in my opinion, there are also not sufficient reasons to recognize the supporting function of the processes. These processes are probably rudiments of embryonic conditions and have no function in the adult worm.

There are also muscles with a specialized function.

1) **Esophageal muscles** (musculi oesophageales) are muscles of the dermo-muscular sac which are attached to the body wall at one end, like

---

[*] 1909, p. 546.

[**] Only some meromyarian Anguillulidae have a flat contractile part (platymyaria).

[***] E.g., in Leptosomatini, see Jägerskiöld, 1901; Türk, 1903, p. 297; de Man, 1904.

[†] These processes have been overlooked for a long time in free-living nematodes because they are very fine. De Man (1886) described them in Adonch. fuscus. They are less clearly described in Rhabditis (Bütschli, 1873, p. 112), Thoracostoma (Eberth, 1863, p. 7; Türk, 1903, p. 297) and Paroncholaimus (Stewart, 1906, p. 112).

[††] Marion recorded this (1870, p. 44) in Thoracostoma, Hallez (1900, p. 599) in Anguillula.

[†††] Such an attachment is also present in parasitic nematodes. See Goldschmidt, 1910; Ehlers, Rauther, 1906, 1909; Hagmeier.

the others; the other end projects from the muscle field, runs obliquely anteriorly or posteriorly and is attached to the surface of the esophagus
436 or the buccal capsule. There are four groups of such muscles, which are usually not all present in the same species:

a) the group extending obliquely anteriorly from the body wall and attached to the anterior end of the esophagus or to the oral cavity – the pharyngeal muscles (m. oes. pharyngeales);

b) the muscles extending obliquely posteriorly and attached in front of the nerve ring – the preneural muscles (musc. oes. praeneurales);

c) the muscles extending anteriorly and attached immediately behind the nerve ring – the postneural muscles (musc. oes. postneurales);

d) the muscles extending anteriorly and attached to the posterior end of the esophagus – the cardial muscles (musc. oes. cardiales).

Marion (1870) observed cardial muscles in Enoplus, but interpreted them incorrectly as nervous elements. De Man described cardial muscles in Enoplus (8) and Adoncholaimus (4) (1886, "vordere Intestinalmuskeln," pp. 5, 19, 43); they have a very muscular sarcoplasmatic part in Adoncholaimus and there are also pharyngeal muscles. Türk described 4 preneural muscles in Fiacra strasseni (1903, "Schlundmuskeln," p. 300). The powerful pharyngeal and preneural muscles which move the oral stylet or buccal capsule (Mononchus) are attached to the buccal cavity in Dorylaimini and Tylenchini (Bastian, 1866, p. 574; Bütschli, 1873, pp. 20, 73; de Man, 1884, p. 62; Strubell, 1888, p. 20; Cobb, 1891, p. 148; 1893, p. 812). Zur Strassen (1904, p. 307) described 4 pre- and postneural muscles united by anastomoses in Siphonolaimini.

Some of these muscles are constantly present in parasites (Leuckart, 1868–76, p. 41). According to Looss (1905, p. 37) the same fibers, altogether 4 pairs, are attached in Ancylostoma both to the esophagus preneurally and to the buccal capsule, and he therefore calls them m. cephalo-oesophageales. This term is not suitable for all the categories described above, and I therefore do not use it.

2) **Intestinal muscles** have been known in parasites for a long time[*]; they surround the posterior part of the intestine in the form of a net. They have not been described in free-living nematodes.

437 3) **Anal muscles** will be discussed in the description of the hindgut.

4) **Vulvar muscles** of the female.

5) **Bursal** and

6) **Spicular muscles** of the male will be discussed in the description of the genital organs.

Attempts have been made to give decisive importance to the structure of the musculature in the systematics of nematodes, e.g., in Schneider's classification. Recently Martini again stressed the great importance of this character. However, the arguments given above support the view that meromyarity is not a primitive but a larval character. We therefore strongly object to its use in systematics, as its practical application will immediately encounter difficulties. Thus, there are not only meromyarian forms in species of Rhabditis but also forms which are transitional to polymyarian forms. Plectus, which is connected by transitional forms with Rhabditis and also resembles it in other characters, is a true

---

[*] See Schneider, 1866, p. 197; Leuckart, 1868–76, p. 54. Particularly Looss (1905, p. 37) and Martini (1916, p. 300 ff.). He described a total of 11 cells in Oxyuris, including the preanal sphincter. They surround the intestine along its entire length as a network of circular (internal) and longitudinal (external) fibers.

polymyarian. Terschellingia and Siphonolaimini are related to Linhomoeus with a small number of muscles and are typical polymyaria.

Thus, we agree entirely with Rauther* that this character cannot be used for the definition of large groups of nematodes.

Muscles of special function have been studied too scantily to draw conclusions about their function.

## 2. INTESTINAL CANAL

The intestine of nematodes is a simple tube extending from the anterior
438 end (the mouth) to the anus, which is situated, with few exceptions, not at the extreme posterior end but anterior to it on the ventral surface. We should distinguish:

a) a small cavity, not always present, formed by the invaginated cuticle of the head – anterior buccal cavity (vestibulum);

b) the muscular esophagus (with the buccal cavity (pharynx) attached to it and the posteriorly attached cardia;

c) the endodermal intestine proper (intestinum);

d) the hindgut (rectum).

These parts are directly connected one behind the other in all free-living and the majority of parasitic nematodes. In some places there are glands opening into the intestinal canal.

### A. Mouth

The form of the mouth depends on the form of the buccal cavity and the lips.

If there is a large buccal capsule, its anterior opening is large, usually round. It may be closed by lips (Oncholaimini, Sphaerolaimini, Halichoanolaimus, Mononchus, Cobbia (p. 19)) or completely without them, as in Eurystoma (Table 5, Figure 29a), Symplocostoma (Table 5, Figures 31a, 32b, 34a) and Anoplostoma (Table 2, Figure 7a).

In Leptosomatini, Anticomini and Acanthopharyngini (Table 6, Figure 36a), the esophageal tube is directly attached to the anterior end of the body and the mouth is therefore triangular, sometimes with its walls projecting inwards (see de Man, 1893, p. 103, Tables 6, 9; Türk, 1903, p. 308). There is the same form of mouth in forms with three large lips, such as Enoplini, Demonema and Selachinema (see p. 20). At the margin of the lips there are sometimes (Enoploides, Selachinema) thin, transversely striated plates which may close the entrance to the mouth tightly. The mouth of these forms may be wide open. The mouth of Dignathonema is generally of this structure; it has the shape of a longitudinal slit, as there are only two lips (see p. 148, Part I, p. 20 and Table 6, Figure 40a–c).

Most other forms have a small, round mouth. In Oxystomini this is caused by the reduction of the musculature of the esophageal tube at the anterior end, which changes its triangular shape into a circular shape. In Chromadoridae and Monhysteridae the cause is different – the walls of the head are invaginated and the esophagus is attached to them below the anterior surface of the body (cf. Table 7, Figure 42c, d; Table 9, Figures 63a, 64a).

### 439 B. Vestibule and Buccal Capsule

The boundary between the cuticle of the head and esophagus is usually sharp, though both are shed at the same time in the larva. The two cuticles stain differently (Jägerskiöld, Rauther). The cavities between the invaginated walls of the head are named vestibule,* while the term buccal capsule refers only to the cuticle of the esophagus. The cuticular cephalic capsule of various species of Leptosomatini, described above, is probably a derivative of the esophagus, as it is directly connected with its cuticle.

The form of the buccal cavity always is triradiate, corresponding to the form of the esophageal tube.** All transitions from complete absence of the buccal cavity to a very complex buccal cavity are found in free-living nematodes. We shall not discuss the origin of these forms, giving only a purely morphological classification:

1) small buccal capsules surrounded by the musculature of the esophagus – enclosed capsules;

2) larger capsules, part of whose walls are not surrounded by musculature – free capsules;

3) capsules armed with large movable appendages, jaws, spines or stylets.

Cobb*** combined the first two categories and distinguished capsules with jaws from capsules with stylets in the third.

Concerning the appendages in the buccal cavity, immovable structures
440 (immovable teeth – onchi, according to Savel'ev†) and movable appendages should be distinguished:

A. Movable in the transverse direction:
  1) small appendages – true movable teeth (dentes);
  2) large structures – jaws (gnathi, according to Savel'ev).
B. Movable in the longitudinal direction:
  1) spines (spinae) with restricted mobility which project from the mouth on contraction of the entire anterior end, caused by the contraction of the walls of the buccal cavity;
  2) stylets (hastae) which are independently movable.

Both the movable and the immovable appendages usually belong to the esophagus and are therefore situated in the dorsal and subventral positions. The description of a ventral tooth in Chromadoridae is very doubtful. The error made by de Man in the case of Hypodontolaimus was recognized by Jägerskiöld. Cobb described a 90° rotation of the anterior end of the

---

* 1909, p. 545.

---

* "Dieser vordere Abschnitt... kann... eigentlich nur als ein in bestimmter Weise modificirter Theil der allgemeinen Cuticularbedeckung des Kopfendes aufgefasst werden" (Bütschli, 1874, p. 11). The term "vestibule" was given by de Man (1884, p. 11).

** Cobb, 1898b, p. 29.

*** 1898b, p. 32.

† It is better to call them buccal tubercles or hooks according to their form, as distinct from movable teeth.

body in one species of Chromadora. Such a rotation may then result in a description of a dorsal tooth.[*]

**a. Enclosed buccal capsules.** Forms without a buccal cavity are numerous, e.g., Oxystomini (Table 2, Figures 8a, 9a), Enchelidium (Table 4, Figure 28a, b), Draconematini (Table 8, Figures 55c, 56), Disconema (Table 10, Figure 74a), Araeolaimoides (Table 10, Figure 73a), Diplopeltis (Table 11, Figure 80) and several other genera. There are also forms in which the buccal cavity is almost absent if the mouth is closed, but may be wide open to swallow food; such forms are Tripyla[**] and Demonema.[***]

441 The mouth of the majority of Leptosomatini also belongs to this category, if only whole mounts are used. But if the head of some of these forms is examined from the front and in sections, it appears that there is a widening of the esophageal tube anteriorly. This widening is formed by the two subventral ridges of the esophagus, while the dorsal ridge narrows the lumen markedly and is therefore difficult to see laterally (Table 1, Figures 1a, b, 2a, 3a, 5d[†]).

The next category consists of narrow, funnel-shaped capsules surrounded on all sides by the musculature of the esophagus. The capsule of Anticoma has this form. It is visible only when the esophagus is relaxed, but completely flattened when the esophagus is contracted (Table 2, Figure 6a and 6b). The capsules of Monhystera and Araeolaimus are generally of this form.

In the majority of Spilipherini and Chromadorini and in Cyatholaimus, the structure is complicated by the presence of a compound vestibule whose walls form 12 pockets[††]; their boundaries are visible laterally in the form of longitudinal ridges. The buccal cavity proper is small and has at least one dorsal[†††] immovable or movable tooth. There is rarely a fairly wide conical cavity (Nannonchus, Achromadora) or a prismatic cavity (Ethymolaimus); the cavity is usually narrow, sometimes hardly marked (Spirina, Table 7, Figures 46a, 47a; Chromaspirina, Table 7, Figure 45a). It is cup-shaped with one dorsal tooth in most genera (figure on Table 8), and its walls are quite thick in some genera (Metachromadora, Table 7, Figure 42b, c, d). In Cyatholaimus the walls are thin but the buccal cavity is wide (Table 5, Figure 37a); the folds of the vestibule may be smoothed, and the open buccal capsule with its teeth is then projected forward.

442 Small cup-shaped capsules completely enclosed by the esophagus are characteristic for Comesomini, Linhomoeus and other forms (Table 9, Figures 57a, 58a; Table 11, Figures 76a, 78a, 79a[‡]).

---

[*] See also p. 150, Part I

[**] De Man, 1884, p. 44.

[***] Cobb, 1893, p. 392.

[†] See also Jägerskiöld, 1901; Türk, 1903; de Man, 1904; Rauther, 1907, p. 726.

[††] See de Man, 1889, Table 6, Figure 6b; Table 7, Figure 9b; 1893, Table 6, Figure 7b; 1907, Table 4, Figure 14.

[†††] Steiner's record (1916, p. 71) of a ventral tooth in Chromadora hyalocephala requires confirmation.

[‡] See also de Man, 1889, p. 207; 1890, p. 171.

Wider funnel-shaped capsules are present in the group Theristus – Cobbia. The boundary of the buccal capsule proper in these genera is demarcated by a chitinized ring, to which the lining of the esophagus is attached, so that the entire colorless anterior part in Figure 63a belongs to the vestibule. There are tubercles in the capsule of Cobbia, on which the esophageal glands open (Table 9, Figure 61a–c). This is the form of the capsule in the freshwater genus Trilobus. In Tripyloides (Table 5, Figure 35a) it is generally the same, but there are also lateral pockets.[*] Cylicolaimus also apparently belongs here.[**]

If the descriptions are carefully studied and the illustrations of Siphonolaimini by de Man,[***] Cobb[†] and particularly Zur Strassen[††] are examined, it appears that they do not resemble the piercing organs of Dorylaimini and others described below. The entire buccal cavity of Dorylaimini consists of a hollow tube whose anterior end is covered with a thin cuticle which may project outside. Cobb did not even describe a stylet as such. The posterior end of the tube is connected broadly with the esophagus, and two esophageal glands open in its lumen. These are its general characters also in Chromagaster stenolaima Steiner.[†††]

**b. Free oral capsules.** There is a long narrow form in Rhabditis and related genera, in Cylindrolaimus and in some species of Dorylaimini. This is a widening of the tube of the esophagus; in Cylindrolaimus, all three ridges are retained as chitinized rods and reduce the 443 lumen of the capsule. There are also several genera of Dorylaimini (listed on p. 126, Part I) with a very long capsule; its anterior end is usually free, while its posterior end is surrounded by the esophagus. There are usually anterior teeth (Ironus, Dolicholaimus, Syringolaimus) or posterior teeth (Cryptonchus). These teeth are shed during the molt. Until then, they are situated in the wall of the esophagus.

The buccal capsule of Axonolaimus and Conolaimus has the form of a pyramid, as in the group Theristus. There is a cone of chitinized rods anterior to it in the wall of the vestibule. Their apex is directed to the opposite side (Table 10, Figures 70a, 71a, 72).

Many genera have a cup-shaped capsule with thick walls. First let us examine forms without hooks. The walls of the capsule of Prismatolaimus[‡] are straight and the thickening of the cuticle does not reach the bottom. There are curved walls with a partly thickened bottom in Anoplostoma (Table 2, Figure 7a[‡‡]) and Pelagonema (Table 3, Figure 19a).

In Sphaerolaimus (Table 10, Figures 67a, 68a, 69a, b[‡‡‡]), there are, in addition to the buccal capsule, thickenings in the wall of the vestibule in

---

[*] See Bütschli, 1874, Table 3, Figure 12; de Man, 1886, Table 11

[**] See Jägerskiöld, 1901.

[***] 1893, p. 100

[†] 1893, p. 416.

[††] 1904, p. 305.

[†††] 1916, p. 632.

[‡] De Man, 1884, p. 79.

[‡‡] See also de Man, 1907, pp. 50, 52.

[‡‡‡] See also de Man, 1907, pp. 54, 58.

the form of a cone of rows anterior to the capsule, as in Axonolaimus. The anterior part of the capsule is markedly thickened and adjacent to the cuticle, taking the place of the cephalic capsule, which is absent. The wall of the capsule is sometimes punctated.

Oncholaimini also have a thickened immovable buccal capsule. It is seen in sections that it consists of three separate plates.[*] The most prominent character is the presence of three hooks on which the esophageal glands open, one on each sector of the esophagus. The teeth are rarely
444 symmetrical — 2 equal teeth subventral and a larger dorsal tooth (Paroncholaimus, Table 3, Figure 18a). One of the subventral teeth is usually the largest (Table 4, Figures 20a, 21b, 23a, 25a, 26a). The tooth is sometimes so large that it fills almost the entire buccal capsule (Onchol aimellus[**]). The buccal cavity of Mononchus generally resembles that of Oncholaimini, but only one tooth is usually present and the buccal capsule is more movable. In addition, there are often other processes and irregularities in the capsule which facilitate the retention of food.[***] Such teeth are present in the short, conical capsule of Demania.[†]

In Symplocostomini, there is a row of rings, punctations and other structures on the wall of the capsule (Table 5, Figures 29a, 31a, 32b, 34a); hooks are also present. Movable spines are described below. The capsule of these forms is very small, but it is fairly large compared with their thin anterior end. Desmolaimus, which belongs to a different group, obtained its name as a result of these rings.[††]

The predaceous Halichoanolaimus has a large buccal cavity whose anterior part is free, but its posterior end is embedded in the esophagus. There is a group of several chitinized denticles at the boundary between them, the largest of several denticles projecting anteriorly (Table 5, Figure 38a—a, b; Table 6, Figures 39b—c, 39c—b, c[†††]). These structures may be called the buccal comb (pecten); it facilitates the retention of prey.[‡] Such a comb is also present in Linhomoeus elongatus Bast.[‡‡]

c. **Buccal capsules with movable parts.** Movable teeth (dentes) are
445 present in many Leptosomatini next to the mouth.[‡‡‡] Another group with such teeth are the Chromadoridae. The tooth here is only slightly movable together with the adjacent parts of the buccal cavity, a transition from hooks to teeth. However, true teeth are also found, usually in forms with a conical buccal cavity, e.g., in Chromadorella, where there are three teeth (Table 8, Figure 53a[*]). In the genera Spiliphera[**] and

---

[*] Rauther, 1907, p. 712.

[**] De Man, 1890, p. 190.

[***] See especially Cobb, 1893, p. 4, 1915.

[†] Southern, 1914, pp. 42, 44.

[††] De Man, 1884, p. 50.

[†††] See also de Man, 1888, p. 37; Savel'ev, 1912, p. 121

[‡] Cobb (1898, p 405) is probably incorrect in stating that these "teeth" have a masticatory function.

[‡‡] De Man, 1890, p. 207, subgenus Eulinhomoeus de Man, 1907.

[‡‡‡] Türk, 1903, pp. 308, 309; de Man, 1904, pp. 29, 30, 38; Filip'ev, 1916, p. 88; Southern, 1914, pp. 36, 37.

[*] See also de Man, 1890, p. 178; Steiner, 1915.

[**] De Man, 1893, Table 5, Figure 6a.

---

Ethmolaimus[*] there are characteristic chitinized processes to which muscles are attached from the teeth inwards ("apophyses chitineuses" of de Man). Teeth projecting outwards are characteristic for Diplogaster, in which they are sometimes very movable.[**]

**Jaws** (gnathi) are best developed in the Enoplini. There are three jaws, corresponding to the three sectors of the esophagus. These are longitudinal structures with two inwardly directed hooks anteriorly and a rounded posterior end (Table 2, Figure 10a, mand). They are widest in the middle and articulate with the ring of the cephalic capsule. A number of narrow canals gives them a longitudinally striated structure. As shown by Rauther,[***] these are local chitinous thickenings of the buccal capsule. Muscles are attached anterior and posterior to the point of articulation, which cause their closing and opening. The esophageal glands open below them.[†]

The jaws of Enoploides form processes in the middle at the place of articulation (Table 3, Figure 12e) and divide into two branches posteriorly. There is an immovable tooth between the branches, at whose end the esophageal glands open (Table 2, Figure 12a, b; Table 3, Figures 12e, 13a,
446 14, 15a). There are immovable ridges instead of movable jaws in Enoplolaimus, which are homologous to jaws as recorded by Savel'ev (Table 3, Figure 16a—a). There is a tooth between the two posterior processes, e.g., in Enoploides (d). The hooks of these forms, as in Oncholaimini, facilitate the swallowing of sand, with which the buccal cavity is usually filled (Savel'ev). The jaws of Triodontolaimus are much shorter and have only one point.[††]

Selachinema Cobb and Dignathonema Fil. of the Cyatholaimini have jaws. Selachinema has three jaws,[†††] Dignathonema has only two subventral jaws. There are accessory lateral parts at the end of the jaws (Table 6, Figure 40a, b, c, f). Both genera are predaceous, with the jaws capturing the prey. To judge from Cobb's short description, similar jaws are also present in Demonema.[‡]

**Spines** (spinae) are rather rare. They are firmly connected with the wall of the buccal cavity and their mobility is therefore restricted. They have also developed independently in several groups. The most typical group is the Symplocostomini, Eurystoma (Table 5, Figure 29a—d. subv. d.) and Symplocostoma (Table 5, Figures 31a, 32b, 34a—d. mob.). If the buccal cavity is contracted, the spine projects outside and probably pierces plants, on which these nematodes feed (Table 5, Figure 31b). The spine of Symplocostoma is close to the immovable tooth of the buccal cavity (d. subv. d., Figure 32b). The spines of both genera are asymmetrical, belonging to one of the subventral sectors.[‡‡] These spines are homologues of the hooks of Oncholaimini, as the esophageal glands apparently open on them.

---

[*] Hofmänner and Menzel, 1915, p. 139.

[**] Bütschli, 1873, p. 119; 1876, p 369; de Man, 1884, p. 84.

[***] 1907, p. 720

[†] Drawing in Marion, 1870, Table G, Figure 1b, c; also de Man, 1886 and especially Rauther, 1907, p. 720.

[††] De Man, 1893, pp. 115, 116.

[†††] See Cobb, 1915; Ybk. Dept. Agric., 1914, p. 486.

[‡] 1894, p. 392: "Three lips are here armed with numerous powerful teeth."

[‡‡] See also de Man, 1888, pp. 25, 28.

447 Another group with spines is Spilipherini. The dorsal tooth may also project anteriorly, but only when the entire buccal cavity is evaginated, and the tooth of these genera, e. g., Metachromadora (Table 7, Figure 42b, c, e, den.), cannot be considered as a buccal spine. The true spine of Onyx is weakly developed (Table 6, Figure 41a, b, den.).[*] There is a well-developed spine only in Hypodontolaimus[**]; it projects downwards from the dorsal ridge of the esophagus to such an extent that de Man at first considered it as a ventral spine. These spines, like the stylet of Dorylaimus, are embedded in the wall of the esophagus before the molt.[***]

The buccal cavity of Acanthopharyngini differs from the usual structure. The dorsal ridge of the esophagus is thickened over a great part and its anterior part enters the vestibule (Table 6, Figure 36a). The anterior free end sometimes has a complicated form.[†] These structures may also be called spines, as they are barely movable.

**Stylets** (hastae) are rare among marine forms, but are present in two large groups of freshwater and terrestrial nematodes – Dorylaimini and Tylenchini. Two types of buccal spine are present in Dorylaimini (see p. 125, Part I). There may be thickenings on all three ridges of the esophagus, which are at first unequal (Diphtherophora[††]) and then fused in the anterior part, while the posterior part is divided (Tylolaimophorus[†††]), and finally there are compound spines, which are thickened at the base in Tylencholaimus and Xiphinema.[‡]

Another structure is present in many species of Dorylaimus[‡‡] and
448 related forms. The stylet is truncate at the tip and belongs to the dorsal sector of the esophagus, as noted by Cobb (1898b, p. 33). It may move forward and backward. It is sometimes very long and thin (Trichodorus[‡‡‡]). The spine is sometimes of complex structure.[*] The boundary of the esophageal part is marked by a chitinized ring, in front of which lies the vestibule, which is sometimes large with thickenings on the walls (Actinolaimus Cobb[**]). The stylet is renewed during the molt and is embedded before the molt in the wall of the esophagus (reserve stylet, "Reservestacheln" of the authors). The stylet of Mermithidae, particularly the larvae, has the same structure (Steiner, 1916).

All Tylenchini have a stylet which is composed of three parts and usually has a swollen base. A very long, stout stylet is present in Hoplolaimus Daday.[***] Reduction of the stylet is often observed, especially in males and in plant parasites.

---

[*] See also Cobb, 1891, p. 146

[**] De Man, 1888, p. 39; Jägerskiöld, 1904.

[***] Cobb, 1891; de Man, 1888, p. 40.

[†] Acanthopharynx Marion, 1870, p 34; see also de Man, 1890, p 184.

[††] See de Man, 1884, p 128.

[†††] Ibid., p. 130.

[‡] Ibid., p. 133; Cobb, 1913, figure in table; 1914 (Yearbook), drawing on p. 469.

[‡‡] Numerous drawings are given in each work on freshwater nematodes. See de Man, 1884; Bütschli, 1873, p. 20.

[‡‡‡] See Cobb, 1913, figure in table; de Man, 1884, p. 163.

[*] E. g., D. macrodorus de Man, l. c., Table 26, Figure 110.

[**] Cobb, l. c.; de Man, l. c., Table 23, Figures 137, 138

[***] Cobb, 1913; 1914 (Ybk.), p. 179; Hofm. and Menz., 1915, p. 207. Synonymy see [Russian] p. 341 [sic]

---

Short stylets are present in both groups or they are really only spines, e. g., in Dorylaimini, Oionchus Cobb[*] and Tylenchini, Neonchus Cobb.[**]

Cobb[***] makes very good suggestions about the function of the stylet. This is certainly a piercing organ, used to puncture the roots of plants. To use the stylet, the nematode has to attach itself to the root. This is usually achieved by the suction of the posterior muscular part of the esophagus. Hoplolaimus (Iota Cobb) has no such muscular apparatus and the attachment is achieved by backwards-directed processes of the
449 cuticle, which become attached to soil particles. When the muscles of the anterior end contract,[†] the stylet projects and pierces the wall of the plant. It has not been proven that Dorylaimus sucks through the hollow spine or if this only pierces – probably the latter. Special muscles activate the stylet.[††] Berliner and Busch (1914) observed the action of the stylet in living Heterodera. It is very slender and is unable to pierce the root of the plant. Only when the nematode has pierced the plant does the stylet begin to act.

Which form of the buccal capsule is more primitive? This is difficult to answer. The absence of the anterior widening of the esophagus is probably more primitive, i. e., a buccal capsule like that in the most primitive species in all groups. The more its triradiate form disappears, the later its origin. Various movable parts have of course developed secondarily.

Marcinowski (1908) considered the buccal capsule of the type of Rhabditis as the primary form and attempted to derive all other forms from it. This form is probably primitive only insofar as it has retained the original triangular shape. However, a large part of the capsule has developed independent walls, which, in my opinion, are secondary. Tylenchus and related forms probably developed from this form, but not Mononchus or Dorylaimus (see p. 125, Part I).

There is almost the same form of buccal cavity in parasites as in free-living nematodes, but the buccal cavity is usually simpler. It would take too much space to enumerate all the different forms.

450 The classification of free-living nematodes has been based on the structure of the buccal capsule since the time of Bastian, and this character has generic importance. The grouping of genera was also based on this character (Bastian, 1865; Bütschli, 1873; de Man, 1884). However, this classification is artificial. A classification based on numerous characters does not correspond to this scheme and very similar capsules are often due to convergence. We mention the wide, thick-walled capsules, occurring independently in Oncholaimini, Cyatholaimini (Halichoanolaimus) and Sphaerolaimus, which belong to the three main families in our classification. Similar jaws have developed independently in different groups, as

---

[*] 1913, drawing in table.

[**] 1893, figure, p 819.

[***] 1891, p. 150; 1914, Ybk., p. 478.

[†] Or by the action of special muscles (see Bütschli, 1873, p 20).

[††] De Man, 1903; Jägerskiöld, 1908.

well as hooks and the oral combs. The structure of the buccal capsule is thus quite unsuitable for the division of families. It is a good generic character, and a subfamiliar character only in a few cases.

The following table, which lists the different forms of the buccal cavity in different groups, may be useful.

### Enoplidae

Leptosomatini – buccal cavity abse[illegible] almost absent except in Cylicolaimus, where it is wide, sm[illegible] and embedded.
Anticomini
Anticoma – small, funnel-sha[illegible]d or almost absent
Anoplostoma – large, thick-walled, free, smooth.
Oxystomini – absent.
Enoplini
Triodontolaimus – three short jaws, each with one point.
Enoplus – elongate jaws with 2 hooks anteriorly.
Enoploides – jaws with 2 or 3 hooks, with an incision posteriorly, sometimes a hook in the incision.
Enoplolaimus – immovable thin ridges with 2 processes posteriorly, and a hook between them.
Demania – partly free, conical, with three short teeth.
Oncholaimini – wide, free with 3 hooks; except in Pelagonema, the same, but without hooks.
451 Enchelidiini – absent.
Symplocostomini – wide, free, with secondary thickenings on the walls and a spine at the bottom.
Dorylaimini
group Mononchus (A, p. 126, Part I) – free, thick-walled, usually with hooks.
group Ironus (B, p. 126, Part I) – very long, usually thick-walled, sometimes with small teeth or hooks.
group Diphtherophora (C, p. 127, Part I) – short with separate rods in wall.
group Tylencholaimus (D, p. 127, Part I) – thin spine, swollen at the end with triple head.
group Actinolaimus (Ea, p. 127, Part I) – thick spine, truncate at end. vestibule wide.
group Dorylaimus (Eb, p. 127, Part I)– similar spine, but vestibule narrow.
group Trichodorus (Ec, p. 128, Part I) – long, thin spine, not swollen at end.

| | |
|---|---|
| Trilobus<br>Trischistoma | conical, fairly large, embedded. |
| Alaimus<br>Deontolaimus<br>Bastiania | absent. |
| Prismatolaimus – | free, smooth, prismatic. |

Tripyloidini
Tripyloides – not very large, conical with lateral pockets.
Bathylaimus – fairly large, two steps, embedded.

### Chromadoridae

Acanthopharyngini – dorsal spine, thickening of dorsal ridge of esophagus extending far posteriorly, sometimes branched anteriorly, except:
Dermatolaimus – very narrow, long, embedded.
Tripylini
Tripyla – absent.

| | |
|---|---|
| Monoposthia<br>Udonchus | small, embedded, with dorsal tooth. |

Rhabdolaimus – long, thin, embedded, with denticle anteriorly.
Cyatholaimini
Richtersia, Necticonema – absent.
Cyatholaimus – fairly large, embedded with dorsal tooth, vestibule folded.
Choanolaimus – folded, fairly large, anterior part free, posterior part embedded.
Halichoanolaimus – anterior part free, thick-walled, with comb posteriorly, posterior part embedded.
452 Demonema – densely folded, with jaws.
Selachinema – three jaws, as in Enoplus.
Dignathonema – two large jaws.
Odontolaimus – very long, with denticles anteriorly.
Nannonchus – conical, embedded, wide, with three teeth.
Spilipherini – with folded vestibule and dorsal hook or tooth, cup-shaped, embedded, except:
Ethmolaimus, Spiliphera – prismatic, with three teeth.
Hypodontolaimus – dorsal tooth turned into spine.
Onyx, Chromaspirina, Spirina, Laxus – vestibule very narrow.
Achromadora, Microlaimus – large, conical, with 1 or 3 teeth.
Chromadorini – the same, except:
Chromadorella – small, conical, with three teeth.
Draconematini – absent.

### Desmoscolecidae – absent.

### Monhysteridae

Monhysterini
group Theristus – conical, fairly large, embedded; Cobbia the same, but with hooks.
Araeolaimus, Monhystera – small, conical, smooth.
Desmolaimus – fairly large, embedded, with constrictions.
Terschellingia, Prosphaerolaimus, Draconema, Aegialoalaimus – absent or almost absent.
Linhomoeus, Metalinhomoeus – cup-shaped, embedded.
Sphaerolaimini – very large, free, thick-walled, vestibule in form of cone of rods.
Axonolaimini – Axonolaimus, Conolaimus – prismatic, partly free, vestibule with cone of rods.
Araeolaimoides, Sphaerocephalus – absent.

Siphonolaimini – long, narrow, round in cross section, may be projected, functioning as piercing organ.
Comesomini – small, embedded, cup-shaped.
Diplopeltini
  Diplopeltis – absent.
  Aemaeolaimus – vestibule conical.

Anguillulidae

group Anguillula-Rhabditis – long, triagonal, partly free.
group Plectus – of varying form, sometimes absent, sometimes changes shape if contracted.
group Diplogaster – wide with teeth, free.
group Tylenchus – stylet of varying structure.

## 453 C. Esophagus

Two parts of the esophagus may be distinguished in adults: the internal cuticular tube, which has a triangular lumen with its angles projecting inwards, and the main, mainly muscular tissue, arranged in the form of three longitudinal chords – the sectors of the esophagus.[*] The sectors project into the lumen of the cuticular tube and compress it; one of the sectors is dorsal and two sectors subventral. There are esophageal glands in the middle of each sector, and between them, at the angles of the tube, epithelial (pigment) stripes.

The structure has been best studied in large parasites, by Looss (1896), K. C. Schneider (1902), Goldschmidt (1904), Martini (1916) and by Rauther (1907) in some free-living forms. The structure is uniform in all forms. The esophagus consists of: 1) muscle cells, 2) epidermal cells, 3) glands, 4) nerve cells. The characteristic structure of the esophagus is produced by the muscle cells and the epidermal cells, which are usually so closely united that the boundaries of the cells are difficult to recognize, or have completely disappeared. The muscle cells form three chords which constitute the main mass of the sectors of the esophagus – the "flat cells" of Looss.[**] The cells enclose radial muscle fibrils,[***] which are attached at one end to the internal angles of the esophageal tube and with the other to the thickened surface layer of the esophagus.[†] Their nuclei are arranged 454 in rows of three on the same level[††]; the sarcoplasma is sometimes well developed (Rauther). The muscle chords may be continuous over the whole length of the esophagus or the epithelial part may be interrupted by the muscles, forming a septum (septum epitheliale Martini). The function of the septum is to give the esophagus greater stability for the formation of bulbs, the musculature of the buccal capsule, etc. Such septa are also present in free-living forms.

There are rows of epidermal cells along the angles of the esophagus – the "marginal" (better "angle") cells of Looss.[*] Their nuclei are also arranged in groups of three on the same level; sometimes they are less numerous and sometimes more numerous than the muscle cells. There are also fibrils from the external angles of the esophageal tube to its surface. However, these are not contractile but elastic elements, as stressed by Looss.[**] This is also confirmed by the direct transition of fibers into the cuticle (Martini). The epidermal cells have processes at both sides of the esophageal tube, which reach almost to its internal angles. These cells produce the cuticle of the esophagus, and only these cells are epithelial; the muscle cells of the sectors are not epithelial, and the name "epithelial-muscular cells" suggested by Goldschmidt is not correct.[***] According to Martini, the dense external cover of the esophagus (membrana propria), is also a derivative of the angle cells. The muscle cells are thus entirely enclosed in the epithelial cells. The combination of the 455 nerves of the anterior papillae with the plasma of the external cover which I recorded in Paroncholaimus also confirms this.[†]

It is surprising that such an obvious interpretation of the angle cells was given clearly only by Martini. It is also clear that the esophagus develops from "stomodeoblasts," which develop from the primary mesodermal cells (Zur Strassen, 1896; Martini, 1903, 1906–1909). Stomodeoblasts do not produce epidermal elements but only muscle cells, and also take part in the formation of the musculature of the anterior end (Martini). The epidermal ("angle") cells probably develop from the ectodermal cells of the anterior end of the body. There is thus a scheme which the stomodeum of all other worms has in common.

In spite of their small size, the muscle and angle cells of the esophagus are more numerous in free-living nematodes than in parasites. Looss found only 24 of 30 cells in different ascarids, while Rauther counted 42 in Fiacra and 54 in Enoplus. Their number is constant in each species.

The nervous system of the esophagus consists of a few cells and fibers; it is present also in free-living forms (up to 24 cells in Cylicolaimus and Fiacra according to Rauther[††] The esophageal glands are discussed below.

The esophagus functions as a sucking organ,[†††] although not exclusively, and also swallows hard food, sometimes even large pieces, e. g., other

---

[*] The term was given by Rauther (1907).

[**] "Flächenzellen.

[***] Martini records transverse striation of the fibrils (1916, p. 242).

[†] Only in Marion (1870, p. 51) and Pérez (1866, p. 190) is there an erroneous record of longitudinal muscle fibers. Longitudinal fibers are present only in the anterior part of the esophagus of a few forms.

[††] Looss described 2 nuclei in each segment in the anterior part of the esophagus in Ancylostoma.

[*] "Kantenzellen.'

[**] Also Rauther, 1907, p. 715. Only Goldschmidt reported individual contractile fibrils among them, but this is doubtful.

[***] This has been particularly stressed by Martini (see p. 218). Rauther interprets this differently: "Es dürfte demnach jeder Sector (bzw. jede Sectorhälfte) als ein syncytiales Gebilde, bzw. als eine einzige mehrkernige Epithelmuskelzelle zu betrachten sein" (1907, p. 714). However, syncytia and multinucleate cells are quite different.

[†] See Filip'ev, 1912, p. 208.

[††] 1907, p. 732. For parasites see Goldschmidt, 1910 and Looss, 1905, p. 83, in addition to the works quoted.

[†††] A. Schneider, 1866, p. 194; Martini, 1916, p. 270.

nematodes in predaceous species (Dignathonema, Halichoanolaimus, Mononchus, etc.). The glands of the esophagus of course have a digestive function.

Rauther (1907) suggested that the esophagus also has an excretory
456 function in free-living nematodes. In his experiments the angular chords discharged methylene blue and neutral red.[*] In his opinion the pigment stripes should be considered as accumulations of excretions. The glands, and partly the muscle cells as well, excrete various substances into the esophagus, which may be useful or harmful (in some forms through special porous plates, see p. 70); the intestine assimilates the useful substances and excretes the harmful ones. The esophagus thus creates a primitive circulation.[**]

The relative length of the esophagus varies greatly; it is usually 10–15% of the body length. Forms with a long esophagus are Phanoderma, especially Sphaerolaimus (a third of the body length in S. hirsutus Bast. and shorter in the Black Sea forms[***]). Dignathonema (Table 6, Figure 40f), Terschellingia (Table 9, Figure 65c), Spira (Table 7, Figure 47a) and related genera have a short esophagus.

The relative length changes with age, the esophagus grows more slowly than the body, so that it is relatively longer in young specimens. The proportions of the parts of the esophagus also change with age. Thus, according to Brakenhoff,[†] the length of the buccal cavity of Ironus ignavus does not change after the last molt, but the esophagus still grows.

The form of the esophagus may be straight, without a thickening posteriorly or only with a gradual thickening. In other cases, there is a more or less marked thickening posteriorly – the bulb,[††] whose function is obviously to strengthen the sucking action of the esophagus. A distinction should be made between true bulbs with a radial arrangement of the muscle fibers and pseudobulbs without such an arrangement.

A thick, straight esophagus developed independently in several groups. A thick esophagus is present in Enoplus and in the Chromadoridae in many species of Cyatholaimini (Cyatholaimus, Halichoanolaimus
457 and in Richtersia, which is related to them). Among the Monhysteridae, such an esophagus is present in Sphaerolaimus and Linhomoeus.

On the other hand, the esophagus of Leptosomatini[†††] and many Monhysteridae (Axonolaimini, Monhystera, Diplopeltis) and apparently of Desmoscolecidae as well,[‡] is very slender and in the latter two groups almost not widened posteriorly.

---

[*] The discharge of stains by the esophagus was also observed by G. Schneider (1906).

[**] 'Die Tätigkeit der Schlundmuskulatur bewirkt demnach eine primitive Circulation' (p. 733); see also p. 37.

[***] De Man, 1907, p. 56; also pp. 223, 225, 227, Part I

[†] 1914, p. 280.

[††] Martini (1916) suggested for Oxuris that a muscular pharynx with corpus, isthmus and bulbus should be distinguished from the non-muscular esophagus behind it (p. 173), but in my opinion the present terminology is more suitable.

[†††] See also p. 25ff, Part I.

[‡] Shchepot'ev, 1908, p. 47; Cobb, 1912, p. 482

Bulbs are common in free-living nematodes. Their absence is characteristic for the Enoplidae. A bulb has been described only for Syringolaimus[*]; Symplocostoma hexabulba Fil. possesses six small bulbs (Table 5, Figure 32a), being a morphological curiosum not only among the Enoplidae but also among all other nematodes. It is interesting that in all other characters, including the slender esophagus, it resembles other species of Symplocostoma so closely that it does not require separation in a separate genus.

Bulbs are particularly characteristic for the Chromadoridae. They are gradual, sometimes weakly marked in some genera; in others they are more marked (Metachromadora, Table 6, Figure 42a; Onyx, Chromadoropsis[**]). The arrangement of the fibers in the bulb may be either simple or double (see figure mentioned above and also Table 8, Figure 54a, Spilophorella). A triple bulb has been described for Sp. ceylonensis Cobb. There is no connection between these species; the bulb is weakly marked in typical Chromadorella[***] but it is double.

In addition to the typical posterior bulb of the Anguillulidae, there are median bulbs anterior to the nerve ring. Sometimes both median and posterior bulbs are present, but they are rarely both fully developed.[†] One or the other bulb; and sometimes the whole posterior part of the esophagus, is usually less developed (see below, p. 71). The double esophagus of Austronema shows the same character (Cobb, 1914). Oerley[††] recorded some variation of the form of the esophagus in Anguillula aceti.

The esophagus is attached anteriorly to the cephalic cuticle or the cephalic capsule. It is attached on a wide area in the primitive Enoplidae
458 (Leptosomatini, Anticomini, Oxystomini, Enoplini) (cf. head on Tables 1, 2). This arrangement is absent in other Enoplidae and also in the other families. The covers are usually invaginated and attached only by a narrow ring (see details on p. 29 ff.).

The presence of complex mouth organs and their musculature sometimes causes a swelling of the anterior part of the esophagus. This is characteristic for many genera of Chromadoridae, Dignathonema (Table 6, Figure 40f), Metachromadora (Table 6, Figure 42a), Ethmolaimus,[†††] Hypodontolaimus,[‡] Monoposthia and others. Longitudinal muscles in the wall of the esophagus are characteristic for these forms (see p. 159, Part I). A description of these muscles in Metachromadora and their boundaries are also shown in Figure 40b. These muscles do not form a single mass with the rest of the esophagus, but are well-differentiated cells. They are attached to a characteristic annular thickening of the cuticle of the head in Dignathonema (Table 6, Figure 40b–c. ceph); in this genus there is another thickened ring of doubtful function on the surface of the anterior part of the esophagus (c. oes.). The muscles of the buccal cavity of Solenolaimus,[‡‡] which

---

[*] De Man, 1888, p. 35, 38: "Un vrai bulbe ovalaire. . . à cavité intérieure dilatée."

[**] De Man, 1907, p. 68.

[***] See p. 184, Part I.

[†] Rhabditis monohystera according to Bütschli (1873, p. 107)

[††] 1880, p. 104.

[†††] De Man, 1884, p. 61.

[‡] De Man, 1888, p. 40; Jägerskiöld, 1905.

[‡‡] 6 "Stachelmuskeln" Zur Strassen (1904, p. 30, 308); Cobb, 1893, p. 419.

also possess two marked swellings, also belong to this group. Two swellings of the esophagus, but without longitudinal muscles, are also present in Draconema (Table 8, Figures 55a, b, 56; details on p. 190, Part I). This anterior part is sometimes separated by a constriction from the rest of the esophagus (Monoposthia and others). Such a separation is rare among Enoplidae. Enoploides amphioxi Fil. is such an example (Table 2, Figure 12a, b).

The internal tube of the esophagus is formed by the cuticle, which differs 459 sharply from the cover of the head. According to Cobb, it refracts light doubly.[*] It is triradiate in section, as the dorsal and two subventral sectors form angles which project inwards and the folds between them project towards the periphery.

There are sometimes swellings in the form of longitudinal bands, which are clearly visible only in sections (Leptosomatini[**]). There may also be widenings of the esophagus, to which muscle fibers run radially, e. g., in Leptosomatum and related forms (Table 1, Figures 1a–a, 3b–d[***]). There are small denticles in Tripyla and Trilobus[†] whose function is not clear, though possibly to break up swallowed particles. There is a second such structure behind the buccal cavity in Plectus cirrhatus Bast. – a widening of the esophagus with thickenings at the internal angles.[††] There is a wide cavity in Araeolaimus, sometimes with a double lumen, and some muscles are apparently attached at this point externally to the esophagus.[†††] Rauther[‡] found radial striation of the cuticle of the esophagus in Cylicolaimus and Fiacra and suggested that there are numerous small pores through which fluid is discharged into the esophagus.

The esophageal tube may not be widened in the bulb, e. g., in Dignathonema (Table 75, Figure 40f), or the widening is small (Metachromadora, Chromadorella and others), or there may be distinct lenticular cavities – indentations of the internal rays of the esophagus – which may be simple or double (Spilophorella). Such a widening, not in the middle but behind the bulb, has been described for Metalinhomoeus.[‡‡] There are denticles in the bulb in many genera of Anguillulidae (Rhabditis and related genera[‡‡‡]) or small punctations and hooks (Plectus[★]). This apparatus is in constant movement in living nematodes, acting as a pump which forces the food into the intestine and crushes hard particles during passage.[★★] Denticles in the bulb are also common in parasitic nematodes.

---

[*] 1916, J. Parasitol., 2, p. 118; see also Martini, 1916, p. 198.

[**] See de Man, 1904, p. 31; Türk, 1903, p. 310; Rauther, 1907, p. 730.

[***] See also de Man, 1893, p. 105; Jägerskiöld, 1901.

[†] De Man, 1884, pp. 10, 74 and pp. 27, 34, Part I of this work; Bütschli, 1873, p. 50, 53

[††] De Man, 1884, p. 110, Table 17, Figure 68.

[†††] See de Man, 1878, p. 107, 1888, p. 15.

[‡] 1907, p 730

[‡‡] De Man, 1907, p. 83.

[‡‡‡] Bütschli, 1873, p. 98; Strubell, 1888, p. 21, Heterodera; Cobb, 1898, 2, p 2; Hallez, 1900, p. 600, Anguillula; Eva Krüger, 1912, p. 92; Steiner, 1916, p. 520, Rhabditis marina Bast.

[★] De Man, 1904, p. 10; Micoletzky, 1914, p. 456.

[★★] Chernai, 1849, p. 288; Pérez, 1866, p. 192.

---

The structure of the esophagus of some species of Enoplidae is interest-
460 ing (Phanoderma, "Thoracostoma" setigerum Marion, some species of Oxystoma,[*] "Enchelidium" polare Steiner,[**] Symplocostoma, Enoploides, Enoplolaimus, one species of Enoplus,[***] Stenolaimus[†] and Linhomoeus[††]). The esophagus has an undulating outline, particularly in the posterior part. This is apparently due to the fact that the cells are not fused into a dense syncytium but remain isolated, as recorded by Bütschli.[†††] The plasmatic chords, formed by the angle cells, have processes which are inserted between the muscle cells. This is particularly evident if the chords are pigmented (Enoploides, according to Bütschli). Some authors thought that these cells are circular muscles in Phanoderma,[‡] or described them as a special cover of the esophagus.[‡‡]

The plasmatic chords of the angle cells are adjacent to the external angles of the lumen of the esophagus. They have often been considered as glands, e. g., by Marion, and Bütschli; only de Man (1886) established that they are different. They often contain pigment, forming processes to the right and left; the anterior pair of these processes produces the pigment of the eyes in Enoplus (oc., Table 2, Figure 10a). The number of these processes is much larger than that of the nuclei in the angle chords (Rauther). Such eyes are present in Thoracostoma denticaudatum Schn., but the pigment of the esophagus is more weakly developed. Pigmentation is often restricted to one eye (see p. 51). There are sometimes pigment stripes in Leptosomatum, but they are straight and without lateral processes (Table 1, Figure 1b). A distinct swelling anterior to the esophagus of Enchelidium corresponds to the accumulation of pigment. Sometimes not only the angle chords but also the muscle
461 cells themselves are pigmented, e. g., in Paroncholaimus.[‡‡‡] In Oncholaimus dujardini de Man, the anterior part is colorless, but the area behind the esophagus is filled with pigment, the pigment being less dense posteriorly.[★]

In some nematodes, particularly in males, the muscle fibrils are reduced. They have disappeared completely or almost completely in Leptosomatum,[★★] in some species of Tylenchini[★★★] and in Araeolaimus cobbi Steiner.[•]

Two parts in the esophagus may be distinguished in many forms: it is narrow anteriorly and the muscle fibers are reduced and it is wider posteriorly and the musculature is normally developed. Forms with a

---

[*] Bütschli, 1874, p. 35.

[**] 1916, p. 597.

[***] Filip'ev, 1916, p. 102.

[†] Southern, 1914, p. 23.

[††] Bütschli, 1874, pp. 12, 32.

[†††] 1874, p. 12.

[‡] Marion, 1870, pp. 15, 19.

[‡‡] Eberth, 1863, pp. 6, 38.

[‡‡‡] See also Rauther, 1907, p. 713.

[★] See p. 95, Part I.

[★★] See p 30, Part I, and Table 1, Figure 1b

[★★★] Bütschli, 1873, p. 42; Cobb, 1914, p. 220, 223.

[•] 1916, p. 637.

narrow anterior end are Symplocostomini (see particularly Table 6, Figure 33a) and Oxystomini (Table 2, Figure 3a). The same is the case in Dorylaimini, where the posterior swelling is usually well marked and elongate, but there are also rounded swellings (Aulolaimus[*]). The tube of the esophagus of Aulolaimus is apparently round to the bulb; this is also the structure of the esophagus in Aegialoalaimus.[**] Mermithidae, particularly their larvae, also resemble Dorylaimini in the structure of the esophagus (Steiner). The short anterior part is completely without musculature, in Enchelidium.

There is instead a marked pigmented widening, and behind it a part with little-marked fibrils and the musculature well developed only behind the nerve ring (Table 4, Figure 28a, b). In Dorylaimus tenuicollis Steiner,[***] the anterior part without muscle fibers is separated by a sharp constriction from the posterior muscular part. The same has been described for Odontolaimus.[†] There are also two parts in Odontopharynx, but both are muscular.[††] See also the remarks on p. 68.

There are often two swellings of the esophagus, sometimes even two bulbs, in Anguillulidae; there is usually a muscular posterior and glandular anterior part. If in the posterior swelling, the anterior bulb is well developed, the musculature of the posterior bulb is usually reduced and its main mass is occupied by glands (Tylenchus, Diplogaster[†††]). The sharp boundary between the posterior part and the midgut has disappeared in Aphelenchus. This part is then distinguished by its light color, but the position of the nerve ring proves that it belongs to the
462 esophagus.[‡] The esophagus is apparently not separated from the midgut in the doubtful Macroposthonia.[‡‡]

There is frequently a special differentiated part at the posterior end of the esophagus – the cardia of Cobb ("Zwischenstück" of the German authors[‡‡‡]). This part consists of cells which are usually without musculature and is well defined; it projects into the beginning of the midgut with three lobes and acts as a valve, preventing regurgitation of food. Rauther considers this to be the epithelial part of the esophagus,[*] which is more muscular in other cases, e.g., in Mermis. It is well developed in Enoplidae and some Monhysteridae (Comesomini). There are numerous nuclei in Paroncholaimus vulgaris[**] and Fiacra.[***] Circular muscle fibrils have also been described in Fiacra. There are also muscle fibers (belonging to three cells) in Enoplus, and the folds of its three lobes are tightly pressed together. Steiner[*] recorded chitinized rods in the cardia of Lept. sabangense, which are absent or almost absent in the Chromadoridae, particularly in forms with a large bulb.

The posterior part without fibrils of the esophagus of Anguillulidae (see above) should not be considered as the cardia; this name refers only to the part behind the posterior bulb. De Man[**] compared the appendage behind the bulb in Desmolaimus zeelandicus with these formations. However, it is situated here behind the posterior bulb and is therefore a true cardia. He described the same for Linhomoeus and Metalinhomoeus.[***]
463 A very large cardia, which forms a "pseudobulb," has been described by Cobb for Trypila lata (1914, p. 83). Among the Anguillulidae, a true cardia is present in Plectus and is sometimes very long.[†] Such formations are probably the three "glands" at the posterior end of the esophagus in Trilobus; they were recorded by Bastian, who named the genus after these lobes.[††] Martini described an "Epithelabschnitt" of the esophagus in Oxyuris, which consists of three annular rows of cells – the first consisting of one gland cell, the second of two gland cells and the third of two epithelial cells. He proposed the name "glandular stomach," ("Drüsenmagen") for the entire part, which is hardly suitable.

The esophageal glands (salivary glands according to many authors) are situated in the middle of the sectors of the esophagus and are common. The anterior part of the gland is simple. They are branched posteriorly between the muscle cells of the esophagus, sometimes forming an entire net.[†††] The dorsal gland is usually different from the two subventral glands. Rauther[‡] found that in Fiacra and Cylicolaimus the narrow duct of the dorsal gland extends further posteriorly than in the subventral glands. The glands are multinucleate in these genera; the subventral glands contain 11 nuclei each, the dorsal glands only 4. The data for parasites are similar. Martini describes only 7 glands in Oxyuris – one dorsal gland and three pairs of subventral glands.[‡‡]

The glands open into the buccal cavity and sometimes form large reservoirs (see Table 1, Figure 5b; Table 2, Figure 12b, gl. oes.). There is sometimes a difference between the dorsal and subventral glands in the situation of the pores. Thus, the pores of the subventral glands are situated more anteriorly in Leptosomatini and Anticoma and those of the dorsal gland more posteriorly (Table 1, Figures 1a, 2a[‡‡‡]). The pores are frequently situated on the hooks of the buccal cavity (Oncholaimini, some species of Enoplini, Cobbia, see p. 60). One of the glands of

---

[*] De Man, 1884, p. 78.

[**] De Man, 1907, p. 35.

[***] 1914, p. 274.

[†] De Man, 1884, p. 127.

[††] De Man, 1912, p. 639.

[†††] Bütschli, 1873, p. 32; 1874, pp. 20, 22; de Man, 1884, pp. 85, 87; Marcinowski, 1908, p. 416.

[‡] Bütschli, 1873, p. 45; Steiner, 1916, p. 562. Jägerskiöld's remark that the bulb is caused by the accumulation of glands posteriorly obviously refers to such bulbs which are also present in parasites. This is a purely muscular structure in other nematodes.

[‡‡] De Man, 1884, p. 124.

[‡‡‡] Looss (1905, p. 95) terms this part in Ancylostoma "intestinal valves" and considers it a part of the intestine, and not of the esophagus.

[*] 1909, p. 554 "epithelialer Abschnitt am Hinterende des Oesophagus."

[**] Rauther, 1907, p. 715.

[***] Türk, 1903, p. 311.

---

[*] 1915, p. 228.

[**] 1884, p. 51.

[***] 1907, pp. 77, 83.

[†] De Man, 1884, 1904, p. 11.

[††] Bastian, 1866, p. 575; Bütschli, 1873, p. 53.

[†††] Türk, 1903, Table 11, Figure 10; Rauther, 1907, p. 731. According to Looss, the three glands unite behind the branches in Ancylostoma (p. 38, 89).

[‡] 1907, p. 731.

[‡‡] 1916, p. 249.

[‡‡‡] See also de Man, 1893, p. 105, 1904, p. 39; Türk, 1903, p. 310.

464 Symplocostomini apparently opens on the subventral spine (see p. 61). According to Zur Strassen,* the dorsal gland of Solenolaimus ends blindly at the base of the buccal cavity (spine) and the two subventral glands open inside it.

In addition to the three usual glands, Rauther also found paired lateral glands in many species of Enoplidae which stain less intensely than the others. They are situated in the upper part of the subventral sectors and open in the middle of the esophagus in Paroncholaimus. The position is the same in Enoplus, but the duct extends forward and its opening may be the "cephalic slit" of these forms (see p. 29); in Fiacra and Cylicolaimus the duct extends to the buccal end and the main part of both glands is situated in the dorsal sector. Rauther suggested that the "cephalic glands" described by Looss for Ancylostoma may be homologous to them; however, they are not connected with the esophagus in this genus. Only de Man made an observation on these glands earlier; he recorded three openings of glands in the dorsal sector in Leptosomatum.**

Rauther*** described for Paroncholaimus a system of special vacuoles next to the esophageal glands; they form a canal which carries excretions accumulated in the esophagus into the buccal cavity.

The nature of the intensely staining bodies immediately behind the buccal cavity in Pelagonema and Fimbrilla is doubtful. They may be some type of gland (Cobb, 1893, pp. 391, 420).

These glands were first described in parasitic nematodes by A. Schneider (1866). They were described by Marion (1870) in free-living nematodes, but he believed that they open behind the esophagus. Bütschli (1874) observed only pigment stripes, not noticing the glands, and related Marion's observations to them, without paying attention to their position opposite
465 the angles and not opposite the sectors of the esophagus. De Man (1886) already gave a correct interpretation of the relationships. Rauther (1907) discovered the lateral glands of the esophagus.

In principle, the structure of the esophagus is the same in parasites. The external appearance of almost all described forms has developed independently. The marked reduction of the musculature of the esophagus in Trichosomatidae and Mermithidae is noteworthy.

The form of the esophagus is a very convenient systematic character, but is not of great importance. Closely related forms frequently have a markedly different shape of esophagus, e. g., many species of Chromadoridae; Linhomoeus without a bulb and Metalinhomoeus with a bulb are closely related, and also Symplocostoma hexabulba Fil. However, some forms of esophagus are present only in certain groups, e. g., the median bulb of Anguillulidae. The absence, almost without exception, of a bulb in Enoplidae may be mentioned again. The slender form of the esophagus may eventually be used for the definition of larger groups.

---

* 1904, p. 307.

** "Au côté dorsal. . . j'ai observé trois tubes de sortie au lieu d'un seul, comme d'ordinaire" (1893, p. 105).

*** p. 715.

† For bibliography, see Rauther, 1909.

---

## D. Intestine

The midgut of free-living nematodes is a tube consisting of a single layer of cells. In free-living nematodes, it does not have the flattened form which is characteristic for parasites. It is always straight and there are no diverticula, as in some species of Ascaris and Oxyuris. It is usually markedly narrower near the genitalia. There is sometimes an inner cuticle, smooth or radially striated (Enoplus, according to Rauther); in Siphonolaimini, this tube is separated from the epithelium and floats freely in the lumen of the gut, a result of degeneration. The cells are bare in other cases and project into the lumen, so that it sometimes
466 becomes irregular (Symplocostoma hexabulba Fil., Enchelidium bierstedti, according to Marion*). There is a basal membrane on the outside formed partly by the cells of the midgut and partly by connective tissue (Martini**).

The number of cells varies greatly. Their number is very great in large marine forms (Paroncholaimus). On the other hand, there are very few cells in the predaceous Halichoanolaimus, Demonema*** and Dignathonema, in which the cells are very large and swollen like a vesicle. The cells of Dignathonema appear to be empty; only a few are filled with a dark substance. Large cells are also present in Enchelidium longicolle Fil. The midgut of many species of Monhystera consists of only one or two rows of large cells; two rows are present in Chromaspirina pontica Fil. and in many species of Rhabditidae.† Characteristic cells are sometimes present between the normal cells. They probably have a different function.††

Marion and Bastian considered the cells of the intestine as hepatic cells and the inconstant internal cuticular tube as the true intestine.

There are inclusions in the cells of the midgut, probably for the most part reserve food. Cobb (1914) made a detailed study of them in Rhabditis. They consist of organic material which forms spherocrystals with double refraction. Cobb called this substance "rhabditin." Yellow fat globules have been described in the gut of Hypodontolaimus.†††

Prolonged vital staining also stains the granules in the midgut, so that
467 it is possible that the midgut also takes part in excretion (Shimkevich, 1894, 1897; Rauther, 1907). Nasonov showed that indigo and iron are discharged by the midgut, but not by phagocytic cells.

The color of the intestine depends on the inclusions. If they are colorless, it is grayish, usually also brownish or reddish; in "Enoplus" coeruleus Eberth it is blue, but its color may vary in the same species, depending on the habitat. Thus, in Paroncholaimus zernovi Fil. the midgut is markedly darker in individuals from the Georgievskii Monastery than in the same species from Kruglaya Bay. The color of the intestine of Solenolaimus and Siphonolaimus is dark purple, almost black. The midgut of Theristus, Sphaerolaimus and many other forms is dark.

---

* 1870, p. 9.

** 1916, p. 298.

*** Cobb, 1893, p. 392.

† Bütschli, 1873, pp. 32, 59; de Man, 1888, p. 5; Maupas, 1901, p. 480 ff.

†† Eberth, 1863, p. 9; Savel'ev, 1912, p. 112; Maupas, 1901, p. 480.

††† G. Schneider, 1906, p. 32.

It is characteristic for Dorylaimus that a posterior part of the midgut (praerectum of Cobb) is light, with the anterior part dark.[*] This was also recorded by Martini for Oxyuris. In some freshwater forms there is a similar differentiation at the beginning of the midgut. Cobb calls this the "cardiac" part of the gut.[**]

There are sometimes glands in the anterior part of the midgut. These are probably the four anterior large cells of the intestine of Dignathonema. According to de Man (1886), this gland is multicellular in Euchromadora. He also found it in Tripyloides. Bütschli[***] recorded such glands for several species of Monhystera. According to Zur Strassen, there are four pockets in the midgut around the cardia in Solenolaimus which resemble the coelomic pockets in sections. The posterior part of the intestine of parasites is sometimes surrounded by characteristic branched "intestinal" muscles (see p. 55).

There is sometimes degeneration of the intestine, e. g., in the males of
468 Leptosomatini, in which the midgut is narrow (see p. 30, Part I). In this case, a kind of shiny crystal, probably reserve food material, is deposited around the midgut. Marion described degeneration of the midgut in Eurystoma.[†]

The midgut of the female of the plant parasite Heterodera grows to a very large size, occupying almost the entire interior of the body (Strubell, 1888).

There are also large- and small-celled intestines in parasites. The internal cuticle is apparently always present.

The presence or absence of this cuticle could probably be used as a systematic character.

## E. Hindgut

The hindgut (rectum) is morphologically an invagination of the external cuticle. This is proven by the fact that the cuticle of the rectum molts together with the external cuticle and that both are in direct connection and do not differ chemically like the cuticle of the esophagus.[††] The genital duct discharges into the hindgut of the male, so that it is a cloaca. It is dorsoventrally flatened, corresponding to the shape of the anal slit. The hindgut is usually short, narrow posteriorly, widened anteriorly and separated by a marked constriction from the midgut. It is usually well developed in marine forms, and less developed in freshwater forms, particularly in Anguillulidae, and Siphonolaimini.[†††] The constriction is surrounded by the rectal sphincter, which consists of a single muscle cell. This sphincter is strongly developed in Leptosomatini.[‡]

---

[*] Bütschli, 1873, p. 24; 1876, p. 381; de Man, 1884, p. 164 ff.

[**] "Cardiac portion of the intestine" in Microlaimus fluviatilis, Alaimus (1914, pp. 82, 86).

[***] 1873, p. 58.

[†] 1870, p. 58

[††] See also Voltzenlogel, 1902, p. 483; Looss, 1905, p. 94; Martini, 1916, p. 308

[†††] Zur Strassen, 1904, p. 309.

[‡] Jägerskiöld, 1901, pp. 16, 43; Türk, 1903, p. 313; de Man, 1904, p. 32. The sphincter usually surrounds the end of the midgut in parasites (see Voltzenlogel, 1902).

469 The anus is a transverse slit and is rarely situated on a tubercle – the anal protuberance (short-tailed Oncholaimini, Table 3, Figure 18ff., Desmoscolecidae[*]). The hindgut passes obliquely to the anus, so that the posterior part of its ventral wall sometimes forms a thin plate, forming a valve at the entrance to the hindgut (Table 7, Figure 44c). The posterior wall is usually swollen in the form of a low transverse ridge. There are usually sensory bristles around the anus.

The hindgut and the anus are reduced in some forms, e. g., in degenerating males of Tylenchulus semiparasiticus Cobb.[**] The same is caused by histolysis of the tail of Linhomoeus and Siphonolaimini (see p. 5).

The anal glands open in the hindgut of very many, if not all, nematodes (glandulae anales). They were already observed by Bastian. They have been found in the following groups: Leptosomatini,[***] Enoplus,[†] Anticoma,[††] Trilobus,[†††] Cyatholaimus,[‡] Linhomoeus,[‡‡] only in female (Table 10, Figure 70c), Anguillulidae.[‡‡‡]

The structure of the hindgut is best recognized in the large parasitic nematodes. According to Voltzenlogel (1902), the epidermis of the hindgut of Ascaris, in contrast to the external "subcuticle," consists of distinctly defined cells. There are 4 large cells anteriorly (3 dorsal and one ventral) and a second ring of 6 cells (3 large gland cells and 3 smaller
470 ventral cells). This was also confirmed by Goldschmidt.[★] Looss[★★] found only 6 cells in Ancylostoma (2 rings of 3 cells) and named them the ligamentum intestino-rectale, rejecting their glandular character. Martini[★★★] described 7 cells in Oxyuris, the anterior three forming an anterior ring and the posteior four arranged one behind the other; in addition, there are three further glandular cells which are of different structure in males and females. Martini thought they had an excretory function, homologous to the Malpighian tubules of arthropods and to the protonephridia of Rotifera.

The musculature of the hindgut of the female consists of one or two dilatatori recti. Two branched cells with fascicles of fibrils have been described in Ascaris, branching in all directions (Gilson and Pantel, Voltzenlogel). There is usually also one cell with two fascicles, united by an H-shaped plasmatic part.[•] This cell apparently raises the rectum and dilates it. There are two further ventral cells in Oxyuris (Martini). In free-living forms,[••] two unicellular muscles are attached to the anus;

---

[*] See drawing of Shchepot'ev, 1908, Table 6, and of Steiner, 1916.

[**] 1914, p. 224.

[***] Türk, 1903, p. 305; Steiner, 1916, p. 615.

[†] De Man, 1886; Filip'ev, 1916, p. 100

[††] Bastian, 1866, p. 582.

[†††] Bütschli, 1873, p. 55.

[‡] Bastian, 1866, p. 582.

[‡‡] Ibid

[‡‡‡] Claus, 1863, p. 356; Bütschli, 1873, p. 108; Hallez, 1900, p. 603; Maupas, 1901, p. 508; E. Krüger, 1913, p. 94.

[★] 1916, p. 317.

[★★] 1904, p. 85.

[★★★] 1905, p. 96.

[•] E. g., in Ancylostomum – musc. anorectalis Looss (1905, p. 98); in Oxyuris, see Martini (1916, p. 321).

[••] See de Man, 1886, 1904; Jägerskiöld, 1901, p. 16; Türk, 1903, p. 313; Steiner, 1916, p. 16.

they function as levator ani. The other end of these cells is attached to the dorsal border of the lateral field. In view of the different function, these muscles are best named rectal muscles (musc. rectales).

### F. Digestion

Little is known about the digestion of nematodes. The predacious *Mononchus* (according to Cobb) and *Dignathonema* digest complete 471 nematodes, including the cuticle, with the exception of the spicules and hard parts of the buccal cavity. In *Dorylaimus brigdammensis* de Man I observed that the pigment of digested algae remains unaltered in the anterior part of the midgut, but becomes brown in the posterior part.

The reaction of different parts of the body of free-living nematodes was determined by placing them in litmus. It appeared (G. Schneider, 1906; Shimkevich, 1899) that the esophagus and the hindgut have an alkaline reaction, while the midgut is strongly acid. This agrees with data on parasites (Nasonov, 1897).

Interesting data are given by Cobb[*] in observations on cultures of *Rhabditis*. He frequently observed that nematodes ingested air; he bred several generations on pure agar and came to the unexpected conclusion that they assimilate part of the absorbed nitrogen.

The esophagus and midgut certainly take some part in excretion (see pp. 67 and 75).

## 3. REPRODUCTIVE SYSTEM

Both parasitic and free-living nematodes are dioecious. Hermaphroditism (see below) is rare and clearly of secondary origin. There is a lack of descriptions of the reproductive system and not all species have been described from mature individuals of both sexes. Material is also often badly preserved, and the genital organs are not recognizable. The available data, particularly on the male genitalia, are therefore not sufficient to allow any conclusions to be drawn.

### 472 A. Male Genitalia

The male genitalia (see Table 7, Figure 42k) consist of one or two testes ((a) in Figure 42k ) opening into the seminal vesicle (b), which is not always developed. The vas deferens is attached (c, d) directly to the seminal vesicle or the testis. The vas deferens has a regular arrangement of cells. The posterior part of the duct is provided with musculature and forms the ejaculatory duct (e), which opens into the cloaca. This terminology was given by de Man (1886).

---

[*] 1915, Journ. Parasitol., 21, p. 154.

The copulatory apparatus, the spicules, which are situated in special pouches, also open into the cloaca. Special movable or immovable structures chitinized in the cloaca or in the pouches of the spicules guide and strengthen the movement of the spicules. They are called the gubernaculum. These parts are moved by a complex musculature. In addition, a row of accessory glands and papillae or bristles are present at the outside of the posterior end of the male.

a. **Testes.** There are one or two testes; the primitive condition is paired testes, and one testis may become reduced. This is not connected with the paired or unpaired condition of the female genitalia. Compared with parasitic nematodes, the testes of free-living nematodes are always very short, thick and straight; only for Anguillulidae have long testes been described, like those of parasites.[*] If there are two testes, the anterior projects forward while the posterior curves backward and is almost always much shorter. This is secondary, and connected with the elongate form of the body: the primitive condition is symmetrical testes (see below, p. 89 ). Cases have been described in which the tip of the posterior testis is recurved and its end directed anteriorly.[**] If there is only one testis, 473 it is usually the anterior, rarely the posterior.[***] Enoplidae almost always have two testes[†]; Chromadoridae usually have one testis[††]; one or two testes are equally common in Monhysteridae.[†††]

The anterior end of the testis is closed, with a short syncytium situated here at the end, producing the spermatogonia which fill its posterior part. Ripe sperm is already present in the posterior end in *Cylicolaimus*[‡] and *Trilobus*[‡‡]; in forms which have a seminal vesicle it is only present there. A rhachis, which corresponds in parasitic nematodes to the syncytium of the free-living nematodes, is apparently absent, except in Anguillulidae. The testis is covered with a thin, delicate epithelium, and outside it there is a thin membrana propria. According to de Man,[‡‡‡] the epithelium consists of longitudinal fusiform cells placed obliquely. However, Bastian described such an epithelium only in the anterior part of the testis in *Enoplus brevis*, and a flat epithelium in the posterior

---

[*] Bütschli, 1873, p. 35; Strubell, 1888

[**] *Onyx* according to Cobb (see p. 156, Part I), *Anticoma* according to de Man (1886, p. 56).

[***] *Monhystera stenosoma* according to de Man (1907, p. 38), *Desmoscolex* (Shchepot'ev, 1908, p. 50), various Anguillulidae (Claus, 1863, p. 356; Hallez, 1900, p. 606; Ditlevsen, 1911, p. 241).

[†] Exceptions are very rare: the posterior testis is only a very short appendage in *Oncholaimus campylocercus* de Man (see p. 97, Part I); single testes have been described for *Tylencholaimus* (Brakenhoff, 1914, p. 297) and *Tripyloides* (de Man, 1886, p. 64).

[††] Double testes are also not rare: *Tripyla* (Bütschli, 1873, p. 51); *Camacolaimus* (de Man, 1890, p. 196); *Halichoanolaimus* (Bütschli, 1874, p. 17); *Monoposthia* (de Man, 1890, p. 196); *Onyx* (Cobb, 1891, see p. 217); *Spilophorella* (de Man, 1888, p. 46); *Rhabdogaster* (Shchepot'ev, 1908, p. 62; there is confusion of terminology in the various parts in his work); *Draconema* (p. 195, Part I); Mechnikov, 1867, describes one testis

[†††] Two testes in *Linhomoeus*, *Terschellingia*, *Sphaerolaimus* (de Man, 1890, p. 207, 1907, pp. 42, 55, 77), *Axonolaimus* (p. 232, Part I), *Penzancia* (Steiner, 1916, p. 647; p. 203, Part I); one in *Monhystera*, *Theristus* (Bütschli, 1873, p. 60; de Man, 1888, p. 9; 1890, p. 183).

[‡] Jägerskiöld, 1901, p. 17.

[‡‡] Brakenhoff, 1914, p. 285.

[‡‡‡] 1886, pp. 6, 22.

part.[*] Jägerskiöld[**] described a thin, flat epithelium on the entire testis in Cylicolaimus.[***]

474 The posterior end of the testis is connected either directly with the histologically distinct vas deferens (Enoplidae) or gradually changes its structure towards the seminal vesicle.

The spermatozoids do not have flagella; they have an amoeboid movement and are sometimes very small. Bastian distinguishes several slightly different forms.[†] They sometimes contain shining rods.[††] Needle-like crystals inside the testis have been observed in Anguillulidae.[†††]

b. **Efferent ducts.** These have hardly been studied and there is no special terminology for them.

The vas deferens of Leptosomatini, studied by Jägerskiöld,[‡] is connected with the testes; it consists of the anterior sperm-filled part of numerous small cells with indistinct boundaries; the cells are less numerous posteriorly and the boundaries are more distinct. A neck[‡‡] then follows and behind it the ejaculatory duct, which consists of two rows of longitudinally compressed cells. There is no musculature anteriorly but it is strongly developed posteriorly. This is the longest part of the genital duct. The musculature of Fiacra acuticaudata is more weakly developed. Türk[‡‡‡] finds the same relationships in related forms. I observed the same in Thoracostoma denticaudatum Schn.[★]

According to de Man,[★★] the epithelium of the vas deferens of Enoplus consists of numerous cells. There is also a neck, which he interpreted as a sphincter. The musculature of the ejaculatory duct begins immediately behind the neck. The epithelium has two rows posteriorly, but there are more numerous rows anteriorly; sometimes there are characteristic
475 glandular (?) cells. I observed the same relationships in Enoplus behringicus Fil.[★★★]

De Man[•] distinguished in Adoncholaimus a vas deferens, a neck with thickened walls and partly cylindrical, partly fusiform epithelial cells, which is followed by the ejaculatory duct without a regular epithelium. According to Stewart[••] the ejaculatory duct of Paroncholaimus is very long and only barely swollen in the beginning; the epithelium consists of many rows of cells and the musculature is weak.

---

[*] Ibid., p. 21.

[**] 1901, p. 17.

[***] See also Türk, 1903, p. 314; Stewart, 1906, p. 121.

[†] 1866, p. 66. Two types of sperm were distinguished by Cobb in Tylenchus polaris (1914a, p. 15).

[††] Bütschli, 1873, p. 100.

[†††] Maupas, 1901, p. 545.

[‡] 1901, pp. 16, 45.

[‡‡] Cobb's observation probably refers to the cells of the neck (1898b, p. 51): "Near the ejaculatory duct, the epithelium bears projections having amoeboid movements or cilia having active vibratile motions."

[‡‡‡] 1903, pp. 314–318.

[★] 1916, p. 92.

[★★] 1886, pp. 22, 30.

[★★★] 1916, p. 99.

[•] 1886, p. 44.

[••] 1906, p. 122.

According to de Man,[*] there is no sharp boundary between the different parts in Anticoma; the neck is absent and the musculature of the ejaculatory duct is weak. There are glands in the middle of the genital tube. Two large testes are connected with a wide vas deferens in Trilobus gracilis Bast.,[**] joined by narrow ducts almost at the same point; then follows the neck (or sphincter) and a short ejaculatory duct. The vas deferens of Tr. pellucidus Bast.[***] is narrow and forms several coils, but the ejaculatory duct is much longer. The cavity of the large testes acts as a seminal vesicle.[†] De Man[††] described a sharp transition of the narrow vas deferens into a wide but short ejaculatory duct in Tripyloides.

According to de Man,[†††] the cells become gradually less numerous posteriorly in Euchromadora, and the posterior end has a weak musculature. The vas deferens of Monoposthia ends in a blind sac, and both testes open into it further posteriorly.[‡]

The testes (a) of Metachromadora (Table 7, Figure 42k[‡‡]) form a short appendage of the wide seminal vesicle (b), which has a large epithelium and
476 a large cavity. The anterior part of the vas deferens does not differ in structure from the vesicle, but its lumen is narrower and there follows a part (c, d) with two rows of cells. The arrangement in the anterior part (d) is not quite regular. The posterior part (e) is surrounded by musculature and represents the ejaculatory duct. The structure in Onyx,[‡‡‡] is the same. A wide seminal vesicle is also present in Spirina, Penzancia and Axonolaimus.[★] The anterior part of the vas deferens of A. setosus Fil. is completely filled with granules, so that it appears dark; the ejaculatory duct tapers gradually. The dark parts of the genital duct are also present in Cyatholaimus elongatus de Man,[★★] but are not always present in Metachromadora.

I do not present the complete observations of other authors. I mention only that the original structure of the ejaculatory duct was already known to Marion.[★★★]

Accessory glands are rarely present, usually opening in the posterior part of the ejaculatory duct; they are particularly well developed in Anguillulidae,[•] and have also been described for Desmoscolex[••] and Euchromadora.[•••]

---

[*] 1886, p. 56.

[**] Bütschli, 1873, Table 4, Figure 23a.

[***] Brakenhoff, 1914, Table 1, Figure 4.

[†] The relationships are also the same in Tr. longus Leidy, according to Cobb (1914, Table 6, Figure 6).

[††] 1886, p. 64.

[†††] 1886, p. 73.

[‡] De Man, 1889, p. 196.

[‡‡] p. 160, Part I.

[‡‡‡] p. 155, Part I, and Cobb, 1891, p. 152.

[★] See also p. 168, Part I.

[★★] 1907, p. 72.

[★★★] 1870, p. 75.

[•] Pérez, 1866, p. 227; Bütschli, 1873, pp. 108, 110; Oerley, 1886, p. 18; Fuchs, 1915, p. 144.

[••] Shchepot'ev, 1906, p. 50.

[•••] De Man, 1886, p. 73.

Voltzenlogel[*] described a network of muscles of the ejaculatory duct in Ascaris – branches of the two dilators of the hindgut.

c. **Copulatory apparatus.** This consists of the paired spicules and the gubernaculum. The spicules are situated at the bottom of a pouch, which is an evagination of the cloaca.[**] The spicules are hollow chinitized
477 structures, usually curved. The chitin of the spicules is solid, often yellow (Enoplus and other large species of Enoplidae) and not soluble in KOH.[***] There is a cytoplasmic core; some of the cells of the core belong to the epidermis which forms the spicules.[†] The structure of the spicule is sometimes rather complex. The spicules have a capitulum and a swollen base, a lumen and longitudinal ridges (costae), and there is a special modification – a thin membranous flange in the curve of the spicule. Muscles are attached to the spicules, which extrude them from the cloaca. Marion[††] described the copulation of Enoplus, and stated that the spicules enter deeply into the vagina. Bütschli[†††] observed copulation in Rhabditis, which has a bursa; the spicules do not enter the vagina in this case, but only make probing movements. The difference between these observations is apparently explained by their objects. Species with a bursa copulate with longer and stronger movements than species without a bursa.[‡]

The term gubernaculum of Looss (accessory organ of most other authors[‡‡]) refers to chitinized thickenings in the wall of the cloaca or in the pouches of the spicules; they are of varying form and guide the spicules sometimes dorsally, sometimes ventrally and sometimes laterally, and sometimes enclose the ends of the pouches of the spicules from both sides. It usually consists of one or two pieces and is rarely absent. Some of its parts may be movable and project from the cloaca together with the spicules, but it is usually immovable. Its purpose, as the term of Looss indicates, is to control the movement of the spicules and give them stability. The literal translation of this term – "rulek" ("rudder") – will perhaps be used in Russian.

478 A compound musculature is attached to the spicules, gubernaculum and walls of the cloaca in the male (see p. 85).

If the numerous different descriptions are compared, several types of copulatory apparatus may be distinguished. These types have to be defined mainly according to the spicules; the less constant gubernaculum can be used only for the definition of smaller subdivisions.

**Simple type:** these are curved, short spicules, which are present in the majority of genera in all families. The following subtypes may be distinguished:

**Simple wide** spicules, sometimes with several facets, e. g., in Leptosomatum (Table 1, Figures 1d, 2d), some species of Enoplus (Table 2,

---

[*] 1902, p. 493.

[**] "Spiculascheide"; Jägerskiöld (1901, p. 24) recorded that it is sometimes little marked; Türk (1903, p. 320) denies their presence.

[***] Jägerskiöld, 1901, p. 23.

[†] Cf. Voltzenlogel (1902, pp. 499, 500), 4 cells in Ascaris

[††] 1870, p. 83.

[†††] 1873, p. 110.

[‡] Bütschli, 1876, p. 368.

[‡‡] "Accessorisches Stück, pièce accessoire.

Figure 11e), some species of Enoploides and Enoplolaimus (Table 3, Figure 15d), Paroncholaimus (Figure 18f, h, i, k), Halicholanolaimus (Table 6, Figure 39h), Onyx (Figure 41d) and the freshwater genera Ironus, Dorylaimus and Mononchus. The spicules of Dorylaimus often have complex longitudinal ridges.[*] A complex gubernaculum is present in Paroncholaimus, with some of its parts projecting together with the spicules; it is otherwise rather simple. A similar type is present in Rhabditis and related forms, but the spicules are usually very short.[**]

**Simple membranous** spicules, with a large membranous flange and a small gubernaculum. This type is present in two groups – in most species of Oxystomini and Anticomini (Table 2, Figures 6e, 8d, 9d) and in Chromadorini and Spilipherini, where it is rather widespread, particularly in Spirina and Chromaspirina (Table 7, Figures 45c, 47d). The gubernaculum is always present and is sometimes of complex structure, especially in the Chromadoridae.

**Simple linear** spicules are narrow, curved, simple, without any differentiation and also with a simple gubernaculum; this type occurs in two modifications – thick in some species of Monhysterini and Sphaerolaimus (Table 9, Figure 62 g) and slender in many species of Chromadoridae (Table 8, Figure 55d, Draconema, and also some species of Chromadora, Desmodora,[***] Hypodontolaimus,[†] Camacolaimus,[††] Richtersia[†††] and Desmoscolecidae[‡]). The spicules of the latter are slightly curved, almost of the straight type (see below). The gubernaculum is always present, but usually simple.

**Spicules with complex gubernaculum.** Very characteristic forms are
479 found in many species of Monhysteridae; these are more or less wide spicules with a gubernaculum which has two processes directed posteriorly to which muscles are attached (group Linhomoeus, Table 9, Figures 57b, 58d, 64d, Parasabatieria, Table 11, Figures 78c, 79b, Axonolaimus, Table 10, Figures 70b, 71b, and also Siphonolaimus and Desmolaimus.[‡‡] A similar structure is also present in several species of Monhystera and Theristus. The same form appears independently in a different group: the gubernaculum is the same, with broad spicules as illustrated by Steiner for Enoplolaimus hamatus.[‡‡‡] The spicules of Eurystoma are slender and curved (linear), with hooks at the end, but the gubernaculum is the same (Table 5, Figure 29c, d, f). Finally, several species of Plectus also have such a gubernaculum.[*] There may be some doubt about Plectus, but Eurystoma and Enoplolaimus have so little in common with the Monhysteridae that it has to be accepted that complex forms of gubernaculum have developed independently in these genera.

---

[*] See de Man, 1884.

[**] See Bütschli, 1873; de Man, 1884.

[***] Steiner, 1916, p. 548.

[†] De Man, 1888, Table 4, Figure 18b.

[††] De Man, 1889, Table 5, Figure 2b.

[†††] Steiner, 1916, Table 26, Figure 18b.

[‡] Steiner, 1916b.

[‡‡] De Man, 1884, 1893.

[‡‡‡] 1916, Table 31, Figure 32c.

[*] Bütschli, Table 7, Figure 47b.

A complex gubernaculum is present in several species of Chromadoridae, e. g., Euchromadora (Table 7, Figure 42a), and also in some other genera.[*] The spicules usually have a membrane.

The most complex gubernaculum is present in typical Cyatholaimus (Table 5, Figure 37b, c). The gubernaculum is dark and larger than the spicules, which are transparent, so that it is easily recognized. It is sometimes divided into two parts, but is usually undivided. The anterior part projects anteriorly and the posterior part is broad and covered with characteristic spines. The structure varies in different species.[**]

**The straight type** resembles the simple type, particularly the thick linear spicules, and differs only in its straight form or very slight curvature.

This type is present in its most characteristic form in Viscosia and Oncholaimus s. str. (Table 4, Figures 20c, 23c, 25c). The straight, short spicules in the genera Trilobus, Tripyla, Rhabdolaimus[***] and Nannonchus[†] have to be considered as a special type.

**The broad type** is not common.

It is present in Tripyloides, Bathylaimus and Dolicholaimus (Table 6, Figure 35b, c; see also de Man, 1886, Table 11; 1889, Table 3, Figure 15b, and Cobb, 1893, p. 410).

480 **The compound type** is present in many species of the highly organized Enoplidae.

Leptosomatides (Table 1, Figure 3e, f), Fiacra, Deontostoma, Thoracostoma, Cylicolaimus,[††] also in Triodontolaimus[†††]; the gubernaculum is always of complex structure, often with two dorsal processes. Different spicules are present in some species of Enoplus (Table 2, Figure 10d, e), where they are strongly curved and have characteristic ridges and cicatrices.[‡] The gubernaculum is also complex.

All these types of spicules are smaller than the diameter of the anus or only slightly larger. The spicules of **the extended type** are markedly larger than the diameter of the anus.

This type is present in Phanoderma (Table 1, Figure 4b), Anoplostoma,[‡‡] Adoncholaimus and Metoncholaimus (Table 4, Figure 27c), Enchelidium (Table 5, Figure 28d), Symplocostoma (Figure 30d), Penzancia (Table 9, Figure 61e), Monhystera,[‡‡‡] Sphaerolaimus (Table 10, Figure 68b) and Comesoma (Table 11, Figures 76c, 77b).

---

[*] "Spilophora" loricata Steiner, 1916, Table 19, Figure 3m; Chromadora sabulicola Fil., Table 8, Figure 50d; "Spilophora' adriatica Daday, 1901, Table 22, Figure 13; Table 23, Figure 1; "Chromadora" papillata Bastian, 1865, Table 13, Figures 247, 248; Spilophorella paradoxa (de Man, 1888), Table 4, Figure 19c.

[**] See de Man, 1889, Table 7, Figures 9c, d; 10e, f; 1890, Table 4, Figure 6c, d, e; 1907, Table 4, Figure 4a, b. A similar structure has been described by Marion for Necticonema (1870, Table J, Figure 2d).

[***] De Man, 1884.

[†] Cobb, 1913, figure in table.

[††] See de Man, 1888, Table 3, Figure 12a; 1893, Table 7, Figure 10d; 1904, Table 9, Figure 8r, s, Table 11, Figure 9n; Jägerskiöld, 1901, pp. 23, 44; Türk, 1903, p. 319; Filip'ev 1916, pp. 73, 92.

[†††] De Man, 1893, Table 7, Figure 12e.

[‡] These notches were described for the first time by Dujardin (1845, p. 234). Better drawings are given by de Man (1886, Table 3, Figures 21, 22; 1904, Table 5). See also Filip'ev, 1916, p. 97.

[‡‡] De Man, 1907, p. 52.

[‡‡‡] De Man, 1888, Table 1, Figure 6.

---

The last type of spicule is **the long type**, in which the spicules are five times longer than the diameter of the anus or even longer.

This type is present in only two groups: some species of Enoploides and Enoplolaimus (Table 3, Figures 12d, 13b[*]) in typical Metoncholaimus (Table 4, Figure 26c, g) and in Oncholaimellus.[**] The spicules are particularly long in Enoploides amphioxi Fil. – 10–12 times longer than the diameter of the anus; the gubernaculum consists of two separate twisted bodies (it is simpler in the other groups) and the end of the spicules bears a characteristic tooth.

The spicules are often of different size, e. g., in Leptosomatides euxina Fil. (Table 1, Figure 3f), Thoracostoma denticaudatum Schneider,[***] Oncholaimellus[†] and Euchromadora vulgaris Bast.[††] This is also reflected in the structure of the gubernaculum.

481 There are rather strange relationships in Monoposthia which are not fully understood. De Man described one large spicule; according to Steiner, there is another single spicule of normal structure in front of this one, so that de Man's spicule is apparently a characteristic gubernaculum, while the true spicule was overlooked. Two spicules have been described in another species, but they apparently correspond to the posterior organ, and not to the anterior spicule (see p. 170, Part I).

The spicules of the parasitic nematodes are generally of the same structure, but belong to even more varied types, which cannot be discussed here for lack of space.

d. **Musculature of the copulatory apparatus.** Jägerskiöld[†††] distinguishes the following unicellular muscles in Cylicolaimus: 1) retractores spiculi from the capitellum of the spicules anteriorly to the dorsal muscle field; 2) protractores spiculi also from the capitellum of the spicule posteriorly, surrounding it – part of them to the gubernaculum and another part to the dorsal muscle field (authors sometimes described a muscular spicule pouch; see Table 4, Figure 27c, pr. sp.); 3) retractores gubernaculi from the gubernaculum to the dorsum; 4) protractores gubernaculi majores from the dorsal side of the capitellum of the gubernaculum to the ventral side and posteriorly; 5) protractores gubernaculi minores parallel to the above but internal to them; 6) dilatatores cloacae from the anus to the dorsum (= musc. anales, see above). Türk[‡] found the same in related forms.

Jägerskiöld (1908) described in Dorylaimus crassoides two pairs of retractores spiculi, branched protractores spiculi, two pairs of retractores, one pair of protractores gubernaculi and a complex dilatator cloacae.

Hallez[‡‡] found in Anguillula aceti only three pairs of muscles (protractor and retractor spiculi and dilatator cloacae). The same was

---

[*] Savel'ev, 1912, p. 112.

[**] De Man, 1890, p. 189.

[***] Filip'ev, 1916, p. 92.

[†] De Man, 1890, p. 189.

[††] De Man, 1886.

[†††] 1901, p. 25.

[‡] 1903, p. 321.

[‡‡] 1900, p. 608.

described by Stewart in Paroncholaimus.[*] I have not studied the
482 genital musculature in detail, but even a cursory examination of the preparations shows that his description is incomplete. All published data on the genital musculature of free-living nematodes give only this information. The protractor and retractor spiculi and the dilatator cloacae are apparently always present; the other muscles are less constant. This requires further study.

The protractor of Ascaris[**] also forms the muscular wall of the sheath of the spicules; in addition, there are two retractors and dilatators of the sheath. According to Martini, the spicule sheath of Oxyuris is fibrous, not muscular, and acts as the exsertor of the spicules. He described four exsertors and two retractors.

e. **Bursal musculature.** This musculature is present in nearly all free-living and parasitic nematodes. Its fibers extend transversely between the dorsal margins of the lateral field and the subventral fields. When they contract, the posterior end becomes flattened, which apparently has some function in copulation. It is particularly well developed in the large Enoplidae (Enoplus, Leptosomatini, Paroncholaimus, Enchelidium), where the number of cells is sometimes very large. The muscle cells are arranged more densely posteriorly, so that there is sometimes hardly any space between them. Some genital muscles are probably modified bursal muscles.

It is difficult to consider the bursal and genital musculature as a common longitudinal muscle. It seems that we must agree with Looss[***] that these are muscles sui generis. Rauther[†] may be correct in suggesting that they are rudiments of a circular or transverse musculature.

f. **External genitalia.**

1. **Bursa.** This name is used for the subventral folds of cuticle on the
483 tail of the male, provided with papillae, which clasp the genital region of the female during copulation. They are present in two groups. A weakly developed bursa is present in Oncholaimellus[††] and Anoplostoma[†††]; it is a fairly long fold, so that the cavity enclosed by it is longitudinal, and the tail is long. The bursa is widely distributed in Anguillulidae, where it bears 9 pairs of papillae; the cavity is usually almost round; the tail is short and pointed, sometimes not projecting behind the bursa.[‡]

2. **Papillae and bristles.** The main papillae and bristles are almost always developed at the posterior end of males. In the rare cases in which they are not visible they are probably present, but small. They are few in number, e.g., in Viscosia (Table 4, Figure 20c) and Leptosomatum.

The usual form of arrangement is straight circumanal rows, e.g., in Enoplus (Table 2, Figure 10c[‡‡]) or some species of Oncholaimus (Table 4, Figure 23c). In Deontostoma and related forms, the circumanal row (Table 1, Figure 3d–a) is connected with an extension in the form of a row of bristles and papillae (b*).

In addition to the usual bristles or papillae, there are sometimes specialized endings which are not found in other parts of the body, e.g., the lemon-shaped papillae of Leptosomatini[**] and some species of Oncholaimus (Table 4, Figure 25c–a) or the clawlike postanal bristles of Enoploides amphioxi Fil. (Table 3, Figure 12d–d). In some species of Metoncholaimus the papillae in the middle of the tail form
484 triangles which may be attached to the tail and straighten when it is curved. In addition to their sensory function, they apparently hold the female during copulation.[***]

The bristles or papillae form definite groups and may be situated on characteristic plates, e.g., in Paroncholaimus zernovi Fil. (Table 3, Figure 18f–$s_1$ and $s_2$; Figure 18m, n[†]). If stained with methylene blue, the lateral endings of the nerve fibers of the papillae are seen to be attached directly to the cuticle. This is also the case in the swellings in the middle of the tail in Oncholaimus campylocercus de Man (Table 4, Figure 25c–c), Axonolaimus setosus Fil. (Table 10, Figure 70b) and Oxystoma clavicauda Fil. (Table 2, Figure 8c[††]). If the papillae are reduced, only a part of the thickened cuticle remains with its perforating canals.[†††] This part sometimes forms a characteristic elevation, e.g., a denticle on the tail in Thoracostoma denticaudatum Schn.[‡] The preanal unannulated plate in Monoposthia may have the same function.[‡‡]

Preanal median papillae are present in several groups. Their absence is characteristic for most of the large marine Enoplidae. There are usually only submedian papillae, which are sometimes markedly displaced towards the ventral line (Paroncholaimus papilliferus Fil.[‡‡‡]). Their number varies from 1–2 to 40–60. Some of these structures are possibly connected with glands, but this seems unlikely for most of them.[✱] Cobb, on the other hand, believed that all median papillae are openings of glands.[✱✱]

485 Among freshwater forms, they have been described in Alaimus, Bastiania and Tripyla.[✱✱✱] They are very well developed in Trilobus, sometimes with claws at the end and small spines at the sides.[•] The papillae

---

[*] 1906, p. 125.

[**] Voltzenlogel, 1902, p. 498 ff.; Goldschmidt, 1904, p. 68 ff.

[***] 1905, p. 61 ff.

[†] 1909, p. 544.

[††] See de Man, 1893, p. 189.

[†††] See de Man, 1907, p. 53.

[‡] Bastian, 1865, p. 125, "caudal alae"; Bütschli, 1873, pp. 33, 96; 1876, p. 367; de Man, 1884, pp. 7, 85. In Dolichodorus the bursa is described as double ("double, crenate," Cobb, 1914, p. 93).

[‡‡] See also Filip'ev, 1916, Table 5, Figures 8c, 9c, d.

---

[*] See also Türk, 1903, pp. 288, 331; de Man, 1904; Filip'ev, 1916, pp. 73, 78 and figures in Table 5.

[**] De Man, 1893, p. 110; 1904, p. 105.

[***] Zur Strassen, 1894.

[†] Also in P. vulgaris Bast.; see Filip'ev, 1916, p. 110.

[††] The same has been observed in Thalassoalaimus (Steiner, 1916, p. 651).

[†††] Thoracostoma caecum Savel'ev, 1912, p. 124.

[‡] Figure, see Filip'ev, 1916, Table 4, Figure 7d.

[‡‡] De Man, 1890, p. 196.

[‡‡‡] 1916, p. 112.

[✱] Bütschli (1876, pp. 382–383) also denies this for Trilobus and Monhystera.

[✱✱] 1893, p. 398, Chromadora minor; 1898b, p. 56.

[✱✱✱] De Man, 1884, pp. 13, 29, 32, 48; Cobb, 1914, Table 8, Figure 23, Bastiania.

[•] De Man, 1884, p. 75; Brakenhoff, 1914, p. 256. "Suckers" or "Sacculi" of Bastian, "Drüschen" of Bütschli, 1873. He later denies their glandular function (1876, p. 382). See also Stefanski, 1914, p. 26.

of Prismatolaimus and Leptolaimus[*] extend to the esophageal part; they are replaced in Leptolaimus by movable tubes of glands (see below). The papillae of Deontolaimus are present only in the esophageal part.[**] A long row of numerous small papillae (up to 70) are present in most species of Dorylaimus[***] and Enchelidium (Table 5, Figure 28d).

These papillae are also common in the Monhysteridae, e.g., in Parasabatieria (Table 11, Figure 79c) and Monhystera mas-papillatus Cobb.[†]

These papillae reach a particular development in the Chromadoridae. They are usually weakly developed, if present at all in the Cyatholaimini (cf. Table 6, Figure 39h–p), but are very well developed and of complex structure in many species of Chromadorini and Spilipherini. In the simplest case, they are barely marked depressions, e.g., in Chromadora poecilosomoides Fil. and Chr. peocilosoma de Man.[††] In Metachromadora, characteristic chitinized parts are marked only on the surface of the cuticle, and a characteristic canal runs from them deeply; the whole row of papillae is situated on a cuticular ridge (Table 7, Figure 42f, g). They are of the same form in Chromadoropsis.[†††] The larger papillae of most other species of Chromadora extend further (Table 8, Figure 51d) and, finally, there are the large structures of a few species of Chromadora and Hypodontolaimus.[‡] The highest development of these papillae is reached in Onyx (Table 6, Figure 41e). There is a characteristic chitinized rod with a hook at the end in connection with the papillae. These rods can apparently be bent and probably hold the female during copulation.

486 Finally, there are 9 pairs of constant papillae in the Anguillulidae (rays of the bursa, if present; see above). These 9 papillae are also present in the bursa of Strongylidae.[‡‡] Their relative position may vary markedly even in different individuals of the same species.[‡‡‡]

**3. Glands and their supports.** The usual papillae are apparently not connected with glands, but there are a number of structures which are connected with them. They sometimes form small chitinized supports of the cuticle, which sometimes extend more or less deeply inwards. These organs are usually called auxiliary or accessory organs.[★] I also used this term in the systematic part. The function of the glands is to assist in copulation, but there is probably also mechanical adhesion.

---

[*] De Man, 1884, pp 80, 81.

[**] Ibid., p. 32.

[***] Except in a few species, in which they are replaced by submedian rows (see de Man, 1884, p. 157; Bütschli, 1876, p 367).

[†] 1890, p. 464; in this species he described glands associated with them.

[††] 1893, Table 6, Figure 7c.

[†††] De Man, 1907, Table 4, Figure 13b.

[‡] De Man, 1888, Table 4, Figure 18b.

[‡‡] Schneider, 1866; Looss, 1905

[‡‡‡] Potts, 1910, p. 483; Johnson, 1913, p. 627. Potts suggests that this is connected with degeneration of males in some species (see below), but this phenomenon has been observed also in forms with well-developed males.

[★] "Hilfsorgan," 'organe supplémentaire.'

The accessory organ of Enoplidae has a varying structure: it lies in the cuticle in Leptosomatini and has the form of a small ring with chitinized supports.[*] In Anticoma (Table 2, Figure 6d) and Enoploides (Table 3, Figure 13b), it is a small tube of varying width. In Phanoderma (Table 1, Figure 4b) there are characteristic thickenings at its base. The most complex form is present in Enoplus (Table 2, Figure 10f): the organ has the form of a funnel with a wide, wrinkled base, enclosing the gland posteriorly; the end of the organ is pointed and oblique, with its opening directed posteriorly. The organ is probably movable, as there is special musculature (de Man). This form is characteristic for all species of Enoplus, except that the organ is tubular in En. behringicus Fil.[**] The organ 487 has a similar form in Paroncholaimus (Table 3, Figure 18n), but it is very small. Steiner[***] described glands under similar tubercles in Thalassoalaimus. There is possibly a similar structure in this genus.

Eurystoma has two such organs (Table 5, Figure 29c), each consisting of a large chitinized ring with anterior and posterior processes. Their homology with the organs of Enoplus was also recognized by A. Schneider.[†] The gland is nearly always distinct and large.

Numerous preanal organs in the form of chitinized points which project during copulation are characteristic for the group of Plectus[††] and other genera. The glands of these organs have been described by Marcinowski[†††]; such organs are also present in other genera: Mononchus[‡] and Cyatholaimus coecus Bast.[‡‡] He stated that the organ may project far outside.

Southern (1914) described several marine genera with numerous preanal organs of the same structure, and all organs are connected with glands. In the genus Halaphanolaimus, the glands are present not only in the preanal region but also in the esophageal part of the body. These and other glands are also present in the female, but in smaller numbers.

**g. Conclusion.** The spicules and the genital armature of the males are a very important systematic character, to which early authors already gave their attention, particularly A. Schneider (1866). However, it was recognized that this armature can be used mainly for the distinction of species, and not of genera. This principle, although in a more general form – the distinction of smaller systematic units – has also been used here. These characters are sometimes useful for the distinction of genera as well – e. g., the division of the Oncholaimini in this book, or the distinction of Sabatieria from Comesoma by Rouville, the division 488 of Monhystera by de Man, etc. However, in some cases, e.g., in Sphaerolaimus, it is definitely not possible to divide genera according to the

---

[*] See de Man, 1893, p. 110; Jägerskiöld, 1901, pp. 27, 38; Türk, 1903, pp. 324, 333; de Man, 1904, pp. 33, 44; Filip'ev, 1916, Table 4.

[**] See Filip'ev, 1916, p. 100.

[***] 1916, p. 651.

[†] 1866, p. 56

[††] Plectus (Bütschli, 1873, p. 89; de Man, 1884, p. 105); Aphanolaimus (de Man, p. 34; Micoletzky, 1914, p 400); Leptolaimus (de Man, p. 81); Pseudobathylaimus (Daday, 1905, p. 61).

[†††] 1908, p. 45.

[‡] Bütschli, 1876, p. 382. However, apparently without aperture; de Man, 1904, p. 7.

[‡‡] De Man, 1890, p. 206.

spicules. The resemblance of the genital armature, on the other hand, often helps in determining the relationship of genera in doubtful cases. The inconstant genital papillae and other external genital organs are of even less importance.

## B. Female Genitalia

The female genitalia consist of one or two tubes in which we distinguish the ovary, oviduct, uterus and vagina. In the typical case, the vagina opens in the female gonopore in the middle of the body; it is rarely displaced to the anterior or posterior end.

The genital tract is usually double, with one branch extending anteriorly and the other posteriorly. However, one of the branches is often reduced and only one tube is present, usually the anterior tube (many species of Oncholaimini, Monhysterini, Sphaerolaimus) and rarely the posterior tube (some species of Oxystomini[*]). The reduction is sometimes incomplete and a rudiment of the other tube is present, which is sometimes small and sometimes larger.[**]

The anterior and posterior position of the genital tracts is secondary. After careful examination, it always appears that one tube is situated to the right and the other to the left of the intestine; one ovary also curves to the right, the other to the left. The anterior ovary of Draconema is the left, the posterior ovary the right[***]; the opposite is the case in Rhabditis and related genera.[†] Thus, the view of Bütschli that the anterior and posterior tubes of the ovaries and the testes are in fact a right and a left tube is confirmed.[††]

489 In cases in which there is unilateral development of the genital tract, the female genital opening is displaced towards one or the other end. In some forms with an anterior tube, it is situated almost in line with the anus (Monoposthia, Tylenchus, some species of Monhysterini). This induced Bastian to describe a male without spicules in species of Monhysterini.[†††] In the forms with only a posterior branch of the genitalia, the gonopore is displaced anteriorly (Thalassoalaimus, Trefusia, Oxystoma). Two female genital openings, which were described by Bütschli[‡] in a species of Linhomoeus, are probably an abnormality.

---

[*] Also some species of Tylencholaimus, Dorylaimus (de Man, 1884, pp 14, 174).

[**] Tylenchus, some species of Rhabditis, Anguillula, Monhystera, Sphaerocephalum, cf. p. 239, Part I. Cobb (1914) states that there may be one or two ovaries in Microlaimus fluviatilis

[***] Claparède, 1863, p. 89.

[†] Maupas, 1901, p. 483; Micoletzky, 1915, p. 260

[††] Cf., however, Rauther, 1909, p 563.

[†††] Monhystera disjuncta, p. 98; cf. Bütschli, 1874, p. 25. Fuchs (1915) described a species of Tylenchus with the oviduct opening into the rectum; the vulva is also displaced far posteriorly in Tylenchulus (Cobb, 1914) and Heterodera (Strubell, 1888).

[‡] 1874, pp 16, 33. Also observed by Hagmeier (1912, p. 551) in Mermis.

---

There is often a row of accessory papillae or bristles around the female genital opening, e.g., in Paroncholaimus and Thoracostoma denticaudatum Schn.[*] Sometimes there are still more strongly modified parts of the cuticle or its fold.

a. **Ovaries and oviduct** (ovaria et tubae). The ovaries of free-living nematodes are of two types: curved or straight. Curved ovaries are present in Chromadoridae and Enoplidae and straight ovaries in the Monhysteridae; both types are represented in the Anguillulidae. The curved type is probably more primitive, as it is present in the most highly organized Enoplidae. Forms with straight ovaries almost always show characters of reduction, and the transition between the two types is evident in the Anguillulidae. This was stated by Bastian.[**] The extreme end of the ovary in both types is a syncytium, from which the oogonia separate; a rachis is absent, also in Anguillulidae.[***] The separated oogonia are at first arranged in several rows, later in one row. The cells are sometimes
490 very short, so that the characteristic figure of a column of coins is obtained; the last cells are rarely situated obliquely (Enoploides). The ovary is covered with a thin epithelium, which consists of flat, extended cells. The surface of the ovary is often irregular, which has also been observed in parasites.[†]

The origin (narrow end) of the ovary in the curved type is directed towards the gonopore and usually coincides with the beginning of the uterus, and the ovary is widened towards the end of the genital tube. The ripening oogonia pass into a blind sac at this end, become detached and pass through the oviduct into the uterus.

The border between ovary and oviduct has been determined differently. De Man used histological characteristics, according to which the oviduct is only a more or less short part attached to the uterus. Jägerskiöld used morphological characteristics, considering the entire part between the uterus and the opening of the narrow part into the blind sac as the oviduct. The latter view seems more correct. The oviduct is not attached to the end of the ovary but at some distance from it, so that a large pouch is formed in which the ripe egg and 1–2 of the following eggs are situated. The first egg must pass the subsequent eggs to pass into the oviduct, and it becomes markedly compressed during passage.[††] The oviduct of Enoplus has its own musculature.[†††] The oviduct sometimes also serves as a seminal receptacle,[‡] in other cases the accumulation of sperm takes place at the beginning of the uterus. At the end of the oviduct, before the uterus, there is a special barrel-shaped part in Anticoma which probably contains contractile elements.[‡‡] A similar structure is also present in Enoploides amphioxi Fil., Paroncholaimus zernovi Fil. and

---

[*] Filip'ev, 1916, p. 92.

[**] 1866, p. 605.

[***] See E. Krüger, 1912; Cobb, 1898b, p. 46.

[†] De Man, 1886, pp 8, 25, 33; see also Jägerskiöld, 1901, p 27; Stewart, 1906, p. 126. Extended cells have also been described in the epithelium of several parts of the ovary of Ascaris (Domaschko, 1905).

[††] Jägerskiöld, 1901, p. 28; Türk, 1903, p. 328; Stewart, 1906, p. 127.

[†††] De Man, 1886, p. 25.

[‡] Leptosomatini, Türk, 1903, p. 325; Paroncholaimus, Stewart, 1906, p. 127; Rhabditis, Maupas, 1901, p. 534.

[‡‡] De Man, 1886, pp. 7, 59; p. 45, Part I.

491 Viscosia[*] Characteristic areas of connective tissue have been described by de Man[**] in Euchromadora

The ovary of Enoplidae is usually long, e. g., in Leptosomatini and Oncholaimini, and sometimes very long, e. g., in Paroncholaimus vulgaris, where it extends along the uterus almost to the gonopore.[***] The origin of the ovary is usually narrow, but it may be wide and blunt.[†] In many species with such an ovary (perhaps in all species) it is at first elongate, with many mature oogonia; they are absorbed when the eggs ripen and the ovary becomes narrower.[††] A short, conical ovary is characteristic for the Chromadoridae. Marion[†††] stated that annulated nematodes have a short ovary. The short ovaries of Metachromadora and Draconema are situated almost transversely because of the great expansion of the body in the region of the genitalia. There is also a short ovary in Enoplidae.[‡]

The syncytial part is situated at the end of the genital tube in the straight type and the oviduct is not separated from the ovary, so that the ovary is attached directly to the uterus. The ovary is usually much longer than in the curved type, sometimes extending into the esophageal part.[‡‡] As in the curved type, there are wider and narrower ovaries, but this is constant within the genus.[‡‡‡] The tip of the straight ovary may be curved (Conolaimus angustilaimus Fil.[*]), possibly an indication of the secondary
492 nature of the straight type. There is a characteristic valve at the origin of the uterus in Axonolaimus. The ovaries of the Desmoscolecidae are apparently also straight.[**]

The straight ovary of Anguillulidae is usually very long, sometimes convoluted, as in parasitic nematodes[***]; it reaches its maximum length in the phytoparasitic forms.[•] The ovary of Plectus[••] is usually of the recurved type. The ovary of Rhabditis is filled with immature eggs. There is thus a clear transition between the two types.

b. **Uterus**. This is a large organ which contains the ripe eggs, and sometimes they develop there too. Its wall consists of the epithelium and a muscle layer. The epithelium is thin in the Enoplidae, but a thick epithelium is characteristic for the Chromadoridae; it sometimes consists of short cells with large nuclei.[*] There is a particularly wide and thick-walled uterus in Metachromadora (see Table 7, Figure 42i), also in Spira, Draconema and Axonolaimus.[**] The musculature of the uterus is usually weak, except in a few forms[***]; Jägerskiöld denies its presence in Leptosomatini. The surface of the uterus is usually irregular, which is due to contractions of the walls (Jägerskiöld[†]). He described multinucleated glands in the uterus of Cylicolaimus,[††] and Bütschli in the uterus of Trilobus.[†††]

The uterus may either have a continuous cavity, so that the vagina is attached to it at a right angle, or the vagina is double and the cavity of the two uteri is separated.

493 The first type is characteristic for Pelagonema, Viscosia and Symplocostoma (Table 5, Figure 31c), Enoplus, Diplopeltis and all species of Chromadoridae; the second type for Leptosomatini, Eurystoma, Paroncholaimus and Axonolaimus.

A further specialized terminal part of the uterus is sometimes differentiated, which is provided with a stronger musculature – the ovejector. In Black Sea nematodes this is present only in Paroncholaimus zernovi Fil. and also in the larger Leptosomatini.[‡]

If there is unilateral development of the genitalia, a rudiment of the uterus of the opposite side is sometimes present, which may function as a seminal receptacle.[‡‡]

The number of eggs in the uterus varies markedly. There are usually only a few, – not more than 5–6 in most species. However, hundreds of eggs may be present in the uterus of Rhabditis[‡‡‡] and Tylenchus tritici.[*] About 20 eggs are present at one time in Symplocostoma and Metoncholaimus. In some Leptosomatini and in Paroncholaimus the length of the uterus depends on the time of fertilization. If this takes place early, the ripe eggs which enter the uterus will be fertilized immediaately and laid. If it takes place late, many eggs are present in the uterus, which is greatly enlarged.[**]

The number of eggs in the uterus also depends on their size and shape. Eggs of the free-living forms (Dorylaimus, some species of Anguillulidae) are relatively large, with few exceptions, as recorded by Eberth and Bastian. They are also long in Deontostoma. They are 6–7 times longer than wide (750–900 $\mu$ × 130–140 $\mu$) in D. papillatum Linst. However,

---

[*] pp. 66, 80, 88, Part I.

[**] 1886, p. 75.

[***] See Jägerskiöld, 1901, p. 27; Stewart, 1906; Filip'ev, 1916, pp. 71, 92.

[†] Trilobus according to Bütschli, 1873, p. 56, Table 4, Figure 27b.

[††] Adoncholaimus fuscus Bast (de Man, 1886, p. 47); Thoracostoma denticaudatum Schn. (Filip'ev, 1916, p. 92), Paroncholaimus zernovi (p. 80, Part I).

[†††] 1870, p. 83

[‡] Pelagonema, Eurystoma, Symplocostoma, pp. 84, 113, 118, Part I.

[‡‡] Steiner, 1916, p. 642.

[‡‡‡] Cf. Bütschli, 1873, pp. 62, 64.

[*] p. 236, Part I.

[**] Cobb, 1912, p. 483; Steiner, 1916.

[***] Cephalobus, Bütschli, 1873, pp 80, 81; de Man, 1884, p. 93; Maupas, 1901, p. 560; Rhabditis, Ditlevsen, 1911, p. 241; Southern, 1909.

[•] Heterodera, see Strubell, 1888, pp. 25, 28; Tylenchus tritici, see Marcinowski, 1908, p. 69.

[••] De Man, 1884, p. 88, Tables 7, 8.

[*] This resembles the warty epithelium of the uterus of Ascaris (see Domaschko, 1905).

[**] Also Euchromadora, de Man, 1886, p. 75, and Heterodera (Strubell, 1888, p. 28).

[***] Some Dorylaimus, Ironus, Trilobus, de Man, 1884, p. 13; Ditlevsen, 1911, p. 232

[†] See also Brakenhoff, 1914, p. 305.

[††] p. 28.

[†††] 1873, p. 56.

[‡] See Filip'ev, 1916, pp. 82, 92

[‡‡] See Steiner, 1916, p. 644, Theristus; Hallez, 1900, p. 610, Anguillula; Southern, 1914, p. 19, Oxystoma.

[‡‡‡] Oerley, 1886, p. 33; Maupas, 1901, p. 483; Ditlevsen, 1911, p. 241.

[*] Marcinowski, 1908, p. 69.

[**] See also pp. 30, 80, Part I.

[***] Filip'ev, 1916, p. 82. Nuada Southern has very long eggs (1914, p. 10), an argument in favor of the fact that its narrow body is secondary.

494 this varies markedly in related species; thus, Leptosomatum grebnickii Fil. and L. behringicum Fil. are easily differentiated by their eggs, which are elongate in the former and round in the latter species. The eggs are usually more or less rounded. Round eggs are characteristic for the larger Chromadoridae (Cyatholaimus, Euchromadora, Metachromadora); they live free in the uterus; the eggs are elongate in the smaller species. The size of the eggs is thus more constant than the size of the body.

The eggs are enclosed in a membrane after fertilization. It is usually thin and very plastic in free-living nematodes.[*] The membrane is rarely thicker and has an irregular surface, e. g., in Plectus and Mononchus. It is also thick in the Anguilullidae.[**]

c. **Vagina**. The walls of the vagina consist of cuticle, a plasmatic layer and muscular elements. The cuticle is the direct continuation of the external cuticle and is shed during the molt together with the latter. There are usually also muscle cells. One of these may form a sphincter at the base of the vagina.

Two forms of the vagina correspond to the two forms of the uterus. The vagina is short if the uterus is continuous; it extends perpendicularly inwards and is usually without muscles. In the Chromadoridae, which belong to this category, the cross section of the vagina is round and the cuticle is thick. There are also two types of vagina if the uterus is divided; they are usually fairly long, extending in an oblique direction, and are provided with muscles. They sometimes diverge almost immediately from the gonopore.[***] If the uterus is unilateral, the vagina is also usually oblique (Oncholaimini, Monhysterini).

Characteristic dilator muscles are attached to the vagina (musculi vaginales s. vulvares, Table 3, Figure 18d). They are part of the general longitudinal musculature of the body. Steiner also distinguishes lateral fascicles in several species in addition to the usual muscle fascicles, which 495 generally run anteriorly and posteriorly.[†] Characteristic chitinized processes are sometimes formed for attachment of the muscles.[††]

The vagina of Leptosomatides has a special form, as described by Steiner.[†††] Strong muscles are present in its walls, resembling the radially arranged muscle fibrils of the esophagus, particularly of its bulb.

Glands also open into the vagina; their numbers vary in different forms, as stated by Bastian.[‡]

d. **Tubular organ** (organon tubiforme). De Man[‡‡] used this term for a characteristic canal at the posterior end of the body of the female of Adoncholaimus fuscus Bast. which is situated on the dorsal side. The posterior end opens laterodorsally to the outside in two short tubes. A fairly long sac follows, whose walls consist of numerous polygonal cells; they are filled with a granular substance. Two protuberances ("Warzen") of modified cells are present at the level of the genital organs. They are filled with bodies of characteristic form (spermatozoa?). A thin connecting canal passes from these protuberances, which is connected with a sphere of cells, and from this runs a thin, narrow canal which opens into the uterus near the oviduct. All typical species of Adoncholaimus and Oncholaimus have an organ of this type.[*]

The tubular organ of Metoncholaimus is of another type (Zur Strassen, 1894). It is connected not with the uterus but with the intestine, into 496 which it opens widely. An unpaired wide canal follows behind it, which branches into two narrow tubes at the posterior end. Their wall consists of rows of cells in the form of a column of coins; the duct is chitinized and displaced to one side. A characteristic "rosette" in the form of a capsule with dense walls and many nuclei is situated lateral to the beginning of these ducts. According to de Man,[**] this rosette communicates with the uterus in M. albidus Bast., but the more detailed examination of Zur Strassen in the closely related M. demani Z. Str. and M. pristiurus Z. Str. did not show such a connection. I can only confirm the results of Zur Strassen for M. demani in the Black Sea. The posterior tubes of this form are illustrated in Table 4, Figure 26c. This type of organ is characteristic for typical species of Metoncholaimus.

The tubular organ develops in females only after the last molt; it is shorter in young females.[***] Its function is not known. A ring of secretions around its opening, which was observed by de Man and myself, may provide an explanation. This may be congealed mucus which covers the eggs of Metoncholaimus when they are deposited.

A characteristic structure was also described by Stewart in Paroncholaimus vulgaris Bast. – the "gonenteric canal," a narrow duct which connects the middle of the uterus with the intestine.[†] It apparently excretes excess sperm into the intestine. Stewart compares it with Laurer's canal of trematodes, a comparison which seems very doubtful.

It seems difficult to ascribe morphological importance to organs of such definitely secondary origin which are only present in such a small group as the Oncholaimini.

e. **Conclusion**. The difference in the development of long genital tracts with many eggs in parasites and short tracts with a few eggs in free-living nematodes is so great that Bastian considered it as characteristic for his 497 family Anguillulidae, which included all free-living nematodes. The difference is in fact very characteristic and should not be overlooked.[††] However, this may be a difference which is more quantitative than qualitative. This is stressed by the transitions in the Anguillulidae in the series Plectus - Cephalobus - Heterodera.

---

[*] Jägerskiöld, 1901, p. 48.

[**] Bütschli, 1873, p. 35; de Man, 1884, p. 108; Brakenhoff, 1914, p. 276.

[***] See Stewart, 1906, p. 128; de Man, 1904, p. 34; Jägerskiöld, 1901, pp 27, 47; Bütschli, 1873, p. 26; Türk, 1903, p. 328; Brakenhoff, 1914, p. 305; Steiner, 1916, p. 618.

[†] 1915, p. 230, Leptosomatum, There are only longitudinal muscles in another species (1916, p. 618). See also 1916, p. 599.

[††] Thoracostoma echinodon Marion, 1870, Table H, Figure 1g; Dolicholaimus, de Man, 1888, p. 34.

[†††] 1916, p [?]

[‡] See especially Jägerskiöld, 1901, p. 75.

[‡‡] 1886, p. 47, Table 7, "Röhrenförmiges Organ," "Organe tubiforme."

[*] See Ditlevsen, 1911, p. 230, and pp. 93, 96, Part I.

[**] 1893, p. 114.

[***] See p. 101, Part I.

[†] 1906, p. 129, 146.

[††] Cf. Jägerskiöld, 1901, p. 27.

I ascribe very great systematic importance to the recurved or straight type of ovaries (except in the Anguillulidae). An entire family – the Monhysteridae, which is very uniform in its composition (see p. 199, Part I)– has been characterized on this basis. The continuous or divided uterus and the corresponding form of the vagina are probably also very important. However, all these characters have been so little studied that no conclusions can be drawn. The paired or unpaired genital tubes are a secondary character. Both types are sometimes present in the same genus.

## C. Gynandromorphism

I use this term for an abnormal development of the male copulatory apparatus in females. The female gonopore is situated in the middle of the body, and the development of the spicules does not impede the full development of the female genitalia. A part of the ejaculatory duct is sometimes also developed. The spicules and the genital papillae are often reduced to some extent. I shall only list the cases known to me and those from the literature.

Thoracostoma figuratum Bast.: de Man, 1893, p. 111.

Enoplus michaelseni Linst.: de Man, 1904, p. 24: two of 8 females with normal copulatory apparatus, one with defective copulatory apparatus.

Trilobus gracilis Bast.: Micoletzky, 1914, p. 509; Ditlevsen, 1911, p. 233: only accessory male papillae in the last case.

Trilobus diversipapillatus Daday: 1905, p. 55.

"Prismatolaimus" microstomus Daday: 1905, p. 57: only single papillae.

Chromadora poecilosoma de Man, 1893, p. 99.

498 Monhystera stagnalis Bast.: Micoletzky, 1914, p. 413.

Monhystera (?) carcinicola Baylis: 1915, p. 420.

Axonolaimus setosus Fil.: see p. 232, Part I.

Mermis albicans Sieb.: Meissner, 1853, pp. 209, 257.

Mermis terricola Hagmeier: 1912, p. 539.

## D. Hermaphroditism and Parthenogenesis

The genital tract of the female of many species of Rhabditis and related genera produces sperm[*] before the development of the eggs. The sperm accumulates at the beginning of the uterus and fertilizes the eggs when they emerge from the ovaries. There are sometimes also males in varying numbers which are often biological rudiments, as they have lost the sexual instinct completely. If a hermaphroditic female is fertilized by a male, a markedly larger than normal percentage of the progeny is male. In some individuals, sperm is produced only in one of the two ovaries. Cobb[**] observed that in one species one gonad was an ovary and the other a small testis. Maupas[*] also observed the development of cells similar to eggs in the testes.

Parthenogenesis was established by Maupas for many species of Anguillulidae; some species of Dorylaimus are also apparently parthenogenetic.[**] Ditlevsen[***] suggested that there are possibly alternating parthenogenetic and bisexual generations in some freshwater forms.

This was discovered by A. Schneider[†]; for details the reader is referred to Vernet (1872), Maupas (1901), Johnson (1913), Potts (1910) and E. Krüger (1912). The latter discusses the maturation of the sexual elements. Most results of these studies were obtained with cultures, as Rhabditis and related forms reproduce well on decomposing meat in the laboratory.

## III. DEVELOPMENT

We know little about the deposition of eggs. Metoncholaimus lays eggs in lumps of mucus, Desmoscolex and Tricoma carry the eggs with them.[††]

Viviparity and development inside the body of the female is widespread
499 in different groups of nematodes.[†††] A nematode is sometimes viviparous only under certain conditions; in others it is oviparous. Thus, Cyatholaimus demani Fil. is viviparous in cold water from the depths at the Georgievskii Monastery, but it is oviparous under other conditions. According to Conte (1900), Rhabditis monohystera Bütsch. cultivated in potato paste is viviparous, but oviparous on peptone. Monhystera stagnalis Bast. also reproduces in both ways, according to the habitat.[‡]

The larvae of Rhabditis which develop in the body are born normally. If the female is weak because of age or other factors, the larvae feed on the tissues and then become free. Such a liberation of eggs is normal in some species, so that birth takes place only after the death of the female.[‡‡]

I shall not describe the embryonic development of nematodes in detail, quoting only the principal studies: Zur Strassen, 1896; Boveri, 1899; Müller, 1903; and several papers by Martini (1903–1909). The development of free-living nematodes has not been studied at all. There are only some old works which are out of date and deal only with such atypical forms as Rhabditis and related genera.[‡‡‡]

The cuticle is periodically shed in the postembryonic development of nematodes. This was recorded by Ehrenberg, but there are more detailed

---

[*] Maupas, 1901, p. 510.

[**] Journal Parasit, 2, p. 195.

---

[*] 1901, p. 491.

[**] 1901, p. 618; Pérez, 1866, p. 299.

[***] 1911, p. 226.

[†] 1866, p. 315 ff.

[††] See Shchepot'ev, 1908; Steiner, 1916b, p. 342.

[†††] Anoplostoma, Monhystera, Rhabditis, many species of Chromadoridae.

[‡] Micoletzky, 1914, p. 412.

[‡‡] Pérez, 1866, p. 295; Oerley, 1886, p. 55; Conte, 1900, p. 374; Maupas, 1901, p. 483; E. Krüger, 1913, p. 95. The same has been observed in the free-living generation of Angiostomum nigrovenosum Duj. (Leuckart, 1863, p. 144).

[‡‡‡] Ganin, 1876; some data in Bütschli, 1873, p. 101; the first stages – 1876b, pp. 20–24; Oerley, 1880, p. 148; 1886, p. 62; Strubell, 1888, p. 34; Hallez, 1900, p. 611.

data in Maupas (1900), who observed 4 molts in a culture, i. e., 5 stages in 500 various species of Anguillulidae. Parasites with rhabditic larvae also have 5 stages (Ancylostoma, Looss, 1909).

Not only the external cuticle is shed but also the invaginated cuticula, buccal cavity (Dorylaimus sheds the stylet, Enoplus the jaws), lining of the esophagus, vagina and hindgut.[*] The molt of the esophagus gave rise to the description of nematodes with a "projecting" tube of the esophagus, e. g., Calyptronema paradoxum Marion, 1870.[**] Bastian (1865) recorded that the cuticle is shed in pieces in Cyatholaimus and Oncholaimus.

The short duration of embryonic and postembryonic development in Rhabditis and related forms is remarkable; the embryonic development lasts 2–3 hours and the full development $1\frac{1}{2}-2$ days. The development lasts much longer in true free-living nematodes.[***]

There is usually no metamorphosis in free-living nematodes, as in many parasites. Young specimens resemble old specimens in all respects, except of the genitalia. Some differences in the structure of the cephalic capsule in young worms have been observed only in some species of Thoracostoma. There are special thickenings on the head in young Plectus which are absent in the old specimens.[†]

The sexual organs develop last. Their development has been fully studied in Anguillulidae, most completely by Maupas (1901) and E. Krüger (1913). There are only four cells in young larvae – two large cells in the middle and two smaller cells at the ends. The cells then divide and produce a longitudinal mass in which the different parts of the genital organs become differentiated.[††] The wall of the genitalia develops from the terminal cells.

501 The phenomena of development also include the so-called encystment of nematodes, which was studied mainly by Schneider[‡] and Maupas (1901). The old cuticle develops a special density after the second molt; it becomes dark and is not shed but persists as a sheath around the body. The sheath is quite impermeable, and the nematode may live for days in this condition in formalin, sublimate and other toxic liquids. The worms may live in this state for months without food. Some forms may become desiccated completely and wrinkled, but remain alive, being one of the best-known examples of anabiosis. When such a desiccated nematode is moistened, the body absorbs water, swells to its normal size and becomes able to move. A classic object for the study of this phenomenon is Tylenchus tritici Bauer, which lives in wheat grains. It was studied by Needham in the 18th century. In his experiments, the nematodes survived 20 years after desiccation.[‡‡] However, recent experiments give a shorter time (5–6 years). The protective cover is sometimes the skin of the female for the embryos inside it.[‡‡‡] The capacity to withstand desiccation is characteristic mainly for terrestrial nematodes (Rhabditis, Plectus, some species of Dorylaimus) and partly for parasitic forms with Rhabditis larvae. It is absent in freshwater and marine forms. There is an extensive literature on this subject, a list of which has been given by Menzel.[*]

## IV. BIOLOGICAL DATA

a. **Movement.** The movement of nematodes takes place in the dorsoventral plane. Movement is sometimes very rapid (Plectus) and sometimes slow (Dorylaimini, Camacolaimus, Thalassoalaimus, Linhomoeus). Some species swim (Symplocostoma and others). Long species coil into a spiral if they are disturbed, e. g., in the Black Sea: Paroncholaimus zernovi Fil., Pelagonema obtusicauda Fil., Linhomoeus, Spirina, Eurystomina and Desmodora. On the other hand, short species of Enoplus, Halichoanolaimus, Sphaerolaimus and Draconema do not coil; they only curve the body and straighten after death. Some species straighten on contact and remain immobile.[**] Many species hook the tail into a substrate and wave the 502 anterior end. Characteristic bending and trembling of the anterior end have been recorded for Cylindrolaimus and Macrolaimus.[***] Symplocostoma and Draconema may bend the head in all directions. Draconema and Rhabdogaster use a progression like larvae of Geometridae, becoming attached alternately with the bristles of the anterior and posterior end.[†] Such a movement has also been described for a species of Chromadora.[††]

b. **Food.** As recorded by Bastian, the structure of the mouth organs of most free-living forms permits suction but not swallowing of food. However, numerous forms with a more or less wide buccal cavity are also able to swallow food, e. g., the predacious Halichoanolaimus,[†††] Dignathonema[‡] and Demonema[‡‡] among marine nematodes and Mononchus and Tripyla among freshwater forms.[‡‡‡] The intestine consists of very large cells in the three marine forms mentioned. They swallow whole nematodes and digest them, including the cuticle. Only the hard buccal and genital parts are not digested. The method of feeding of Enoploides and Enoplolaimus is doubtful. The structure of the buccal organs and

---

[*] See Steiner, 1916, p. 603.

[**] See also Claus, 1863.

[***] Cf. Micoletzky, 1914, pp. 388, 509.

[†] See Steiner, 1916, p. 623; Filip'ev, 1916, p. 91.

[††] Micoletzky, 1914, pp. 458, 463.

[†††] Also in Schneider, 1866, p. 263; Marion, 1870, p. 73.

[‡] 1866, pp. 149, 293.

[‡‡] See Bastian, 1866, p. 613.

[‡‡‡] Hallez, 1900, p. 592.

[*] 1914, p. 83.

[**] Diplogaster (Bastian, 1865, p. 117; Hofmänner, 1913, p. 630). Also Chromadoropsis vivipara, Spirina parasitifera, Desmodora scaldensis (de Man, 1907).

[***] ". . . the animal is trembling as if very miserable and piteous" (Ditlevsen, 1911, p. 235); on the second genus see Maupas, 1901, p. 581.

[†] Mechnikov, 1867, p. 543. Shchepot'ev, 1908, p. 66.

[††] Cobb, 1893, p. 396.

[†††] Savel'ev, 1912, p. 121.

[‡] See p. 149, Part I.

[‡‡] Cobb, 1893, p. 394.

[‡‡‡] De Man, 1884, p. 22; Cobb, 1915, p. 488, J. Parasit, 2, p. 198; Micoletzky, 1917, p. 469. However, there are also indications of herbivorous feeding for Mononchus (Cobb, 1893, p. 816).

the large-celled intestine suggests that they are predacious, but neither Savel'ev nor myself found nematodes in the intestine. The denticles of the buccal cavity may only retain sand and not prey, as Savel'ev suggests.

503 Other forms, mainly Monhystera, Theristus and related forms, feed exclusively on diatoms. They sometimes swallow shells which are so large that the nematode becomes a "veritable sword swallower," in Cobb's phrase.[*] Some species of Tripyla also belong here; they also feed on green algae if there are no diatoms.[**] Diplogaster and Mononchus vulgaris feed on algae.[***]

Most actively swallowing forms feed on decomposing plant and animal detritus, e.g., Paroncholaimus, Enoplus,[†] Phanoderma and Leptosomatum in the Black Sea. According to Cobb, Oncholaimus orientalis also swallows diatoms,[††] as do Cyatholaimus and Spilipherini.

Rhabditis and other terrestrial forms feed on decomposing animal material (see below).

Forms provided with a stylet usually pierce the membranes of plant cells and suck them out. Thus, I observed that one Dorylaimus in lake mud with numerous blue-green algae had the anterior part of the intestine filled with a green mass without cell membranes. The chlorophyll had already become grayish brown in the posterior part of the intestine.[†††] The terrestrial Dorylaimus, many species of Tylenchus and others suck on the roots of plants.[‡] Micoletzky[‡‡] found that Dorylaimus also feeds on detritus.

504 Plant parasites (see below) also obtain plant juices with the aid of the stylet. However, the stylet does not pierce the root, acting only when the nematode has already pierced it (see p. 63).

Feeding on animals has been suggested for other forms with spines. Such a suggestion for Onyx is based only on the fact that it lives in sand, where there are no large algae (Cobb[‡‡‡]), which is doubtful. It has been suggested for Siphonolaimini because of their black intestine – the color of digested blood.[*] De Man observed that Dorylaimus fed on Cephalobus.[**]

c. **Regenerative capacity.** Completely absent in nematodes. Bastian and Golovin cut Enoplus and Paroncholaimus in half; the nematodes lived for several days, but the wound did not heal. I repeated these experiments with the same result.

---

[*] "... a veritable sword swallower" (1893, p. 402). See also G. Schneider, 1906, p. 12; Hofmänner, 1913, p. 653.

[**] Micoletzky, 1914, p. 386; 1914a, p. 11; Stefanski, 1917, p. 361.

[***] Micoletzky, 1917, p. 469.

[†] Rauther (1907, p. 726) suggests that the dark inclusions in the intestine possibly originate from swallowed blood.

[††] 1890, p. 459.

[†††] See also Micoletzky, 1917, p. 469.

[‡] For the mechanism of sucking, see p. 488; see also de Man, 1884, p. 21.

[‡‡] 1914, p. 386.

[‡‡‡] 1891, p. 55.

[*] Zur Strassen, 1904, pp. 302, 309, 311.

[**] 1884, p. 22.

d. **Paleontology.** It may seem odd, but it is true: nematodes have been described from Baltic amber; but the descriptions and drawings are too schematic to permit identification (Duisberg, 1862; Menge, 1866).

e. **Sex ratio.** In general, females are more numerous, but in hermaphrodites and parthenogenetic species only females are present.[*] An exception is Enchelidium, where females are known only in one species. I did not find females of the Black Sea species E. longicolle Fil., though males are fairly numerous. This phenomenon is quite unexplained.

f. **Diseases and parasites.** Degeneration of the intestine in adult Leptosomatini.[**] has been discussed above. A similar physiological degeneration
505 has been described by Hagmeier[***] for Mermis. The cells of the intestine swell, become filled with deuteroplasmatic inclusions and lose their form, so that authors speak of a "fat body." The epidermis also degenerates. Males of Tylenchulus and Hoplolaimus also degenerate normally, losing even the stylet in the adult state, which is characteristic for the young (Cobb[†]).

The physiological nature of degeneration is not in doubt in the cases described, but histolysis of the tail in Linhomoeus and Siphonolaimini is possibly of parasitic origin. For example, Table 4, Figure 17b of the study of Bütschli (1874) shows a large number of cells in the tail cavity, possibly parasites. According to Zur Strassen, the females of Solenolaimus may thus lose up to one-fifth of their total length. The region of the anus also undergoes histolysis, so that the intestine has a blind end.[††]

Injured parts of the body are often infected by bacteria, while other parts remain healthy. This resembles gangrene in nematodes. As a result, one cuticle becomes detached on the infected part of the body.[†††]

Numerous cases of endoparasites and ectoparasites in free-living nematodes have been recorded. Endoparasites:

Sporozoa in Aphelenchus parietinus Bastian, 1865, p. 122.
" " in Mononchus macrostoma de Man, 1884, p. 22.
" " (Gregarine?) – Dorylaimus brigdammensis de Man, 1884, p. 22.
" " (swellings with Coccidia) – Monhystera macrura Steiner, 1916a, p. 339.
" " (in the intestine and body cavity) – Plectus Micoletzky, 1914, p. 386.
" " (cysts and spindles) – Mononehus vulgaris Micoletzky, 1917, p. 470.
Bacteria in Cephalobus oxyuroides de Man, 1884, p. 22.
506 " " in Linhomoeus attenuatus de Man, 1907, p. 81.
Suctoria in Desmodora scaldensis de Man, 1890, p. 192 ("les animaux étaient paralisés").

Low fungi which trap nematodes are interesting (Zopf, 1888). The hypae form loops. When a nematode enters such a loop it is caught: the fungus grasps it, pierces the cuticle and sucks out the body contents.

---

[*] See also Micoletzky, 1914, p. 390; 1914a, p. 12; 1917, p. 472. There are more males in the cold season.

[**] See p. 30, Part I.

[***] 1912, p. 581.

[†] See p. 62.

[††] 1904, p. 303.

[†††] See also Marion, 1870, p. 6.

Ectoparasites are filamentous algae, diatoms, low fungi, Acineta and Vorticellae. These parasites are usually attached only to a hard cuticle. I observed such parasites in Spirina and Metachromadora. They have also been recorded in Desmodora, Paroncholaimus, Aphelenchus and Chromadoropsis.[*] Species with a smooth, easily swelling cuticle, e. g., Leptosomatini, are always without them.

g. **Distribution by habitat** As a result of my investigations, I am inclined to believe that these free nematodes will be found to constitute one of the most widely diffused and numerically abundant groups in the whole animal kingdom, rivaling, in the first respect at least, the almost ubiquitous Diatomaceae." Bastian. Mon. on the Aguillulidae, 1865, p. 75.

Bastian's comparison seems too narrow: the group with which the conditions of habitat of nematodes should be compared are not the diatoms but the even more widely distributed Protozoa. In fact, nematodes are ubiquitous – in fresh and sea water, in the soil and in plants and animals. 507 The distribution of nematodes in different biocenoses of the sea will be given below. The richest freshwater biocenoses are crusts on stones ("Krustensteine"), which consist mainly of diatoms and mud. Next is the sand and mud-sand bottom. Nematodes are relatively rare on aquatic plants, but there are some characteristic forms, e. g., species of Monhystera. Mud is also poor in nematodes.[**] There are very few species of nematodes at the bottom of Lake Geneva. All belong to the group of not very particular cosmopolites.[***] There are few species in running water, forms with a well-developed cement gland predominating. The variety of species in small pools, particularly in pools with polluted water, is much smaller; some specialized species are very numerous in such places,[†] while other species which occur everywhere are also found in polluted water.[††]

Terrestrial species are concentrated in the superficial 10 cm soil layer. They are numerous near the roots of plants, fungi and moss.[†††] They are present at all altitudes in mountains, apparently carried by birds and wind.[‡] Distribution is obviously assisted by the ability to withstand desiccation and to revive when moistened.

De Man (1884) distinguishes the following 5 groups in Holland: 1) ubiquitous species; 2) species in forest and meadow soil rich in humus; 3) species in the sandy soil of dunes; 4) species in brackish water or in soil soaked in it; 5) freshwater nematodes.

Some species also live on plants, in the sheaths of grass (Bastian) and between the leaves of moss (Bütschli), while some species of Anguillulidae are true plant parasites. Many of them cause serious damage to cultivated plants. Species of Tylenchus and Aphelenchus, some of which are

---

[*] Bastian, 1865, pp. 81, 123; de Man, 1890, p. 176; 1907, p. 69.

[**] Micoletzky, 1914, p. 353.

[***] Hofmänner and Menzel, 1915, p. 216.

[†] Ditlevsen, 1911, pp. 214, 219, Monhystera crasissima Ditl.; Hofmänner, 1913, p. 653, Diplogaster rivalis Leyd.

[††] Micoletzky, 1914, p. 460.

[†††] Cobb, 1915, p. 459.

[‡] Hofmänner and Menzel, 1915, p. 223.

free-living, are relatively little changed by parasitism.[*] Cephalobus elongatus de Man occurs under suitable conditions, e. g., it develops poorly on fungi but well on wheat.[**] Tylenchus dipsaci Kühn (devastatrix Kühn) is also parasitic on many different plants.[***] 508 Many species which have been described as parasites causing disease, develop in already-diseased fruit or other parts of the plant.[†] Tylenchulus semipenetrans Cobb, a parasite of the roots of lemon and orange trees, does not enter completely into the tissues but penetrates only with its anterior half. The body then becomes swollen. The males cease feeding early, degenerate, and become smaller in the latest stage. The little-known genus Macroposthonia de Man, which shows traces of degeneration, may be a parasite. The well-known beet nematode Heterodera, in contrast to Tylenchulus, enters at first into the root, but later tears the tissue of the plant and hangs outside in the form of a sac. Some species produce galls and live inside them. Tylenchus fucorum de Man, 1895, produces galls on Fucus; it is the sole marine representative of this genus.

Species of the genus Anguillula and others live in fermenting liquids – in vinegar and the oozing sap of trees.[††]

Many species of Rhabditis feed on decaying animal matter. Their "encysted" larvae are regularly found in the soil (see p. 98). If decaying meat, manure, milk, etc., are available, the larvae crawl to it, multiply rapidly and produce several generations. Reproduction takes place only at a temperature below 31° and if there is sufficient oxygen. Meat buried in the ground is therefore always without nematodes.[†††] The intensity of growth, reproduction and the deposition of grains of "rhabditin" in the intestine may vary greatly according to the nutritional value of the substrate.[‡] Other species infect earthworms and snails and become encysted in a special capsule or remain free, but do not grow or feed. Feeding and reproduction take place only after the death of the host. When decay becomes further advanced, the larvae crawl away and migrate until they die or find a new suitable substrate. Such migrations probably caused the development of hermaphroditism, as the chance of finding a suitable substrate is very small, and it is important that even a single individual may be able to reproduce.[‡‡]

Another type of parasitism has been recorded in insects. The original substrate in which beetles and nematodes occur is manure (dung beetles) and the bark of trees (bark beetles and weevils). Some nematodes live in dung and the galleries of bark beetles. Encysted larvae are present under the elytra or are attached to the body or tarsi of beetles and carried to a

---

[*] Bütschli, 1873, p. 31.

[**] Marcinowski, 1908, p. 30

[***] Ibid., pp. 62–63.

[†] Ibid., p. 13.

[††] See de Man, 1912a, b, 1913.

[†††] Oerley, 1886, p. 57.

[‡] Conte, 1900, p. 374.

[‡‡] See Schneider, 1866, pp. 149, 302; Bütschli, 1873, p. 17; Maupas, 1900, 1901; E. Krüger, 1913, et al.; Oerley, 1886, p. 39.

509 new place. It is not a large step from this to true parasitism, which sometimes changes the nematode, so that it is completely unrecognizable.[*]

Among the aquatic nematodes, the Dorylaimini have passed to parasitism, and an interesting group – the Mermithidae – developed. The larvae of Mermithidae resemble the free-living forms mentioned so closely that this hypothesis of Steiner (1916) seems well based.

Owing to the difficulty of penetrating the skin, many free-living nematodes have been found in the intestine of various animals as pseudoparasites: Aphelenchus erraticus Linstow (1876, p. 10) in the intestine of Lacerta; Dorylaimus stagnalis Dujardin (1845) in the carp; according to Davaine, embryos of Tylenchus triciti entered the intestine of frogs and fish without causing injury; Mononchus muscorum Dujardin (1845, p. 237) was found in the intestine of a stickleback.

h. **Seasonal distribution.** The marine forms will be discussed in the next section. De Man[**] and Micoletzky[***] observed mature individuals of many freshwater species throughout the year. However, de Man observed only immature Trilobus gracilis Bast.[†] in early spring and Mycoletzky[††] assumes that there is only one generation per year in Dorylaimus.

i. **Geographical distribution.** Recent data on terrestrial and aquatic forms suggest their cosmopolitan or, at least, very wide distribution. For example, Bunonema richtersi Jägerskiöld was found on the Kerguelen Islands and in Europe. Several European species were found by Cobb in Australia, by Daday and Micoletzky in Africa and by Daday in South America. This is not very suprising in view of the ability of nematodes to withstand desiccation and the distant migrations of birds. However, when the study of free-living nematodes is further advanced, forms characteristic for certain
510 zoogeographical regions will probably be found among the forms which are unable to withstand desiccation in addition to cosmopolitan species. Purely geographical factors and cold and warm water play only a secondary role.[†††]

The marine fauna is more differentiated. There are local forms in each region constituting the larger part of the fauna, while widely distributed forms are a small minority. If we compare the large forms of the North Sea and Mediterranean Sea (the small forms are insufficiently studied), we find that most species are different. The differences between the species on the Murmansk Coast and the North Sea are less marked, but the same has been observed in other groups.[‡]

Steiner (1915) had a different view. He found 8 species in a sediment washed free of algae near the coast of Sumatra, three of which were also known from the coasts of Europe, and came to the following conclusion: "Geographical zones and regions do not play any part in the geographical distribution of free-living nematodes; only physicochemical and biological factors in their habitats are important." Eight species of a local fauna of 100–200 species are a very inadequate material for such a far-reaching conclusion. Cosmopolitans among marine forms are present in many groups, but this does not prove that a local fauna does not exist. If we remember that the marine zoogeographical zones are determined mainly by physicochemical factors,[*] the force of Steiner's conclusion is much reduced.

## V. ADDITIONAL DATA ON THE SYSTEMATICS AND PHYLOGENY OF FREE-LIVING NEMATODES

511 The main systematic principles of this work have been given on pp. 21–22, Part I. As the work was submitted in parts, the general picture was different when Part I was printed (November, 1915). Since then I have reexamined the entire literature and my own material. In the summer of 1916 I had the opportunity to study many freshwater genera. In addition, some very important studies published abroad have only recently reached me. All this necessarily influenced my views on the system of free-living nematodes. Some changes were so fundamental that I included them in the proofs. Others are given here.

1) The composition of Leptosomatini and Anticomini must be reexamined. In addition to Platycoma and Synonchus of Cobb (see Appendix), several new genera from Murmansk belong to these tribes, probably Thalassoalaimus and Triodontolaimus. Phanoderma should probably form a separate subfamily. Anoplostoma should probably be transferred to the Oncholaimini; the resemblance of the genital system to that of Oncholaimellus is evident. I was influenced too greatly by de Man's comparison of this genus with Anticoma.

2) Symplocostoma is a relative of Enchelidium, while Eurystoma has an isolated position. It may be related to Phanoderma. The cuticular bodies of the first two genera should be considered as homologues of the teeth of Ironus, etc. In this case, Enchelidium would be related to the Dorylaimini.

3) The position of forms near Trilobus (p. 128, Part I) and Tripyla (p. 131, Part I) is very doubtful. These forms seem to be transitional between Enoplidae and Chromadoridae, which are sharply differentiated in the sea. However, some characters relate them to the group of Plectus (Anguillulidae).

4) The Desmoscolecidae, to judge from the work of Steiner (1916, 1916a) and my own material, are relatives or only a subfamily of Monhysteridae.

512 5) In the Monhysteridae, I apparently ascribed too much importance to some easily recognized characters (shape of lateral and oral organs), disregarding less-marked but more fundamental characters. In particular, the group Linhomoeus of the Monhysterini and related genera are isolated and closely related to the Siphonolaimini, Axonolaimini and Diplopeltini. The Comesomini are more closely related to the true Monhystera and the marine group Theristus–Cobbia.

---

[*] See Leuckart, 1886, 1891; Zur Strassen, 1892; Merrill and Ford, 1916, particularly Fuchs, 1915. The classification of the typical parasitic species in these genera and that of the typical free-living species is not correct in the latter work.

[**] 1884, p. 18.

[***] 1914, p 374.

[†] Ibid., p. 75.

[††] Ibid., p. 388

[†††] Micoletzky (1914a, p. 1) believed that all non-stenothermic species of the European fauna are cosmopolitan; alpine individuals are smaller in the plains (1917, p. 469).

[‡] Cf. Deryugin, 1915, quoted in the next section.

[*] Ortmann, quoted after the next section.

6) The position of the group Plectus and related genera in the Anguillulidae is doubtful. It is possibly related to the groups of Trilobus and Dorylaimus (Mononchus), as the early authors suggested.

In general, if the marine genera fit well into the system, the position of the freshwater forms is only approximately defined. In any case, the majority of genera belong to distinct groups (subfamilies or families) which are not represented in the sea.

No organ develops suddenly in phylogenetic development. Therefore, if we have on the one hand a fully organized form and on the other a form in which some organs are absent, the simpler organization will be secondary, as it is justified to assume that these organs have disappeared. Parallel with this process of simplification, however, there is a process of differentiation and development of the remaining rudiments, so that the picture may change either towards complication or towards simplification. A typical case of simplification in nematodes is the phenomenon of a state with a small number of cells, which results in a halt of development.

It is therefore accepted to consider the most fully organized and also the most simply organized forms, without reduction of the number of cells, as the most primitive: Leptosomatum in the Enoplidae and Paroncholaimus in the Oncholaimini. Among Chromadoridae and Monhysteridae,
513 there are apparently several parallel series. Draconematini and Desmoscolecidae are the most specialized lateral branches of these groups, and not transitional to the more primitive forms, as suggested by Shchepot'ev (see p. 189, Part I).

The transition to neotenic forms with few cells has been observed independently in several groups. As the embryonic development of nematodes is strictly determinative, the number of cells in the different organs of these forms will also be constant. In other words, the constancy of the cell composition is a purely larval characteristic. Some organs may pass from the "infantile" state and become multicellular; in this case, we have some degree of cell constancy. I therefore do not consider species of Rhabditis as primitive forms, but only as secondarily simplified forms (see pp. 21, 251, Part I, 38, 53, etc.).

We must again discuss the phenomenon of convergence, which is so widely developed in free-living nematodes. There is no organ of which similar types have not developed in different groups, e. g., the jaws of Enoplus and Cyatholaimini ( p. 61 ) and the stylet of Dorylaimini and Tylenchini ( p. 62 ). There are examples for every organ. The organization of different groups of nematodes is apparently so similar that equal biological factors cause equal morphological results.

There are two cases in the subdivision of smaller groups: either some organs vary more or less in parallel, and the definition of genera is not difficult in this case (e. g., Oncholaimini, p. 77, Part I; Monhystera, pp. 199, 210, Part I); or, on the other hand, difficulties in the group Chromadorini (pp. 150, 171, Part I) of this type have not yet been overcome. In this group, the cuticle, oral capsule, bulb of the esophagus and copulatory apparatus vary, apparently independently, so that the attempt to establish a system according to one character interferes with a system established according to other characters. It seems necessary for the time being to
514 restrict ourselves to the establishment of small genera which differ slightly but are natural, leaving a definitive system to future work.

## REFERENCES TO PARASITIC NEMATODES QUOTED IN THIS SECTION

See the general list at the end of the book for the bibliography on free-living nematodes.

### Publications in Russian

Deineka, D. I. Nervnaya sistema askaridy. Gistologicheskoe issledovanie (The Nervous System of Ascaris. Histological Study). — Trudy SPb Obshchestva Estestvoispytatelei, Zool., 42 (2):1(1—359. 1912 9 pl. 57 fig.

Fedchenko, A. P. Zoologicheskie zametki. III. K anatomii kruglykh chervei (Zoological Notes. III. The Anatomy of Round Worms). — Izv. Imp. Obshch. Lyub. Estest. Antrop. Etnogr. Imp. Mosk. Univ., 2 (14) 18.

Metal'nikov, C. O vydelitel'nykh organakh Ascaris megalocephala (The Excretory Organs of Ascaris megalocephala). — Izvestiya Akademii Nauk, 7, pp. 473—480. 1897.

Nasonov, N. K anatomii i biologii kruglykh chervei (The Anatomy and Biology of Round-Worms): I. Oxyuris flagellum — Raboty Zoologicheskoi Laboratorii Varshavskago Universiteta, pp. 1—31. 1897. II. Ascaris lumbricoides. — Ibid., pp. 133—174. 1897. III. Ascaris decipiens etc. — Ibid., pp. 61—86. 1898. Also published as supplement to Varshavskie Universitetskie Izvestiya in 1897, 1898.

### Publications in Other Languages

Augstein, O. Strongylus filaria R. — Arch. Natg. Anno 60, 1 (13—14): 255—304, 1894.

Bömmel, van. Über Cuticularbildungen bei einigen Nematoden. — Arb. Z. Inst. Würzburg, 10 (11):189—212. 1895.

Boveri, Th. Die Entwicklungsgeschichte von Ascaris megalocephala mit besonderer Rücksicht auf die Kernverhältnisse. — Festschr. Kupffer, p. 383—430, t. 40—45, Jena. 1899. 6 fg.

Brandes, G. Das Nervensystem der als Nemathelminthen zusammengefassten Wurmtypen. — Abh. naturf. Ges. Halle, 21, p. 271—299. 1899.

Bütschli, O. Gibt es Holomyarier ? — Zeit. wiss. Zool., 23 (22):402—422. 1873.

Bütschli, O. Zur Herleitung des Nervensystems der Nematoden. — Morph. Jahr., 10, p. 486—493. 1895.

Cloquet, J. G. Anatomie des vers intestinaux, Ascaride lombricoide et Echinorhynque géant. Paris, 4°, 106 pp., 1824. 8 pl.

Cobb, N. A. Oxyuris Larvae Hatched in the Human Stomach Under Normal Conditions. — Proc. Linn. Soc. N. S. W., 5 (8):168—185. 1891.

Deineka, D. Das Nervensystem von Ascaris — Zeit. wiss. Zool., 89 (18—20):242—307. 1908.

Domaschko, Ad. Die Wandung der Gonade von Ascaris megalocephala. Ein Beitrag zur Zellenlehre. — Arb. Zool. Inst. Wien, 15, pp. 275—280, 1905. 2 pl.

Ehlers, P. Zur Kenntnis der Anatomie und Biologie von Oxyuris curvula. – Arch. Naturg. Jg. 65, Vol. 1, p. 1–26. 1899.

Gilson, G. et Pantel, J. Sur quelques cellules musculaires de l'Ascaris. – Anat. Anz., 9, pp. 724–727. 1894.

Goldschmidt, R. Histologische Untersuchungen an Nematoden I. Sinnesorgane von Ascaris lumbricoides und A. megalocephala. – Zool. Jahrb. Anat., 18 (1–4):1–57. 1903.

Goldschmidt, R. II. Der Chromidialapparat lebhaft funktionierender Gewebszellen. – Ibid., 21 (3–8):49–140. 1904.

Goldschmidt, R. Über die Cuticula von Ascaris. – Zool. Anz., 28, p. 259–266. 1904.

Goldschmidt, R. Mittheilungen zur Histologie von Ascaris. – Ibid., 29, p. 719–737. 1906.

Goldschmidt, R. Das Nervensystem von Ascaris lumbricoides und megalocephala. Part I. – Zeit. wiss. Zool., 90, pp. 73–136, 1908. 3 pl.; Part II. Ibid., 92, p. 306–357, 1909. 21 fig. 3 pl. Part III. – Festschr. Hertwig II, p. 253–354, 1910. 3 pl.

Hagmeier, A. Beiträge zur Kenntnis der Mermithiden. 1. Biologische Notizen und systematische Beschreibung einiger alter und neuer Arten. – Zool. Jahrb. Syst. 32 (17–21):521–612. 1912.

Hamann, H. Die Nemathelminthen II. Die Nematoden. Jena. 8°. 1895.

Hesse, R. Über das Nervensystem von Ascaris megalocephala. – Zeit. wiss. Zool., 54, p. 548–568. 1892.

Jägerskiöld, L. A. Beiträge zur Kenntnis der Nematoden. – Zool. Jahrb. Anat., 7 (24–28): 449–532. 1894.

Jägerskiöld, L. A. Über die büschelförmigen Organe bei Ascaris – Arten. – Cbl. Bakt. Parasitk. (1) 24, pp. 737–741, 785–793. 1898.

Leuckart, R. Die menschlichen Parasiten und die von ihnen herrührenden Krankheiten. Leipzig u. Heidelberg 8°. 1868–76. VIII–882 pp. 401 fig.

Linstow, Osyuris paronai und Cheiracanthus hispidus. – Arch. Naturg. Jg. 59, 1 (7):201–208. 1893.

Linstow. Zur Kenntniss der Genera Hystrichtis und Tropidocerca. – Arch. Naturg. Jg. 65, 1 (13–14):155–164. 1899.

Looss, A. Über den Bau des Ösophagus bei einigen Ascariden. – Cbl. Bakt. Parasitk. (1) 19, pp. 5–13. 1896.

Looss, A. Zur Kenntnis des Baues der Filaria loa Guyot. – Zool. Jahrb. Syst. 20. 1904.

Looss, A. The Anatomy and Life History of Ancylostoma duodenale Dubini. A Monograph. Part I. – Rec. Egypt. Gov. School. Medic. 3 (1–10):5–158, Cairo. 1905.

Looss, A. The same. Part II. – Ibid., 4 (11–19):159–613. 1911.

Martini, E. Über Furchung und Gastrulation des Cucullanus elegans Zed. – Zeit. wiss. Zool. 74, p. 501–556. 1903.

Martini, E. Über Subcuticula und Seitenfelder einiger Nematoden 1906: I, Ibid; 81 (31–33):699–766. 1906; 8 fig. II, Ibid., 86 (1–3):1–54. 1907; 2 fig. III, Ibid., 91, pp. 191–235. 1908; IV–V, Ibid., 93, pp. 535–624. 1909.

Martini, E. Die Nematodenentwickelung als Mosaikarbeit. – Verh. Anat. Ges., 20, p. 266–274. 1906.

Martini, E. Die Konstanz histologischer Elemente bei Nematoden nach Abschluss der Entwickelungsperiode. Ibid., 22, p. 132–134. 1908.

Martini, E. Zur Anatomie der Gattung Oxyuris und zur Systematik der Nematoden. – Zool. Anz., 32, p. 551. 1908.

Martini, E. Über die Stellung der Nematoden im System. – Verh. D. Zool. Ges., 23, p. 233–248, 1913. 2 fig.

Martini, E. Die Anatomie der Oxyuris curvula. I. – Zeit. wiss. Zool. 116 (6–20):137–525. 1916.

Meissner, G. Beiträge zur Anatomie und Physiologie von Mermis albicans. – Zeit. wiss. Zool. 5 (11–15):207–284. 1853.

Müller, H. Beiträge zur Embryonalentwicklung der Ascaris megalocephala. – Zoologica, No. 41, 30 pp., 1903, 5 pl. 12 fig.

Rauther, Max. Beiträge zur Kenntniss von Mermis albicans v. Sieb. mit besonderer Berücksichtigung des Haut-Nerven-Muskelsystems. – Zool. Jahrb. Anat., 23 (1–3):1–7b. 1906.

Rauther, Max. Morphologie und Verwandtschaftsbeziehungen der Nematoden. – Erg. Fortschr. Zool. 1, p. 491–596. 1909.

Rohde, E. Beiträge zur Kenntniss der Anatomie der Nematoden. – Zool. Beiträge I. 1885.

Toldt, Carl. Über den feineren Bau der Cuticula von Ascaris megalocephala Cloquet nebst Bemerkungen über die Subcuticula desselben Tieres. – Arb. Zool. Inst. Wien, 11 (27):289–326. 1899.

Voltzenlogel, E. Untersuchungen über den anatomischen un histologischen Bau des Hinterendes von Ascaris megalocephala und Ascaris lumbricoides. – Zool. Jahrb. Anat. 16 (34–36): 491–510. 1902.

Zur Strassen, O. Bradynema rigidum v. Sieb. – Zeit. wiss. Zool., 54 (29–33):655–747. 1892.

Zur Strassen, O. Embryonalentwickelung der Ascaris megalocephala. – Arch. Entwmech., 3, pp. 27–105, 133–190. 1896.

## 517 *BIOLOGY AND GEOGRAPHY OF THE FREE-LIVING NEMATODES OF THE BLACK SEA*

519 In this section I present the general characteristics of the nematode fauna of the Black Sea, its distribution according to facies and a zoogeographical characterization.

There are few data from other seas on this subject. The studies on marine nematodes are generally based on fragmentary data, mainly on easily obtained littoral forms. Data on habitats are not compared and often even not given. Studies are rarely based on a more or less complete study of even a single facies. An exception is the work of Rouville (1905) and Steiner (1916), who gave a more complete picture, but only of a single facies. I intend to deal with the work of Steiner after studying my Murmansk material. The work of Rouville will be discussed below.

During my stay in Sevastopol I did not study the fauna of the stony bottom, which is certainly interesting. Shchepot'ev (1908) collected his material of Desmoscolex, Draconema, Rhabdogaster and Trichoderma on a stony bottom. In his opinion, the fauna of stones is cosmopolitan, as the same species have been found in Bergen and Naples. Commensal nematodes, living in sponges, Bryozoa, Ascidia and the tubes of annelides, have also been insufficiently studied. Sufficient material was collected only from clusters of mussels and Botryllus from the pier.* I also did not examine marine plankton; but nematodes are apparently very rare in plankton. Mechnikov (1868) mentioned only a larva of Desmoscolex from the plankton near Odessa. We also did not collect nematodes with bait. Buerkel (1901) stated that Adoncholaimus fuscus Bast. and Paron. vulgaris Bast. were collected in large numbers in dredge nets with a bait of decomposing mussels.

### FACIES OR BIOCENOSES ?

Zernov (1913), in his great work on the Black Sea fauna, distinguished these two concepts sharply, considering as facies in recent seas the physical properties of the bottom and as biocenosis (Moebius' term) the complex of organisms which inhabits a given facies. If we translate the
520 two terms, "facies" is rendered as "properties of the bottom" and biocenosis as the "community of animals" or, if we accept Zernov's arguments against "community," as the "population of a certain facies."

The term facies has been interpreted in different ways. The term was first used by geologists, who defined it as the modification of a geological horizon in different places. We also are justified in using facies in a recent geological horizon – at the bottom of the sea. The geologist Walther (1893–1894) defined facies as the "physical properties of the sea bed which conditions the distribution of organisms in the sea." Zernov rejects the second part of the definition, as it obscures its meaning, and retains only the first part.

Facies has been defined in this sense in many zoological studies. The concept of facies was closely related to that of biocenosis and certain organisms were used for a characterization of the facies. This was done in the work of Lorenz (1863) on the distribution of animals in Quarnero, in the work of Pruvot (1893–1895) and in the preliminary study of Zernov (1908).

Deryugin (1915) does not accept Zernov's view, stating that for "facies" the concept of the combination of a definite type of bottom with a definite complex of animal forms must be retained regardless of whether such combinations are present in geological deposits or recent formations" (p. 723).

This quotation thus seems to suggest that Deryugin considered organisms as the main characteristic of the "facies," but this is not the case:

"The complex of forms which enters the composition of the facies may be called biocenosis, but the facies should be defined according to the type of substrate, i. e., the bottom sediment, and not according to the type of the biocenoses, as the latter depend on the substrate, and not the reverse" (p. 724).

The two above quotations seem to contradict each other. In a later discussion, Deryugin follows the second concept, describing facies of "rocks and stones," "sand," etc., and biocenoses of "sponges and ascidia" on the
521 rocks, "Phallusia obliqua," etc. If he had followed the first concept, however, including organisms in the characterization of the facies, he would have had to describe a "facies or rock with Phallusia," etc. However, in his characterization of sands he follows the first concept, describing a subfacies of "Dentalium sand," etc.

Thus, in practice Deryugin accepts the view and definitions of Zernov, and the disagreement is apparently based on a misunderstanding. I may have given Zernov's views incorrectly, but my interpretation is based on frequent discussions with him and on a letter in which he dispelled some of the doubts caused by Deryugin's criticism.

A few words on the methods of study of biocenoses: Should we, as Deryugin suggests in the second quotation, establish a bottom-facies and then describe the distribution of the various biocenoses on the facies, or should we define the biocenoses and describe them? This depends mainly on the author: for the geologist the bottom-facies is the most important, and he describes it as the main subject; for the zoologist the population of the facies is more important, and he describes the biocenoses first. The minerologist Thoulet therefore adopted the first point of view and suggested exact subdivisions of the bottom sediment. Other examples are the work of Sudry on the Thau lagoon ("étang de Thau") and that of the zoologist Pruvot. Sudry (1894) gave a purely lithological map of the environs of Banyuls, and Pruvot described the distribution of animals on the different

---

* Cf. Bastian, 1865, p. 89; Bütschli, 1873; Villot, 1876.

facies which had been determined before. Deryugin also follows this course, while the work of Zernov takes a mainly zoological approach.

Each approach has its advantages. If the form of the bottom has been determined exactly, there is a different basis for the study of their biocenoses and sources of inaccuracy are eliminated. However:

522 1) Uniform bottoms may lie at very different depths, particularly where there are strong tidal currents. A good example is the "facies of rocks and stones" in the Kola Gulf, according to Deryugin, where he defined different biocenoses. The same applies to the various mud or sand biocenoses of the Black Sea.

2) "... do not interpret the narrow, small subdivisions of the bottom on the basis of the predominating animals... But they react very strongly to coarse subdivisions, such as rocks, sand, mud" (Zernov, 1913, p. 15).

3) The distribution of some marine plants (e.g., Zostera) depends, in addition to the bottom, on other factors which have nothing to do with the bottom, since a characteristic biocenosis is always associated with plants.

4) The distribution of animals depends on other conditions in addition to the bottom: temperature, salinity.

These arguments also suggest that the zoologist should first of all consider the facts when determining biocenoses: the presence of populations in a given place. He should not hesitate to combine different facies (e.g., sand, mud-sand, gravel) or divide a facies (e.g., different types of mud in the Black Sea, rocks in the Kola Gulf). In short, the zoologist should consider the facies only insofar as it conditions the distribution of animals.

Zagorovskii and Rubinshtein also followed Zernov in this interpretation of biocenosis and in their method when they described the biocenoses of the Odessa Bay. However, Odessa Bay also created objections to exaggerated enthusiasm for the study of facies, as it explained the causes of the distribution of animals inadequately (Kudelin, 1912). Thus, the differences in the composition of the mussel mud near Odessa and Sevastopol caused him to state that it was not possible to use the same terms for both. Zernov objected to this (1913, p. 138), by stating that it is obviously impossible to 523 find two places in the sea with exactly the same fauna. The fauna of Odessa Bay with its sharp fluctuations of temperature and salinity is certainly poor compared with that of Sevastopol, but the disappearance of some form is no argument against the close resemblance of the biocenoses in Odessa and Sevastopol. Some differences in the Odessa biocenoses according to Zagorovskii and Rubinshtein will be discussed below.

## DEPTH ZONES IN THE BLACK SEA

When the biocenoses are established in general outline, the next question is their classification. One of the main characteristics here is the depth at which a given biocenosis develops and its restriction to a particular vertical zone. Life in the depths is absent in the Black Sea and is present only on the continental plateau, demarcated by the 200 m isobath.

"Another essential boundary in the open sea is the 30–60 m isobath. This is probably the lower boundary of biocenoses associated with a hard substrate – sand, rock and shell bottom, which are also the lower limit of action of the waves. Mud begins to be deposited below it. In bays protected against heavy storms, the mud is deposited much higher and the corresponding boundary is situated on the 8–18 m isobath" (Zernov, pp. 135–136).

Zervnov called the zone above this line the littoral zone, and the zone below the sublittoral zone. Voronikhin (1908), on the basis of the distribution of algae, distinguished in the littoral zone of Zernov a littoral zone proper (at the surface), a sublittoral zone and an elittoral zone (the deepest horizon of the littoral zone of Zernov – the biocenosis of shell bottom).

Deryugin (p. 769) considered the term "littoral" used by Zernov to be incorrect and retained this term only for the tidal zone. As there are no tides in the Black Sea, this term can be used only for a narrow strip near the water, as used by Voronikhin.

Not only for the Black Sea, but in general, the separation of a surface strip is hardly natural. Thus, Pruvot (1897, p. 607) recorded for the English 524 Channel that the fauna of the upper strip of the tidal zone differs markedly from that of the lower strip. The low-tide mark divides such well-defined and natural biocenoses as, for example, meadows of Zostera. The fauna which cannot withstand complete desiccation persists in pools above the tide mark and is characteristic for the deeper horizons. The classical zone of Laminaria is considered to be situated below the tide mark, but Joubin gives very informative photographs of this zone, which is dry during low tide.

Thus, the biocenoses in the Black Sea are grouped only in two principal zones – the sublittoral and the elittoral (the littoral and sublittoral strips of Zernov).

Voronikhin divides the flora of the open sea from that of the protected parts, chiefly of Bol'shoi Roadstead. A degree of protection also has a great influence on the distribution of zoological biocenoses. The biocenosis of muddy coasts is present only in enclosed bays. Zostera also requires a more or less protected location. Zernov stated that all biocenoses become weaker towards the surface the further they are from the open sea: rocks descend not deeper than 2 m in the depth of the roadstead as opposed to 10–22 m in the open sea; the lower border of coquina is 24–70 m in the open sea and 12–20 m in the roadstead. Mud lies below the shell bottom, both in the open sea and in the roadstead, and Zernov related the same mussel-mud biocenosis to this. We cannot accept this view. The mud of the open sea is very pure; it is, in fact, a clay deposit, each particle of which is worked through by the sea. The temperature in this zone is almost constant and this biocenosis is one of the richest and most characteristic of the Black Sea. The mud of the roadstead (and also of the Kherson and Strelets bays) is markedly richer in organic material, carried by the freshwater flow from the shore and deposited; it is greatly polluted by wastes from the city, becomes heated in summer and cooled in winter, and its fauna is therefore also much poorer and cannot be compared with 525 true mussel mud. I suggest considering it as a special biocenosis of bay mud.

I also object to the term "biocenosis of sand" used by Zernov (p. 74), as it suggests a population of sand, as if it were a well-defined unit. But Zernov (p. 82) mentions a "biocenosis of littoral sand near the water level," and later he mentions "shell sand from Peschanaya Bay." It is thus not entirely clear whether we should distinguish one common biocenosis of sand or several different biocenoses. There is a much clearer distinction in his preliminary report (1908, p. 887): he distinguishes between facies 5 — "littoral sand near the water level," facies 6 — "sand further from the shore," facies 7 — "Amphioxus sand." This subdivision of the different zones of sand appears more correct from the zoological point of view, as their populations are very different. The combination of these zones in the final work appears an unnecessary concession to the geological approach in the study of biocenoses which was proposed by Thoulet and to which Zernov objects on p. 15.

Thus, if Zernov's table (p. 134) is modified to some extent, we obtain the following scheme (see below). This scheme is of course not definite and does not reflect all the combinations. The disappearance of intermediate biocenoses is particularly common, as it depends mainly on the steep inclination of the bottom at the corresponding depth, so that there is not sufficient space for the full development of the fauna (see also p. 137 in Zernov). In this scheme, bay mud is related to the sublittoral zone and not to the elittoral zone, although it lies outside the direct action of the waves. However, it is always situated within the isobath given and its presence is due only to the particular complication of the coast line. Too strict an application of the principle of protection from waves would make it necessary to consider the biocenosis of the muddy shore also as elittoral.

528 We shall now discuss the various biocenoses and the nematodes characteristic for them, arranging the biocenoses in three main groups: sublittoral of the open sea, elittoral of the open sea and biocenoses of sheltered parts.

## A. Biocenoses of the Sublittoral Strip of Open Parts

### 1. Biocenosis of rocks

The barnacle Chthamalus, the snail Littorina neritoides, the shore crab Pachygrapsus marmoratus and the isopod Lygia brandti are characteristic for this biocenosis above the water level. Along the water extends a pink strip of coralline algae resembling the coralline pavements described from the Mediterranean by Marion, Pruvot and Joubin. The annual death of the coralline algae and the fauna associated with them resulting from the fall of the water level in autumn is characteristic.

The following nematodes were collected from the corelline algae:

Enoplus euxinus Fil. } in large numbers, distributed
Eurystoma assimile Fil. } everywhere.

In addition, isolated specimens of other species were distributed throughout the whole coastal facies.

Lower down, in places which are not uncovered during wave action, joining the coralline algae above, grows a dense ridge of Cystoseira which shelters a specialized fauna: shrimps (Rissoa), polychaetes on leaves and stalks, Spirorbis and Pileolaria in tubes, various hydroids, sponges.

526-527

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Region of strong wave action | sublittoral zone | Open sea and open bays | | | | | Protected, quiet bays and main roadstead | | |
| | | coastal facies: | | | | | coastal facies: | | |
| | | rocks | shingle | coarse sand (gravel) | fine sand | clay | rocks, artificial structures | sand | mud |
| | | biocenosis of rocks sprayed by surf | biocenosis of shingle | biocenosis of Saccocirrus sand | biocenosis of fine sand and dead plants on shore | biocenosis of clay burrowed by Pholas | biocenosis of rocks above sea level | mud-sand coast | biocenosis of muddy coast |
| | | biocenosis of thickets of Cystoseira, upper and lower layer | | biocenosis of Diogenes sand (biocenosis of dead plants in depressions as a particular case) | biocenosis of Zostera (in calm places) | | biocenosis of Cystoseira in muddy areas of Ulva | biocenosis of Zostera | biocenosis of Ulva |
| | | biocenosis of Amphioxus sand | | | | | Capitella sand | | |
| | | biocenosis of shell bottom (sometimes overgrown with Phyllophora) | | | | | biocenosis of oysters | | |
| | | isobath 30–60 m | | | | | isobath 8–16 m | | |
| Region of weak wave action | elittoral zone | biocenosis of mussel mud 60–70 m | | | | | biocenosis of bay mud | | |
| | | biocenosis of Phaseolina mud | | | | | | | |
| | | isobath 200 m | | | | | | | |
| | bathyal zone | hydrogen sulfide realm | | | | | | | |

Zernov distinguished an upper and lower horizon. The bryozoan Lepralia covers the Cystoseira in the lower horizon. Tikhii recorded characteristic species of Caprella from this layer.

I had samples of the upper layer from the boulevard roadstead, Shmit Bay and the Spasenie rock from Georgievskii Monastery; deep Cystoseira from Shmit Bay and from the boulevard roadstead. The fauna of nematodes is rather similar in all these places.

529 a) Mass occurrence:

Anticoma pontica Fil.– only in upper zone.
Enoplus euxinus Fil. – everywhere.
Symplocostoma longicolle Bast.– everywhere.
Cyatholaimus demani Fil. – particularly in the lower zone.
Euchromadora striata Eb. – everywhere, species characteristic for littoral zone.
Chromadorina obtusa Fil.–found everywhere, but in large numbers only in Georgievskii Monastery in July. Only found in Cystoseira.

b) Forms that were found only or mainly in Cystoseira, but as single specimens:

Phanoderma albidum Bast.– few specimens, but everywhere.
Anoplostoma viviparum Fil. – in deep zone
Oncholaimus? dujardini de Man – Georgievskii Monastery in July Identification doubtful, found also in deep sand.
Symplocostoma marioni Fil.– one specimen in May from boulevard roadstead.
Metachromadora cystoseira Fil. – one specimen in June from the same place.
Sphaerocephalum crassicauda Fil.–one specimen in deep zone in June.

Clumps of mussels sometimes develop in large quantities on the rocks, particularly in winter on the piers. The mussels are fairly large in winter, overgrown with Botryllus and between them shelters a large fauna, not very rich in species and characterized by various species of Syllidae, Nereidae and Polyophthalmus. I found only 5 species in the sample collected in January, 1912, but all of them in large numbers:

Cyatholaimus demani Fil.
Enoplus euxinus Fil. } found everywhere.
Enchelidium longicolle Fil. – also in sand.
Symplocostoma longicolle Bast.
Euchromadora striata Eb. } in various coastal biocenoses.

The clumps of small mussels from the rocks below the station in June, 1912, provided a less rich but more varied collection. Mass species were:

Anticoma pontica Fil.
Enoplus euxinus Fil.
Cyatholaimus demani Fil.
Eurystomina assimilis de Man } found everywhere.
Euchromadora striata Eb. – found in various coastal facies.
Oncholaimus campylocercus de Man – mainly a coastal form, but found also in the depths.

530 The following are also characteristic:

Chromadorella mytilicola Fil.
Chromadora quadrilinea Fil. } only here.
Sphaerocephalum crassicauda Fil. – also in Cystoseira.

Unfortunately, during my stay in Sevastopol I could not obtain pieces of wood bored by Teredo, rocks with burrows of Pholas and specimens from overgrown vessels. I would probably have obtained new data, particularly in the last case.

The nematode fauna collected by Rouville in Sète, Canal de Bourdigues, consists of different species, but mainly of the same genera as the Sevastopol fauna of rocks.

## 2. Biocenosis of clay burrowed by Pholas

Sarmatian clay is directly washed by the sea in some places. The burrowing mollusk Barnea candida occurs here in large numbers. This biocenosis, defined by Zernov in 1908, is combined with the biocenosis of the rocks in the final work. It is probably more correct to keep it separate, even if there is no overgrowth. Large numbers of nematodes, but only of three species, were found in the burrows of Barnea in July. There were mainly:

Oncholaimus campylocercus de Man – large numbers; mainly a coastal species, but found also deeper in sand.
Enoplus euxinus Fil. – common everywhere.
Tripyloides demani Fil. – one specimen, also in Zostera.

## 3. Biocenosis of littoral shingle

I washed several pails of shingle from Georgievskii Monastery. The biocenosis was very poor. Only one Nereis was found and only four nematodes, all of them characteristic for the fauna of the nearby rocks, so that their presence in the shingle was accidental (see chart, pp. 128–135).

## 531 4. Biocenosis of Saccocirrus sand

This biocenosis is connected with coarse sand from broken rocks. I usually obtained it from the boulevard roadstead, not far from the station.

"It is sufficient to keep sand from the Yachting Club near the station in a vessel for one day without blowing through, and pink clumps of Protodrilus, white clumps of Procerodes and Cercyra (Triclada) and green clumps of Saccocirrus crawl out and lie on the surface; it is enough to agitate the water slightly for all the Saccocirrus and Protodrilus to hide suddenly in the sand and not a living creature to remain on the surface. The same occurs on the seashore during a storm: when the sea is not calm it is very difficult to find even a few of these animals, but there are large numbers in good weather" (Zernov, p. 82).

I had samples of this sand from the boulevard roadstead and Shmit Bay. There were few nematodes. A few specimens of the following were found:

Enoploides cirrhatus Fil. – in Shmit Bay.

Oncholaimus brevicaudatus Fil. – near the boulevard roadstead.

The other species are characteristic mainly for deeper sand.

I neglected the fauna under stones at shallow depths. All authors found a rich fauna under stones in the Atlantic (Southern, 1914; Villot, 1876), and I found this also at Murmansk.

### 5. Biocenosis of fine littoral sand

This biocenosis develops where the coast consists of fine sand, e.g., in Peschanaya Bay. A special case is the "biocenosis of dead plants and algae on the shore" (Zernov, p. 104). The fauna of stranded plants and the fauna of plants in the water near the shore seem indistinguishable.

There are numerous amphipods, and littoral oligochaetes are characteristic. Nematodes are very numerous, but except for one specimen of
532 Eurystomina assimilis de Man all belong to one species which has been formed only here:

Enoplus littoralis Fil., immature, June, July.

### 6. Biocenosis of Diogenes sand

This name was proposed by Zagorovskii and Rubinshtein for deep, fine sand (2–10 m) which follows the above littoral biocenoses in Odessa. The predominant form is the gastropod Cerithiolum reticulatum and the hermit crab Diogenes, which lives in the shell of Nassa.

This sand is identical with facies No. 6 of Zernov – "sand further from the shore" (p. 74). This sand is connected by transitions with the lower Amphioxus sand and contains a distinct biocenosis which should not be combined with the deeper biocenosis of Amphioxus sand. This combination induced Zagorovskii and Rubinshtein to make a mistaken comparison of the Odessa Diogenes sand with the Sevastopol Amphioxus sand. The Diogenes sand in Sevastopol is the same as in Odessa, while Amphioxus sand is absent in Odessa.

Several fishes are characteristic for this sand: Uranoscopus, Trachinus, Solea, Mullus; the mollusks Loripes, Cardium, Tapes, Venus, Cerithium; the crustaceans Gebia in burrows; Arenicola.

I did not examine the fauna of this sand in detail, but there were few nematodes in the Kazach'ya Bay. Nematodes generally do not like this fine, disturbed sand.

I was unable to obtain samples of dead algae, which are deposited in depressions in Kazach'ya Bay. This biocenosis, which was considered by Zernov (p. 105) as distinct, should probably be considered a modified Diogenes sand.

### 533 7. Biocenosis of Amphioxus sand

This is one of the richest and most interesting biocenoses at Sevastopol. From 10–12 m it descends to 20–34 m near Sevastopol, and to 50–52 m in the open sea. There is shell bottom near Georgievskii Monastery at 54 m. This sand is present near Sevastopol in two modifications.

Between Sevastopol and the Kherson lighthouse, it consists of broken shells with an admixture of fine greenish-brown mud.

There is thus, as noted by Zernov (p. 88), a clear disruption of the usual sequence of sediments – coarser sand near the coast, finer sand further out to sea. The shells which constitute this sand are probably broken by the action of waves on the rocks (Zernov). However, this is caused in part by living organisms – fishes and crustaceans which grind the shells and burrowing sponges, in addition to the action of the waves. The direct dissolving action of the sea water probably also has some effect.

Zernov's view is supported by the fact that the sand is disposed chiefly against rocky promontories and is apparently only secondarily carried to calmer parts opposite the bays. Another factor possibly has an effect: the shells are flat and have a relatively larger surface area than the small but round sand grains. They are therefore washed from the sand by the waves and carried away by the deep surf currents. The chemical and mechanical process breaks them into fine particles.

The origin of Amphioxus sand at Georgievskii Monastery is different: there is a regular sequence, shingle near the coast, mainly the product of the break-up of local trachytic rocks; the greater the depth the finer the
534 sand, but it is still fairly large gravel at 36 m. There is no fine sand. Deeper mud adheres to the gravel and the shell bottom develops on this mixture (see below).

The fauna of this sand is very rich and characterisitic; all the animals burrow into the sand or crawl between the sand grains. Most characteristic is Amphioxus, Ammodytes, the crustacean Portunus, particularly many worms: pink Polygordius, Glycera and Ophelia are typical forms. There are large numbers of various turbellaria, Rhabdocoela and Acoela. The mollusks Tapes, Venus and Meretrix are characteristic (Zernov, p. 76); Modiola adriatica is attached to the sand by byssus; Calyptraea chinensis is attached to larger fragments.

The fauna of the Georgievskii Monastery is qualitatively and quantitatively richer than the sand at Peschanaya Bay. Amphioxus is far more numerous; the small, naked mollusk Hedyle is numerous.

The nematode fauna is also very rich qualitatively and quantitatively. This is the richest biocenosis, with only Zostera comparable in the number of species, but not in the number of individuals and their size.

The following species, arranged according to size, were found in numerous samples from Peschanaya Bay (marked*) and in summer samples from Georgievskii Monastery (marked † ):

*† Paroncholaimus zernovi Fil. – adults in winter, not less numerous in summer, but all individuals immature. The Georgievskii specimens are darker than the Sevastopol specimens.

* Metoncholaimus demani Z. Str. – particularly on filamentous algae collected in the same place together with the sand.

*† Symplocostoma ponticum Fil. – in large numbers only at the Georgievskii Monastery, much less numerous in Peschanaya Bay.
*† Enoploides amphioxi Fil.
*† Eurystomina assimilis de Man – numerous in winter, fewer in summer.
*† Symplocostoma hexabulba Fil.
† Enchelidium longicolle Fil. – only at Georgievskii Monastery.
* Comesoma stenocephalum Fil.
* Axonolaimus setosus Fil. }
*† Axonolaimus ponticus Fil. } only young in winter. Only one specimen of A. setosus at Georgievskii Monastery.
* Oncholaimus campylocercus de Man – adults were found in summer and winter, but they were less numerous in winter.
535 *† Metachromadora macroutera Fil. – adults in winter, numerous in summer, but all immature.
*† Anticoma pontica Fil. – only in clumps of algae on sand, a few at Georgievskii Monastery.
*† Onyx perfectus Cobb – adults in summer, particularly numerous at Georgievskii Monastery in samples from 36 m.
*† Chromadora poecilosomoides Fil. – a few at Georgievskii Monastery.
5–10 of the following:
* Leptosomatum bacillatum Eb. – adult females in July–August.
* Lept. punctatum Eb.
*† (Enoplus euxinus Fil.‡)
*† Viscosia cobbi Fil. – adults in May.
*† Dignathonema bulbosa Fil.
* Pelagonema obtusicauda Fil. – only in winter.
*† Oxystomina filiformis Fil.
* Halichoanolaimus clavicauda Fil.
* Disconema alaima Fil.
*† Oncholaimus dujardini de Man.
Single specimens:
* (Cyatholaimus demani Fil.‡)
*† Chromadora sabulicola Fil.
† (Euchromadora striata Eb.‡)
* Spirina sabulicola Fil.
† Acmaeolaimus diplopeltoides Fil.
* Diplopeltis eberthi Fil.
† Symplocostoma sabulicola Fil.
*† Oxystomina clavicauda Fil.
* Enoplolaimus conicus Fil.
† Enoplolaimus dubius Fil.
* Draconema cephalatum Cobb.

The fauna of the Georgievskii Monastery and Peschanaya Bay are thus very similar in spite of the great chemical differences of the substrate. This is a good illustration of a facies of different origin which contains similar biocenoses. The records of nematodes, except for some differences in rare species which may be disregarded as the records were accidental, differ as follows:

There are far fewer Symplocostoma ponticum Fil. in Peschanaya Bay. Enchelidium longicolle Fil. is absent, but littoral and 536 mud species flourish: Metoncholaimus demani Z. Str., Oncholaimus campylocercus de Man, Anticoma pontica Fil. Axonolaimus setosus Fil. is only present in Kruglaya Bay, while A. ponticus Fil. also flourishes at Georgievskii Monastery; the reasons for this are not known. It is interesting that Paron. zernovi Fil. is not found in large numbers nearer to Kruglaya Bay, though the composition of the sand is the same. It apparently withstands pollution well, lives for a long time in an aquarium, and was formed in single specimens even in the muddy Capitella sand (see below).

The most important conditions for the population of this sand are: coarse sand outside the tidal zone. The tide touches it only slightly, or at any rate rarely. It usually does not disturb large sand grains, and only cleans the sand from mud. The current also cleans the sand, especially at Georgievskii Monastery. This also explains the abundance of small turbellaria, which are easily concealed in crevices of undisturbed sand.

There are analogies in other seas to the Amphioxus sand of the Black Sea. The Amphioxus sand in Naples lies at a depth of 2–4 m (Zernov, p. 75). The sand consists of fragments of recent volcanic rocks. Toward the coast it is found near sheltering rock and in small inlets (Porto Margellina, Posilippo). Amphioxus and Polygordius flourish here also, and several interesting nematodes have been described (Türk, Zur Strassen). There was no systematic research, but the large Fiacra and Cylicolaimus are particularly characteristic. Saccocirrus is sometimes found together with Amphioxus, which would not be possible in Sevastopol, where the habitats of two forms are separated by a wide strip of Diogenes sand.

537 Another classic location of Amphioxus is the Straits of Messina where the swell in the narrow straits is weak but there are strong currents which clean the sand.

Cori (pp. 705–706) described shell sand below rocks near Trieste: Amphioxus and a typical worm fauna is found "wherever it is sufficiently loose."

Pruvot (1894) also described sand in Banyuls with broken shells from a depth of 20–40 m with numerous Amphioxus, Polygordius and Ophelia. An abundant nematode fauna will probably be found to exist there also.

Jägeskiöld wrote on Cylicolaimus magnus Villot:

"I found this species near the outer (Swedish) marine station in Kristineberg, near the rocky Island of Bonden far from the coast, where it is abundant in sand, which consists of broken shells, and lives together with Amphioxus, Cyprina islandica, Polygordius sp. and Fiacra described below. I found it also near Flattholmen Island near Kristineberg. The depth at both locations was 10–20 m."

Southern (1914) described a dredge from Clew Bay on the west coast of Ireland from a depth of 48 m:

"The dredge was filled with gravel, sand and broken shells. Part of it was washed, and the water was filtered throught a fine net. Several ounces

---

‡ Species in parentheses also occur in other biocenoses.

of sediment were obtained and this material provided an apparently inexhaustable source of new and interesting species. . . Most species had not been described, because this particular habitat had never been examined in detail. Because of the presence of many Polygordius . . . this type of bottom should be called Polygordius ground. . . The same type of bottom, which provides shelter for the same community of species, was found in Dingle Bay and is undoubtedly widespread in sublittoral waters."

Among the nematodes found by Southern, species of the genera Nuada, *Diplopeltis, Stenolaimus, Fiacra, Cylicolaimus, Demania, *Paroncholaimus, *Enoploides, Enoplolaimus, *Draconema and Desmoscolex are particularly characteristic. If we compare this list with the list given above, it appears that the genera marked with an asterisk are characteristic for the Sevastopol Amphioxus sand, while Fiacra and Cylicolaimus are characteristic for the Neapolitan and Swedish Amphioxus sands.

The origin of the fauna of the three localities is probably due to the
538 strong tidal or other underwater currents.

According to Deryugin (pp. 743–744), "a subfacies of coarse sand or gravel" is quite poor in Murmansk. The fauna of the deep shingle (p. 740) is fairly rich. I examined broken shells from Letninskii Cape at the Murman Coast from a depth of 100–120 m. After seeing the material collected by a dredge, I found that its fauna was much poorer than I had imagined. On the other hand, the muddy sand from that area yielded about 70 species of nematodes in one dredge. I did not study the "coarse sand with an admixture of finely broken shells in the Korabel'naya Inlet (Pala-Guba)" mentioned by Deryugin, in which Ophelia occurs.

Thus, Polygordius, Amphioxus and a rich fauna of nematodes of characteristic genera occur wherever there are suitable conditions – coarse sand in a calm sea, outside the direct action of the waves.

### 8. Biocenosis of the shell bottom

The biocenosis of the shell bottom (Zernov, p. 87) consists of a mass of living and dead mollusks, mainly bivalves. This is present almost everywhere at the boundary of sand and mud, where the bottom has become hard through a substantial admixture of mud and provides conditions for the settlement of mollusks.

The shell bottom at Peschanaya Bay (34 m, Zernov, p. 95) consists mainly of mussels, mainly Meretrix, Gouldia and Tellina donacina. Modiola adriatica is common and Pecten ponticus is rare. Only shells of oysters are found.

The shell bottom at Georgievskii Monastery from 54 m consists mainly of Pecten ponticus and Modiola adriatica. The latter are particularly large. Almost all shells with a marked pink pigment, Pecten as well, and white shells were found only in small numbers. The wide
539 plates of the brown alga Zonardinia and large red sponges, not idendified exactly but probably belonging to the genus Reniera, according to Zernov, are common.

The nematode fauna in the latter shell bottom is very poor and not very characteristic. Only the following, which occurs everywhere, was found in large numbers:

Anticoma pontica Fil.

The following species were also found:

* Leptosomatum punctatum Eb.
Enoplus euxinus Fil. – this species was found alive everywhere, but here they were particularly large individuals and fully mature in the summer, which was not observed on the surface.
Paroncholaimus zernovi Fil.
Symplocostoma ponticum Fil.

Species marked with an asterisk are very abundant here, the others are visitors from sand and are not common. Isolated specimens of the following were found:

* Leptosomatides euxina Fil. }
* Spilophorella euxina Fil. } only in this sample.
Phanoderma tuberculatum Fil. – also on Phyllophora.
Draconema cephalatum Cobb – also in sand.

Phyllophora near Sevastopol also grows on shells. Only the widely distributed Enoplus euxinus Fil. occurred in large numbers:

In addition, the following were found:

Leptosomatum bacillatum Eb.
* Phanoderma tuberculatum Eb.
Enchelidium longicolle Fil.
Symplocostoma hexabulba Fil.
Cyatholaimus demani Fil.
Axonolaimus setosus Fil.

Phyllophora is a center of concentration only for Phanoderma (*); Enchelidium and Cyatholaimus have their center of concentration in the littoral algae, the others in Amphioxus sand.

## B. Biocenoses of the Elittoral Zone

540

### 9. Biocenosis of mussel mud

A sample of this mud from Kacha consisted of gray, slightly sandy clay. The predominant forms are Mytilus galloprovincialis, overgrown with the hydroid Sertularella, various sponges and the ascidia Ascidiella aspersa and Ciona intestinalis. Botryllus is also abundant.

The nematode fauna, although not very rich, contains numerous characteristic forms. Only the following were numerous:

Sphaerolaimus dispar Fil. – characteristic for the biocenosis.
Parasabatieria abyssalis Fil. – also found deeper in Phaseolina mud.

In addition, the following were found:

Enoploides brevis Fil. – characteristic for the biocenosis.

Metoncholaimus eberthi Fil. } characteristic for the
Sphaerolaimus macrocirculus Fil. } biocenosis.
Oncholaimus campylocercus de Man – widely distributed.

### 10. Biocenosis of Phaseolina mud

Deeper than the mussel mud, from 60–72 m to the boundary of life at 200 m, extends a biocenosis characterized by Modiola phaseolina Phil., which flourishes in the northern seas and has almost died out in the Mediterranean. The annelid Terebellides carnea is common in the upper layers, so that Zernov created for them a special biocenosis of terebellid mud. Melinna adriatica also occurs, living in elastic tubes. There are the following ascidia: Ciona intestinalis, Eugyra adriatica and Ctenicella appendiculata, the latter occurring in higher levels and characteristic for the biocenosis.

Nematodes are rare in this mud. Only the following widely distributed species are more or less numerous:

Enoplus euxinus Fil.
Oncholaimus campylocercus Fil.
Parasabatieria abyssalis Fil. – also fairly numerous, but its main habitat is in a higher level, in the mussel mud.
Enoploides hirsutus Fil. was found only in this habitat.

### 541 11. Biocenosis of Phyllophora meadow

This characteristic biocenosis was not examined, except for the small overgrowths of Phyllophora on mussels (see p. 123).

## C. Biocenoses of Sheltered Locations

### 12. Biocenosis of Ulva (muddy coast, according to Zernov)

This biocenosis is developed in the depths of calm, sheltered bays, mainly polluted, but not fresh, e. g., in the depths of Kherson Bay or Novaya Hollandiya. Arenicola, Glycera and Nereidae, which burrow in the mud, are characteristic; there are many Hydracarina (Pontarachna). Nematodes are rare; all are widely distributed littoral forms, only Euchromadora striata Eb. occurred in large numbers.

### 13. Biocenosis of meadows of marine plants

In protected bays, where the tide is light, overgrowths of Zostera develop; where the water is more brackish, e. g., in the depths of the roadstead and in Streletskaya, Kamysheva and Kazach'ya, overgrowth of Potamogeton pectinatus develops. I did not study Potamogeton very much, but it should probably to be considered a separate biocenosis.

**Meadows of Zostera** may also be referred to the biocenoses of the open sea, or at least of open bays. However, such a division is always conditional, and I prefer to place them in this section, as they are most typically developed in the sheltered parts of the Bol'shoi Roadstead and a necessary condition for their development is usually protection. The bottom is mud-sand. A similar biocenosis of the open sea is Diogenes sand.

The fauna of the Zostera meadows is very rich:

Between the leaves of Zostera swim large numbers of mysids, amphipods, isopods, shrimps, various genera and species of Syngnathus, Crenilabrus tinca (Labridae) and other fishes (medusae Cladonema) and the Sagitta and Spadella. Numerous Rissoa crawl on the leaves. There are large numbers of various species of Rhabdocoela and
542 Acoela. Cerithiolum is present in immense numbers along with Trochus and other mollusks. The leaves of Zostera are entirely covered with Bryozoa towards autumn: Lepralia, Membranipora and the tunicata Didemnidae; they die in winter, the weight of these overgrowths killing them. There are also Spirorbis and hydroids on the leaves – among the roots of Zostera Ophyurids hide: Sthenelais, Lagis koreni, Gebia and Calianassa, and there are also mollusks living in the sand (Zernov, pp. 97–98).

In the Mediterranean Sea the role of the Black Sea Zostera is played by Posidonia, which descends, however, to 25 m, while Zostera is found no deeper than 6–10 m. Zostera grows only in less saline and colder regions, e. g., in the estuaries of the Rhone and in the Adriatic (Cori). The fauna of Posidonia and Zostera is much richer in the Mediterranean, but many characteristic animals (Rissoa, Spadella, Cladonema) occur there also. Issel made a special study of the biology of the fauna of Posidonia and established several categories of animals: animals living on the leaves, in incrustations on the leaves, etc. I did not even distinguish between the fauna of the roots and the leaves of Zostera, but placed them all together.

Zostera is also widely distributed in the English Channel and the Baltic Sea (Zernov, p. 99; Pruvot, 1897) and their fauna resembles that of the Black Sea in many respects.

The nematode fauna is very rich qualitatively and quantitatively. The absence of large forms is characteristic. The biocenosis of Zostera competes with Amphioxus sand in the number of species, but the latter is certainly richer, particularly in larger species. The following species were very common:

Anticoma pontica Fil. } found in all littoral biocenoses.
Enoplus euxinus Fil. }
Chromaspirina pontica Fil. } characteristic only for Zostera.
Spirina zosterae Fil. }

Other species are fairly numerous, but I list only the more characteristic species (the other species are given in the table at the end of this section):

Enoplolaimus conicus Fil. – was found in Amphioxus sand at Kruglaya Bay.

Tripyloides demani Fil. – found on Potamageton in a few specimens and in clay with Barnea.
Dignathonema bulbosa Fil. – also from Amphioxus sand at Georgievskii Monastery.
Monoposthia costata Bast. – also with coralline algae.
543 Parasabatieria clavicauda Fil. – also in bay mud, probably present in the bottom sediment.

Halichoanolaimus filicaūda Fil.
Paramonhystera setosa Fil.
Cobbia triodonta Fil.
Linhomoeus filiformis Fil.
Metalinhomoeus zosterae Fil.
Terschellingia pontica Fil.
Prosphaerolaimus eurypharynx Fil.
Araeolaimoides zosterae Fil.
Comesoma dubia Fil.
} mainly single specimens, but found only in Zostera.

I had a deposit from the leaves of Potamogeton from Streletskaya Bay collected by Zernov. Only a few species of nematodes were found, but in large numbers:

Metoncholaimus demani Z. Str. – species of dirty water.

Anticoma pontica Fil.
Eurystomina assimilis de Man
Cyatholaimus demani Fil.
} widely distributed in coastal biocenoses and sand.

Axonolaimus ponticus Fil. – species characteristic for deep sand.

## 14. Biocenosis of Capitella sand

Capitella sand consists of fairly coarse gravel like Amphioxus sand, strongly polluted by waste and mixed with black mud. It was collected from the wharves of ROP & T [a shipping company] in January 1912; there is little present there in summer.

If a sample is left to stand, numerous Capitella capitata and Metoncholaimus demani Z. Str. crawl out, forming red and light-orange clumps, like worms in Saccocirrus sand. M. demani lays eggs in these clumps in mucous balls.

Also found singly were:

Paroncholaimus zernovi Fil.
Penzancia euxina Fil.
} also in Amphioxus sand.

Their presence confirms the relationship of this biocenosis with Amphioxus sand and possibly also its origin from Amphioxus sand. Some accidental nematodes characteristic for other coastal biocenoses were also found.

544 I studied the same biocenosis in spring 1911 at Villefranche, where it is situated in a depression below a sewer pipe. The fauna was richer than in Sevastopol: in addition to Capitella capitata, there were numerous Ototyphlonemertes, Met. demani, a related species, Met. pristiurus Z. Str., and the interesting Siphonolaimus sagax Z. Str.

## 15. Biocenosis of oysters

This biocenosis replaces the biocenosis of the shell bottom in the roadstead (Zernov, p. 86 ff.). The oysters lie on the mud bottom below the Zostera, i. e., from a depth of 4–6 m to 8–10 m at the Chernaya River and to 19 m at Primorskii Boulevard.

Oysters predominate among mollusks. There are also different polychaetes, Nemertina and large infusoria on the shells (Folliculina). The nematode fauna contains several characteristic species. The following were found in considerable numbers:

Phanoderma tuberculatum Eb. – also on shells.
Cyatholaimus demani Fil. – distributed everywhere.
Paramonhystera elliptica Fil. – also in Amphioxus sand.
Linhomoeus ostraearum Fil. – characteristic.

Present in single specimens were:

Viscosia minor Fil.
V. glabra Bast.
Sphaerolaimus ostreae Fil.
Conolaimus angustilaimus Fil.
} found only in this biocenosis.

Oysters are not found near Odessa and the oyster shells there are replaced by "a biocenosis of mussel bed" (Zagorovskii and Rubinshtein, p. 227) with a rich fauna. The mussels are almost all alive and covered with sponges (Reniera); polychaetes are numerous.

## 16. Biocenosis of bay mud

It would be more correct to say "biocenoses" of bay mud, as, according to Zernov (p. 114), it shows marked differences in different places at Glavnyi Roadstead. It would be incorrect to refer this biocenosis to mussel
545 mud like Zernov (he separates a special Mellina mud in his preliminary work). This mud is connected directly with the coast and consists of debris of various small rivers, rivulets, and streams with a large content of organic matter. The temperature fluctuates widely.

However, true mussel mud is mainly the product of abrasion of parts of the sea bed near the shore and consists mainly of inorganic particles. I therefore relate this biocenosis to the sublittoral and not the ellitoral zone, like true mussel mud. The fauna confirms this – there is no trace of the special character of the fauna of true mussel mud. The fauna consists mainly of visitors from the neighboring coastal facies. Mussels are present in places in large numbers in some localities but are absent in others. I studied this mud from two localities.

**Mellina mud** from the Chernaya River contained numerous tubes of Mellina and delicate shells of Syndesmya. Common nematodes were only the following:

Parasabatieria clavicauda Fil. – characteristic for the biocenosis and a few specimens of the common Enoplus euxinus.
Enoplus euxinus Fil.

## Distribution of Black Sea nematodes according to various biocenoses

546-
547

- ● Very numerous
- o Numerous
- × Single specimens

Roman numbers indicate months
in which adult individuals were found.

| | Biocenoses of the open sea | | | | | | | | | | | | | | | Biocenoses of sheltered locations | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | sublittoral zone | | | | | | | | | | | | | elittoral zone | | | | | | | | | |
| | biocenosis of rocks | | | | | | | | | biocenosis of Amphioxus sand | | biocenosis of the shell bottom | | | | | biocenosis of meadows of marine plants | | | | biocenosis of bay mud | | |
| | coralline algae | upper layer of Cystoseira | lower layer of Cystoseira | mussels on rocks | mussels on piers | biocenosis of clay burrowed by Pholas | biocenosis of littoral shingle | biocenosis of Saccocirrus sand | biocenosis of fine littoral sand with dead plants | Kruglaya Bay | Georgievskii Monastery | shell bottom | Phyllophora | biocenosis of mussel mud | biocenosis of Phaseolina mud | biocenosis of Ulva | Zostera | Potamogeton | biocenosis of Capitella sand | biocenosis of oysters | Mellina mud | Nassa mud | |
| Enoplidae | | | | | | | | | | | | | | | | | | | | | | | |
| 1. Leptosomatum bacillatum Eb. | . | . | . | ×<br>VI | . | . | . | . | . | o<br>VI, VIII | . | × | o<br>VI | . | × | . | . | . | . | × | . | . | 1 |
| 2. Lept. punctatum Eb. | . | . | . | . | . | . | . | . | . | × | . | o | . | . | . | . | . | . | . | . | . | . | 2 |
| 3. Leptosomatides euxina Fil. | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | 3 |
| 4. Phanoderma tuberculatum Eb. | . | . | . | . | . | . | . | . | . | . | . | ×<br>VII | o<br>VI | . | . | . | . | | . | o<br>VI | . | . | 4 |
| 5. Ph. albidum Bast. | . | × | ×<br>VII | . | . | . | . | . | . | . | . | . | . | . | . | . | . | | . | × | . | ×<br>I | 5 |
| 6. Anticoma pontica Fil. | ×<br>VII | ●<br>VII | o<br>VII | ● | . | . | × | . | . | ● | o | ● | . | . | . | . | ●<br>V | ● | × | . | . | ● | 6 |
| 7. Anoplostoma viviparum Bast. | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 7 |
| 8. Oxystomina clavicauda Fil. | . | . | . | . | . | . | . | . | . | × | o | . | . | . | . | . | . | . | . | . | . | . | 8 |
| 9. O. filiformis Fil. | . | . | . | . | . | . | . | . | . | ×<br>V | × | . | . | . | | . | . | . | . | . | . | . | 9 |
| 10. Enoplus euxinus Fil. | ● | ● | ● | ● | ●<br>I | ● | . | . | . | o | o<br>VII | o | ●<br>VII | . | o | o | ● | . | ×<br>I | × | o | o | 10 |
| 11. E. littoralis Fil. | . | . | . | . | . | . | . | . | ● | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 |
| 12. Enoploides amphioxi Fil. | . | × | . | . | . | . | . | . | . | ●<br>V | ●<br>VII | . | . | . | . | . | . | . | . | . | . | . | 12 |
| 13. E. hirsutus Fil. | . | | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | 13 |
| 14. E. brevis Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | 14 |
| 15. E. cirrhatus Fil. | . | . | . | . | . | . | . | o | . | . | . | . | × | . | . | . | . | . | . | . | . | . | 15 |
| 16. Enoplolaimus conicus Fil. | . | . | . | . | . | . | . | . | . | ×<br>I | . | . | . | . | . | . | o | . | . | . | . | . | 16 |
| 17. E. dubius Fil. | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | 17 |
| 18. Paroncholaimus zernovi Fil. | . | . | . | . | . | . | . | × | . | ●<br>XII—III | ● | o | . | . | . | . | . | . | × | . | . | . | 18 |
| 19. Pelagonema obtusicauda Fil. | . | . | . | . | . | . | . | . | . | o<br>I | . | . | . | . | . | . | . | . | . | . | . | . | 19 |
| 20. Viscosia cobbi Fil. | . | . | . | . | . | . | . | . | . | o | o | . | . | . | . | . | . | . | . | . | . | . | 20 |
| 21. V. minor. Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | ×<br>VI | . | . | 21 |
| 22. V. glabra Bast. | . | . | . | . | . | . | . | . | . | : | : | : | : | : | : | : | : | . | . | × | . | . | 22 |
| 23. Oncholaimus brevicaudatus Fil. | . | . | . | . | . | . | . | ×<br>I | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 23 |
| 24. Oncholaimus dujardini Fil. | . | o* | . | . | . | . | | o* | . | ×<br>I | ×<br>VII | . | ×<br>VI | . | . | . | . | . | . | . | . | . | 24 |

---

* Identification doubtful, see p. 149.

Distribution (continued)

548-549

- ● Very numerous
- o Numerous
- × Single specimens

Roman numbers indicate months in which adult individuals were found.

| | Biocenoses of the open sea | | | | | | | | | | | | | | | Biocenoses of sheltered locations | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | sublittoral zone | | | | | | | | | | | | | elittoral zone | | | | | | | | | |
| | biocenosis of rocks | | | | | | | | | biocenosis of Amphioxus sand | | biocenosis of the shell bottom | | | | | biocenosis of meadows of marine plants | | | | biocenosis of bay mud | | |
| | coralline algae | upper layer of Cystoseira | lower layer of Cystoseira | mussels on rocks | mussels on piers | biocenosis of clay burrowed by Pholas | biocenosis of littoral shingle | biocenosis of Saccocirrus sand | biocenosis of fine littoral sand with dead plants | Kruglaya Bay | Georgievskii Monastery | shell bottom | Phyllophora | biocenosis of mussel mud | biocenosis of Phaseolina mud | biocenosis of Ulva | Zostera | Potamogeton | biocenosis of Capitella sand | biocenosis of oysters | Mellina mud | Nassa mud | |
| 25. O. campylocercus de Man | . | . | . | ●<br>VII | . | ● | . | o<br>I, VII | . | o<br>I, VI | . | . | . | ×<br>VIII | o<br>VII | ×<br>VI | . | . | ×<br>I | . | . | o<br>VII | 25 |
| Adoncholaimus fuscus Bast.* | . | . | . | . | . | . | . | . | . | o | . | . | . | . | . | . | . | . | . | . | . | . | |
| 26. Metoncholaimus demani Z. Str. | . | . | . | o<br>VI | . | . | . | . | . | ●<br>VI | . | . | . | . | . | . | . | ●<br>III | ●<br>I | . | . | ×<br>VII | 26 |
| 27. M. eberthi Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | o<br>VIII | . | . | . | . | . | . | . | . | 27 |
| 28. Enchelidium longicolle Fil. | . | × | . | . | ● | . | . | × | . | . | o | . | o | . | . | . | o | . | . | . | . | . | 28 |
| 29. Eurystomina assimilis de Man | ●<br>VII | o | ×<br>VII | ●<br>VI | . | . | × | . | × | ●<br>I | ●<br>VII | × | . | . | . | × | o | ●<br>III | . | . | . | . | 29 |
| 30. Symplocostoma longicolle Bast. | o<br>VII | o<br>VII | o<br>VI | o | ●<br>I | . | . | . | . | . | . | . | ×<br>VI | . | . | . | o<br>V | . | . | . | . | o | 30 |
| 31. S. ponticum Fil. | . | . | . | . | . | . | . | . | . | o<br>I, V | ●<br>VII | o | . | . | . | . | . | . | . | . | . | . | 31 |
| 32. S. hexabulba Fil. | . | . | . | . | . | . | . | . | . | ●<br>VI | ●<br>VII | . | o<br>V | . | . | . | . | . | . | . | . | . | 32 |
| 33. S. sabulicola Fil. | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | 33 |
| 34. S. marioni Fil. | . | ×<br>V | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 34 |
| 35. Tripyloides demani Fil. | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | ×<br>III | × | . | . | . | . | 35 |
| Chromadoridae | | | | | | | | | | | | | | | | | | | | | | | |
| 36. Acontiolaimus zostericola Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 36 |
| 37. Cyatholaimus demani Fil. | . | o | o<br>VII | ●<br>VI | . | . | . | . | . | × | . | o | o | . | . | o<br>VII | . | ●<br>III | . | o<br>VI | . | o<br>I | 37 |
| 38. Halichoanolaimus clavicauda Fil. | . | . | . | . | . | . | . | . | . | o<br>VI, VII | . | . | . | . | . | . | . | . | . | . | . | . | 38 |
| 39. H. filicauda Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o<br>VI–VII | . | . | . | . | . | 39 |
| 40. Dignathonema bulbosa Fil. | . | . | . | . | . | . | . | . | . | o<br>V–VI | o<br>VII | . | . | . | . | . | . | . | . | . | . | . | 40 |
| 41. Onyx perfectus Cobb. | . | . | | . | . | . | . | . | . | . | ●<br>VII | . | . | . | . | . | . | . | . | . | . | . | 41 |

---

* See first footnote on p. 77, Part I.

Distribution (continued)

550-551

- ● Very numerous
- o Numerous
- × Single specimens

Roman numbers indicate months in which adult individuals were found.

| | Biocenoses of the open sea | | | | | | | | | | | | | | Biocenoses of sheltered locations | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | sublittoral zone | | | | | | | | | | | | | elittoral zone | | | | | | | | | |
| | biocenosis of rocks | | | | | | | | | biocenosis of Amphioxus sand | | biocenosis of the shell bottom | | | | | biocenosis of meadows of marine plants | | | | biocenosis of bay mud | | |
| | coralline algae | upper layer of Cystoseira | lower layer of Cystoseira | mussels on rocks | mussels on piers | biocenosis of clay burrowed by Pholas | biocenosis of littoral shingle | biocenosis of Saccocirrus sand | biocenosis of fine littoral sand with dead plants | Kruglaya Bay | Georgievskii Monastery | shell bottom | Phyllophora | biocenosis of mussel mud | biocenosis of Phaseolina mud | biocenosis of Ulva | Zostera | Potamogeton | biocenosis of Capitella sand | biocenosis of oysters | Mellina mud | Nassa mud | |
| 42. Metachromadora macroutera Fil. | . | . | . | . | . | . | . | . | . | ●<br>I | ● | . | . | . | . | . | . | . | . | × | . | . | 42 |
| 43. M. cystoserrae Fil. | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 43 |
| 44. Chromadorina obtusa Fil. | . | ● | o | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 44 |
| 45. Chromaspirina pontica Fil | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | ●<br>V, VII | . | . | . | . | . | 45 |
| 46. Spirina sabulicola Fil. | . | . | . | . | . | . | . | . | . | ×<br>VII | . | . | . | . | . | . | . | . | . | ×<br>VI | . | . | 46 |
| 47. Sp. zosterae Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | ●<br>V, VII | . | . | . | . | . | 47 |
| 48. Monoposthia costata Bast. | o | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o | . | . | . | . | . | 48 |
| 49. Euchromadora striata Eb. | . | ●<br>VI | ●<br>VII | o<br>VI | o<br>I | . | . | × | . | . | × | . | . | . | . | ●<br>VI | ×<br>V | . | . | . | . | . | 49 |
| 50. Chromadora sabulicola Fil. | . | . | . | . | . | . | . | . | . | × | . | × | . | . | . | . | . | . | . | . | . | . | 50 |
| 51. Chr. quadrilinea Fil. | . | . | . | ×<br>VI | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 51 |
| 52. Chr. poecilosomoides Fil. | . | . | | . | . | . | × | . | . | ●<br>VI, VII | ●<br>VII | . | . | . | . | . | . | . | . | . | . | o | 52 |
| 53. Chromadorella mytilicola Fil. | . | . | . | ×<br>VI | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 53 |
| 54. Spilophorella euxina Fil. | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | 54 |
| 55. Draconema cephalatum Cobb | . | . | . | . | . | . | . | . | . | × | . | × | . | . | . | . | . | . | . | . | . | . | 55 |
| 56. Dr. ponticum Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 56 |
| Desmoscolecidae | | | | | | | | | | | | | | | | | | | | | | | |
| Desmoscolex greefi Reinhard. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o* | . | |
| D. medius Reinhard. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o* | . | |
| D. minutus Clap. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o* | . | |
| Monhysteridae | | | | | | | | | | | | | | | | | | | | | | | |
| 57. Paramonhystera elliptica Fil. | . | . | . | . | . | . | . | . | . | o<br>VI, VIII | . | . | . | . | . | . | . | . | . | o<br>VI | . | . | 57 |
| 58. P. setosa Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 58 |
| 59. Penzancia euxina Fil. | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | o<br>I | . | . | . | 59 |

---

* These species were apparently from Odessa mussel mud, which is compared with the Sevastopol bay mud (see p. 136).

Distribution (continued)

552-
553

- ● Very numerous
- o Numerous
- × Single specimens

Roman numbers indicate months in which adult individuals were found.

| | Biocenoses of the open sea | | | | | | | | | | | | | | | | Biocenoses of sheltered locations | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | sublittoral zone | | | | | | | | | | | | | elittoral zone | | | | | | | | | |
| | biocenosis of rocks | | | | | | | | | biocenosis of Amphioxus sand | | biocenosis of the shell bottom | | | | | | biocenosis of meadows of marine plants | | | | biocenosis of bay mud | | |
| | coralline algae | upper layer of Cystoseira | lower layer of Cystoseira | mussels on rocks | mussels on piers | biocenosis of clay burrowed by Pholas | biocenosis of littoral shingle | biocenosis of Saccocirrus sand | biocenosis of fine littoral sand with dead plants | Kruglaya Bay | Georgievskii Monastery | shell bottom | Phyllophora | biocenosis of mussel mud | biocenosis of Phaseolina mud | biocenosis of Ulva | Zostera | Potamogeton | biocenosis of Capitella sand | biocenosis of oysters | Mellina mud | Nassa mud | |
| 60. Cobbia triodonta Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | ×<br>V | . | . | . | . | . | 60 |
| 61. Cobbia sabulicola Fil. | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | 61 |
| 62. Linhomoeus filiformis Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 62 |
| 63. L. ostraearum Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o | . | . | 63 |
| 64. Metalinhomoeus zosterae Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | o | . | . | . | . | . | 64 |
| 65. Terschellingia pontica Fil. | | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | ×<br>XI | . | . | . | . | . | 65 |
| 66. Prosphaerolaimus eurypharynx Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 66 |
| 67. Disconema alaima Fil. | . | . | . | . | . | . | . | . | . | o | . | . | . | . | . | . | . | . | . | . | . | . | 67 |
| 68. Sphaerolaimus ostreae Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | 68 |
| 69. Sph. macrocirculus Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | 69 |
| 70. Sph. dispar Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | ● | . | . | . | . | . | . | . | . | 70 |
| 71. Axonolaimus setosus Fil. | . | × | . | . | . | . | . | . | . | ●<br>VI | × | × | o | . | . | . | . | . | . | . | . | . | 71 |
| 72. Ax. ponticus Fil. | . | . | . | . | . | . | . | . | . | ●<br>V, VI | ●<br>VII | . | . | . | . | . | ×<br>V | ●<br>III juv. | . | . | . | . | 72 |
| 73. Conolaimus angustilaimus Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | 73 |
| 74. Araeolaimoides zosterae Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 74 |
| 75. Sphaerocephalum crassicauda Fil. | . | . | ×<br>VI | ×<br>VI | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 75 |
| 76. Comesoma stenocephalum Fil. | . | . | . | . | . | . | . | × | . | ●<br>V, VI | . | . | ×<br>VI | . | . | . | . | . | . | . | . | . | 76 |
| 77. C. dubia Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | 77 |
| 78. Parasabatieria clavicauda Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | ●<br>VI | . | 78 |
| 79. P. abyssalis Fil. | . | . | . | . | . | . | . | . | . | . | . | . | . | ●<br>VIII | o<br>VII | . | . | . | . | . | . | . | 79 |
| 80. Diplopeltis eberthi Fil. | . | . | . | . | . | . | . | . | . | ×<br>VII | . | . | . | . | . | . | . | . | . | . | . | . | 80 |
| 81. Acmaeolaimus diplopeltoides Fil. | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | 81 |
| Total number of species (data from other seas are not included) | 5 | 14 | 10 | 12 | 4 | 3 | 3 | 8 | 2 | 33 | 21 | 14 | 10 | 6 | 5 | 5 | 23 | 6 | 6 | 13 | 2 | 8 | |
| | | 16 | | | | | | | | 39 | | 19 | | 9 | | | | | | | | | |
| | 22 | | | | | | | | | | | | | | | | | | | | | | |
| | 29 | | | | | | | | | | | | | | | | | | | | | | |

Dirty **Nassa** mud from Artilleriiskaya Bay was richer:

Anticoma pontica Fil. was common.

Other species were present in small numbers. All species are coastal forms.

Thus, the characteristic nematodes of true mussel mud are absent (p. 123). Only forms which have entered accidentally from other coastal biocenoses are present.

The fauna of mussel mud near Odessa, which should be compared with this bay mud and not with true mussel mud, is apparently richer. Reinhard found three species of Desmoscolex there.

## 554 TIME OF SEXUAL MATURITY

Lo Bianco (1911) wrote the only paper on this subject, discussing the factors which influence the time of sexual maturity in marine animals. He distinguished four groups:

1) Littoral forms reproduce when the sea is calm; in summer, forms which lay free eggs deposit them mainly at night, when there is a coastal breeze which carries the eggs into the sea. Forms which attach their eggs have either a protective capsule or cover the eggs with mucus. In winter the sea is rough and therefore these animals rarely lay eggs in this season. Exceptions are Patella, Lineus lacteus and Eunemertes gracilis, which reproduce in winter.

Twelve of the 20 species of nematodes which are characteristic for the surf zone (uncharacteristic forms are omitted) (see No. 3) reproduce in summer; 6 species were found to be fully mature only in summer and 6 also in winter. Exceptions are Enoplus euxinus Fil., Oncholaimus brevicaudatus Fil. and probably also Enoplus littoralis Fil., which are mature only in winter.

2) Animals in harbors or polluted localities usually reproduce in winter, as the contamination of the harbors is too great in summer. Many species form resting stages at this time, e. g., Metoncholaimus demani Z. Str., which occurs in large numbers in dirty Capitella sand and reproduces in winter. It reproduces in summer in other localities as well. It reproduces in winter and spring in Villefranche, when the water is cold under these conditions.

3) Widely distributed animals, which are not exacting in their requirements from external conditions, reproduce throughout the year. Lo Bianco
555 stated that this applies only to plankton organisms. If we include benthic species, the following species of 6 benthic nematodes behave in this manner: Oncholaimus campylocercus de Man, Metoncholaimus demani Z. Str., Eurystomina assimilis de Man and Cyatholaimus demani Fil. However, adults of Anticoma pontica Fil. were not found in winter; on the other hand, Enoplus euximus Fil., is mature only in winter.

Lo Bianco's other category does not refer to nematodes.

Lo Bianco discussed only progressive factors which influence the reproduction of animals and factors of natural selection which induce animals to reproduce at the most favorable time. However, not only these factors play a part in the life of animals, but also conservative factors: animals strive to maintain conditions of reproduction which have proven to be most favorable in their main habitats. It is therefore clear that boreal forms, some of which also occur in the Mediterranean, reproduce there at the coldest time, which corresponds to the greatest warmth in their original habitat. This probably explains the time of reproduction of Lineus lacteus and other forms, and also of Carcinus moenas. Lo Bianco placed the latter in the category of harbor forms, but it also occurs and reproduces in winter outside harbors; moreover, individuals from colder seas, including the Black Sea, are larger and the best conditions of existence are therefore found in colder waters. Apellöff gave interesting data for the northern Cucumaria orientalis, which reproduces near the coasts of Norway only in winter.

The largest Black Sea nematode, Paroncholaimus zernovi Fil., also belongs to this category; it reproduces only in winter, from December to February according to my data. Its closest relative, P. similis Southern, is very common near the coasts of Ireland and may be considered a northern form.

556 Enoplus euxinus Fil. also reproduces only in winter near coasts, but I found adults in summer in the shell bottom at Georgievskii Monastery and in Phaseolina mud. This is apparently due to the lower temperature in the depths.

Other data are given in the systematic part and in the table on pp. 128–135.

## ZOOGEOGRAPHICAL CHARACTERISTICS OF FREE-LIVING NEMATODE FAUNA OF THE SEVASTOPOL AREA

This is an impoverished Mediterranean fauna.* The main Pontic-Caspian fauna died out when the Bosphorus was formed, persisting only in the brackish northern parts of the sea. The Sevastopol fauna, however, developed from immigrants from the Mediterranean. Omitting the new species, nearly all the others have been described from the Mediterranean. Such species are the following:

Leptosomatum bacillatum Eberth – Naples, Nice.
L. punctatum Eberth – Nice.
Phanoderma tuberculatum Eberth – Nice (Englush coast).
Oncholaimus dujardini de Man – Naples (Sumatra).
O. campylocercus de Man – Naples.
Metoncholaimus demani Zur Strassen – Naples, Villefranche.
Eurystomina assimilis de Man – Naples, Sète, Fiume.
Onyx perfectus Cobb – Naples.
Euchromadora striata Eberth – Naples.
Draconema cephalatum Cobb – Naples (cosmopolitan).
Desmoscolex minutus Claparède – all European coasts
D. medius Reihard – Naples.
D. greefi Reinhard – Naples.

---

* This is also Zernov's conclusion for all the fauna and Dekenbakh's conclusion for algae.

The following species have not yet been found in the Mediterranean:
Phanoderma albidum Bastian – English coast.
Anoplostoma viviparum Bastian – English Channel, North Sea, Baltic Sea, Murman.
Viscosia glabra Bastian – English Channel, North Sea.
557 Symplocostoma longicolle Bastian – English Channel, North Sea.
Cyatholaimus demani nom. nov. (ocellatus de Man) – North Sea.
Monoposthia costata Bastian – English Channel, North Sea, Baltic Sea, Murman.

Most of them have probably not yet been found in the Mediterranean, which is still insufficiently studied, particularly as regards small forms. However, immigrants from the Mediterranean are subjected to a double selection in the Black Sea – low salinity and low temperature. Forms of a northern character are therefore found in the Black Sea and develop abundantly. The Black Sea apparently selects the northern forms of the Mediterranean fauna (Sovinskii). Carcinus maenas is found in the Mediterranean in much smaller numbers than in the Black Sea. Modiola phaseolina forms an entire biocenosis in the Black Sea, but is known only from a few specimens in the Mediterranean. However, there are Quaternary strata in Sicily where Phaseolina is very numerous (it was described from Sicily). The Mediterranean was apparently colder at that time than at present – the result of the ice age. The largest Black Sea nematode, Paroncholaimus zernovi Fil., should be considered as such a northern relict.

This species occurs in large numbers in Amphioxus sand. It reproduces in winter and is closely related, or only a variant, of the northern P. similis Southern. This species was not found, although Amphioxus sand was examined there and this large nematode would not have been overlooked. This species belongs to the same category as Modiola phaseolina and others. If P. zernovi is found in the Mediterranean, it will probably be found in the northern Adriatic (Quarnero), where, as a result of the cold winter, selection of northern forms also takes place and they find a suitable time for reproduction.

558 As regards the 65 new species (80% of the fauna), it is premature to draw zoogeographical conclusions. This large number of new species proves only that the free-living nematodes in general and the Mediterranean fauna in particular have been insufficiently studied.

Thoracostoma and related genera, which are well represented in the Mediterranean, are completely absent.

As regards the proof that the Black Sea fauna is an impoverished Mediterranean fauna, the total number of species cannot be compared, as there are only fragmentary data for the entire Mediterranean. Only the larger species can therefore be considered.

The following 40 species larger than 5 mm are known from the Mediterranean; a third of these species are longer than 10 mm:

from the English Channel and the Mediterranean, 27 species longer than 5 mm – of these 6 longer than 10 mm;

from the Murman coast, 23 species longer than 5 mm – of these 8 longer than 10 mm;

from the Black Sea, only 10 species longer than 5 mm– of these one longer than 10 mm.

It is unlikely that the latter figure will increase. The Black Sea fauna is thus 2.5–3 times poorer than that of the northern seas and 4 times poorer than that of the Mediterranean. These figures would be even larger if the incomplete study of the nematode fauna in these areas were considered.

The following list gives the mean measurements in microns of adult individuals (length/width):

Paroncholaimus zernovi Fil., 12–13500/160.
Leptosomatum bacillatum Eb., 9000/120.
Leptosomatides euxina Fil., 9000/100.
Leptosomatum punctatum Eb., 8500/120.
559 Symplocostoma ponticum Fil., 7200/140.
Metoncholaimus demani Zur Str., 6700/90.
Enoplus euxinus Fil., 5–6000/140–180.
Eurystomina assimilis de Man, 6000/60.
Enoploides amphioxi Fil., 5500/150.
Symplocostoma marioni Fil., 5400/115
Sympl. longicolle Bast., 5400/95.
Sympl. hexabulba Fil., 5300/85.
Phanoderma tuberculatum Eb., 5000/120.
Comesoma stenocephalum Fil., 4600/90
Viscosia cobbi Fil., 4600/60.
Enoploides cirrhatus Fil., 4400/105.
Dignathonema bulbosa Fil., 4300/110.
Linhomoeus ostraerum Fil., 4300/80
Axonolaimus setosus Fil., 4100/50
Pelagonema obtusicauda Fil., 4000/95.
Oncholaimus campylocercus de Man, 4000/70.
Axonolaimus ponticus Fil., 4000/65
Oxystomina filiformis Fil., 4000/35.
Enchelidium longicolle Fil., 3900/65.
Enoplolaimus conicus Fil., 3800/150.
Oncholaimus brevicaudatus Fil., 3800/80.
Metoncholaimus eberthi Fil., 3700/90.
Diplopeltis eberthi Fil., 3600/95
Disconema alaima Fil., 3600/50.
Phanoderma albidum Bast., 3500/105
Oncholaimus dujardini de Man, 3500/70.
Oxystomina clavicauda Fil., 3500/40.
Enoplolaimus dubius Fil., 3400/80.
Acmaeolaimus diplopeltoides Fil., 3400/65.
Metalinhomoeus zosterae Fil., 3200/40.
Halichoanolaimus filicauda Fil., 3100/125.
Enoplus littoralis Fil., 3000/70
Cobbia triodonta Fil., 2900/65.
Enoploides hirsutus Fil., 2800/120.
Cyatholaimus demani Fil., 2800/110.
Paramonhystera elliptica Fil., 2800/85.
Penzancia euxina Fil., 2800/60.

Comesoma dubia Fil., 2800/60.
Chromaspirina pontica Fil., 2800/55.
Sphaerocephalum crassicauda Fil., 2800/47.
Spirina zosterae Fil., 2700/75.
Acontiolaimus zostericola Fil., 2700/55.
Metachromadora macroutera Fil., female, 2600/150.
Met. cystoscirae Fil., female, 2600/130.
Paramonhystera setosa Fil., 2600/105.
Metachromadora macroutera Fil., male, 2600/70–100.
560 Halichoanolaimus clavicauda Fil., 2500/70.
Anticoma pontica Fil., 2500/60.
Sphaerolaimus dispar Fil., 2400/135.
Symplocostoma sabulicola Fil., 2400/55.
Conolaimus angustilaimus Fil., 2400/50.
Enoploides brevis Fil., 2300/120.
Prosphaerolaimus eurypharynx Fil., 2300/80.
Euchromadora striata Eb., 2100/70–90.
Onyx perfectus Cobb, 2100/65.
Cobbia sabulicola Fil., 1900/55.
Chromadora sabulicola Fil., 1900/55.
Viscosia glabra Bast., 1900/50.
V. minor Fil., 1900/35.
Linhomoeus filiformis Fil., 1900/35.
Draconema cephalatum Cobb, 1800/100–125.
Sphaerolaimus macrocirculus Fil., 1800/100.
Spirina sabulicola Fil., 1800/55.
Tripyloides demani Fil., 1700/35.
Sphaerolaimus ostreae Fil., 1600/65.
Parasabatieria abyssalis Fil., 1600/60.
Par. clavicauda Fil., 1600/55.
Terschellingia pontica Fil., 1400/45.
Araeolaimoides zostericola Fil., 1400/35.
Anoplostoma viviparum Bast., 1250/60.
Chromadora poecilosomoides Fil., 1200/40.
Draconema ponticum Fil., 1100/50.
Monopostia costata Bast., 1100/40–55.
Chromadorella mytilicola Fil., 1000/70.
Spilophorella euxina Fil., 1000/50.
Chromadora quadrilinea Fil., 900/50.
Chromadorina obtusa Fil., 800/45.

## Bibliography for Zoogeographical Section

### Publications in Russian

Dekenbakh, K. N. K kharakteristike flory vodoroslei Chernogo Morya (Characteristics of Alga Flora of the Black Sea). – Trudy SPb. Obshchestva Estestvoispytatelei, Botanika, Vol. 37; pp. 47-52. 1908.

Deryugin, K. M. Fauna Kol'skago Zaliva i usloviya eya sushchestvovaniya (The Fauna of Kola Gulf and its Life Conditions). – Zapiski Imperatorskoi AN Fiz. Mat. Otd. (8), 34 (1):IX + 929. 1915. 55 figs. 14 pls. 14 maps.

Kudelin, N. O raspredelenii zhivotnykh v Chernom more v svyazi s voprosom o proiskhozhdenii presnovodnoi fauny (Distribution of Animals in the Black Sea in Connection with the Origin of Freshwater Fauna). – Zapiski Novorossiiskogo Obshchestva Estestvoispytatelei, 39, pp. 45–84. 1914.

Kudelin, N. K voprosu o fatsiyakh Chernogo Morya (Facies of the Black Sea). – Ibid., pp. 85–94. 1914.

Kudelin, N. K voprosu o morskoi faune proniknoveniya v presnyya vody (On the Marine Fauna Penetrating into Freshwaters). – Ibid., pp. 345–394. 1914.

Sovinskii, V. K. Vvedenie v izuchenie fauny Ponto-Kaspiisko-Aral'skogo morskogo basseina, razsmatrivaemoi s tochki zreniya samostoyatel'noi zoogeograficheskoi provintsii (Introduction to the Study of Fauna of the Pontic-Caspian-Aral Marine Basin as an Independent Zoogeographical Province). – Zapiski Kievskogo Obshchestva Estestvoispytatelei, 18, XIII + 487 + 217 + 111 pp. 1904. 4 plates.

Voronikhin, N. N. O raspredelenii vodoroslei v Chernom more u Sevastopolya (Distribution of Algae in the Black Sea near Sevastopol). – Trudy SPb. Obshchestva Estestvoispytatelei, Botanika, 37, pp. 181–198. 1902.

Zagorskii, N. and D. Rubinshtein. Materialy k sisteme biotsenozov Odeskago zaliva (Data on the Biocenosis System of Odessa Bay). – Zapiski Obshchestva Sel'skogo Khozyaistva Yuzhnoi Rossii, 86, pp. 203–244. 1916.

Zernov, S. A. Osnovnye cherty raspredeleniya zhivotnykh v Chernom more u Sevastopolya (Main Features of Animal Distribution in the Black Sea near Sevastopol). – Izvestiya Imperatorskoi Akademii Nauk (6) 2. p. 881–901. 1908.

Zernov, S. A. Fatsiya fillofory (Algae-Rhodophycae)– fillofornoe pole v severo-zapadnoi chasti Chernogo morya. Zoologicheskaya ekskursiya na parokhode Fedya, 11–14 Aprelya 1907 g. (Phyllophora facies – Phyllophora Field in the Northwestern Part of the Black Sea. Zoological Excursion on the Steamer Fedya 11–14 April 1907). – Ezhegodnik Zoologicheskogo Muzeya Imperatorskoi Akademii Nauk, 14, pp. 181–194. 1907. 4 plates.

Zernov, S. A. K voprosu ob izuchenii zhizni Chernogo morya (Study of Life in the Black Sea). – Zapiski Imperatorskoi AN, Fiz. Mat. Otdelenie (8) 32, No. 1. 299 pp. 10 plates. 1913.

### Publications in Other Languages

Appelof, A. Über die Beziehungen zwischen Fortpflanzung und Verbreitung mariner Tierformen. – Verh. VIII Intern. Zool. Kongr. Graz., p. 303–311. 1912.

Cori, C. J. Charakteristik der Fauna der nördlichen Adria. –Ibid., p. 689–711. 1912.

Issel, R. Biologia neritica mediterranea: Il bentos animale delle foglie di Posidonia studiata dal punto di vista bionomico. – Zool. Jahrb. Syst. 33, p. 379–420, 1912, t. 11–12, fig.

Joubin, L. La répartition des animaux marins sur les côtes françaises de la Méditerranée. – Bull. Mus. Océan. No. 74, Monaco, 1906, 25 pp., 4 pl.

Krummel, O. Handbuch der Ozeanographie. Stuttgart. 526 pp. 1907.

Lo Bianco, S. Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del Golfo di Napoli. – Mitth. Zool. Stat. Neapel 19, p. 513–573 (editions 1 and 2 appeared in volumes 8 (1888) and 13 (1899) of Mitth. Third, supplemented edition. Their content has not varied).

Lo Bianco, S. L'influenza dell' ambiente sul periodo riproduttivo degli animali marini. – Ibid., 20, p. 129–156. 1911.

Lorenz, R. J. Physikalische Verhältnisse und Vertheiluug der Organismen im Quarnerischen Golfe. Wien. 369 pp., 1863, 5 tt, carta.

Marion, M. A. F. Exquisse d'une topographie zoologique du Golfe de Marseille. – Ann. Mus. Hist. Nat. 1883, Marseille, 1. Mém. No. 1. 108 pp., 1 carte.

Marion, M. A. F. Considérations sur les faunes profondes de la Méditerranée opérés au large des côtes méridionales de France. – Ibid., Mém. No. 2, 50 pp., 1883, avec carte.

Ortmann, A. E. Grundzüge der marinen Tiergeographie. 96 pp., 1 car. 1896, Jena.

Pruvot, G. Essai sur la topographie et les fonds sous-marins de la région de Banyuls. – Arch. Zool. Exp. (3) 2, p. 599–672, 1894, carte.

Pruvot, G. Coup d'oeil sur la distribution génerale des Invertébrés dans la région de Banyuls (Golfe de Lion). – Ibid., (3) 3 p. 629–658, 1895, carte.

Pruvot, G. Essai sur les fonds et la faune de la Manche occidentale (côtes de Bretagne), comparés à ceux du Golfe de Lion. – Ibid. (3) 5, p. 510–617+22, Vol. 21–26. 1897.

Steuer, A. Veränderungen der nordadriatischen Flora und Fauna während der letzten Dezennien. – Int. Revue. Ges. Hydrobiol. Hydrogr., 3 pp. 6–16, 1910.

Sudry, L. L'étang de Thau. Essai de Monographie Océanographique. – Ann. Inst. Océan. Monaco 1. Fasc. 10 (en même temps: Travail du Lab. de Minér. de Nancy et de la Station Zool. Cette. Série mixte, No. 3), 208 pp., carte.

Thoulet, J. L'océan, Paris. 1904.

Thoulet, J. Précis d'analyse des fonds sous-marins actuels et anciens. Paris, 220 pp. 1907.

Thoulet, J. Instruction pratique pour l'établissement d'une carte bathymétrique-lithologique sous-marine. – Bull. Inst. Océan. Monaco, No. 169. 1910.

## 562 ADDENDA AND ERRATA

P. 4, Part I. The same method of washing nematodes from sand has been suggested by Cobb (1890) and Southern (1914).

P. 7, Part I. It is useful to add chloral hydrate to the water, to keep the nematodes immobilized, as suggested by Davaine (1857) and Cobb (1890).

Pp. 24, 25, Part I. Genus Demania Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 41; 2 species: (1) D. major Southern, 1914, p. 42, Table 7, Figure 20 A–C; west coast of Ireland: sand and shell bottom with Polygordius 40–48 m. (2) D. minor Southern, 1914, p. 43, Table 7, Figure 21 A–C; at a depth of 28–52 m.

This genus resembles the Leptosomatini (Cylicolaimus) in some characters and also the Oncholaimini, but is probably a separate subfamily. It has a three-faceted free buccal capsule, which is closed by lips. Its three rays are thickened and each bears a solid tooth. One species was found at Murmansk.

P. 25, Part I. The following genera probably also belong to the Leptosomatini:

— 8) Platycoma Cobb, 1893 (one species, Pl. cephalata, Cobb, 1893: Proc. Linn. Soc. N. S. W. 8, p. 339, Figure 7, marine sand Naples; an apparently different species was described by Southern under the same name: 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 33, Table 7, Figure 22 A–C, west coast of Ireland in sand and shell bottom with Polygordius at 48 m, adults in May).

— 9) Synochus Cobb, 1893; l. c., p. 411 (two species: S. fasciculatus Cobb, 1893, p. 411, Figure 10; S. hirsutus Cobb, 1893, p. 413. Both from marine sand, Naples).

— To the same subfamily (group Phanoderma) probably belongs a new genus, a species of which is Enchelidium polare Steiner, 1916: Z. J. Syst., 39, p. 596, Tables 16, 30, Figure 28 a–h. White Sea Strait, on algae. It is possibly related to the genus Stenolaimus Marion (see note to p. 43, Part I).

563 — Genus Thoracostoma Marion.

— Th. denticaudatum Schneider was found on the west coast of Ireland under stones among tubes of Spirorbis, adults in September (Southern); Thoracostoma sp. Steiner, 1919: Zool. Jahrb. Syst., 39, p. 620, Table 16, Figure 29a: Table 31, Figure 29b: White Sea Strait, on algae; apparently young specimens of this species. Hemipsilus trichodes Leuckart, 1849 (Arch. Naturg., 15 (1), p. 157) from Ireland possibly also belongs here.

— Th. figuratum Bast. is very common on the west coast of Ireland under stones near the shore on algae and almost in each dredge; adults in May, September, October (Southern).

— Th. lobatum Steiner, 1916: Zool. Jahrb. Syst., 39, p. 620, Table 16, Figure 29a; Table 31, Figure 29b: White Sea Strait, on algae, apparently only young specimens of Deontostoma arcticum Savel'ev.

— Th. polare Cobb, 1914: Nem. Shackleton Exp., p. 31. South Polar Sea, near Ross Island 20–100 m.

— Odontobius filiformis Eberth, 1863: Untersuch. über Nematoden, p. 29, Table 1, Figures 10–12, certainly belongs to the genus Thoracostoma. This species has been omitted in the survey of species of this genus.

P. 25, Part I. The genus Jägerskiöldia Fil. had already been described under the names:

— 5) Fiacra Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 34; the author adds two further new species: F. longisetosa Southern, 1914 (type): l. c., p. 35, Table 5, Figure 14 A–F and F. brevisetosa Southern, 1914, l. c., p. 37, Figure 14 A–E. Both species from the west coast of Ireland from a depth of 48–54 m, in sand with Polygordius; adults in May.

— Cylicolaimus magnus Villot redescription by Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 39, Tables 6–7, Figure 19 A–F; west coast of Ireland: 1 specimen under a stone on the coast; many from 48 m – coquina and sand with Polygordius; adults in May.

P. 27, Part I. Genus Leptosomatum Bast.

— L. indicum Stewart, 1914: Rec. Ind. Mus., 10, p. 249, Table 31, Figures 11–14. Cbilka Lake, east India, on algae; I could not obtain the paper.

— Lept. sabangense Steiner, 1916: (L. elongatum v. sab.: Zool. Jahrb. Syst., 38, p. 226, Tables 22–23, Figures 94–11. Sabang Sumatra, on algae) – according to the key identified together with L. elongatum Bastian, but it differs by its longer tail (twice diameter of anus), slightly more than one diameter in L. elongatum.

P. 33, Part I. Genus Leptosomatides Fil.

— Steiner (1916) described Leptosomatum gracile Bastian, 1865: Zool. Jahrb. Syst., 39, p. 610, Table 16, Figure 27 c, d; Table 29, Figure 27a, b, e–g; Table 30, Figure 27 h–o. White Sea Strait, on algae. This species is characterized by a special development of the vagina. The vagina is exactly as in L. euxina Fil. The species described by Steiner should therefore be 564 placed in this genus. L. gracile Bastian nec Steiner, L. tetrophthalmum Sav., L. grebnickii Fil. and L. arcticum Fil. belong thus to the genus Leptosomatum.

Pp. 36–37, Part I. Phanoderma gracile de Man, recorded from Clew Bay on the west coast of Ireland from a depth of 36 m.

— Ph. parvum Villot, probably belongs to another genus.

— Thoracostoma conicaudatum Steiner, 1916: Zool. Jahrb. Syst., 39, p. 642, Table 17, Figure 31a; Table 31, Figure 31b. – White Sea Strait, on algae; belongs to the genus Phanoderma; it is closely related to Ph. tuberculatum (Eberth) = Ph. cocksi Bastian, but differs in its shorter tail which is only 1.5 times longer than wide. However, Steiner had only one young specimen, and the species are probably identical.

Pp. 41–43, Part I. Genus Anticoma Bastian.

— A. eberthi Bastian, 1865, should be regarded as the type of the genus, according to a letter from the author to Stiles (see Stiles and Hassal, 1905, p. 87).

— 2) Anticoma subsimilis Cobb, 1914: Nem Shackleton Exp., p. 11. Ross Island, South Polar Sea. Compared by the author with A. similis; distinguished by 5 cervical bristles, longer cephalic bristles and esophagus without widening behind the nerve ring. The lateral organ seems to be situated more posteriorly than in A. pellucida Bast., A. pontica Fil. and A. similis, which it resembles closely. However, the species was described from inadequate material.

— 3) A. eberthi Bast.– recorded by Southern from rocks on Clare Island on the west coast of Ireland. Adults in May.

— 8) A. pellucida Bast., according to Southern, very abundant on the west coast of Ireland in pure sand, Zostera, sponges, among Spirorbis and in the littoral zone. Adults in May–September.

— A. pellucida Bast. var limalis Bast., under this name. Steiner, 1916 (Zool. Jahrb. Syst., 39, p. 654, Table 36, Figure 46) described a nematode from the White Sea Strait from algae. A. limalis Bast. is retained as a long-tailed variant of pellucida.

— 14) A. arctica Steiner, 1916. (l. c., p. 656, Table 36, Figure 45 a–f; (from the same locality), closely related to A. similis Cobb, possibly identical.

P. 43, Part I. Genus Stenolaimus Marion, 1870.

If Southern is correct, Stenolaimus lepturus Marion is not related to Anticoma, but forms a separate genus together with the species described which belongs to the Anticomini. It differs from Anticoma by the cellular structure of the posterior end of the esophagus. "Enchelidium" polare Steiner possibly belongs here (note to p. 25, Part I).

— Stenolaimus marioni Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 23, Table 4, Figure 12 A–E. Described from the west coast of Ireland. In sand and shell bottom with Polygordius at 48 m.

565 P. 47, Part I. 4) Anoplostoma heterura (Cobb, 1914); Oncholaimellus h.: Trans. Amer. Micr. Soc., 33, p. 100, Table 7, Figure 21. In freshwater pond near Ocala, Florida, U. S. A. Possibly only a synonym of A. vivipara Bast.

— Anoplostoma longisetum Steiner, 1916, possibly related to the genus Bathylaimus Cobb: see p. 128, Part I.

P. 48, Part I. The genus Alaimus de Man apparently belongs to a different group. In addition to the other three genera, the following genera are probably also related:

— 4) Trefusia de Man, 1893, not as elongate, but with a very long tail (one species: Tr. longicauda de Man, 1893: Mém. Soc. Zool. France, 6, p. 85, Table 5, Figure 3; coastal rocks near Trefusis in English Channel).

— 5) Acoma Steiner, 1916: Z. Jahrb. Syst., 39, p. 652; with one species A. borealis Steiner, 1916: l. c., p. 652, Table 34, Figure 43a – White Sea Strait, very similar, possibly not different from Oxystoma.

— 6) Nuada Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 9; species: N. leptosoma Southern, 1914: Ibid., p. 10. – West coast of Ireland, sand and shell bottom with Polygordius at a depth of 48 m. It differs from other genera by its slender form and by a constriction which separates the head.

— There is one further species of the genus Thalassolaimus – Th. egregius Steiner, 1916. Z. J. Syst., 39, p. 649, Table 35, Figure 44 a–f; White Sea Strait, on algae.

— I propose for Oxystoma Bütschli, 1874 (nomen praeocc. in coleopt.: Duméril, 1806) the name Oxystomina nom. nov.

P. 49, Part I. Oxystoma asetosa Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 18, Table 1, Figure 3 a–d. In sand and shell bottom with Polygordius (48 m) from the west coast of Ireland. It differs from Ox. pellucidum Cobb by the absence of bristles.

P. 54, Part I. Enoplus communis Bast. West coast of Ireland, near the coast and from 48 m. (Southern).

— E. crassus Fil; Steiner, 1916, records it from the White Sea Strait, as E. communis Bastian (Z. J. Syst., 39, p. 625).

P. 55, Part I. Enoplus inermis Bastian belongs to the genus Triodontolaimus de Man (see p. 53, Part I).

Pp. 62–64, Part I. Instead of the correct separation of Enoploides as a different genus, Southern suggested the unification of Enoplolaimus with Enoplus, as there are transitional forms, i. e., Enoploides. This seems quite unjustified and is due to a lack of knowledge of the work of Savel'ev. He described two new species:

— 10) E. labrostriatus Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 53, Table 8, Figure 24 A–F. West coast of Ireland from a depth of 48 m, sand and shell bottom with Polygordius.

566 — 11) E. bütschlii Southern, 1914: l. c., p. 50, Table 8, Figure 23 A–F. From the same locality, sand from 28–34 m.

— The key should be changed from No. 5 on as follows:

5 (8). Buccal musculature separated in form of a characteristic marginal swelling.
6 (7). Angles of mouth at half the distance from margin of lips to end of oral musculature. Spicules smooth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. labrostriatus (Southern)**
7 (6). Angles of mouth one-third of this distance. Spicules ribbed. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. amphioxi Fil.**
8 (5). Buccal musculature not forming special part.
9 (12). Cephalic bristles as long or almost as long as width of head, labial bristles about half as long. Jaws markedly diverging posteriorly.
10 (11). Crown of supplementary cephalic bristles very dense, situated immediately behind the main crown. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. cirrhatus Fil.**
11 (10). If present, not very dense and displaced far posteriorly.
11a (11b). Cephalic bristles very thick at base, then suddenly tapering, longer than width of head. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. typicus Savel'ev**
11b (11a). Cephalic bristles shorter than width of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. labiatus (Bütschli)**
16 (15). Definition of width of end of tail to be deleted.
17 (18). Tail not swollen at end; small cephalic bristles half as long as the bristles . . . . . . . . . . . . . . . . **E. hirsutus Fil.**
18 (17). Tail distinctly swollen at end; small cephalic bristles $^2/_3$ as long as large bristles. Ring of cephalic capsule narrower and jaws and teeth relatively smaller than in E. hirsutus. . . . . . . . . . . . . . . **E. bütschli (Southern)**

P. 72, Part I. Genus Enoplolaimus de Man. The following 3 species have been described:

— 8) Enoplolaimus (Enoplus) diplechma (Southern, 1914): Proc. Roy. Irish Acad., 31, pt. 54, p. 55, Tables 8–9, Figure 25 A–G; west coast of Ireland, in sand, 28–34 m.

— 9) E. (Enoplus) longicaudatus (Southern, 1914): l. c., p. 57, Table 9, Figure 26 A–D. From the same locality from a depth of 48 m, sand and shell bottom with Polygordius. The latter species closely resembles E. dubius Fil.

— 10) Enoplolaimus hamatus Steiner, 1916: Z. J. Syst., 39, p. 626, Table 31, Figure 32 a–c. White Sea Strait, on algae, inadequately described, apparently related to the group acantholaimus-australis.

— The genus Labyrinthostoma, which has been named but not described, probably also belongs here, Cobb, 1898: Agric. Gaz. N. S. W., 1898, p. 29 (reprint).

— The key on p. 73, Part I, should be revised as follows:

1 (10, 11). Cephalic bristles as long as head, or slightly shorter.
2 (5). Tail 9–10 times longer than width at base.
3 (4). All three teeth uniform. A crown of supplementary bristles behind the cephalic bristles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. longicaudatus Southern**
4 (3). Dorsal tooth shorter, supplementary crown of bristles absent. . . . . . . . . . . . . . . . . . . . . . . . . **E. dubius Fil.**
567 5 (2). Tail 4–5 times longer than width at base.
6 (7). A crown of supplementary bristles of same length behind the cephalic bristles; spicules as long as the tail; posterior $^5/_6$ of tail forming a flagellum. . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. tenuicaudatus Savel'ev**

7 (6). Supplementary cephalic bristles much shorter than main bristles
8 (9). Spicules short . . . . . . . . . . . . . . **E. vulgaris** de Man
9 (8). Spicules long, 2.5 times as long as tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. deplechma** Southern
10 (1, 11). Cephalic bristles $^2/_3$ of length of head. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **E. hamatus** Steiner
11 (1, 10). Cephalic bristles not longer than half the length of the head (identical with No. 6 of the key).

P. 77, Part I. The species of Oncholaimellus, described by Cobb (1914), belongs to Anoplostoma (see note to p. 47, Part I).

P. 77, Part I. According to Golovin (1901, p. 86) O. fuscus is found in Amphioxus sand much more rarely than P. zernovi. This record possibly refers to O. campylocercus de Man or Meton. demani Z. Str.

— E. Buerkel collected it in large numbers with bait of decomposing mussels at Kiev; in addition to Par. vulgaris Bast. (see p. 76, Part I), also Adon. lepidus de Man.

— Adoncholaimus punctatus (Cobb, 1914): Oncholaimus p.: Trans. Amer. Micr. Soc., 33, p. 91, Table 5, Figure 14: in fresh water, Cape Breton Island., Canada.

P. 78, Part I. Genus Paroncholaimus:

— 4) P. (Oncholaimus) macrolaimus (Southern, 1914): Proc. Roy. Irish Acad., 31, pt. 54, p. 44, Table 6, Figure 16 A–D, west coast of Ireland, sand and shell bottom from 48 m with Polygordius.

— 5) P. (Onch.) similis (Southern, 1914); l. c., p. 47, Table 6, Figure 17 A–D; same locality, near coast, under stones, adults in summer.

— P. vulgaris Bast., new description: Southern, 1914: l. c., p. 46, Table 5, Figure 15 A–D together with P. vulgaris, adults in March, May, September.

— P. similis Southern, which resembles P. zernovi Fil. closely, has almost exactly the same genital armature and oral cavity. However, some differences given in the key (see below) make their identity doubtful.

The following shoud be included in the key on p. 78, Part I:

2a (2b). Lateral organ large, about $^1/_4$ of the corresponding width, spicules narrow, markedly curved, slightly different. . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. macrolaimus** Southern
2b (2a). Lateral organ very small, $^1/_8$–$^1/_{10}$ of corresponding width.
5 (6). Subventral teeth extend through $^3/_4$ of oral cavity; base of spicules twice as wide as the following thin part; gubernaculum distinctly separate, with a hook at the end. Adult females to 18 mm, $\alpha = 53–64$. . . . . **P. similis** Southern
6 (5). Subventral teeth extend through $^2/_3$ of buccal cavity; base of spicules 1.3 times wider than following narrow part; gubernaculum adjacent to spicules, without hook at the end. Not longer than 12 mm, $\alpha$ = 70–84 . . . . . . **P. zernovi** Fil.

P. 90, Part I. Oncholaimus attenuatus Duj., west coast of Ireland, adults in May (Southern).

— O. brachycercus de Man: Steiner, 1916: Zool. Jahrb. Syst., 39, p. 603, Table 28, Figure 23 a–b: White Sea Strait, on algae.

— Oncholaimus chilkensis Stewart, 1914: Rec. Ind. Mus. Calcutta, 10, p. 245, Table 30, Figures 1–4; Table 31, Figures 15, 17, 18. Chilka Lake, East India, algae. I could not obtain the description.

P. 94, Part I. Oncholaimus dujardini de Man. The following references have been omitted:

— De Man, 1878: Tijd. Nederl. Dierk. Vereen., 3, p. 94, Table 7, Figure 4 a–c; Rouville, 1904: CR. Ass. Franç. Av. Sci., p. 793; Steiner, 1915: Zool. Jahrb. Syst., 38, p. 238, Table 24, Figures 28–30.

It is possible that the species described by Steiner from Sumatra (Sabang, mud with diatoms) does not belong here. I did not find males, and the description of de Man is not quite correct. To judge from the drawings, the spicules have a different shape and the perianal bristles are arranged differently. Steiner's species also lacks pigment spots.

P. 106, Part I. Enchelidium tenuicolle Eb.: Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 14, west coast of Ireland, sand near coast, and at a depth of 14 m.

P. 109, Part I. Eurystoma Marion, 1870 is a nomen praeoccupatum (Rafinesque, 1818, mollusk, Koell., 1853–coleopt.), and I propose the name Eurystomina nom. nov.

Pp. 110, 111, Part I. Omitted in survey of species is: Eu. acuminata de Man, 1889: Mém. Soc. Zool. France, 2, p. 6; Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 41; Penzance, rare (de Man); in sand under Zostera at west coast of Ireland (S). The following is added to the key:

— 2a (2b). Tail narrow at end, pointed; processes of accessory organs not longer than half their diameter. . . . . . **Eu. acuminata** de Man

— 2b (2a). Tail blunt at end; processes of accessory organs longer.

P. 114, Part I. Eu. assimilis de Man (like Eu. filiforme de Man) recorded from the west coast of Ireland: 2 mature males under stones near coast, among Spirorbis in September and in sand and shell bottom with Polygordius from a depth of 48 m in May. (Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 41, Table 6, Figure 18).

Pp. 114, 116, Part I. The type of the genus Amphistenus Marion, 1879, becomes a synonym and has to be Symplocostoma tenuicolle Eberth, 1863 = A. agilis Marion, 1870.

P. 119, Part I. Symplocostoma longicolle Bast. recorded from the west coast of Ireland: very common in algae near the coast and in dredges down to 16 m, adults in September (Southern).

P. 126, Part I. Cobb, 1916: Journ. Parasitol. 2, p. 195. I suggest a division of the genus Mononchus into 5 subgenera according to the structure of the buccal cavity.

P. 126, Part I. The genus Cephalonema Cobb, 1893, is a nomen praeoccupatum (Stimpson ante, 1884 – vermis) should have the name Nanonema Cobb, 1905 (Stiles and Hassal, p. 92).

— Thalassironus britannicus de Man, recorded from the west coast of Ireland in pure sand and sand under Zostera (Southern).

To group E. also belongs:

— Brachynema Cobb, 1893 (nom. praeocc.): Agric. Gaz. N. S. W., 4, p. 811. 1 freshwater Australian species.

P. 135, Part I. The genus Selachinema Cobb has three high lips like Enoploides and Enoplolaimus which are compressed between the teeth and spiral lateral organs. I have not seen the original description and quote from Yearbook U. S. Dept. Agric., 1914, pp. 484, 486.

— 1) Nannonchus lacustris Mic. Bukovina in mountain lake (Mic.).

— Richtersia Steiner (1916): Zool. Jahrb. Syst., 39, p. 583–1 species: R. collaris Steiner, 1916, l. c., Table 26, Figure 18 a–g. White Sea Strait, on algae. Very aberrant from: cuticle covered with hairs as in Trichoderma, while the thick, straight esophagus and spiral lateral organs relate it to the Cyatholaimini.

P. 137, Part I. Cyatholaimus ocellatus Bast. recorded by Southern from the west coast of Ireland near the shore, at 8–12 m, in sponges; adults in September.

P. 138, Part I. Cyatholaimus dubiosus Bütschli. Southern (1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 29) believed that C. caecus de Man is different from Bastian's description and is possibly identical with C. dubiosus Bast. Adults in March and September in sand under Zostera, under stones among Spirorbis, and from a depth of 36 m near the west coast of Ireland.

— 10a) Cyatholaimus truncatus Cobb, 1914: Trans. Amer. Micr. Soc., 33, p. 94, Table 6, Figure 17. In fresh water: Silver Springs, Florida.

P. 139, Part I. Cyatholaimus tenax de Man recorded from Lake Pyukhaselka in Finland, common on muddy and sandy bottom and among algae (Sheider).

P. 143, Part I. Halichoanolaimus robustus Bast. recorded from the west coast of Ireland, under stones near shore among Spirorbis and among algae (Southern).

Genus Desmodora de Man.

P. 151, Part I. D. sanguinea Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 27, Table 3, Figure 9 A–E. Many adults and immature individuals in May, Clew Bay, 48 m in sand and shell bottom with Polygordius.

— 8) Chromadora cincta Villot, not Desmodora, but the type of a different genus.

— Genus Hypodontolaimus. Cobb (1914) did not describe new species of this genus. A misunderstanding based on an inaccurate quotation.

P. 152, Part I. Genus Spiliphera Bast. Bastian originally gave this name, but corrected it to Spilophora in the same work. As Spilophora is nomen praeocc. in coleopt. (Bohemann, 1850), the former name has to be used. I learned this from Stiles and Hassal, 1905, during proofreading and corrected the name where possible.

— Spiliphera gracilicauda de Man, recorded by Southern from the west coast of Ireland under stones near the shore between tubes of Spirorbis.

— Achromadora minima (Cobb, 1893); 1914: Trans. Amer. Micr. Soc., 33, Table 5, Figure 11.

Genus Ethmolaimus de Man:

— 6) E. alpinus Mic. (syn. E. foreli Hofm.); Micoletzky, 1917: Z. J. Syst., 40, p. 552. Lake Lunz in Austria; Bukovina in mountain lake and in spring below it (Mic.); Lake Geneva (Hofm.).

— 8) Ethmolaimus americanus Cobb, 1914: Trans. Amer. Micr. Soc., 33, p. 96, Table 7, Figure 19. Spring, Washington Country Club, Chevy Chase Maryland, U. S. A.

— 4) Microlaimus fluviatilis Cobb, 1914: Trans. Amer. Micr. Soc., 33, p. 81, Table 3, Figure 6; Maple River, Michigan U. S. A.

P. 153, Part I. 3) Laxus septentrionalis Cobb, 1914: Nem. Shackleton Exp., p. 29. South Polar Sea near Ross Island, 26–100 m.

P. 166, Part I. Southern records Spirina parasitifera Bast., Sp. schneideri Villot and Sp. laevis Bast. Blacksod Bay (west coast of Ireland) in sand under Zostera (January, February) and near shore (February, March). He does not give a detailed description of Sp. schneideri.

— 7) Spirina septentrionalis (Cobb, 1914) Nem. Shackleton Exp., p. 11. Ross Island; South Polar Sea. Closely related to Sp. parasitifera Bast.

P. 171, Part I. Genus Chromadorissa Fil. Chr. beklemishevi Fil. described in: Revue Zool. Russe, 2, p. 25, figs.

— To the same genus is apparently related also: 3) Chromadora mucrodonta Steiner, 1916: Zool. Jahrb. Syst., 39, p. 538, Table 16, Figure 5c; Table 20, Figure 5 a–b, d–g. White Sea Strait, on algae.

— 4) Chromadora meridiana Cobb, 1914: Nem. Shackleton Exp., p. 22. South Polar Sea near Ross Island, 20–40 m.

— 5) Spilophora edentata Cobb, 1914: Nem. Shackleton Exp., p. 24, from the same locality.

P. 172, Part I. Genus Euchromadora de Man.

— Eu. vulgaris Bast., recorded by Southern from the west coast of Ireland: rocks and sand near shore; adults in August and September.

— 4) Eu. meridiana Cobb, 1914: Nem. Shackleton Exp., p. 28. South Polar Sea, near Ross Island, 20–40 m.

P. 173, Part I: Instead of (Table 7, Figure 47), read: (Table 7, Figure 49).

571 P. 175, Part I. Cobb (1914, Nem. Shackleton Exp.) gave a detailed diagnosis of Spilophora and Euchromadora and described two species of Chromadora. I was unable to discover why he placed any of these species in these genera. His genera do not correspond to the genera of de Man. I place his species differently.

P. 176, Part I. Genus Chromadora Bast.

— 2a) Chr. septentrionalis (Cobb, 1914): Euchromadora s.: Nem. Shackleton Exp., p. 26. South Polar Sea, near Ross Island, 20–100 m.

— 2b) Chr. (Spilophora) canadensis (Cobb, 1914): Trans. Amer. Micr. Soc., 33, p. 80, Table 3, Figure 5. In freshwater ponds, Cape Breton Island, Canada.

— 6a) Chr. (Spilophora) serrata Cobb, 1914, Nem. Shackleton Exp., p. 25, South Polar Sea, near Ross Island (depth 20–40 m). Related to Chr. macrolaima de Man.

— 7) Chromadora nudicapitata Bast., found by Southern on the west coast of Ireland on rocks, adults in September.

— 9a) Chr. antarctica (Cobb, 1914): Spilophora a. Nem. Shackleton Exp., p. 24. South Polar Sea, near Ross Island, 20–100 m. Closely related to Chr. (Sp.) parva de Man.

— 13) Chr. polaris Cobb, 1914: Nem. Shackleton Exp., p. 22. South Polar Sea, 20–40 m, near Ross Island. Differs from Chr. poecilosomoides Fil. by the distinct preanal papillae.

P. 177, Part I. 2) Chromadora bioculata M. Sch.; Micoletzky, 1917: Z. J. Syst., 40, p. 551. Bukovina; Lake Pyukhasel'kya in Finland, common on muddy bottom and among algae (Shneider) and in Ireland in stagnant water (Southern).

P. 178, Part I. 7) Chr. leuckarti de Man, recorded from brooks in Ireland (Southern) from the Pyukhasel'kya Lake in Finland, common on muddy bottom and among algae (Schneider).

— 8) Chr. ratzeburgensis Linst., from the same locality, in decomposing Equisetum and Phragmites on algae on muddy and sandy bottom.

P. 179, Part I. 14a) Euchromadora antarctica Cobb, 1914: Nem. Shackleton Exp., p. 27. South Polar Sea, near Ross Island, 20–100 m.

— 15a) Euchr. denticulata Cobb, 1914: l. c., p. 27, from the same locality.

— 16–19) Related to Chromadorella.

— 20) To Chromadora, group $\alpha$.

P. 192, Part I. Genus Draconema Cobb.

— Chaetosoma hibernicum Southern, 1914: Proc. Roy. Irish Acad., 31, pt. 54, p. 59, Table 10, Figure 27 A–H. From west coast of Ireland from a depth of 48 m, sand and shell bottom, synonym of Draconema cephalatum Cobb, 1913.

— Dr. (Chaetosoma) spinosum (Southern, 1914): l. c., p. 60, Table 19, Figure 28 A–E, from the same dredge; this is the second
572 species with four rows of bristles; differs in its narrower neck, which is four times narrower than the head and a lateral organ in the form of a round closed spiral.

P. 197, Part I. 5) Desmoscolex chaetogaster Greef belongs to the genus Eudesmoscolex Steiner.
Genus Theristus Bast.

P. 200, Part I. 5) Th. pseudosetosus Fil.: M. setosa Büt. Micoletzky, 1917: Zool. Jahrb. Syst., 40, p. 499; Bukovina, in Pruth and its backwaters. Micoletzky agrees with Hofmänner's identification, but gives a very wide variation, which in my opinion exceeds the limits of the species; he believes, however, that M. dubia Büt. may be a different species. He places his M. crassoides (p. 213, Part I) among the synonyms.

— 3a) Th. pilosus (Cobb, 1914): Monhystera p.: Nem. Shackleton Exp., p. 17, near Ross Isalnd, South Polar Sea, 60–100 m.

— 3b) M. polaris Cobb, 1914: l. c., p. 19, from the same locality, 26–100 m.

— 13a) M. meridiana Cobb, 1914, l. c., p. 20, from the same locality.

P. 201, Part I. 6a) Austronema Cobb, 1914: Nem. Shackleton Exp., p. 16; 1 species: Au. spirurum Cobb, 1914: l. c., Ross Island, South Polar Sea, 14–28 m. This genus is closely related to Theristus and Monhystera, but distinguished by the posterior part of the esophagus, which is separated by a constriction behind the nerve ring.

— 15) For Th. articus read: Th. arcticus (Steiner).
Genus Monhystera Bast.

P. 211, Part I. 13) M. uniformis Cobb, 1914: Nem. Shackleton Exp., p. 18. South Polar Sea, near Ross Island, 50–100 m.

— 13a) M. frigida Cobb, 1914: l. c., p. 19, from the same locality.

— 13b) M. septentrionalis Cobb, 1914: l. c., p. 20, from the same locality.

— 13c) M. antarctica Cobb, 1914: l. c., p. 21, from the same locality.

— 14) M. alpina Fil. (M. demani Menzel) = M. stagnalis Bast. sec. Micoletzky, 1917- Zool. Jahrb. Syst., 40, p. 487.

— 16) M. dispar Bast.: Micoletzky, 1917: l. c., p. 495: Bukovina.

— 17) M. filiformis Bast.: Micoletzky, 1917: l. c., p. 497: Bukovina.

P. 212, Part I. 25) M. paludicola de Man: Micoletzky, 1917: Zool. Jahrb. Syst., 40, p. 491: Bukovina.

— 26) M. stagnalis Bast.: Micoletzky, 1917: l. c., p. 487: very common in Bukovina.

— 33) M. similis Büt.: Bukovina, rare (Micoletzky).

— 37) M. vulgaris de Man: Micoletzky, 1917: Zool. Jahrb. Syst., 40, p. 493: Bukovina, common.

— 38) M. sentiens Cobb, 1914: Trans. Amer. Micr. Soc., 33, p. 97, Table 7, Figure 20. Potomac River in eastern U. S. A.

P. 213, Part I. for M. crasissides read M. crassoides.
Also described were the following species, but the descriptions were not available:
Monh. diria Stewart, 1914: Rec. Indian Mus., 10, p. 247, Tables 30–31, Figures 8–10. Chilka Lake, East India, on a species of Eunicidae.

— M. megalaima Stewart, 1914: l. c., p. 250, Table 32, Figures 21–27. On algae from the same locality.

P. 219, Part I. 6) Terschellingia polaris Cobb, 1914: Nem. Shackleton Exp., p. 14. Ross Island, South Polar Sea, 28–100 m.
573 Differs from all other species by the much displaced (2 lengths of head) lateral organs; possibly belongs to another genus.

P. 230, 235, Part I. 5) Conolaimus (Axonolaimus) polaris Cobb, 1914: Nem. Shackleton Exp., p. 30. South Polar Sea, near Ross Island, 60–100 m. Closely related to C. angustilaimus Fil., but differs by the better developed lips.

P. 244, Part I. Only males of P. abyssalis Fil. have lateral organs which are $^5/_6$ of width of head, females have lateral organs $^2/_3$ of width of head, as P. clavicauda Fil. This species is therefore probably only a coastal variant of P. abyssalis.

P. 252, Part I. 3a) Aulolaimoides Micoletzky, 1917: Zool. Jahrb. Syst., 40, p. 516, one species, closely related to Plectus.

— 5a) Cryptonchus Cobb, 1913: J. Washington Ac. Sci., 3, p. 441; one species.

P. 253, Part I. Acrobeles Linstow, 1877: Arch. Naturg., 43, Vol. 1, p. 2 (type A. ciliatus Linstow) and Aloionema A. Schneider, 1859, Z. w. Z., 10, p. 176 (type A. appendiculatum A. Schn.) remain so far synonyms to Cephalobus Bastian.

— 8) Diplogasteroides de Man: Micoletzky, 1915: Denkschr. Ak. Wiss. Wien., 92, p. 158.

P. 19. Cobb (1914, pp. 78, 79) described 14 labial leaflets for Diplogaster fictor and 6 for Prismatolaimus.

## BIBLIOGRAPHY FOR MARINE AND FRESHWATER FREE-LIVING NEMATODES AND PLANT PARASITES

Only the major works of the earlier literature are listed. Studies which deal with marine nematodes are given in large type, the others in small type.* Publications marked with an asterisk have not been perused by me. Works containing only faunistic data are given in square brackets; for more detailed information on the earlier literature see Diesing, 1851, 1863; Bastian, 1865; on plant pests see Marcinowski, 1908; on the Swiss fauna see Hofmänner and Menzel, 1915.

Müller, O. F. Vermium terrestrium et fluviatilium seu Animalium infusoriorum, helminthicorum et testaceorum non marinorum succinta Historia. – Havniae, I pars 1–1773; I pars 2–1774. 1773–1774.

Müller, O. F. Animalcula Infusoria fluviatilia et marina, quae detexit, systematice descripsit et ad vivum delineari curavit. Opus posthumum, cura O. Fabricii editus. – Havniae. 1786.

Bauer, Fr. The Croonian Lecture. Microscopical Observations on the Suspension of the Muscular Motions of the Vibrio tritici. – Philos. Trans. R. Soc. Lond., pp. 1–16. 1823. Plates 1–2.

Dugès. Recherches sur l'organisation de quelques espèces d'Oxyures et de Vibrions. – Ann. Sci. nat., (1) 9, pp. 225–251. 1826. 2 tt.

Hemprich, F. G. and Chr. G. Ehrenberg. Symbolae physicae seu icones et descriptiones corporum naturalium novorum ant minus cognitorum, quae in itineribus per Libyam, Aegyptum studio annis 1820 – 1825 redierunt. Pars Zoologica. Decas prima. Phytozoa, Entozoa, Berolini. 1828.

Ehrenberg, C. G. Organisation, Systematik und geographisches Verhältnis der Infusionsthierchen, Berlin. 1830. 108 pp. 8 plates.

Ehrenberg, C. G. Die Acalephen des rothen Meeres und der Organismus der Medusen der Ostsee erläutert und auf Systematik angewendet, Berlin. 1836. 82 pp. 8 plates.

Lamarck, I. B. P. A. Histoire naturelle des Animaux sans Vertèbres, 2me ed., Vol. 3 (Nématodes par Nordmann). 1840.

Dujardin, Histoire naturelle des helminthes ou vers intestinaux, Paris. 1845. 16 + 654 pp. 12 tt.

*Kolliker r, A. Über drei neue Gattungen von Würmern. – Verh. naturf. Ges., Zurich. 1845.

Quatrefages, A. de. Note sur un genre d'anguillules marines, pourvues de soies, Hemipsile. – Ann. Sci. nat., (3) 6, Zool., pp. 131–132. 1846.

Leuckart, Rud. Zur Kenntnis der Fauna von Island. Erster Beitrag (Würmer). – Arch. Naturg., 15 (1):149–208. 1849. 3 plates.

Czernay, A. Monographie des Essigälchens. – Bull. Soc. Imp. Nat. Moscou, 22 (3/4):232–256. 1849. 6 plates.

Grube, Ed. Über einige Anguillulen und die Entwicklung von Gordius aquaticus. – Arch. Naturg., 15 (1):348–375, 1849, 1 plate.

Diesing, C. M. Systema Helminthum, Vol 2, Vindobona. 1851. 588 pp.

*Leidy. Contributions to Helminthology. – Proc. Acad. Nat. Sci., Philadelphia, Vol. 5, pp. 205–209, 224–227, 239–244, 349–351. 1852.

Czernay, A. Über eine neue, der Anguillula zunächst stehende Gattung der Flusswasserwürmer. – Bull. Soc. Imp. Nat. Moscou, Vol. 26. pp. 205–208. 1853. 1 fig.

Berlin, W. Über einen neuen Wurm aus der Gruppe der Anguillulae, Enoplus quadridentatus. – Arch. Anat. Phys., pp. 431–441. 1853. Plates 14, 15.

Dalyeli, The Powers of the Creator Displayed in Creation, Vol. 2. 1853. (Dilettante publication of no scientific importance.)

Leydig, Fr. Zoologisches Arch. Anat. Phys., pp. 284–295. 1854, plate 11.

Grube, Ed. Bemerkungen über einige Helminthen und Meerwürmer. – Arch. Naturg., 21 (1):136–158. 1855. Plates 6, 7.

Leidy, J. Contributions Towards the Knowledge of the Marine Invertebrate Fauna of the Coasts of Rhode Island and New Jersey. – J. Acad. Nat. Sci., Philadelphia, Vol. 3: 135–152. 1855. Plates 10–11.

*Leidy, J. A Synopsis of Entozoa and Some of their Ectocongeners Observed by the Author. – Proc. Acad. Nat. Sci., Philadelphia, Vol. 8, pp. 42–58. 1857.

---

* [In Russian original.]

Davaine. Recherches sur l'Anguillule du blé niellé, Paris. 1857. 80 pp.

Kühn, I. Über das Vorkommen von Anguillulen in erkrankten Blüthenköpfen von Dipsacus fullonum L. – Zeitschr. wiss. Zool., Vol. 9:129–137. 1857. Plate 7c.

*Cohn, F. Über das Wiederaufleben der durch Austrocknen in Scheintod versetzten Tiere und Pflanzen. – Jahresb. schles. Ges. vaterl. Kultur, pp. 48–50. 1857.

*Cohn, F. Über Anguillula tritici in sogenannten gichtigen Weizenkörnern. – Ibid., p. 73. 1857.

Schultze, M. Nematodes. – In: V. Carus. Icones zootomicae, Leipzig. 1858. Plate 8.

Barthélemy, M. A. Études sur le developpement et les migrations d'un Nématoide parasite de l'oeuf de la Limace grise. – Ann. Sci. Nat. Zool., (4) 10:41–48. 1858.

Gavarret. Quelques expériences sur les Rotifères, les Tardigrades et les Anguillules des mousses des toits. – Ann. Sci. Nat. Zool., (4) 11:315–330. 1859.

Carter, H. I. On Dracunculus and Microscopic Filaridae in the Island of Bombay. – Ann. Mag. Nat. Hist., (3) 4:28–44. 1859. Plates 1–3.

Schneider, A. Über eine Nematodenlarve und gewisse Verschiedenheiten in den Geschlechtsorganen der Nematoden. – Zeitschr. wiss. Zool., Vol. 10:176–178. 1860.

Grube, A. E. Ein Ausflug nach Triest und dem Quarnero, Berlin. 1861.

Diesing, K. M. Revision der Nematoden. – Sitz. Ber. math. – naturw. Cl. Kais. Akad. Wiss., Wien, Vol. 42:595–736, 2 plates (Bibliography of the years 1850–1860).

Dulsberg, H. Beitrag zur Bernstein Fauna. – Schr. phys. -ök. Ges., Königsberg, pp. 31–36. 1862. 1 plate (Nematodes in Amber).

Mecznikow, E. Bemerkungen über einen neuen Diplogaster. – Art. Arch. f. Anat. Phys., pp. 502–509. 1863. Plate 12.

Mechnikov, I. Zametka o novom vide Diplogaster (A Note on a New Species of Diplogaster). – Zapiski Imperatorskoi Akademii Nauk. 1863.

Eberth, C. J. Untersuchungen über Nematoden, Leipzig. 1863. 77 pp. 9 plates.

Claparède, R. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Tiere, Leipzig. 1863. 120 pp. 18 plates.

Claus. Über einige im Humus lebende Anguilluliden. – Zeitschr. wiss. Zool., Vol. 12:354–359. 1863. Plate 35.

*Claus. Beobachtungen über die Organisation und Fortpflanzung von Leptodera appendiculata. – Schr. Ges. Marburg. Suppl. 3, p. 24. 1864. 3 plates.

*Greef. Über die hier lebenden Nematoden. – Verh. Nat. Ver. Preuss. Rheinl., pp. 112, 113. 1864.

Metshnikov, E. Über einige wenig bekannte niedere Tierformen. – Zeitschr. wiss. Zool., Vol. 15:328–341. 1865. Plate 35.

Bastian, H. Ch. Monograph on the Anguillulidae, or Free Nematoids, Marine, Land and Freshwater, with Descriptions of 100 New Species. – Trans. Linn. Soc., Vol. 25:73–184. 1865. Plates 9–13.

Bastian, H. Ch. On the Anatomy and Physiology of the Nematoids, Parasitic and Free. – Philos. Trans. R. Soc., London, Vol. 156. 1866.

Pérez, M. Recherches anatomiques et physiologiques sur l'Anguillule terrestre (Rhabditis terricola Dujardin). – Ann. Sci. Nat., (5) Zool., Vol. 6:152–307. 1866. Tt 5–10.

*Leuckart, R. Sur les vers Nématodes. – Bull. Acad. Roy. Belgique, Vol. 21:208. 1866. L'Institut, pp. 245–247. 1866. (Quoted after Oerley.)

Menge, A. Über ein Rhipidopteron und einige andere im Bernstein eingeschlossene Tiere. – Schr. naturf. Ges., Danzig I, Lfg. 3/4, No. 3. 1866. 8 pp. 22 figs. (Nematodes in Amber).

Schneider, A. Monographie der Nematoden, Berlin. 1866. 357 pp. 28 plates.

Metschnikoff, E. Beiträge zur Naturgeschichte der Würmer I. Über Chaetosoma und Rhabdogaster. – Zeitschr. wiss. Zool., Vol. 17:539–544. 1867. Plate 31.

[Mechnikov, Il. Zametki o pelagicheskoi faune Chernago morya (Notes on the Pelagic Fauna of the Black Sea). – Trudy I s"ezda Russkikh Estestvoispytatelei i Vrachei, Otdel Zoologicheskii, pp. 267–270. 1868.]

Greef, R. Untersuchungen über einige merkwürdige Thiergruppen der Arthropoden und Wurmtypus. – Arch. Naturg., 35 (1):71–121. 1869. Plates 4–7.

*Claus, C. Beobachtungen über die Organisation und Fortpflanzung von Leptodera appendiculata. – Schr. Beförd. Ges. Naturwiss., Marburg. Suppl. No. 3. 1869.

*[Claus, C. Rhabditen in faulenden Kartoffeln. – Sitz. Ber. niederrheinischen Ges. Natur- und Heilkunde. 1869.]

*Claus, C. Untersuchungen über freilebende Nematoden. – Ibid., 1870.

Marion, M. A. F. Recherches zoologiques et anatomiques sur des Nématoides non parasites, marins. – Ann. Sci. Nat. (5) Zool., 13, Art. 14. 1870a. 102 pp. Tt. 16–26.

Marion, M. A. F. Additions aux recherches sur les Nématoides libres du Golfe de Marseille. – Ibid., 14, Art. 1. 1870b. 16 pp. 20 pl.

*Schmidt. Über die Rübennematoden. – Zeitschr. d. Verein. f. Rüben-Industrie im Zollverein. 1871.

*Greef, R. Über die frei in Wasser und in der Erde lebenden Nematoden, namentlich die Meeresbewohner. – Sitz. Ber. naturf. Ver. Preuss-Rheinland, Vol. 27, p. 87. 1872.

Vernet, H. Quelques mots sur la reproduction de deux espèces hermaphrodites du genre Rhabditis. – Arch. Sci. Phys. et Nat., Vol. 45:60–75. 1872. T. 1.

*[Frauenfeld. – Verh. Zool. bot. Ver. Wien. 1872. (Quoted after Oerley.)]

*[Thomas. Beiträge zur Kenntnis der Milbengallen. – Holl. Zeitschr. f. ges. Naturwiss. Vol. 42. 1873. (Quoted after Oerley).]

*[Ercolani. – Mem. Ac. Sci. Ist. Bologna (3) 4, 1873. (Quoted after Oerley).]

Bütschli, O. Beiträge zur Kenntnis der freilebenden Nematoden. – N. Acta Acad. Caes. Leop. - Carol. Germ., Vol. 36, No. 5. 1873. 144 pp. Plates 17–27.

Bütschli, O. Zur Kenntniss der freilebenden Nematoden, insbesondere der des Kieler Hafens. – Abh. Senck. naturf. Ges., Vol. 9:1–56. 1874. Plates 1–9.

Löw, Franz. Tylenchus millefolii n. sp., eine neue, gallenerzeugende Anguillulide. – Verh. zool.-bot. Ges. Wien, Vol. 24: 16–24. 1874. Plate 13.

*[Braun, A. Gallenbildung durch Aelchen. – Sitz. Ber. Ges. naturf. Freunde, 15 März, Berlin. 1875. (Quoted after Oerley.)]

*[Braun, A. Über Gallen am Edelweiss (Tylenchus nivalis Kühn) und über Anguillula–Gallen überhaupt. – Ibid., 1875.]

Villot, A. Sur le système nerveux périférique des Nématoides marins. – C. R. Ac. Sci., Paris, Vol. 80:400–402. 1875.

Villot, A. Recherches sur les helminthes libres ou parasites des côtes de la Bretagne. – Arch. Z. Exp. (1) 4:451–482. 1875. Tt. 11–14.

Marion, M. A. F. Révision des Nématodes du Golfe de Marseille. – C. R. Ac. Sci., Paris, Vol. 80:499–501. 1875. (Notes synonymiques.)

Barrois, J. and A. Giard. Note sur un Chaetosoma et une Sagitta. – Rev. sci. nat. Montpellier, pp. 513–532. 1875. T. 9.

Bütschli, O. Vorläufige Mitteilung über die Untersuchungen, betreffend die ersten Entwicklungsvorgänge im befruchteten Ei von Nematoden und Schnecken. – Zeitschr. wiss. Zool., Vol. 25:201–213. 1875.

Bütschli, O. Studien über die ersten Entwicklungsvorgänge der Eizelle, die Zelltheilung und Konjugation der Infusorien. – Abh. Senck. naturf. Ges., Vol. 10: 1876. 250 pp. 15 plates. (Nematodes pp. 19–26.)

Bütschli, O. Untersuchungen über freilebende Nematoden und die Gattung Chaetonotus. – Zeitschr. f. wiss. Zool., Vol. 26:363–413. 1876. Plates 23–26.

*Panceri, P. Osservazioni intorno a nuove formi di Vermi Nematoidi marini. – Rend. Accad. sci. fis-matem., Napoli, Vol. 7:225. 1876.

De Man, J. G. Onderzoekingen over vrij in de aarde levende Nematoden. – Tijd. Nederl. Dierk., 2:78–196. 1876. Plates 3–13.

Grimm, O. A. Kaspiiskoe more i ego fauna (The Caspian Sea and its Fauna). Fasc. 1. – Trudy Aralo-Kaspiiskoi Ekspeditsii, No. 2, Sankt-Peterburg. 1876. 168 pp. 6 plates.

Linstow, von O. Helminthologische Beobachtungen. – Arch. f. Naturg., Vol. 42:1–18. 1876. Plates 1–2.

Linstow, von O. Helminthologica. – Ibid., Vol. 43:1–14. 1877. Plate 1.

[Grimm, O. K poznaniyu fauny Baltiiskogo morya (Contribution to the Study of the Fauna of the Baltic Sea). – Trudy Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Vol. 8:107–138. 1877.]

Ganin, M. S. Nablyudeniya nad embrional'nym razvitiem Pelodera teres (Observations on the Embryonal Development of Pelodera teres). – Trudy V S"ezda Russkikh Estestvoispytatelei i Vrachei, Otdel Zoologicheskii, pp. 147–184, Warszawa. 1877. Plate 9. (Abstract: Zeitschr. wiss. Zool., Vol. 28:412–413).

*Hallez. Sur le développement d'Anguillula aceti. – Rev. Sci. Nat. 5. (Quoted after Oerley.)

*[Brown. – In: Sitz. Ber. Ges. naturf. Freunde, Berlin. 1878. (Quoted after Oerley.)]

*Oerley, L. Adatok a Nematodák fejlödé séhez., Budapest. 1878. (Development of Anguillula aceti.)

De Man, J. G. Contribution à la connaissance des Nématoïdes marins du Golfe de Naples. – Tijd. Nederl. Dierk., Ver. 3:88–118. 1878. Tt. 7–9.

Linstow, von O. Helminthologische Beobachtungen. – Arch. f. Naturg. Vol. 45:165–188. 1879. Plates 11–12.

*[Liebscher, G. Über die Beziehungen der Heterodera schachti zur Rübenmüdigkeit, Halle. 1879. (Diss.).]

*[Huber, I. Ch. Über Tylenchus scandens Bast. – Ber. naturhist. Ver. Augsburg, Vol. 25:41. 1879.]

[Joseph, G. Über die in den Kreiner Tropfsteingrotten einheimischen freilebenden Rundwürmer (Nematoden). – Zool. Anz., Vol. 2: 275–277. 1879.]

Oerley, L. Monographie der Anguilluliden. – Termesz. Füzetek, Vol. 4:1–165. 1880. Plates 1–7.

De Man, J. G. Die einheimischen, frei in der reinen Erde und im süssen Wasser lebenden Nematoden, monographisch bearbeitet. – Vorläufiger Bericht und deskriptiv-systematischer Teil. – Tijd. Nederl. Dierk., Ver. 5:1–104. 1880. (Completely contained in the Large Monograph of 1884.)

De Man, J. G. Über einige neue oder noch unvollständig bekannte Arten von frei in der reinen Erde lebenden Nematoden: 1. Supplement zu dem Aufsatz auf S. 1 dieses Bandes. – Ibid., pp. 138–143. 1881. (Supplement to the preceding paper.)

Reinhard, W. Über Echinoderes und Desmoscolex der Umgegend von Odessa. – Zool. Anz., Vol. 4:588–592. 1881.

Levinsen, I. Smoa Bidrag til den grönlandske Fauna. – Vedensk. Meddelser naturh. Fören. Kjöbenhavn, 1881, pp. 132–133. 1881.

*Kühn, J. Untersuchungen über die Ursachen der Rübenmüdigkeit. – Ber. physiol. Labor. landw. Inst., Halle, No. 3. 1882.

Joseph, G. Beiträge zur Kenntnis des Nervensystems der Nematoden. – Zool. Anz., Vol. 7:264–266. 1882.

Linstow, von O. Helminthologische Studien. – Arch. f. Naturg. Vol. 48: 1–25. 1882. Plates 1–2.

*Müller, K. Neue Helminthocoecidien und deren Erzeuger. Inaug. Diss., Berlin. 1883. 50 pp. 4 plates.

*Chatin, J. Recherches sur l'Anguillule de l'oignon, Paris. 1884. 2 tt.

[Braun, M. Physikalische und biologische Untersuchungen im westlichen Theile des finnischen Meerbusens. – Arch. Naturk. Liv-, Est- und Kurlands, Vol. 10:1–34. 1884.]

De Man, J. G. Die frei in der reinen Erde und im süssen Wasser lebenden Nematoden der Niederländischen Fauna. Eine systematisch-faunistische Monographie. Leiden, E. J. Brill. 1884. 206 pp. 84 plates.

De Man, J. G. Helminthologische Beiträge. – Tijd. Nederl. Dierk., Ver. (2) 1:1–26. 1885. Plates 1–3.

Schöyen, M. Bygaalen. Tylenchus hordei n. sp., en ny, for Biggit skadelig Planteparasit blandt Rundarmene. – Forhan. Vidensk. Selskabet Christiania, 1885, No. 22. 1885. 16 pp. 1 plate.

De Man, J. G. Anatomische Untersuchungen über freilebende Nordsee-Nematoden, Leipzig. 1886. 82 pp. 13 plates.

Oerley, L. Die Rhabditiden und ihre medizinische Bedeutung, Berlin. 1886. 84 pp. 6 plates.

[Treub, M. Quelques mots sur les effets du parasitisme d'Heterodera javanica dans les racines de la canne à sucre. – Ann. Jard. Botan. Buitenzorg, Vol. 6:93–96. 1886. T. 10.]

*Treub, M. and J. Kühn. Bericht über die weiteren Versuche mit Nematoden (Heterodera) Fangpflanzen. – Ber. phys. Labor. Inst. Univ. Halle., No. 6:163–175. 1886.

Pennetier, G. Limite de la résistance vitale des Anguillules de nielle. – C. R. Ac. Sci., Paris, Vol. 103:284–286. 1887.

Linstow, O. V. Helminthologische Untersuchungen – Zool. Jahrb. Syst. 3, p. 12. 1887. Plate 2.

*Ludwig. Ein Verwandter des Essigälchens in den Gährungsproducten der Eichenrinde. – Monatl. Mitt. Huth, 5 (7):160. 1887.

Ritzema-Bos, J. Untersuchungen über Tylenchus devastatrix Kühn. I–II. – Biol. Centralbl. VII, pp. 232–243, 257–271, 646–659; VIII, pp. 129–138, 164–178. 1887–1888.

Ritzema-Bos, J. L'Anguillule de la tige (Tylenchus devastatrix Kühn) et les maladies des plantes dues à ce nématode. – Arch. Mus. Teyler (2) 3 Haarlem, pp. 161–348. 1888. Tt. 1–10.

Strubell, A. Untersuchungen über den Bau und die Entwicklung des Rübennematoden – Heterodera schachti Schmidt. – Bibl. Zool., Vol. 2. 1888. 52 pp. 2 plates.

Zopf, W. Zur Kenntnis der Infektionskrankheiten niederer Tiere und Pflanzen. I. Über einige durch Schimmelpilze verursachte Krankheiten Nematoden-artiger Würmer. – N. Acta Ac. Leop.-Car., Vol. 52:313–341. 1888. Plates 1–3.

Chatin, I. Sur la structure des téguments de l'Heterodera schachti et sur les modifications qu'ils présentent chez les femelles fécondées. – C. R. Ac. Sci., Paris, Vol. 107:139. 1888.

Michel, De l'existence d'un véritable épiderme cellulaire chez les nématodes. – C. R. Ac. Sci., Paris, Vol. 107:1175. 1888.

[Prillieux, M. Maladie vermiculaire des avoines. – C. R. Ac. Sci., Paris, Vol. 107:51–53. 1888.]

Cobb, N. A. Beiträge zur Anatomie und Ontogenie der Nematoden. – Jen. Zeit. Naturw., Vol. 23:41–76. 1888. Plates 3–5.

De Man, J. G. Sur quelques Nématodes libres de la mer du Nord, nouveaux ou peu connus. – Mém. Soc. Zool. France 1:1–51. 1888. Tt. 1–4.

De Man, J. G. Espèces et genres nouveaux de Nématodes libres de la mer du Nord et de la Manche. – Ibid., pp. Vol. 2:1–10. 1889.

De Man, J. G. Troisième note sur les Nématodes libres de la mer du Nord et de la Manche. – Ibid., Vol. 2:182–216. 1889. Tt. 5–8.

De Man, J. G. Über zwei in der feuchten Erde lebende Arten der Gattung Oncholaimus Duj. – Tijd. Nederl. Dierk., Ver. (2) 2:162–169. 1889. Plate 6.

Dureau, G. Le nématode de la betterave à sucre (Heterodera schachti), Paris. 1889.

*[Atkinson. Nematode Root-Galls. – Journ. Elisha Mitchell Sci. Soc., Vol. 6, No. 2. 1889.]

*[Horn. Die Älchen-Gallen auf Phleum behmeri. – Wibel. Arch. Ver. Freunde. Naturgesch. Mecklenburg, Vol. 42:139–156. 1889. 2 plates.

Certes, A. Organismes divers appartenant à la faune microscopique de la Terre de Feu. – Mission scient. du Cap Horn. 1882–1883, Zool., Vol. 6:47. 1889.

Göldi, E. A. Relatorio sobre e molestia do cafeeiro na Provincia do Rio de Janeiro. – Archivos do Museu Nacional de Rio de Janeiro, Vide. – Zool. Jahrb. Syst. 4:262–267. 1889. 4 tt.

Moniez, R. Sur la métamorphose et la migration d'un Nématode libre (Rhabditis oxyuris Cls). – C. R. Ac. Sci., Paris, Vol. 109: 506–507. 1889. (Biology.)

Moniez, R. Faune des eaux souterraines du département du Nord et en particulier de la ville de Lille. – Revue Biol. Nord. France, Vol. 1: 9–10. 1889.

*Voigt. Infektionsversuche zur Unterscheidung von Heterodera radicicola Greef und H. schachti Schmidt. – Sitzb. Niederrhein. Ges. Bonn, pp. 66–74. 1890. (According to Centralbl Bakt., Vol. 9:21.)

De Man, J. B. Quatrième note sur les Nématodes libres de la mer du Nord et de la Manche. – Mém. Soc. Zool. France, Vol. 3:169–194. 1890. Tt. 3–5.

[Chatin, J. Sur la présence de l'Heterodera schachti dans les cultures d'oeillets à Nice. – C. R. Ac. Sci., Paris, Vol. 113: 1066–1067. 1891.]

*Chatin, J. Recherches sur l'Anguillule de la betterave publiées par les soins du Ministère de l'Agriculture, Paris. 1891.

*Ritzema-Bos, J. Tierische Schädlinge und Nützlinge. 1891.

Cobb, N. A. Arabian Nematodes. – Proc. Linn. Soc. N. S. W., Vol. 5: 449–468. 1891.

Cobb, N. A. Anticoma: a Genus of Free-Living Marine Nematodes. – Ibid., Vol. 5: 765–774. 1891.

Cobb, N. A. Onyx and Dipeltis, New Nematode Genera, with a Note on Dorylaimus. – Ibid., Vol. 6:143–158. 1891.

Leuckart, R. Über einen an Aphodius fimetarius sich verpuppenden freilebenden Rundwurm – Rhabditis coarctata n. sp. – Verh. deutsch. Zool. Ges., Vol. 1:54–56. 1891.

*Massalongo, C. Sul elmintocecidio (Tylenchus invalis) dell' Edelweiss. N. Giorn. Botan. Ital., Firenze, Vol. 23 (2):375. 1891.

Ritzema-Bos, J. Zwei neue Nematodenkrankheiten der Erdbeerpflanze. – Zeitschr. f. Pflanzenkrankheiten, Vol. 1:1. 1891.

*Ritzema-Bos, J. Aphelenchus olesistus n. sp. een Nematode schadelijk aan Begonia's en Varens. – Maandbl. Natuurw., Vol. 17:101–112. 1892. Plate 8.

[Fritsch and Vavra. Vorläufiger Bericht über die Fauna der Unter-Počernitzer und Gatterschlager Teiche. – Zool. Anz., Vol. 15:26–30. 1892.]

Göldi, E. A. Relatorio sobre a molestia do cafeeiro na provincia do Rio de Janeiro. – Archivios Mus. Nacion. Rio de Janeiro, Vol. 8: 1–123. 1892. Plates 1–4.

[Kojevnikov, Gr. La faune de la mer Baltique orientale et les problèmes des explorations prochaines de cette faune. – Congrès Int. Zool. 2 sess. Moscou, Vol. 1:132–157. 1892.

Linstow, von O. Helminthen von Süd-Georgien. – Jahrb. Hamburger wiss. Anstalt. Anno IX, Vol. 2:59–77. 1892. 3 plates.

Vaňha, Jan. J. O nových listech řepních, jejich škůdnosti a rozsíření. Sitzb.– Kgl. Böhm. Ges. Wiss. Math-Nat. 1892, pp. 311–323. 1892. Plate 8.

De Man, J. G. Über eine neue, in Gallen einer Meeresalge lebende Art der Gattung Tylenchus Bast. – Festschr. Leuckart, pp. 121–125. 1892. Plate 16. 3 figs.

De Man, J. G. Cinquième note sur les Nématodes libres de la mer du Nord et de la Manche. – Mém. Soc. Zool. France, Vol. 6:81–125. 1893. Tt. 5–7.

*Cobb, N. A. Nematodes, Mostly Australian and Fijian. – Macleay Memorial Volume of the Linnean Society N. S. W., pp. 252–308. 1893. Plates 36–42.

Cobb, N. A. Plant Diseases and their Remedies. – Agric. Gaz. N. S. W., Vol. 4:778–883. 1893.

Cobb, N. A. Tricoma and Other New Nematode Genera. – Proc. Linn. Soc. N. S. W., Vol. 8:389–420. 1893. 15 figs.

[Zacharias, O. Fauna des Grossen Plöner See's. – Forschungsber. biol. Stat. Plön., Vol. 1:1–13 (Nematodes, p. 6). 1893.]

*Müller, W. Tierische Zuckerrübenschädlinge, Berlin. 1893.

*[Frič, A. and V. Vávra. Untersuchungen über die Fauna der Gewässer Böhmens. IV. Die Tierwelt des Unterpočernitzer und Gatterschlager Teiches. – Arch. Landesdurchf. Böhmens, Vol. 9, No. 2. 1894.]

Zur Strassen, O. Über das röhrenförmige Organ von Oncholaimus. – Zeitschr. f. wiss. Zool., Vol. 58:460–474. 1894. Plate 29.

Janet, Ch. Études sur les fourmis: 4 notes: Pelodera des glandes pharyngiennes de Formica rufa. – Mém. Soc. Zool., France, Vol. 7:45–62. 1894. 11 figs.

Daday, E. Ujabb adatok a Balaton mikrofaunájak ismertéhez, – Math. termt. Ertesitö Magyar Ak., Vol. 12:122–145. 1894. (Published in 1897.)

Schimkevitsch, W. Über die excretorische Thätigkeit des Mitteldarmes der Würmer. – Biol. Centralbl., Vol. 14:838–841. 1894.

Jammes, Léon. Recherches sur l'organisation et le développement des Nématodes, Paris. 1894. XV + 205 pp. 11 tt. 11 figs.

De Man, J. G. Note supplémentaire sur la Rhabditis janeti Lac. Duth. – Mém. Soc. Zool. France, Vol. 7:363–371. 1894. T. 5.

De Man, J. G. Description of Three Species of Anguillulidae, Observed in Diseased Pseudo-Bulbs of Tropical Orchids. – Proc. Liverpool Biol. Soc., Vol. 9:76–96. 1895. Plates 3–5.

*[Spiegler, J. Praktische Anleitung zur Bekämpfung der Rüben-Nematoden. 2 Aufl., Wien. 1895.]

*[Ormerod, E. A. Report of Observations of Injurious Insects and Common Farm Pests during the Year 1894. – Eelworms, pp. 47–61, London. 1895.]

[Garbini, A. Appunte per una limnobiotica italiana. II. -- Zool. Anz., Vol. 18:105–108. 1895.]

*Debray, J. and E. Maupas. Le Tylenchus devastatrix Kühn et la maladie vermiculaire des fèves en Algérie. – Algérie agricole. 1896. 55 pp. 1 t.

Linstow, von O. Nemathelminthen. – Erg. Hamburger Magalhaenischen Sammelreise, Vol. 1, No. 7. 1896. 22 pp. 1 Plate.

*Vaňha, Joh. and Jul. Stocklasa. Die Rüben-Nematoden, Berlin, Parey. 1896. 97 pp.

[Stocklasa, J. Heterodera radicicola. – Zeit. f. Zuckerindustrie Böhmens, Vol. 21:92 (Ref. Centralbl. Bakt. (2) 2:772). 1896.]

[Tarnani, J. K. Nematody buraczne v Panstwie Rossyjskiem. – Gazeta cukrownicza 1896, pp. 445–448. 1896.]

Tarnani, I. K. Sveklovichnaya nematoda (Heterodera schachti Schmidt). Obraz zhizni, sposoby izsledovaniya i bor'ba s sveklovichnoi nematodoi. S prilozheniem programmy dlya sobiraniya svdenii o nematodnoi bolezni rastenii (The Beet Nematode (Heterodera schachti Schmidt). Mode of Life, Methods of Study and Control. Instructions for Collection of Information on the Plant Nematode Disease). – Nasekomyya i drugiya zhivotnyya nanosyashchiya vred v sel'skom khozyaistve. II. Ministerstvo Zemledeliya i Gosudarstvennyi Imperatorskii Departament Zemledeliya, Sankt-Petersburg. 1897. 62 pp. 10 figs.

*Frič, A. and V. Vávra. Untersuchungen zweier Böhmerwaldseen, des Schwarzen und des Teufelsees. – Arch. Landesdurchf. Böhmens, Vol. 10, No. 3. 1897.

Chatin, J. Sur les noyaux hypodermiques des Anguillulides. – C. R. Ac. Sci., Paris, Vol. 125:57–59. 1897.

Erlanger, R. Beobachtungen über die Befruchtung und ersten zwei Teilungen an den lebenden Eiern kleiner Nematoden. I. – Biol. Chl., Vol. 17:152. 1897.

Daday, E. Die freilebenden Süsswasser-Nematoden Ungarns. – Zool. Jahrb. Syst., Vol. 10:92–134. 1897. Plates 11–14.

Daday, E. Nematoden. – Res. wiss. Erforsch. Balatonsees. Vol. 2, Part 1:81–119, Wien. 1897. 55 figs. (Contained completely in the preceding work.)

Daday, E. Beiträge zur Kenntnis der Microfauna der Tatra-Seen. – Termész. Füzetek, Vol. 20:149–196. 1897. (Nematodes contained completely in the work in Zool. Jahrb.)

Daday, E. Microscopische Süsswasserthiere aus Ceylon. – Termész. Füzetek, 21, Appendix (Nematodes, p. 10). 1898. 123 pp.

Cobb, N. A. Extract from M. S. Report on the Parasites of Stock. – Agric. Mag. N. S. W., Vol. 9:296–321, 419–454. 1898.

Daday, E. Australian Free-Living Marine Nematodes. – Proc. Linn. Soc. N. S. W., Vol. 23:383–407. 1898.

Noack, F. Die Pfahlwurzelfäule des Kaffees, eine Nematodenkrankheit. – Zeitschr. f. Pflanzenkrankheiten, Vol. 8. 1898.

Fritsch, G. Ein Beitrag zur Beurteilung der Vitalität jugendlicher Rundwürmer. – Zool. Anz., Vol. 21:110–112. 1898.

Shimkevich, V. M. O nekotorykh primeneniyakh okraski metilenovoi sin'yu (On the Methods of Staining with Methylene Blue). – Trudy Imperatorskogo Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Vol. 29:320–323.

Schimkewitsch, W. Über besondere Zellen in der Leibeshöhle der Nematoden. – Biol. Centralbl., Vol. 19:407. 1899.

[Plotnikov, V. K faune chervei ozera Bologova i ego okrestnostei (On the Fauna of Worms of the Bologov Lake and its Vicinity). – Trudy Imperatorskogo Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Vol. 30, Proceedings. 1899.

Daday, E. Uj-guineai szabadon élö Nematodák. – Math. termt. Ertesitö, Vol. 17:557. 1899. (German Translation see under 1901).

*Henneberg, W. Zur Biologie des Essigaales (Anguillula aceti). – Deutsche Essigindustrie. Inst. f. Gärungsgewerbe, Berlin. 1899, Nos. 45–52. 1900; Nos. 1–5. 1899–1900. 10 figs. (Biology; Abstr. see Centralbl. Bakt., (2) 6:180).

Maupas, E. La mue et l'enkystement chez les Nématodes. – Arch. Zool. Exp., (3) 7:562–668. 1899. Tt. 16–18.

Maupas, E. Modes et formes de reproduction chez les Nématodes. – Arch. Zool. Exp., (3) 8:463–624. 1900. tt. 16–26.

Hallez, Paul. Nématodes. L'Anguillule du vinaigre. (Anguillula oxophila Schneider). – Zoologie descriptive, T. 1:585–622, Paris. 1900.

*Zimmermann, A. De Nematoden der Koffiewortels. II. – Meddel. uit s'lands Platentuin, Vol. 37. 1900.

Conte, M. A. De l'influence du milieu nutritif sur le développement des Nématodes libres. – C. R. Soc. Biol., Vol. 52:374–375. 1900.

Conte, M. A. Sur les conditions de ponte des Nématodes. – Ibid., pp. 375–376. 1900.

*Buerkell, E. Biologische Studien über die Fauna der Kieler Föhrde (158 Reusenversuche). (Nematodes, pp. 22–24), Kiel-Leipzig. 1900.

Linstow, von O. Die Nematoden. – Fauna Arctica, Vol. 1: 117–132. 1900. Plates 6–7.

Linstow, von O. Beobachtungen an Helminthen des Senckenbergschen naturhistorischen Museums, des Breslauer zoologischen Instituts und anderen. – Arch. mikr. Anat., Vol. 58:182–198. 1901. Plates 8–9.

Linstow, von O. Dorylaimus atratus n. sp. – Boll. Mus. Zool. Anat. Compar. R. Univ. Genova, No. 109. 1901. 2 pp.

Plotnikov, V. Nematoda, Oligochaeta i Hirudinei, naidennyya v Bologovskom ozer i ego okrestnostyakh v 1899 g. (Nematoda, Oligochaeta and Hirudinei, found in the Bologov Lake and its Vicinity in 1899). – Trudy Presnovskoi Biologicheskoi Stantsii Imperatorskogo Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Vol. 1: 244–251. 1901.

Jägerskiöld, L. Weitere Beiträge zur Kenntnis der Nematoden. – Kgl. Svenska Vetensk. Ak. Handl., Vol. 35, No. 2. 1901.

Golovin, E. P. Nablyudeniya nad nematodami I. Fagotsitarnye organy (Observations on Nematodes. I. Phagocytic Organs), Kazan. 1901–1902. 149 pp. 3 plates; II. Ekskretornyi apparat (Excretory Apparatus), Kazan: 1902. VI+ 120 pp. 4 plates.

Daday, E. Mikroskopische Süsswasserthiere aus Deutsch-Neu-Guinea. – Termész. Füzetek, Vol. 24: 1–56. 1901. Plates 1–3.

Daday, E. Freilebende Nematoden aus dem Quarnero. – Termesz. Füzetek, Vol. 24:433–437. 1901. Plates 21–23.

Cobb, N. A. A New Eel-Worm Infesting the Roots of Passion-Vine. – Agric. Gaz. N. S. W., Vol. 12:115–117. 1901.

Cobb, N. A. Root-Gall. – Ibid., Vol. 12:1041–1052. 1901.

Cobb, N. A. The Nematode Formula. – Ibid., Vol. 13:1023–1030. 1902.

*Cobb, N. A. Internal Structure of the Gall-Worm. – Ibid., Vol. 13:1031–1033. 1902.

Daday, E. Mikroskopische Süsswasserthiere aus Patagonien, gesammelt von Dr. Filippo Silvestri. – Termesz. Füzetek, Vol. 25:201–310. 1902. (A Note on One Species on Page 203.).

Daday, E. Mikroskopische Süsswasserthiere. – Zool. Erg., 3 asiat. Forschungsreise Zichu, Budapest. 1902.

*[Jacobi, A. Die Rüben- und Hafernematode (Heterodera schachti und ihre Bekämpfung) – Arb. Kais. Gesundheitsamt, Biol. Abth. Land. Forstw. Flugbl., XI, pp. 1–4. 1902. 12 figs.]

Shipley, A. E. On the Nematodes Parasitic in the Earthworm. – Arch. Parasitol., Vol. 6:619. 1902.

Michel, A. Sur les formes nouvelles ou peu connues de Rhabditis. – C. R. Ac. Sci., Paris, Vol. 135:907–910. 1902.

Metcalf. Cultural Studies of a Nematode Associated with Plant Decay. – Trans. Amer. Soc. Microsc., Vol. 24:89–102. 1903. 1 plate.

Türk, F. Über einige im Golfe von Neapel freilebende Nematoden. – Mitt. Zool. Stat. Neapel., Vol. 16:281–347. 1903. Plates 10, 11.

Linstow, von O. Entozoa des Zoologischen Museums der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. II. – Ann. Mus. Zool. St. Petersbourg, Vol. 8:265–294. 1903. Plates 17–19.

Daday, E. Microscopische Süsswassertiere der Umgebung des Balaton. – Zool. Jahrb. Syst., Vol. 19:37–98. 1903. Plates 5–6.

Daday, E. Microscopische Süsswassertiere aus Kleinasien. – Sitzb. Kais. Ak. Wien. 29. 1903.

Zynov, V. P. Materialy po faune Volgi i gidrofaune Saratovskoi gubernii (Data on the Fauna of the Volga and on the Hydrofauna of Saratov Province). – Bull. Soc. Imp. Nat. Moscou, Vol. 17:1–148, (Nematodes, p. 57). 1903. 2 plates.

Rouville, E. Révision des Nématodes libres de la région de Cette. – C. R. Acad. Sci., Vol. 137–1002–1003. 1903. (Preliminary note to the following work.)

Rouville, E. Révision des Nématodes libres marins de la région de Cette. – C. R. Ass. Franc. pour l'avancement des Sciences, pp. 788–797. 1904.

Jägerskiöld, L. A. Zum Bau des Hypodontolaimus inaequalis Bast., einer eigentümlichen Meeresnematode. – Zool. Anz., Vol. 27:417–421. 1904.

Cobb, N. A. Free-Living Freshwater New Zealand Nematodes. – Proc. Cambridge Philos. Soc., Vol. 12:363–374. 1904.

Zur Strassen, O. L. Anthraconema, eine neue Gattung freilebender Nematoden. – Zool. Jahrb. Suppl., Vol. 7:301–346. 1904. Plates 14–15.

De Man, J. G. Ein neuer freilebender Rundwurm aus Patagonien – Plectus (Plectoides) patagonicus n. sp. – Ber. Senck. Naturf. Ges., Frankfurth, pp. 41–45. 1904. 6 figs.

De Man, J. G. Nématodes libres. Résultats du voyage "Belgica."– Rapp. scientif. Zool. 1904. 51 pp. 11 tt.

Daday, E. Mikroskopische Süsswassertiere aus Turkestan. – Zool. Jahrb. Syst., Vol. 19:469–553. 1904. Plates 27–30. 5 figs.

Daday, E. Untersuchungen über die Süsswasser-Mikrofauna Paraguays. – Zoologica, No. 44. 1905. 374 pp. 23 plates.

Jägerskiöld, L. A. Bunonema richtersi n. g., n. sp. Ein eigentümlicher neuer Landnematode aus dem Schwarzwald, von Kerguelen und Possession-Island (Crozet-Inseln). – Zool. Anz., Vol. 28:557–561. 1905.

Richters, F. Bunonema richtersi und B. reticulatum. – Verh. D. Zool. Ges., Vol. 15:46–47. 1905.

Stiles, Ch. W. and A. Hassal. The Determination of Roundworm Genera, with their Original and Type Species. – Bull. No. 79, Bureau of Animal Industry, U. S. Dept. Agric. 1905. 150 pp.

Retzius, G. Zur Kenntnis der Hautschicht der Nematoden. – Biol. Unters. (2) 13:101–106. 1906. figs. a–f.

Stewart, F. H. The Anatomy of Oncholaimus vulgaris Bast. with Notes on Two Parasitic Nematodes. – Quart. Journ. Micr. Sci., Vol. 50:101–150. 1906. Plates 7–9.

*[Murray. Some Interesting Nematodes in the Forth Area. – Ann. Scott. Nat. Hist., p. 164. 1906.]

Plotnikov, V. K faune chervei presnykh vod okrestnostei Bologovskoi biologicheskoi stantsii (On the Fauna of Helminths of Fresh Waters in the Vicinity of Bologov Biological Station). – Trudy Presnovskoi Biologicheskoi Stantsii Imperatorskogo Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Vol. 2:30-41. 1906. Plate 2.

Schneider, G. Zur Kenntnis der frei im Finnischen Meerbusen vorkommenden Nematoden. – Zool. Anz., Vol. 29-625-627. 1906. (Preliminary Note to the Following Paper.).

Schneider, G. Beitrag zur Kenntnis der im Uferschlamm des Finnischen Meerbusens freilebenden Nematoden. – Acta Soc., Fauna Flora Fennica, Vol. 27, No. 7. 1906. 42 pp. 1 plate.

Schneider, G. Süsswassernematoden aus Estland. – Zool. Anz., Vol. 29:679–683. 1906. 5 figs.

Cobb, N. A. Fungus Maladies of Sugar Cane. – IX. Free-Living Nematodes Inhabiting the Soil about the Roots of Cane and their Relation to Root-Diseases. Report of the Work of the Experiment Station of the Hawaiian Sugar Planter's Association. – Divis. Pathol. Physiol. Bull., No. 5: 163–195. 1906.

Daday, E. Zwei bathybische Nematoden aus dem Vierwaldstädter See. – Zool. Anz., Vol. 30:413–415. 1906. 5 figs.

Daday, E. Édesvízi Mikroskopi Allatok Mongoliából. – Math. termész. Értesitö, Vol. 24:34–77. 1906. (German Translation see under 1908.).

[Schorler, B. and J. Thallwitz. Pflanzen und Tierwelt des Moritzburger Grossteiches bei Dresden. – Ann. biol. lac. I, pp. 193–310. 1906.]

Marcinowski, Kati. Zur Biologie und Morphologie von Cephalobus elongatus de Man und Rhabditis brevispina Claus, nebst Bemerkungen über einige andere Nematodenarten. – Arb. Kais. biol. Anst., Berlin, Vol. 5:216–236. 1906. 9 figs. (There are many short notes in this work which are not included in this list.)

Linstow, von O. Neue und bekannte Helminthen. – Zool. Jahrb. Syst., Vol. 24:1–20. 1906. Plate 1.

Linstow, von O. Nematoda. – Nat. Antarct. Exp. 1901–1904. Nat Hist., Vol. 3:1–4. 1906. 1 plate.

[Linstow, von O. Nematodes of the Scottish National Expedition 1902–1904. – Proc. R. Soc., Edinburgh, Vol. 26:464–472. 1907.]

Linstow, von O. The Fauna of Brackish Ponds at Port Cunning, Lower Bengal, Pt. 2, A New Nematode of the Genus Oncholaimus. – Rec. Indian Mus., Calcutta, Vol. 1:45–46. 1907. 2 figs.

Linstow, von O. Nematoden aus dem zoologischen Museum zu Berlin. – Mitt. Zool. Mus., Berlin, Vol. 3:251–259. 1907. Plates 6–7.

Rauther, Max. Über den Bau des Ösophagus und die Lokalisation der Nierenfunktion bei freilebenden Nematoden. (Zweite Studie über die Organisation der Nematoden). – Zool. Jahrb. Anat., Vol. 23:703–740. 1907. Plate 38, 7 figs.

[Le Roux, M. Recherches biologiques sur le lac d'Annecy. – Ann. biol. lac., Vol. 2:220:387. 1907. (Nematodes, pp. 267, 369.)]

De Man, J. G. Sur quelques espèces nouvelles ou peu connues de Nématodes libres vivant sur les côtes de la Zélande. – Tijd. Nederl. Dierk. Ver. (2) 10:227–244. 1907. (Preliminary note to the following paper.)

De Man, J. G. Sur quelques espèces nouvelles ou peu connues de Nématodes libres habitant les côtes de la Zélande. – Mém. Soc. Zool. France, Vol. 20:33–90. 1907. Tt. 1–4.

De Man, J. G. Observations sur quelques espèces de Nématodes terrestres libres de l'ile de Walcheren. – Ann. Soc. R. Zod. Malacol., Belgique, Vol. 41–156–174. 1907. 17 figs.

De Man, J. G. Contribution à la connaissance des Nématodes libres de la Seine et des environs de Paris. – Ann. biol. lac., Vol. 2:9–29. 1907. Tt. 1–3.

Schepotieff, A. Zur Systematik der Nematoiden. – Zool. Anz., Vol. 31:132–161. 1907.

Schepotieff, A. Die Desmoscoleciden. – Zeitschr. wiss. Zool., Vol. 90:179–204. 1908. Plates 8–10.

Schepotieff, A. Trichoderma oxycaudatum Greef. – Zool. Jahrb. Syst., Vol. 26:386–392. 1908. Plate 25.

Schepotieff, A. Rhabdogaster cygnoides Metschn. – Ibid., Vol. 26-393–400. 1908. Plate 26.

Schepotieff, A. Die Chaetosomatiden. – Ibid., Vol. 26:401–414. 1908. Plates 27–28.

Shchepot'ev, A. O nematodakh i blizkikh k nim gruppakh (On Nematodes and Related Groups). – Sankt-Peterburg. 1908. 91 pp. 13 plates. (Shortened edition of the preceding papers.)

[Heinis, F. Beitrag zur Kenntnis der Moosfauna der Kanarischen Inseln. – Zool. Anz., Vol. 33:711. 1908.]

Jägerskiöld, L. A. Ein neuer Nematode, Dorylaimus crassoides, aus dem Thuner See in der Schweiz. – Zool. Anz., Vol. 33:673–677. 1908.

Linstow, von O. Helminthes, Nematoden und Acanthocephalen in L. Schulze. – Zool. u. anthrop. Ergebn. einer Forschungsreise in Südafrika, Bd. I, Lfg. 4, Denkschr. med. – naturwiss Ges., Jena, Vol. 13: 19–28. 1908. 1 plate.

De Man, J. G. Plectus sp. (in Richters: Beitrag etc.). – Zool. Jahrb. Syst., Vol. 26:199–202. 1908. 4 figs.

[De Man, J. G. Note on a Free-Living Nematode from Rhamtso Lake, Tibet. – Rec. Indian Mus., Calcutta, Vol. 2:314–315. 1908.]

Richters, F. Moosfauna-Studien. – Ber. Senck. Ges., Frankfurt, pp. 14–30. 1908. Plates 1–2.

Richters, F. Die Fauna der Moosrasen des Gaussberges und einiger südlicher Inseln. – D. Südpolar Exp. 1901–1903, Bd. 9 (Zool., Bd.1) : 272–312. 1908. 4 plates.

Schneider, Guido. Der Obersee bei Reval. – Arch. Biontol., Berlin, Vol. 2:1–192. 1908.

Marcinowski, Kati. Zur Kenntnis von Aphelenchus ormerodis Ritzema Bos. – Arb. Kais. Biol. Anst., Vol. 6:407–444. 1908.

Marcinowski, Kati. Parasitisch und semiparasitisch an Pflanzen lebende Nematoden. – Arb. Kais. Biol. Anst., Vol. 6:1–192. 1908. 1 plate. 76 figs. (A large agricultural literature not listed above in this paper.)

Daday, E. Beiträge zur Kenntniss der Mikrofauna des Kossogolbeckens in der nordwestlichen Mongolei. – Math. naturwiss. Ber. Ungarn., Vol. 26:274–360. 1908.

[Daday, E. Beiträge zur Kenntnis der Fauna Turkestans auf Grund des von D. D. Pedashchenko gesammelten Materials (1904–1906). V. – Ostracoden und Plankton der Seen Issyk-Kul und Tschatyr-Kul. Trudy Imperatorskogo Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Zool., Vol. 39:1–58. 1909. 1 plate. 8 figs. (Nematodes pp. 6, 36.)]

Faber, von F. C. Die Krankheiten und Schädlinge des Kaffees. II. Centralbl. Bakt. (2) 23. 1909.

Horn, P. Beitrag zur Kenntnis der Moos bewohnenden Tylenchus-Arten. – Arch. Ver. Freunde Naturgesch. Mecklenburg, Vol. 63:67–77. 1909. Plate 11.

Jägerskiöld, L. A. Freilebende Süsswassernematoden. – Süsswasserfauna Deutschlands, Heft. 15:1–15. 1909. (A very convenient compilation.)

Linstow, von O. Parasitische Nematoden. –Ibid., pp. 47–83. 1909. (Description of a semiparasitic species of Rhabditis.)

Molz, E. Über Aphelenchus olesistus Ritzema Bos und die durch ihn hervorgerufene Aelchenkrankheit des Chrysanthemum. – Centralbl. Bakt. (2) 23:656–641 [sic]. 1909. 1 plate.

Rauther, Max. Morphologie und Verwandschaftsbeziehungen der Nematoden. – Erg. Fortschr. Zool., Vol. 1:491–596. 1909.

Southern, R. On the Anatomy and Life History of Rhabditis brassicae n. sp. – J. econ. Biol. Lond., Vol. 4:91–95. 1909. Plate 8.

Cobb, N. A. Fungus Maladies of the Sugar Cane, VIII. – Nematodes. Report of Work of the Experiment Station of the Hawaiian Sugar Planter's Association. – Divis. Pathol. Physiol. Bull., No. 6: 51–73. 1909.

De Man, J. G. Beiträge zur Kenntnis der in dem weissen Schleimfluss der Eichen lebenden Anguilluliden, nebst Untersuchungen über den Bau des Essigälchens und der Gattung Anguillula Ehrb. – Zool. Jahrb. Syst., Vol. 29:359–394. 1910. Plates 14–16.

Potts, F. A. Notes on the Free-Living Nematodes. – Quart. Journ. Microsc. Sci., Vol. 55:433–484. 1910. 11 figs.

[Vaňha, I. I. Die Kräusel- oder Rollkrankheit der Kartoffel, ihre Ursache und Bekämpfung. – Landw. Monatshefte. Wien, Vol. 3:268–276. 1910.]

Daday, E. Untersuchungen über die Süsswasser-Mikrofauna Deutsch-Ostafrikas. – Zoologica, No. 59. 1910. 314 pp. 18 plates.

[Daday, E. Beiträge zur Kenntnis der Mikrofauna des Nils. – Sitzber. Akad. Wiss., Wien, Math. Naturw. Kl., Vol. 119:537–589. 1910. 3 plates.

Daday, E. Freilebende Süsswasser-Nemathelminthen aus der Schweiz. – Revue Suisse Zool., Vol. 19:501–536. 1911. Plates 15–17.

[Richters, F. Faune des mousses. Tardigrades. In: Duc d'Orléans Compagne arctique. 1907. 1911. 8 pp. 2tt.]

[Micoletzky, H. Zur Kenntnis des Faistenauer Hintersees bei Salzburg mit besonderer Berücksichtigung faunistischer und fischereilicher Verhältnisse. – Int. Revue ges. Hydr., Vol. 3:506–542. 1911. Plates 5–8. (Nematodes, p. 520).]

Ditlevsen, H. Danish Free-Living Nematodes. – Vidensk. Meddelser naturh. Fören Kjöbenhavn, Vol. 63:212–256. 1911. Plates 2–5.

Grochmalicki, J. Trilobus lomnickii n. sp. nowy gatunek nicienia z Siwey Wody (Trilobus lomnickii n. sp., eine neue Nematoden-Art aus der Siwa-Woda), Kosmos Lwow, Vol. 36: 372–376. 1911.

Schwartz, M. Die Aphelenchen der Veilchengallen und der Blattflecken an Farnen und Chrysanthemum. – Arb. Kais. Biol. Anst., Vol. 8:303–334. 1911. 20 figs.

[Schwartz, M. Zur Bekämpfung der Rübennematoden in den Schlammteichen der Zuckerrübenfabriken. – Arb. Kais. Biol. Anst., Vol. 8:335–341. 1911.]

Schwartz, M. Nematodenuntersuchungen. – Mitt. Kais. Biol. Anst., No. 12:5–6. 1912.

De Man, J. G. Odontopharynx longicaudata n. g., n. sp. Eine neue Form von Anguilluliden. – Zool. Jahrb. Syst., Vol. 33:637–642. 1912a. Plate 18.

De Man, J. G. Helminthologische Beiträge. – Zool. Jahrb. Suppl. 15, Bd. 1:439–461. 1912b. Plates 22–23.

Menzel, Rich. Über freilebende Nematoden aus der Umgebung von Triest. – Revue Suisse Zool., Vol. 20:535–542. 1912. 2 figs.

Saweljew, S. Zur Kenntnis der freilebenden Nematoden des Kolafjords und des Relictensee Mogilnoje. – Trav. Soc. Imp. Nat., St.-Petersbourg, 43, Comptes rendus, pp. 108–126. 1912.

Filip'ev, I. K voprosu o stroenii nervnoi sistemy u svobodnozhivushchikh nematod (On the Structure of the Nervous System in Free-Living Nematodes). – Trudy Imperatorskogo Sankt-Peterburskogo Obshchestva Estestvoispytatelei, Vol. 43:205–215. 1912. 8 figs.

Krüger, Eva. Die phyletische Entwicklung der Keimzellenbildung einer freilebenden Rhabditis. – Zool. Anz., Vol. 40:233–237. 1912. (Preliminary Note to the Following Paper).

Krüger, Eva. Fortpflanzung und Keimzellenbildung von Rhabditis aberrans, nov. sp. – Zeitschr. f. wiss. Zool., Vol. 105:87–124. 1913. Plates 3–6.

Cobb, N. A. Further Notes on Tricoma. – J. Wash. Acad. Sci., Vol. 2:480–484. 1912. 2 figs.

Cobb, N. A. New Nematode Genera Found Inhabiting Fresh Waters and Nonbrackish Soils. – Ibid., Vol. 3:432–444. 1913. i fig.

Cobb, N. A. Draconema, a Remarkable Genus of Marine Free-Living Nematodes. – Ibid., 3. 1913.

*Cobb, N. A. Notes on Mononchus and Tylenchulus. – Ibid., Vol. 3:288. 1913.

Ditlevsen, Hj. A. Marine Dorylaimus from Greenland Waters. – Dorylaimus maritimus n. sp. – Meddleser om Grönland., Vol. 43:429–430. 1913. Plate 18. (Danmark Ekspeditionen til Grönlands Nordostkyst, Bd. 3, No. 15. 1906–1908.) 1913.

[Hewitt, T. R. A Few Species of Nematoda from Co. Dublin. – Irish Naturalist, Vol. 22:147–151. 1913.]

Hofmänner, B. Beiträge zur Kenntnis der freilebenden Nematoden. – Zool. Anz., Vol. 42:413–418. 1913. 4 figs.

Hofmänner, B. Contribution à l'étude des Nématodes libres du lac Léman. – Revue Suisse Zool., 21 (16): 589–658. 1913. Tt. 15–16.

Johnson, G. E. On the Nematodes of the Common Earthworm. – Quart. Journ. Microsc. Sci., Vol. 58:605–652. 1913. 1 plate. 2 figs.

[Zernov, S. A. K voprosu ob izuchenii zhizni Chernogo morya (On the Problem of Studying the Life in the Black Sea). – Zapiski Imperatorskoi Akademii Nauk, Fiziko-Matematicheskii Otdel (8) 32, No. 1. 1913. 299 pp. 7 figs. 8 plates. 2 maps.]

De Man, J. G. Anguillula silusiae n. sp., eine neue, in den sogenannten "Bierfilzen" lebende Art der Gattung Anguillula Ehrb. – Centralbl. Bakt. (2) 39:74. 1913.

Menzel, Rich. Mononchus zschokkei n. sp. und einige wenig bekannte, für die Schweiz neue freilebende Nematoden. – Zool. Anz., Vol. 42:408–413. 1913.

Steiner, G. Ein Beitrag zur Kenntnis der Tierwelt des Zürichersees (Monohystera dubia Bütschli und Ethmolaimus revaliensis Schneider). – Arch. Hydrobiol. Planktonk., Vol. 8: 451–457. 1913. 5 figs.

Zograf, N. Bunonema bogdanovi. – Zool. Anz., Vol. 41:162–164. 1913. 6 figs.

Micoletzky, H. Die freilebenden Nematoden der Ostalpen, 1. Teil, d. vorläuf. – Mitt. Stzber. Akad. Wiss, Wien, Abt. 1, Vol. 122: 111–112, 2. Teil, Ibid., pp. 1913.

Micoletzky, H. Die freilebenden Süsswasser-Nematoden der Ost-Alpen mit besonderer Berücksichtigung des Lunzer-Seengebietes. – Zool. Jahrb. Syst., Vol. 36:331–546. 1914. Plates 9–19. 1 map.

Micoletzky, H. Oekologie alpiner Süsswasser-Nematoden mit besonderer Berücksichtigung des Lunzer Seengebietes. – Verh. Ges. deutsch. Naturf. u Ärzte, 85, Vers., Th. 2, H. 1:692–695. 1914.

Micoletzky, H. Ökologie ostalpiner Süsswasser-Nematoden. – Intern. Revue Hydrobiol., Hydrogr. 1914. 12 pp.

Brakenhoff, H. Beitrag zur Kenntnis der Nematodenfauna des nordwestdeutschen Flachlandes. – Abh. naturwiss. Ver. Bremen, Vol. 22: 267–311. 1914. Plates 1–3.

Stefanski, W. Deux espèces nouvelles de Bunonema, Nématode à segment céphalique. – Zool. Anz., Vol. 43:461–483. 1914. 3 figs.

Stefanski, W. Recherches sur la faune des Nématodes libres du bassin du Léman. Thèse de l'Université, Genève. 1914. 72 pp. 2 tt.

Steiner, Dr. G. Freilebende Nematoden aus der Schweiz. 1. Teil, einer vorläufigen Mitteilung. – Arch. Hydrobiol. Planktonk., Vol. 9:259–276. 1914. 29 figs; 2. Teil. – Ibid., pp. 420–438. 1914. 38 figs.

Menzel, R. Über die mikroskopische Landfauna der schweizerischen Hochalpen. – Arch. Naturg. Jg. 1914, Abt. A, Heft. 3:31–91. 1914.

Berliner, E. and K. Busch. Über die Züchtung des Rübennematoden (Heterodera schachti Schmidt) auf Agar. – Biol. Centralbl., Vol. 34:349–356. 1914. 1 plate.

*Daday, E. Voyage d'exploration scientifique en Colombie. Freilebende Nematoden. – Mém. Soc. Neuchâteloise Sci. Nat., Vol. 5:664–668. 1914.

Turner, Ch. The Microscopy of the Manchester Water Supply. – Trans. Manchester Microsc. Soc. 1913, pp. 44–58. 1914. 1 plate.

Cobb, N. A. Antarctic Free-Living Nematodes of the Shackleton Expedition. Contributions to a Science of Nematology I., Baltimore. 1914. 33 pp. 50 figs.

Cobb, N. A. Rhabditin. Contribution to a Science of Nematology II. – J. Parasitol., Vol. 1:40–41. 1914. 1 plate.

Cobb, N. A. The North American Free-Living Fresh Water Nematodes. Contribution etc. II. – Trans. Am. Microsc. Soc., Vol. 33:69–119. 1914. Plates 2–8.

Cobb, N. A. Citrus-Root Nematode. – J. Agric. Research, Vol. 2:217–230. 1914. 13 figs.

*[Wagner. Das Vorkommen von Aelchen in einem Hopfengarten in Pörnbach. – Prakt. Blätter Pflanzenbau u. Pflanzenschutz, Vol. 12:67–68. 1914. 1 fig.

Southern, R. Nematelmia, Kinorhyncha, Chaetognatha. Clare Island Survey. – Proc. R. Irish Acad., Vol. 31, Part 54. 1914. 79 pp. 12 plates.

*Stewart, F. H. Report on a Collection of Free-Living Nematodes from the Chilka Lake on the East Coast of India. – Rec. Ind. Mus., Calcutta, Vol. 10:245–254. 1914. Plates 30–32.

*[Heinis, Fr. Die Moosfauna Columbiens. – Mém. Soc. Neuchâteloise Sci. Nat., Nos. 5–2:675–730. 1914. 47 figs.

*[Melchers, L. E. Heterodera radicicola Attacking the Canada Thistle. – Science, N. S., Vol. 40:241. 1914.

Hofmänner, B. and R. Menzel. Neue Arten freilebender Nematoden aus der Schweiz. – Zool. Anz., Vol. 44:80–91. 1914.

Hofmänner, B. Die freilebenden Nematoden der Schweiz. – Revue Suisse Zool., 23 (5):109–244. 1915. Plates 4–6. (This is a summary of the entire Swiss literature on the hydrobiology of free-living Nematodes. This is the reason that it is omitted above.)

*Leiper, R. T. and R. W. Atkinson. Parasitic Worms, with a Note on a Free-Living Nematode. – British Museum (Nat. Hist.) British Antarctic (Terra Nova) Exp. 1910, Zool., Vol. 2:19–60. 1915. 11 figs. 5 plates.

*Osterwalder, A. Durch das Blatt- und Stengelälchen, Aphelenchus ormerodis Ritz. Bos. und Tylenchus dipsaci Kühn, verursachte Krankheiten an Zierpflanzen. – Landw. Jahrbuch d. Schweiz, pp. 520–522. 1915. (Abstr. Review Applied Entom., 4 A, p. 136.)

Micoletzky, H. Freilebende Süsswasser-Nematoden der Ost-Alpen. Nachtrag. Die Nematodenfauna des Grundl- Hallstätter- Ossiacher- und Millstätter-Sees. – Zool. Jahrb. Syst., Vol. 38: 245–274. 1915. 1 plate.

Micoletzky, H. Süsswasser-Nematoden aus Südafrika. – Denkschr. Kais. Ak. Wiss. Wien. Math. Naturw. Kl., Vol. 92:149–171. 1915. Plates 1–4.

Fuchs, G. Die Naturgeschichte der Nematoden und einiger Parasiten: 1) des Ips typographus L. and 2) des Hylobius abietis L. – Zool. Jahrb. Syst., Vol. 38:108–222. 1915. Plates 17–21. 2 figs.

Fuchs, G. Tylenchus dispar curvidentis n. sp. und Tylenchus dispar cryphali n. sp. – Zool. Anz., Vol. 45:195. 1915.

Stefanski, W. Nouvelles espèces de Nématodes provenant de la Pologne. – Zool. Anz., Vol. 45:346–349. 1915. 6 figs.

Baylis, H. A. Two New Species of Monhystera Inhabiting the Gillchambers of Land-Crabs. – Ann. Mag. Nat. Hist., (8) 16: 414–421. 1915. 6 figs.

*Maupas, E. Un nouveau Rhabditis. – Bull. Soc. Hist. Nat. Afrique du Nord, Vol. 7:51–52. 1915.

*Maupas, E. Sur un champignon parasite des Ryabditis. – Ibid., Vol. 7: 34–49. 1915. 13 figs.

*Trabut. Un Nématode (Tylenchus semipenetrans Cobb), sur les racines des Citrus. – Ibid., Vol. 7:118–119. 1915. 2 figs.

Steiner, G. Freilebende marine Nematoden von der Ostküste Sumatras. – Zool. Jahrb. Syst., Vol. 38:223–244. 1915. 3 plates.

Cobb, N. A. Tylenchus similis, the Cause of a Root-Disease of Sugar Cane and Banana. – J. Agric. Research, Vol. 4:561–568. 1915. 2 figs.

Cobb, N. A. Nematodes and their Relationships. – Yearbook U. S. Dept. Agric. 1914, pp. 457–490. 1915. 20 figs.

*Cobb, N. A. (Free-Living Nematodes from Douglas Lake, Mich.). – Trans. Am. microsc. Soc., Vol. 34:21–47. 1915. (Quoted after J. microsc. Soc.)

*Cobb, N. A. The Asymmetry of the Nematode Bunonema inaequale n. sp. Contribution etc. III. 1915.

Cobb, N. A. (On Parthenogenesis). – J. Parasitol., Vol. 2:95. 1915.

Cobb, N. A. (The Mechanism of the Spinneret of a Free-Living Nematode). – Ibid., p. 95. 1915.

Cobb, N. A. Notes on New Genera and Species of Nematodes. – Ibid., Vol. 2:195–196. 1916.

Cobb, N. A. Notes on Filter-Bed Nematodes. – Ibid., pp. 198–200. 1916.

Steiner, G. Beiträge zur geographischen Verbreitung freilebender Nematoden. – Zool. Anz., Vol. 46:311–347. 1916. 11 figs.

Steiner, G. Freilebende Nematoden von Novaja Zemlja. – Zool. Anz., Vol. 47:50–74. 1916. 8 figs.

Steiner, G. Das Männchen des Dorylaimus lugdunensis de Man. – Zool. Anz., Vol. 47:99–100. 1916. 1 fig.

Steiner, G. Neue und wenig bekannte Nematoden von der Westküste Afrikas. – Zool. Anz., Vol. 47:322–350. 1916. 22 figs.

Steiner, G. Freilebende Nematoden aus der Barentssee. – Zool. Jahrb. Syst., Vol. 39: 511–576. 1916. Plates 16–36.

*Steiner, G. Nematodes. – Beiträge zur Kenntnis der Land- und Süsswasserfauna D. S. W. Afrikas herausg. v. Michelsen. 1916.

Stefanski, W. Die freilebenden Nematoden des Inn, ihre Verbreitung und Systematik. – Zool. Anz., Vol. 46:363–384. 1916. 4 figs. 1 Kartenskizze.

Merrill, I. H. and A. L. Ford. Life, History and Habits of Two New Nematodes Parasitic on Insects. – J. Agrc. Research, Vol. 6: 115–127. 1916. 3 figs.

Filip'ev, I. N. Svobodnodvizhushchiya nematody kollektsii Zoologicheskogo Muzeya Imperatorskoi Akademii Nauk (Free-Living Nematodes of the Collection of Zoological Museum of the Imperial Academy of Sciences). – Ezhegodnik Zoologicheskogo Muzeya I. A. N., Vol. 21: 59–116. 1916. Plates 4, 5.

Filip'ev, I. N. Novaya svobodnaya nematoda iz Kaspiiskogo morya Chromadorissa gen. nov. (Chromadoridae, Chromadorini) (A New Free-Living Nematode from the Caspian Sea Chromadorissa gen. nov. (Chromadoridae, Chromadorini)). – Russkii Zoologicheskii Zhurnal, pp. 24–29. 1917. fig. Filipjev, I. Un Nématode libre nouveau de la mer Caspienne, pp. 29–30.

Schneider, G. K poznaniyu fauny svobodno zhivushchikh kruglikh chervei Finlyandii. – Russkii Zoologicheskii Zhurnal, Vol. 2:40–43. 1917.

Schneider, G. Quaedam ad cognitionen nematodarum Finlandiae liberarum, pp. 44–45.

Stefanski, W. Contribution à l'étude de l'excrétion chez les Nématodes libres. – Biol. Centralbl., Vol. 37:294–311. 1917.

Stefanski, W. Sur les races de Trilobus gracilis Bast. – Revue Suisse Zool., Vol. 25:163–168. 1917.

Micoletzky, H. Freilebende Süsswasser-Nematoden der Bukowina. – Zool. Jahrb. Syst., Vol. 40:441–586. 1917. Plates 19–22.

Steiner, G. Über die Verwandtschaftsverhältnisse und die systematische Stellung der Mermithidae. – Zool. Anz., Vol. 48:263–267. 1917.

*Steiner, G. Über das Verhältnis der marinen freilebenden Nematoden zu denen des Süsswassers und des Landes. – Biol. Centralbl., Vol. 37. 1917.

Menzel, R. Zur Kenntnis der freilebenden Nematodengattung Hoplolaimus Daday. – Revue Suisse Zool., Vol. 25:154–162. 1917.
*Cobb, N. A. Tylenchus penetrans. New Parasitic Nema Found Infesting Cotton and Potatoes. – J. Agric. Research, Vol. 11. 1917, No. 1:27–33. 1917.

The bibliography purports to be complete until 1914 but many short faunistic or agricultural notes may have been overlooked. The years 1915 and 1916 are more or less complete, but I did not see the "Zoological Record" for these years, and some publications in these years may have been overlooked. The year 1917 is obviously not complete. No data from 1918 onward is included, as it is only fragmentary.

---

## LEGENDS TO TABLES

Table 1.

### 1. Leptosomatum bacillatum (Eberth, 1863).

| | |
|---|---|
| Figure 1a | Cephalic end of female; obj. $^1/_{16}$, oc, 1; a – widening of esophageal tube; c. ceph. – cephalic capsule; gl. oes. d. – dorsal esophageal gland (incompletely shaded); or. gl. oes. d. – opening of this gland; or. gl. oes. v. – opening of ventral esophageal gland; p. subceph. – papillae between anterior end and eye. |
| Figure 1b. | Cephalic end of male; obj. $^1/_{16}$, oc. 1; gl. oes. – esophageal gland. |
| Figure 1c. | Tail of female; obj. 7, oc. 1. |
| Figure 1d. | Spicules; obj. $^1/_{16}$, oc. 1; a – thickening in middle of posterior part of spicule. |

### 2. Leptosomatum punctatum (Eberth, 1863).

| | |
|---|---|
| Figure 2a | Anterior end of male; obj. $^1/_{16}$, oc. 1; pōckets at angles of esophageal lumen; p. lab. – labial papillae. |
| Figure 2b. | Posterior end of male; obj. 3, oc. 5. |
| Figure 2c. | Posterior tip under high magnification; obj. $^1/_{16}$, oc. 1; a – plug closing porus caudalis, to which glands are attached; b – space between two layers of cuticle. |
| Figure 2d | Spicules; obj. $^1/_{16}$, oc. 1; gub. – gubernaculum; x – part of unknown function, probably in intestine. |

### 3. Leptosomatides euxina n. g., n. sp.

| | |
|---|---|
| Figure 3a. | Anterior end of male; obj. $^1/_{16}$, oc. $\gamma$ 0; set. – lateral bristles between anterior end and eye. |
| Figure 3b. | The same under higher magnification; obj. $^1/_{16}$, oc. 3; p. lab. – labial papillae; vest. – vestibule. Parts of cephalic capsule: a – anterior vault; b – dorsal process; c – lateral subcuticular parts; d – depression on ventral ridges of esophagus. |
| Figure 3c. | Eye, obj. $^1/_{16}$, oc. 1. |
| Figure 3d. | Posterior end of male; obj. 3, oc. 5; a – posterior subventral row of usual bristles; b – anterior subventral row of modified bristles; org. acc. – accessory organ. |
| Figure 3e. | Spicular apparatus from left side; obj. 7, oc. 3; a – manubrium of spicules; b – lateral flanges in its middle; c – end of spicule with two irregular tubercles, clasped by middle of gubernaculum; d – capitellum of gubernaculum (only the left capitellum drawn); e – terminal widening of gubernaculum. |
| Figure 3f. | Spicules from ventral side; obj. 7, oc. 1; the spicules are different; e – terminal widening of gubernaculum. |

### 4. Phanoderma tuberculatum (Eberth, 1863).

| | |
|---|---|
| Figure 4a. | Cephalic end of female; obj. $^1/_{16}$, oc. 1; the specimen from which the drawing was made was slightly curved, the body should therefore be wider posteriorly; a – longitudinal striation in posterior part of cephalic capsule. |

| | |
|---|---|
| Figure 4b. | Posterior end of male; obj. 7, oc. 1. |
| Figure 4c. | Accessory organ of male; obj. 7, oc. 3; a – outline of its sheath. |

### 5. Phanoderma albidum Bastian, 1865.

| | |
|---|---|
| Figure 5a. | Anterior end of female; obj. $^1/_{16}$, oc. 1; gl. excr. – excretory gland. |
| Figure 5b | Same, ventral view; obj. $^1/_{16}$, oc. 3; p. lab – labial papillae; gl. oes. – reservoir of esophageal gland. |
| Figure 5c. | Same, dorsal view; a – cuticular bodies at base of dorsal tooth. |
| Figure 5d. | Same, lateral view; a – thickening of cephalic capsule on ventral side, extending also laterally. |
| Figure 5e. | Tail of female; obj. 3, oc. 5. |

Table 2.

### 6. Anticoma pontica n. sp.

| | |
|---|---|
| Figure 6a. | Anterior end with esophagus not compressed; obj. $^1/_{16}$, oc. 3; por. excr. – porus excretorius; gl. oes. – esophageal glands; s. cerv. – cervical bristles. |
| Figure 6b. | Same, but esophagus compressed. |
| Figure 6c. | Tail of female; obj. 7, oc. 0. |
| Figure 6d. | Tail of male, same magnification. |
| Figure 6e. | Spicules; obj. $^1/_{16}$, oc. 1. |

### 7. Anoplostoma vivipara (Bastian, 1865).

| | |
|---|---|
| Figure 7a. | Anterior end of female; obj. $^1/_{16}$, oc. 3. |
| Figure 7b. | Tail of female; obj. $^1/_{16}$, oc. 0 |

### 8. Oxystomina clavicauda n. sp.

| | |
|---|---|
| Figure 8a. | Anterior end of female; obj. $^1/_{16}$, oc. 1. |
| Figure 8b. | Same, higher magnification; obj. $^1/_{16}$, oc. 5. |
| Figure 8c. | Posterior end of male; obj. 7, oc. 1; s – special supplementary bristles. |
| Figure 8d. | Spicules; obj. $^1/_{16}$, oc. 1. |
| Figure 8e. | Bristles (s – Figure 8c); obj. $^1/_{16}$, oc. 3. |

597

### 9. Oxystomina filiformis n. sp.

| | |
|---|---|
| Figure 9a. | Anterior end of male; obj. $^1/_{16}$, oc. 3; cel. – special large cells in body cavity, displaced towards esophagus – oes. |
| Figure 9b. | Tail of female; obj. $^1/_{16}$, oc. 1. |
| Figure 9c. | Tail of male, obj. $^1/_{16}$, oc. 3. |
| Figure 9d. | Spicules, obj. $^1/_{16}$, oc. 3. |

### 10. Enoplus euxinus n. sp.

| | |
|---|---|
| Figure 10a. | Head of female, obj. 7, oc. 3; lab. – lips; p. lab. – labial papillae; c. ceph. – capsule, shown here as a ring surrounding the jaws – mand; fiss. ceph. – cephalic slit; l. ceph. – cephalic line; oc. – pigment spot – eye. |
| Figure 10b. | Tail of female; obj. 3, oc. 5. |
| Figure 10c. | Tail of male; obj. 3, oc. 5; $s_1$ – stout bristles behind anus; $s_2$ – slender bristles between anus and accessory organ; p. – sensory preanal papillae. |
| Figure 10d. | Spicules, lateral view; obj. 7, oc. 1; a – lateral tubular part of gubernaculum; b – its middle plastic part; c – upper processes of tubular part. |
| Figure 10e. | Same, ventral view; obj. 7, oc. 3; legend as for Figure 10d. |
| Figure 10f. | Accessory organ of male; obj. 7, oc. 1. |

### 11. Enoplus littoralis n. sp.

| | |
|---|---|
| Figure 11a. | Head of female; obj. $^1/_{16}$, oc. 1; p. lab. – labial papillae; l. ceph. – cephalic line. |
| Figure 11b. | Tail of female; obj. 7, oc. 0. |
| Figure 11c. | Tail of male; obj. 7, oc. 0. |
| Figure 11d. | Spicules from the right; obj. $^1/_{16}$, oc. 1. |
| Figure 11e. | End of spicules and gubernaculum, ventral view; obj. $^1/_{16}$, oc. 1; a – thickening in middle part of gubernaculum. |

### 12. Enoploides amphioxi n. sp.

| | |
|---|---|
| Figure 12a. | Head from subventral side; superficial structures omitted so as not to obscure the drawing; obj. $^1/_{16}$, oc. 3; s. l. – bristles; lab. – lips; mand. – jaws; c. ceph. – cephalic capsule; a – ridges on internal cuticle of esophagus near base of jaws; b – thick posterior rim of cephalic capsule; c – ganglion on flattened cephalic capsule; d – lateral processes of jaws articulating with cephalic capsule. |
| Figure 12b. | Same, ventral side. Superficial structures omitted; all lateral parts drawn schematically; obj. 7, oc. 3; lab. – lips; c. ceph. – cephalic capsule; mand. – jaws; e – chitinized structure between jaws for attachment of muscles; gl. oes. – end of esophageal gland. |
| Figure 12c. | Base of lateral bristle and lateral organ; obj. $^1/_{16}$, oc. 1. |

598 Table 3.

| | |
|---|---|
| Figure 12d. | Posterior end of male; as complete spicules could not be drawn, because of the high magnification, only their characteristic parts are drawn; obj. 7, oc. 1; gub. – gubernaculum; o. acc. – accessory organ; a – capitellum of spicule; b – middle part of spicule; c – terminal hook; d – claw at base of tail of male. |
| Figure 12e. | Jaw, internal view; obj. $^1/_{16}$, oc. 1; a – terminal hook; d – anlage of tooth – chitinized protuberance at apex of mandibular notch; p. a – anterior lateral process; p. p. – posterior lateral process. |

### 13. Enoploides hirsutus n. sp.

| | |
|---|---|
| Figure 13a. | Anterior end of male; obj. 7, oc. 3; lab. – lips; c. ceph. – internal cephalic capsule; x – points of attachment of muscles to superficial cephalic capsule. Lateral organs not drawn exactly (see text). |
| Figure 13b. | Posterior end of male; obj. 3, oc. 5; org. acc. – accessory organ; s – supplementary bristles. |
| Figure 13c. | End of spicules with gubernaculum; obj. 7, oc. 3. |
| Figure 13d. | End of tail, reservoir at its end visible; obj. $^1/_{16}$, oc. 1. |

### 14. Enoploides brevis n. sp.

| | |
|---|---|
| Figure 14. | Anterior end of female; obj. 7, oc. 1; a – special plates at angles of buccal cavity. |

### 15. Enoploides cirrhatus n. sp.

Figure 15a. Anterior end of male; obj. $^1/_{16}$, oc. 1; gl. oes. – reservoir of esophageal gland, opening on tooth.

Figure 15b. Jaw and tooth; obj. $^1/_{16}$, oc. 1.

Figure 15c. Tail of male; obj. 3, oc. 5.

Figure 15d. Spicules; obj. $^1/_{16}$, oc. 1.

### 16. Enoplolaimus conicus n. sp.

Figure 16a. Anterior end of female; obj. $^1/_{16}$, oc. 1; a – apparatus supporting lip, homologous to jaws of Enoplus; d – tooth; c. ceph. – narrow part of cephalic end (capsule).

Figure 16b. Posterior end of female; obj. 3, oc. 5.

### 17. Enoplolaimus dubius n. sp.

Figure 17. Tail of female; obj. 3, oc. 5.

### 18. Paroncholaimus zernovi n. sp.

Figure 18a. Anterior end of male; obj. 7, oc. 3; lab. – lips; p. lab. – labial papillae; a – space between 599 external and internal layer of cuticle on cephalic end; den. d. – dorsal tooth; gl. oes. – terminal widening of esophageal gland.

Figure 18b. Same, anterior view; obj. 7, oc. 3; p. lab. subd. – subdorsal dental papillae (projection of their sensory bulb); lab. – terminal thin part of lip. o. s. l. – sensory bulb of lateral cephalic bristle; o. l. – lateral organ.

Figure 18c. Lateral cephalic bristle and lateral organ; obj. $^1/_{16}$, oc. 3; s. l. – lateral cephalic bristle; o. s. l. – its sensory organ; a. o. l. – sensory apparatus of lateral organ. Boundaries of epithelial cells and enclosed granules marked.

Figure 18d. Vulva, ventrally; obj. 7, oc. 1.

Figure 18e. Tail of female; obj. 7, oc. 1; cel. – phagocytic cells.

Figure 18f. Tail of male; Zeiss obj. E, oc. 4; $s_1$ – posterior preanal group of bristles; $s_2$ – anterior preanal group of bristles with accessory organ.

Figure 18g. End of tail of male; obj. $^1/_{16}$, oc. 1; a – chitinous ring reinforcing caudal pore; b – central porous cone; c – cavity at end of pore.

Figure 18h. Spicules and gubernaculum laterally; obj. 7, oc. 1; legend as for Figure 18i.

Figure 18i. Spicules and gubernaculum ventral; obj. 7, oc. 1; a – posterior capitellum of gubernaculum; b – lateral processes clasping spicules; c – central ridge; d – process along spicules.

Figure 18k. Spicules laterally; obj. 7, oc. 3; v – velum.

Figure 18m. Posterior preanal group of bristles; obj. $^1/_{16}$, oc. 3.

Figure 18n. Anterior preanal group of bristles with accessory organ; obj. $^1/_{16}$, oc. 3.

### 19. Pelagonema obtusicauda n. sp.

Figure 19a. Anterior end of female; obj. $^1/_{16}$, oc. 1.

Table 4.

Figure 19b. Posterior end of female; obj. 7, oc. 1.

### 20. Viscosia cobbi n. sp.

Figure 20a. Anterior end of male; obj. $^1/_{16}$, oc. 1; lab. – lip, sections of angles of mouth at its margins visible; a. o. l. – sensory apparatus of lateral organ.

Figure 20b. Tail of female; obj. 7, oc. 1.

Figure 20c. Tail of male; obj. 7, oc. 1.

Figure 20d. Anal region of male; obj. $^1/_{16}$, oc. 1; $s_1$, $s_2$, $s_3$ – groups of bristles (see text).

### 21. Viscosia minor n. sp.

Figure 21a. Anterior end of female; obj. $^1/_{16}$, oc. 3.

Figure 21b. Posterior end of female; obj. 7, oc. 1.

600

### 23* Oncholaimus brevicaudatus n. sp.

Figure 23a. Head of male; obj. $^1/_{16}$, oc. 1.

Figure 23b. Tail of female; obj. 7, oc. 3.

Figure 23c. Tail of male; obj. $^1/_{16}$, oc. 1; por. caud. – porus caudalis; s. caud. – caudal bristles; $s_1$ – median of 5 bristles of anal row; $s_2$ – preanal oblique row of large bristles; $s_3$ – preanal median group of smaller bristles, third from anus; $s_4$, $s_5$ – 1st and 2nd preanal median groups of bristles.

### 24. Oncholaimus dujardini de Man, 1878.

Figure 24a. Head of female; obj. $^1/_{16}$, oc. 1.

Figure 24b. Tail of female; obj. $^1/_{16}$, oc. 1; thickening of cuticle at end visible, also long porus caudalis and cone, in which the caudal glands end.

### 25. Oncholaimus campylocercus de Man, 1878.

Figure 25a. Head of female; obj. $^1/_{16}$, oc. 1; d. d. – dorsal tooth, its hooklike form recognizable.

Figure 25b. Tail of female; obj. 7, oc. 1; int. – intestine; o. t. – tubular organ.

Figure 25c. Tail of male; obj. 7, oc. 3; a – preanal bulb (see text); b – preanal papillae; c – thickening of cuticle on tail; $s_1$ – forward-displaced pair of bristles; $s_2$ – 6 pairs of anal, larger bristles; $s_3$ – 3 pairs of postanal smaller bristles.

### 26. Metoncholaimus demani (Zur Strassen, 1894).

Figure 26a. Head of female; obj. $^1/_{16}$, oc. 1; lab. – lips; o. l. – lateral organ; a – round space below anterior surface of head between two layers of cuticle; b – dorsal wall of buccal cavity; c – projection of subventral sector of esophagus; d – process of buccal capsule inside space between two sectors of esophagus.

Figure 26b. Caudal part of female, with posterior part of tubular organ; obj. 3, oc. 5; b – rosette; c – part of anterior sac behind rosette; d – posterior paired canal; e – its opening.

Figure 26c. Posterior part of tubular organ, ventral; obj. 7, oc. 3; cel. – nucleus of cell forming duct of the posterior tube.

Figure 26d. Perianal part of male, ventral; obj. $^1/_{16}$, oc. 1; a – sensory tubercle with papillae in front of an anus; p – 2 postanal papillae; $s_1$ – posterior; $s_2$ – anterior preanal group of bristles; $s_3$ – origin of postanal row of bristles.

Figure 26e. Same, lateral; obj. $^1/_{16}$, oc. 1; $s_1$ – posterior preanal group of bristles; $s_2$ – 2 anterior, short, inconstant pairs; $s_3$ – beginning of postanal row; a – sensory bulb.

---

* [Figure 22 is omitted in the Russian ]

| | |
|---|---|
| Figure 26f. | Sensory bulb (a) in front of anus; obj. $^{1}/_{16}$, oc. 3; $s_1$ — bristles of posterior postanal group. |
| Figure 26g. | Posterior part of male, lateral; obj. 3, oc. 5. |

### 601 27. Metoncholaimus eberthi n. sp.

| | |
|---|---|
| Figure 27a. | Head of female; obj. $^{1}/_{16}$, oc. 1. |
| Figure 27b. | Tail of female; obj. 7, oc. 1. |
| Figure 27c. | Tail of male; obj. 7, oc. 1; pr. sp. — protractor spicularum; a — manubrium of spicule; b — its terminal widening; c — terminal flattening of spicule; gub. — gubernaculum. |
| Figure 27d. | Anal region of male under higher magnification; obj. $^{1}/_{16}$, oc. 3; con. — cone of caudal glands. |

### 28. Enchelidium longicolle n. sp.

| | |
|---|---|
| Figure 28a. | Head dorsal; obj. $^{1}/_{16}$, oc. 1; c. ceph. — cephalic capsule; o. l. — opening of lateral organ; widening of esophageal lumen in front of eyes accidental. |
| Figure 28b. | Head lateral; obj. $^{1}/_{16}$, oc. 1; c. ceph. — cephalic capsule. Inner structure in front of eyes marked approximately. |
| Figure 28c. | Detail of end of spicule; obj. $^{1}/_{16}$, oc. 1; $s_1$ — unpaired large preanal bristle; $s_2$ — paired preanal bristles; gub. — gubernaculum. |

Table 5.

| | |
|---|---|
| Figure 28d. | Tail of male; obj. 7, oc. 1. |

### 29. Eurystomina assimilis de Man.

| | |
|---|---|
| Figure 29a. | Anterior end of male; obj. $^{1}/_{16}$, oc. 3; a — first annular thickening of wall of buccal cavity; b — second thickening consisting of short rods; lin. — line around labial papillae on head; d. d. v. — right subventral tooth (large); d. d. — dorsal tooth. |
| Figure 29b. | Tail of male; obj. 7, oc. 1. |
| Figure 29c. | Tail of male; obj. 7, oc. 1; gub. — gubernaculum; $a_1$ — posterior, $a_2$ — anterior accessory organ; $s_1, s_2, s_3, p_4, s_5, p_6$ — different categories of supplementary bristles (see text, p. 114, Part I). |
| Figure 29d. | End of spicules with hooks; obj. $^{1}/_{16}$, oc. 1. |
| Figure 29e. | Posterior accessory organ; obj. $^{1}/_{16}$, oc. 1. |
| Figure 29f. | Posterior end of specimen with shortened space between accessory organ and with short tail; obj. 7, oc. 1. |

### 30. Symplocostoma longicolle Bastian.

| | |
|---|---|
| Figure 30a. | Head of female; obj. $^{1}/_{16}$, oc. 3; d. imm. — immovable tooth; d. mob. — movable tooth; corp. — cuticular body. |
| Figure 30b. | End of tail, cone of caudal glands visible; obj. $^{1}/_{16}$, oc. 1. |
| Figure 30c. | Tail of female; obj. 3, oc. 5. |
| Figure 30d. | Tail of male; obj. 3, oc. 5. |
| Figure 30e. | Anal region of male; obj. $^{1}/_{16}$, oc. 1. End of spicules and gubernaculum visible. |

### 602 31. Symplocostoma ponticum n. sp.

| | |
|---|---|
| Figure 31a. | Head of female; Zeiss apochr. 2 mm, comp. oc. 12. |
| Figure 31b. | Same, young specimen with projecting tooth; obj. $^{1}/_{16}$, oc. 3. |
| Figure 31c. | Region of female gonopore, lateral; obj. 3, oc. 3. |
| Figure 31d. | Tail of female; obj. 7, oc. 0. |

### 32. Symplocostoma hexabulba n. sp.

| | |
|---|---|
| Figure 32a. | Anterior end of body of female, six bulbs with cavities visible; obj. 7, oc. 0. |
| Figure 32b. | Anterior end of female; obj. Zeiss apochr. 2 mm, comp. oc. 12 (magnification about 2,000); d. subv. d. — right subventral tooth (immovable); d. mob. — adjacent spine of buccal cavity; cut. — cuticular thickening on bottom of buccal cavity; oc. — eyes.; p. lab. — labial papilla (its chitinized canal); d. d. — dorsal tooth; cůt. — internal layer of cuticle attached separately to buccal capsule; o. l. — lateral organ; gl. oes. — esophageal gland; c. cut. — cuticular body; oes. — internal chitinized tube of esophagus. |
| Figure 32c. | Tail of female; obj. 7, oc. 1. |

### 33. Symplocostoma sabulicola n. sp.

| | |
|---|---|
| Figure 33a. | Anterior end of female; obj. $^{1}/_{16}$, oc. 3; d. mob. — movable tooth; o. l. — lateral organ. |
| Figure 33b. | Tail of female; obj. 7, oc. 3. |

### 34. Symplocostoma marioni n. sp.

| | |
|---|---|
| Figure 34a. | Head of female; obj. $^{1}/_{16}$, oc. 3. Left: an. cut. — cuticular ring near anterior margin of buccal cavity; d. sv. d. — subventral immovable tooth; d. mob. — end of movable spine; b — internal layer of cuticle separately attached to buccal capsule; c. cut. — cuticular body; c — widening of lumen at beginning of esophagus. Right: d. d. — dorsal immovable tooth; a — cuticular ring forming a constriction on the buccal cavity; o. l. — lateral organ; den. — posterior true tooth with opening of esophageal gland; gl. oes. — esophageal gland. |
| Figure 34b. | Tail of female; obj. 7, oc. 0. |

### 37.* Cyatholaimus demani nom. nov.

| | |
|---|---|
| Figure 37a. | Head of male; obj. $^{1}/_{16}$, oc. 1. |
| Figure 37b. | Spicular apparatus, ventral; obj. 7, oc. 3; sp. — spicules; gub$_1$ — unpaired part of gubernaculum; gub$_2$ — paired posterior part of gubernaculum. |
| Figure 37c. | Tail of male, lateral; obj. 7, oc. 0; sp. spicule; gub. — gubernaculum. |

### 603 38.* Halichoanolaimus clavicauda n. sp.

| | |
|---|---|
| Figure 38a. | Head of female in subventral position; obj. $^{1}/_{16}$, oc. 1; a — posterior symmetrical denticles of oral comb; b — anterior unpaired denticle of comb; c — skeletal parts of posterior half of buccal cavity in plane; d — same parts in profile; s. cerv. — cervical bristles. |
| Figure 38b. | Tail of female; obj. 7, oc. 1. |
| Figure 38c. | See following plate. |

Table 6.

### 35 Tripyloides demani n. sp.

| | |
|---|---|
| Figure 35a. | Anterior end of male; obj. $^{1}/_{16}$, oc. 3. |
| Figure 35b. | Spicules, laterally; obj. $^{1}/_{16}$, oc. 3; b — posterior hook of gubernaculum. |
| Figure 35c. | Spicules and gubernaculum, ventral; obj. $^{1}/_{16}$, oc. 3; a — median process of gubernaculum; b — posterior hooks of gubernaculum. |

### 36. Acontiolaimus zostericola n. g., n. sp.

| | |
|---|---|
| Figure 36a. | Anterior end of female; obj. Zeiss apochr. 2 mm, comp. oc. 12; a — process of cuticle to which wall of buccal cavity is attached. |
| Figure 36b. | Tail of female; obj. 7, oc. 1. |

* [Figures 37 and 38 appear in this order in the Russian.]

### 38. Halichoanolaimus clavicauda n. sp.

| | |
|---|---|
| Figure 38c. | Tail of male; obj. 7, oc. 1. |

### 39. Halichoanolaimus filicauda n. sp.

| | |
|---|---|
| Figure 39a. | Head of female, lateral; obj. $^{1}/_{16}$, oc. 1; s. ceph. — cephalic bristles; a — ridge of anterior part of oral cavity. |
| Figure 39b. | Same, dorsal; obj. $^{1}/_{16}$, oc. 1; c. ceph. — cephalic capsule; a — ridges of anterior part of buccal cavity; b — supplementary ridges; c — comb; d — plates demarcating side of posterior part of buccal cavity; e — plate at bottom of buccal cavity. |
| Figure 39c. | Same, anterior; obj. $^{1}/_{16}$, oc. 1; a — lamellar part of lip; b — its plasmatic base; c — processes of cephalic capsule, strengthening lips; p. lab. — labial papillae; n. p. lab. — nerve of labial papillae; s. ceph. — cephalic bristles; c. ceph. — cephalic capsule. |
| Figure 39d. | Optical section of anterior part of buccal capsule and its comb; obj. $^{1}/_{16}$, oc. 1; a — ridge of anterior part of buccal cavity; b — lateral denticles of comb; c — median denticle of comb. |
| Figure 39e. | Tail of female; obj. e, oc. 5. |
| Figure 39f. | End of tail of female; obj. $^{1}/_{16}$, oc. 1. |
| Figure 39g. | Tail of male; obj. 3, oc. 5. |
| Figure 39h. | Spicular apparatus; obj. $^{1}/_{16}$, oc. 0; gub. — gubernaculum; pap. — supplementary papillae; a — internal velum of spicule; b — tubercle at end of spicule. |

604

### 40. Dignathonema bulbosa n. g., n. sp.

| | |
|---|---|
| Figure 40a. | Head of female, lateral; obj. $^{1}/_{16}$, oc. 1; p. lab. lat. — lateral labial papillae; lab. — lips; md. c. — median part of jaw; md. l. lateral part of jaw; md. p. — posterior part of jaw; c. ceph. — cephalic capsule. |
| Figure 40b. | Same, anterior; obj. $^{1}/_{16}$, oc. 1; c. ceph. — cephalic capsule; c. oes. — esophageal capsule; md. p. — posterior parts of jaw. |
| Figure 40c. | Same anterior; obj. $^{1}/_{16}$, oc. 1. Left: c. oes. — esophageal capsule; s. c. l. — lateral cephalic bristles; md. c. — median part of jaw; md. l. lateral part of jaw; sect. sv. — subventral sector of esophagus. Right: p. l. sd. — subdorsal labial papillae; sect. drs. — dorsal sector of esophagus; d. d. — one of dorsal teeth; p. l. l. — lateral labial papilla; os. — line demarcating mouth; p. l. sv. — subventral lateral papilla; s. c. sl. — subventral (large) cephalic bristle. |
| Figure 40d. | Part of intestine, large cells visible, swollen by contents; obj. 7, oc. 1. |
| Figure 40e. | Tail of female; obj. 3, oc. 5. |
| Figure 40f. | Esophageal part of female; obj. 3, oc. 5; anterior and posterior swellings of esophagus visible. |

### 41. Onyx perfectus Cobb.

| | |
|---|---|
| Figure 41a. | Head of male with open lips; obj. $^{1}/_{16}$, oc. 1; s. cerv. — cervical bristles; s. c. ant. — anterior cephalic bristles; s. c. post. — posterior cephalic bristles; lab. — lips; c. or. — wall of buccal capsule; den. — tooth. |
| Figure 41b. | Same, but with closed lips; obj. $^{1}/_{16}$, oc. 0; lab. — lips. |
| Figure 41c. | Tail of male; obj. 7, oc. 0. |
| Figure 41d. | Spicules; obj. $^{1}/_{16}$, oc. 1; a — median part of gubernaculum; b — lateral angle of gubernaculum. |
| Figure 41e. | End of spicules and some posterior accessory organs; obj. $^{1}/_{16}$, oc. 1. |

### 42. Metachromadora macroutera n. g., n. sp.

| | |
|---|---|
| Figure 42a. | Anterior end of female; obj. 3, oc. 5. |

Table 7.

| | |
|---|---|
| Figure 42b. | Anterior end of female, lateral; obj. $^{1}/_{16}$, oc. 3; den. — dorsal tooth; a — place where one of cuticular annules ends; s. c. post. — posterior cephalic bristles; vest. — vestibule; s. subc. — characteristic bristles near lateral organ; c. or. — buccal capsule. |
| Figure 42c. | Same, dorsal; obj. $^{1}/_{16}$, oc. 3; s. c. ant. — anterior cephalic bristles; other letters as for Figure 42b. |
| Figure 42d. | Same, anterior. View of external surface; obj. $^{1}/_{16}$, oc. 3; p. lab. — labial papillae; os. — mouth opening; other letters as above. |
| 605 Figure 42e. | Same, but deeper focus; obj. $^{1}/_{16}$, oc. 4; m. int. — internal layer of musculature of buccal cavity; m. ext.$_1$ — external layer at level of wall of buccal capsule (c. or.); m. ext.$_2$ — the same at the level of the vestibule (vest. — wall of vestibule); den. — dorsal tooth. |
| Figure 42f. | Tail of male; obj. 7, oc. 1; s. subd. — subdorsal row of bristles; s. lat. — lateral row; s. subv. — subventral row; pap. — supplementary papillae; a — sensory tubercles on tail; b — posterior part of tail, without annules. |
| Figure 42g. | Supplementary papillae of male; obj. $^{1}/_{16}$, oc. 3. |
| Figure 42h. | Posterior part of tail of male with sensory tubercles; obj. $^{1}/_{16}$, oc. 1. |
| Figure 42i. | General view of female; obj. 3, oc. 0. |
| Figure 42k. | Male genital organs; obj. 3, oc. 3; a — testis; b — seminal vesicle; c — origin of vas deferens; d — vas deferens; e — ejaculatory duct. |

### 43. Metachromadora cystoseirae n. g., n. sp.

| | |
|---|---|
| Figure 43. | Anterior end of female; obj. $^{1}/_{16}$, oc. 1; vest. — vestibule; c. or. — wall or buccal capsule. |

### 44. Chromadorina obtusa n. g., n. sp.

| | |
|---|---|
| Figure 44a. | Anterior end of female; obj. Zeiss apochr. 2 mm, oc. 1. |
| Figure 44b. | Same, higher magnification; ob. Zeiss apochr. 2 mm., comp. oc. 12; den. — dorsal tooth. |
| Figure 44c. | Tail of female; obj. 7, oc. 3; r — reservoir of caudal glands. |
| Figure 44d. | Tail of male; obj. 7, oc. 3; r — reservoir of caudal glands. |
| Figure 44e. | Spicular apparatus; obj. Zeiss apochr. 2 mm, comp. oc. 12. |

### 45. Chromaspirina pontica n. g., n. sp.

| | |
|---|---|
| Figure 45a. | Head of female; obj. $^{1}/_{16}$, oc. 1; den. — dorsal tooth; s. lab. — labial bristles; s. ceph.$_1$ — anterior bristles; s. ceph.$_2$ — posterior cephalic bristles. |
| Figure 45b. | Tail of female; obj. 7, oc. 0. |
| Figure 45c. | Spicules; obj. $^{1}/_{16}$, oc. 1. |

### 46. Spirina sabulicola n. sp.

| | |
|---|---|
| Figure 46a. | Anterior end of female; obj. $^{1}/_{16}$, oc. 3; p. ceph. — cephalic papillae (anterior ring of cephalic bristles); s. ceph. — cephalic bristles (posterior ring). |
| Figure 46b. | Tail of female; obj. 7, oc. 1. |

### 47. Spirina zosterae n. sp.

| | |
|---|---|
| Figure 47a. | Anterior end of female; obj. 7, oc. 1. |
| Figure 47b. | Same, higher magnification; obj. Zeiss apochr. 2 mm, comp. oc. 12. |
| Figure 47c. | Tail of male; obj. 7, oc. 1. |
| Figure 47d. | Spicular apparatus; obj. $^{1}/_{16}$, oc. 1. |

606

### 48. Monoposthia costata (Bastian, 1865).

| | |
|---|---|
| Figure 48. | Esophageal region of female; obj. 7, oc. 1. |

### 49. Euchromadora striata (Eberth, 1863).

| | |
|---|---|
| Figure 49a. | Spicules; obj. $^{1}/_{16}$, oc. 1; sp. sin. — left spicule; sp. d. — right spicule; gub. m. — median part of gubernaculum; gub. l. — lateral part. |
| Figure 49b. | Tail of male; obj. 7, oc. 0. |

Table 8.

### 50. Chromadora sabulicola n. sp.

| | |
|---|---|
| Figure 50a. | Head of young female; obj. $^{1}/_{16}$, oc. 3; 0. 1. — lateral organs; d. d. — dorsal tooth. |
| Figure 50b. | Structure of cuticle next to posterior half of esophagus; obj. Zeiss apochr. 2 mm, comp. oc. 1 oc. 12; l. lat. — lateral line; l. subv. — subventral lines. |
| Figure 50c. | Same, near posterior end. Same magnification. |
| Figure 50d. | Tail of male; obj. 7, oc. 3 (slightly compressed). |

### 51. Chromadora quadrilinea n. sp.

| | |
|---|---|
| Figure 51a. | Anterior end of male; obj. Zeiss apochr. 2 mm, comp. oc. 12. |
| Figure 51b. | Same; obj. 2 mm, oc. 0. |
| Figure 51c. | Posterior end of male; obj. 2 mm, oc. 0. |
| Figure 51d. | Spicules and posterior preanal papilla; obj. 2 mm, oc. 12. |

### 52. Chromadora poecilosomoides n. sp.

| | |
|---|---|
| Figure 52a. | Anterior end of male; obj. Zeiss apochr. 2 mm, comp. oc. 12. |
| Figure 52b. | Structure of cuticle, lateral, near end of esophagus. Gradual transition from section without lateral punctations to section with punctations visible. Same magnification. |
| Figure 52c. | Structure of cuticle in middle of body. Same magnification. |
| Figure 52d. | Bulb; obj. $^{1}/_{16}$, oc. 1. |
| Figure 52e. | Tail of male; obj. 7, oc. 1. |
| Figure 52f. | Spicules; obj. $^{1}/_{16}$, oc. 1; pap. — posterior preanal papilla. |

### 53. Chromadorella mytilicola n. g., n. sp.

| | |
|---|---|
| Figure 53a. | Anterior end of female; obj. Zeiss apochr. 2 mm, comp. oc. 12. |
| Figure 53b. | Structure of cuticle of female at posterior end. Same magnification. |
| Figure 53c. | Tail of female; obj. 7, oc. 3. |

### 54. Spilophorella euxina n. g., n. sp.

| | |
|---|---|
| Figure 54a. | Anterior end of female; obj. Zeiss apochr. 2 mm, comp. oc. 12; p. ceph. — cephalic papillae; vest. — vestibule, posterior part; s. subc. — supplementary cephalic bristles. |
| 607 Figure 54b. | Bulb; obj. Zeiss apochr. 2 mm, oc. 1. |
| Figure 54c. | Tail of female; obj. 7, oc. 1; por. caud. — caudal pore. |

### 55. Draconema cephalatum Cobb, 1913.

| | |
|---|---|
| Figure 55a. | General view of male; obj. 3, oc. 3. |
| Figure 55b. | General view of female; obj. 3, oc. 3. |
| Figure 55c. | Anterior end of male; obj. $^{1}/_{16}$, oc. 0. Preparation compressed; set. — thick cephalic bristles; s.c. — cephalic brsitles; o. 1. — lateral organ. |
| Figure 55d. | Tail of male; obj. 7, oc. 1.; set. — posterior bristle of lateral row. |
| Figure 55e. | One of bristles of the external posterior row; obj. $^{1}/_{16}$, oc. 3. |

### 56. Draconema ponticum n. sp.

| | |
|---|---|
| Figure 56. | Anterior end; obj. $^{1}/_{16}$, oc. 0. |

Table 9.

### 57. Linhomoeus (Paralinhomoeus) filiformis n. sp.

| | |
|---|---|
| Figure 57a. | Cephalic end, dorsal, slightly asymmetrical; obj. $^{1}/_{16}$, oc. 1. |
| Figure 57b. | Tail, straightened; obj. $^{1}/_{16}$, oc. 0. |

### 58. Linhomoeus (Paralinhomoeus) ostraearum n. sp.

| | |
|---|---|
| Figure 58a. | Anterior end of male; obj. $^{1}/_{16}$, oc. 1; dors. — dorsal side. |
| Figure 58b. | Tail of female; obj. 7, oc. 1. |
| Figure 58c. | Tail of male; obj. 3, oc. 5. |
| Figure 58d. | Spicules; obj. $^{1}/_{16}$, oc. 1; a — posterior process of gubernaculum; b — lateral sheath enclosing spicules; c — process between spicules; d — preanal part. |

### 59. Paramonhystera elliptica n. sp.

| | |
|---|---|
| Figure 59a. | Anterior end of female; obj. $^{1}/_{16}$, oc. 1; a — papilla with bristles, on which the nerves of lateral organ end. |
| Figure 59b. | Lateral organ, profile; obj. $^{1}/_{16}$, oc. 1; a — as for Figure 59a. |
| Figure 59c. | Tail of female; obj. 3, oc. 5. |
| Figure 59d. | Spicules; obj. $^{1}/_{16}$, oc. 1. |

### 60. Paramonhystera setosa n. sp.

| | |
|---|---|
| Figure 60a. | Head of young female; obj. $^{1}/_{16}$, oc. 1. |
| Figure 60b. | Tail of female; obj. 3, oc. 5. |

608

### 61. Penzancia euxina n. sp.

| | |
|---|---|
| Figure 61a. | Head of female; obj. $^{1}/_{16}$, oc. 0. |
| Figure 61b. | Lateral organ, profile; obj. $^{1}/_{16}$, oc. 1. |
| Figure 61c. | Tail of female; obj. 7, oc. 0. |
| Figure 61d. | Tail of male; obj. 7, oc. 1. |
| Figure 61e. | Spicules, gubernaculum visible, external part projecting near end; obj. $^{1}/_{16}$, oc. 1. |

### 62. Cobbia triodonta n. sp.

Figure 62a. Anterior end of female, obj. $^{1}/_{16}$, oc. 1.
Figure 62b. Same, deeper focus; obj. $^{1}/_{16}$, oc. 1 ; a — dorsal side; b — ventral side; gl. oes. — duct of esophageal gland.
Figure 62c. Same, anterior view; obj. $^{1}/_{16}$, oc. 3.
Figure 62d. Cuticle in middle of body, lateral; obj. $^{1}/_{16}$, oc. 5.
Figure 62e. Tail of female; obj. 7, oc. 0.
Figure 62f. Tail of male; obj. 7, oc. 0.
Figure 62g. Spicules; obj. $^{1}/_{16}$, oc. 3.

### 63. Cobbia sabulicola n. sp.

Figure 63a. Anterior end of female; obj. $^{1}/_{16}$, oc. 3.
Figure 63b. Tail of female; obj. 7, oc. 0.

### 64. Metalinhomoeus zosterae n. sp.

Figure 64a. Head of female; obj. $^{1}/_{16}$, oc. 3.
Figure 64b. Tail of young female; obj. 7, oc. 1.
Figure 64c. Tail of old female, its end subject to histolysis; obj. 7, oc. 1.
Figure 64d. Tail of male; obj. 7, oc. 3.

### 65. Terschellingia pontica n. sp.

Figure 65a. Anterior part of female; obj. Zeiss apochr. 2mm, comp. oc. 12.
Figure 65b. Tail of female; obj. 7, oc. 1.
Figure 65c. Esophageal part of body; obj. 7, oc. 1.

### 66. Prosphaerolaimus eurypharynx n. g., n. sp.

Figure 66a. Anterior part of female; obj. $^{1}/_{16}$, oc. 1; lab. — lips turned inside out,
Figure 66b. Tail of female; obj. 7, oc. 0.

Table 10.

### 67. Sphaerolaimus ostreae n. sp.

Figure 67a. Head of male; obj. $^{1}/_{16}$, oc. 1. Letters mark different parts of buccal capsule: a — part with
609 denser punctations, descending posteriorly in form of a tongue; b — processes at posterior
margin; c — dorsal sector; d — space between ventral sectors.
Figure 67b. Tail of male; obj. 7, oc. 0.
Figure 67c. Spicules; obj. $^{1}/_{16}$, oc. 0; gub. — gubernaculum.

### 68. Sphaerolaimus macrocirculus n. sp.

Figure 68a. Head of male; obj. $^{1}/_{16}$, oc. 1; a — cone of rods; b — posterior process near lateral organ; c — dorsal sector; d — ventral sector; e — depressions at anterior margin.
Figure 68b. Tail of male; obj. 7, oc. 1.
Figure 68c. End of spicules; obj. $^{1}/_{16}$, oc. 3; a — upper, b — posterior process of gubernaculum.

### 69. Sphaerolaimus dispar n. sp.

Figure 69a. Head of male; obj. $^{1}/_{16}$, oc. 1.
Figure 69b. Head of female; obj. $^{1}/_{16}$, oc. 1; s. lab. — labial bristles; s. ceph. cephalic bristles; vest. — vestibule ; a — cone of rods; b — space between cone and cuticle; c — first band of oral capsule; d — second band; e — third band.
Figure 69c. Tail of female; obj. 7, oc. 0; a — valve at entrance to hindgut.
Figure 69d. Tail of male; obj. 7, oc. 0.
Figure 69e. Spicules; obj. $^{1}/_{16}$, oc. 0.
Figure 69f. Head of young female with undeveloped cephalic capsule; obj. $^{1}/_{16}$, oc. 1.

### 70. Axonolaimus setosus n. sp.

Figure 70a. Cephalic end; obj. $^{1}/_{16}$, oc. 3.
Figure 70b. Tail of male; obj. 7, oc. 3.
Figure 70c. Tail of female; obj. 7, oc. 0.

### 71. Axonolaimus ponticus n. sp.

Figure 71a. Cephalic end; obj. $^{1}/_{16}$, oc. 3.
Figure 71b. Tail of male; obj. 7, oc. 3.
Figure 71c. Tail of female; obj. 7, oc. 3.

### 72. Conolaimus angustilaimus n. g., n. sp.

Figure 72. Cephalic end of female; obj. $^{1}/_{16}$, oc. 3.

### 73. Araeolaimodes zosterae n. sp.

Figure 73a. Head of male, obj. $^{1}/_{16}$; oc. 3.
Figure 73b. Esophagus and eye; obj. $^{1}/_{16}$, oc. 3.
Figure 73c. Tail of male; obj. 7, oc. 1.
Figure 73d. Spicules; obj. $^{1}/_{16}$, oc. 3.

### 74. Disconema alaima n. g., n. sp.

Figure 74a. Anterior end of female; obj. $^{1}/_{16}$, oc. 1. Lateral organs in superficial focus.
Figure 74b. Lateral organs in deep focus; obj. $^{1}/_{16}$, oc. 1.

610 Table 11.

Figure 74c. Anterior part of female; obj. 7, oc. 0.
Figure 74d. Tail of female; obj. 7, oc. 0.

### 75. Sphaerocephalum crassicauda n. g., n. sp.

Figure 75a. Anterior end of female; obj. 3, oc. 5.
Figure 75b. Same, higher magnification; obj. Zeiss. apochr. 2mm, oc. 3.
Figure 75c. Tail of female; obj. 7, oc. 1.

### 76. Comesoma stenocephalum n. sp.

| | |
|---|---|
| Figure 76a. | Anterior end of male; obj. $^1/_{16}$, oc. 3. |
| Figure 76b. | Tail of female; obj. 3, oc. 5. |
| Figure 76c. | Tail of male; obj. 7, oc. 0. |
| Figure 76d. | End of spicules and gubernaculum; obj. $^1/_{16}$, oc. 1; gub. m. — median part of gubernaculum; gub. l. — lateral part. |

### 77. Comesoma (?) dubia n. sp.

| | |
|---|---|
| Figure 77a. | Cephalic end; obj. $^1/_{16}$, oc. 3; den. — dorsal spine; a — subventral chitinized tubercle. |
| Figure 77b. | Tail of male; obj. $^1/_{16}$, oc. 0. |
| Figure 77c. | End of spicules and gubernaculum; obj. $^1/_{16}$, oc. 3; gub. a — upper gub g — lower part of gubernaculum. |

### 78. Parasabatieria clavicauda n. sp.

| | |
|---|---|
| Figure 78a. | Head, obj. $^1/_{16}$, oc. 3. |
| Figure 78b. | Tail of female; obj. 7, oc. 0. |
| Figure 78c. | Spicules; obj. $^1/_{16}$, oc. 3; a — transparent median parts of gubernaculum. |

### 79. Parasabatieria abyssalis n. sp.

| | |
|---|---|
| Figure 79a. | Head; obj. $^1/_{16}$, oc. 3. |
| Figure 79b. | Tail of female; obj. 7, oc. 1. |
| Figure 79c. | Tail of male; obj. 7, oc. 1. |
| Figure 79d. | Spicules; obj. $^1/_{16}$, oc. 1. |

### 80. Diplopeltis eberthi n. sp.

| | |
|---|---|
| Figure 80. | Head of female; obj. $^1/_{16}$, oc. 1; p. ex. — cervical pore; gl. ex. — end of cervical gland; a — opening of lateral organ; b — sensory bulb of lateral organ; c — internal spiral of lateral organ; d — ? lens; e — terminal duct of cervical gland. |

### 81. Acmaeolaimus diplopeltoides n. gen., n. sp.

| | |
|---|---|
| Figure 81. | Anterior end of female; obj. $^1/_{16}$, oc. 3. |

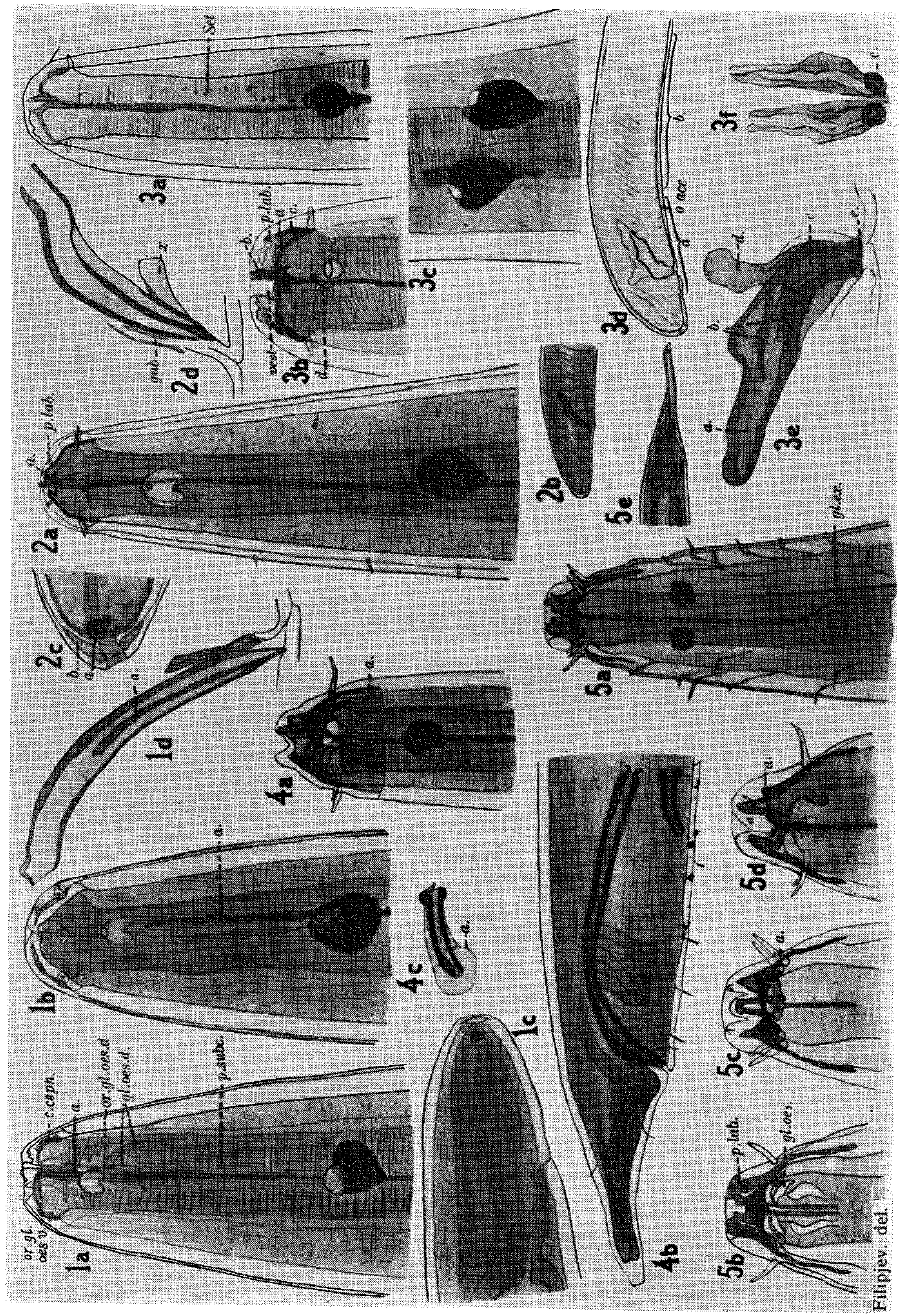


TABLE 1

TABLE 2

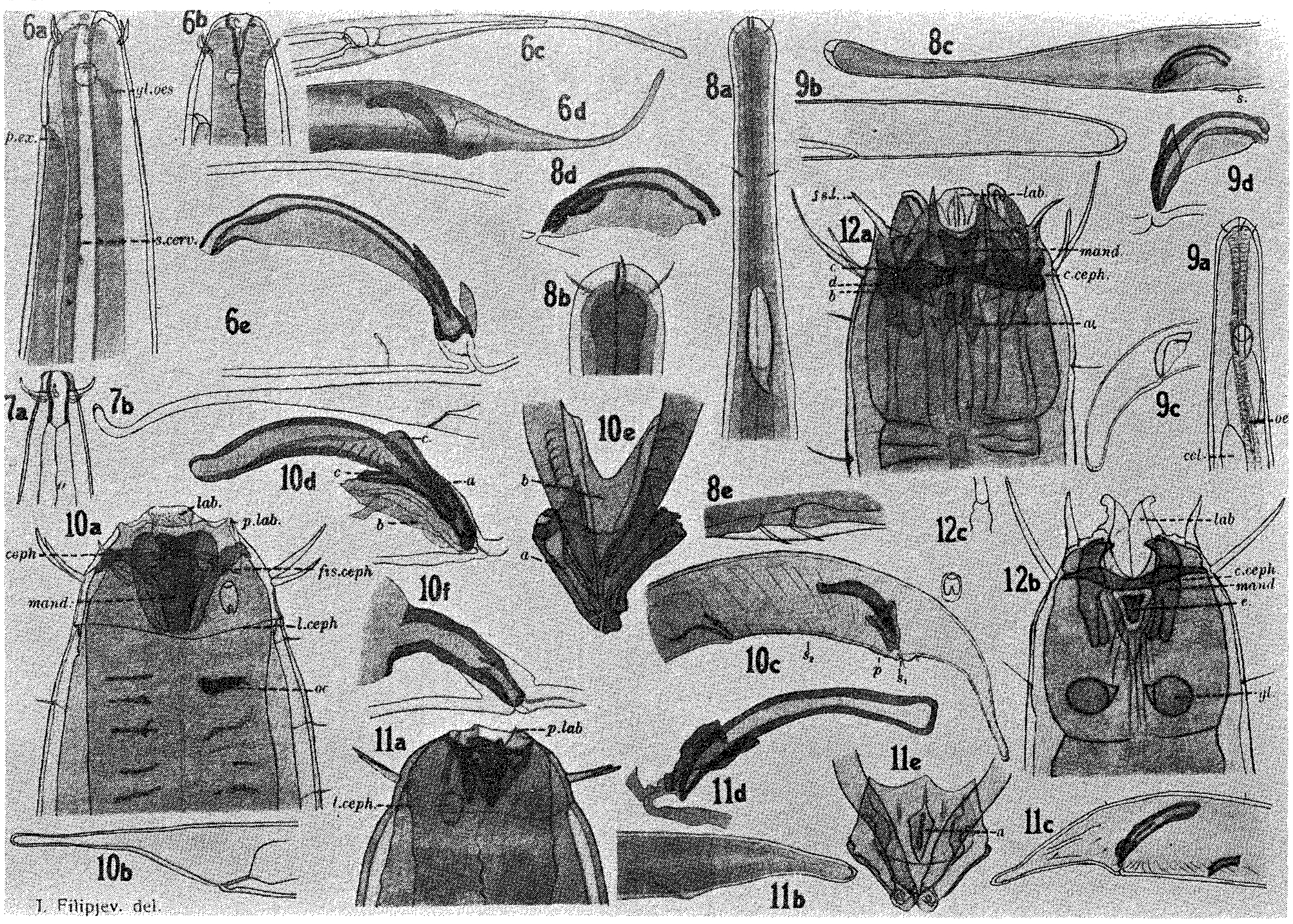


TABLE 3

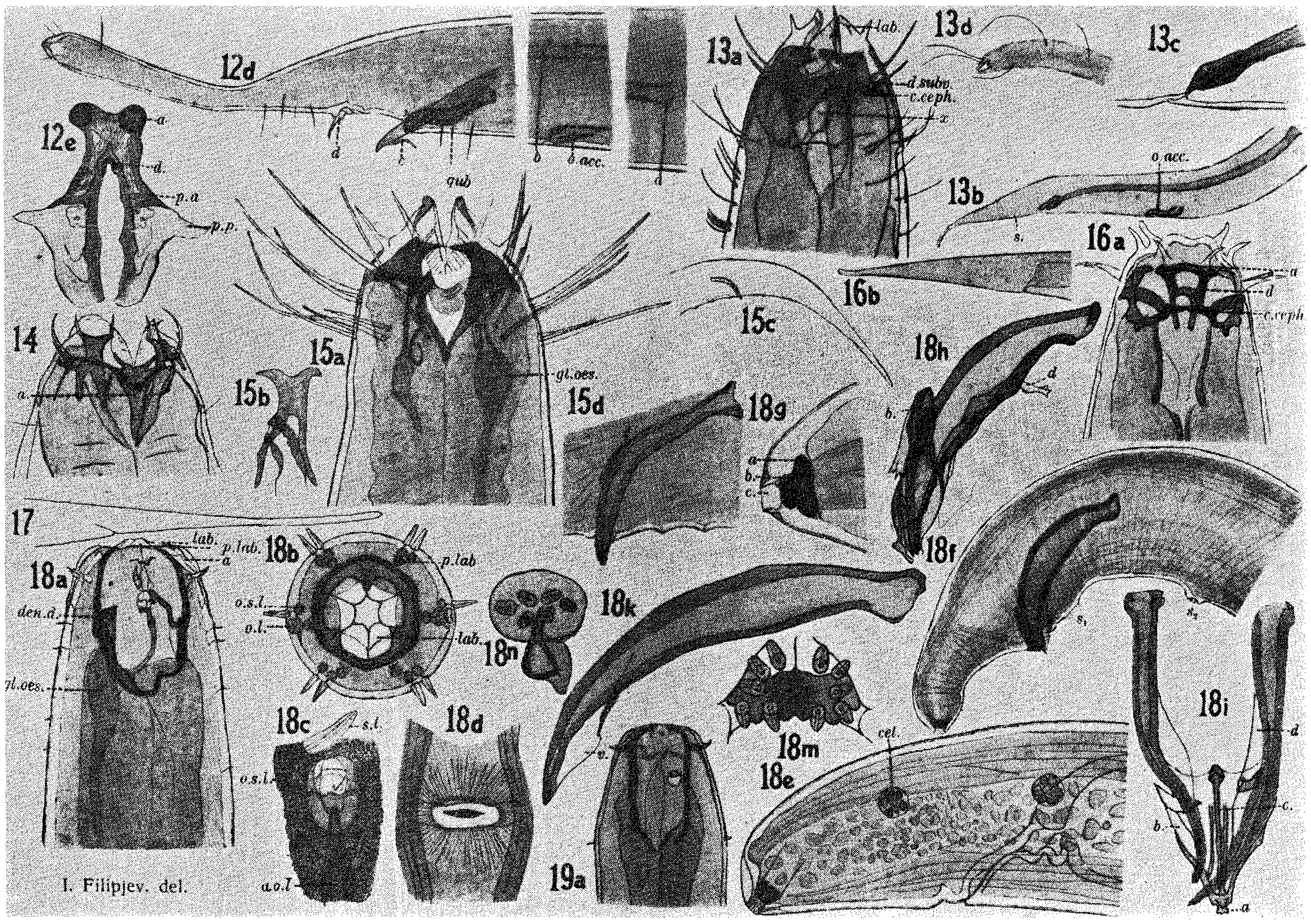
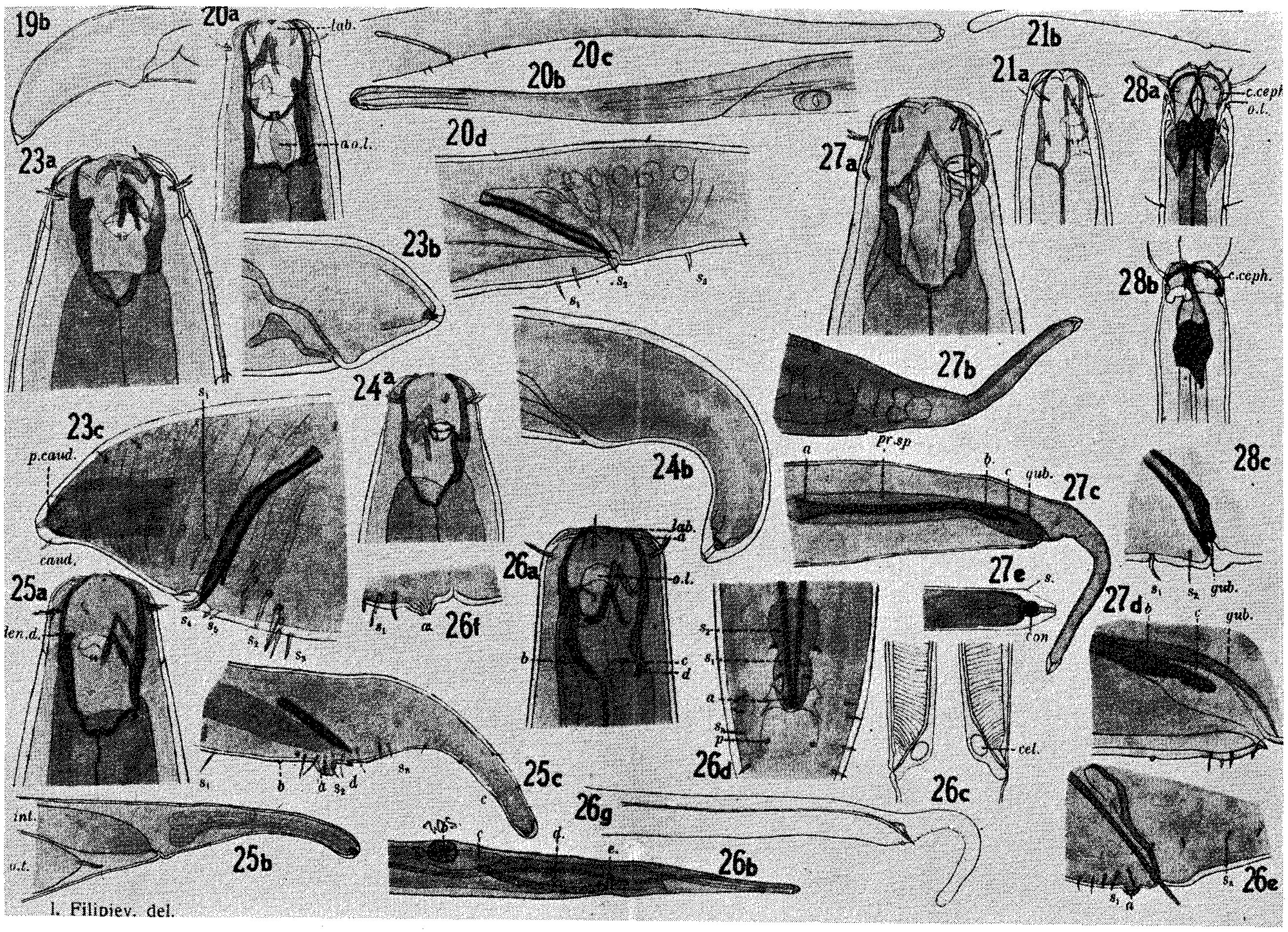
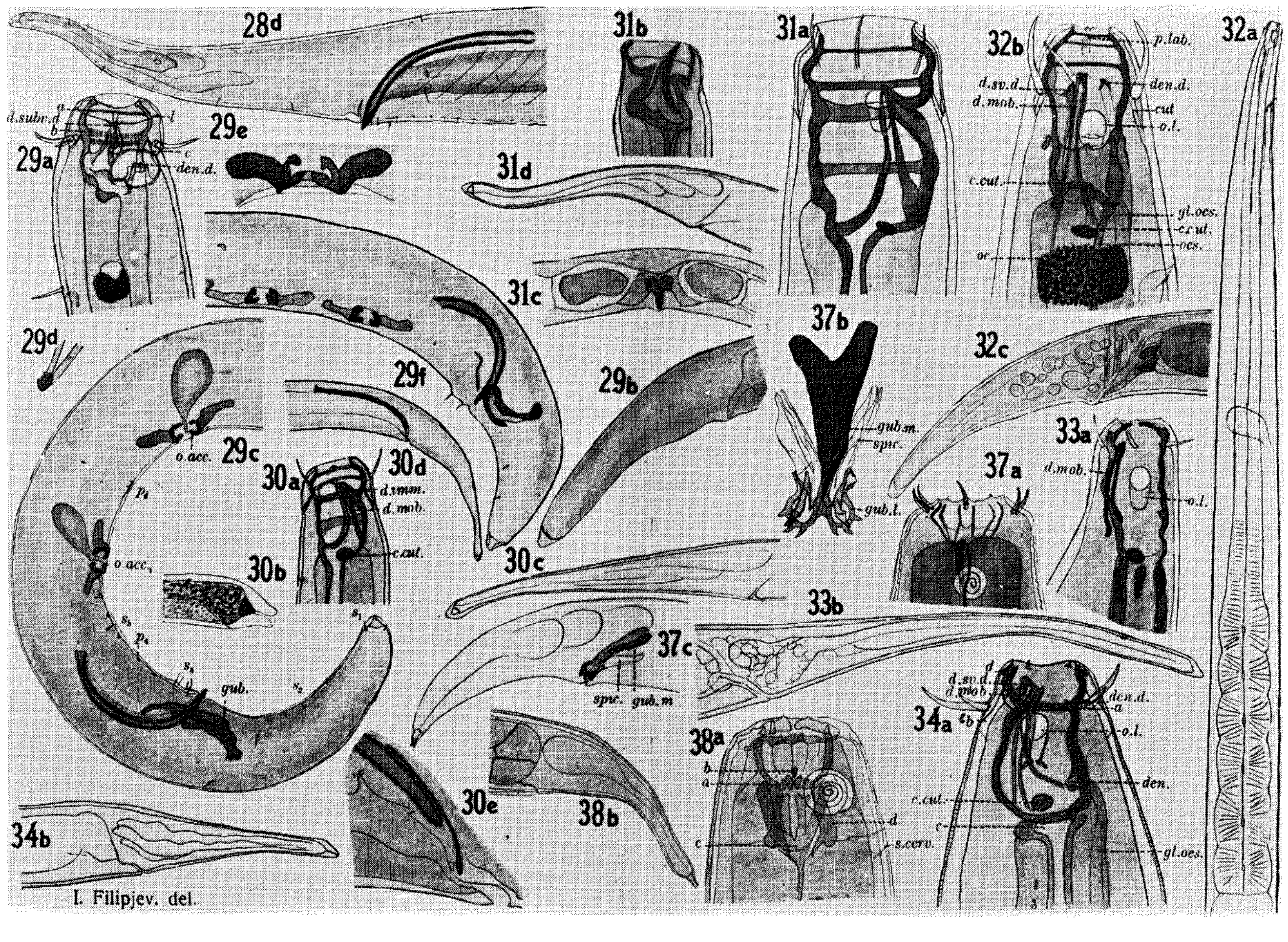


TABLE 4



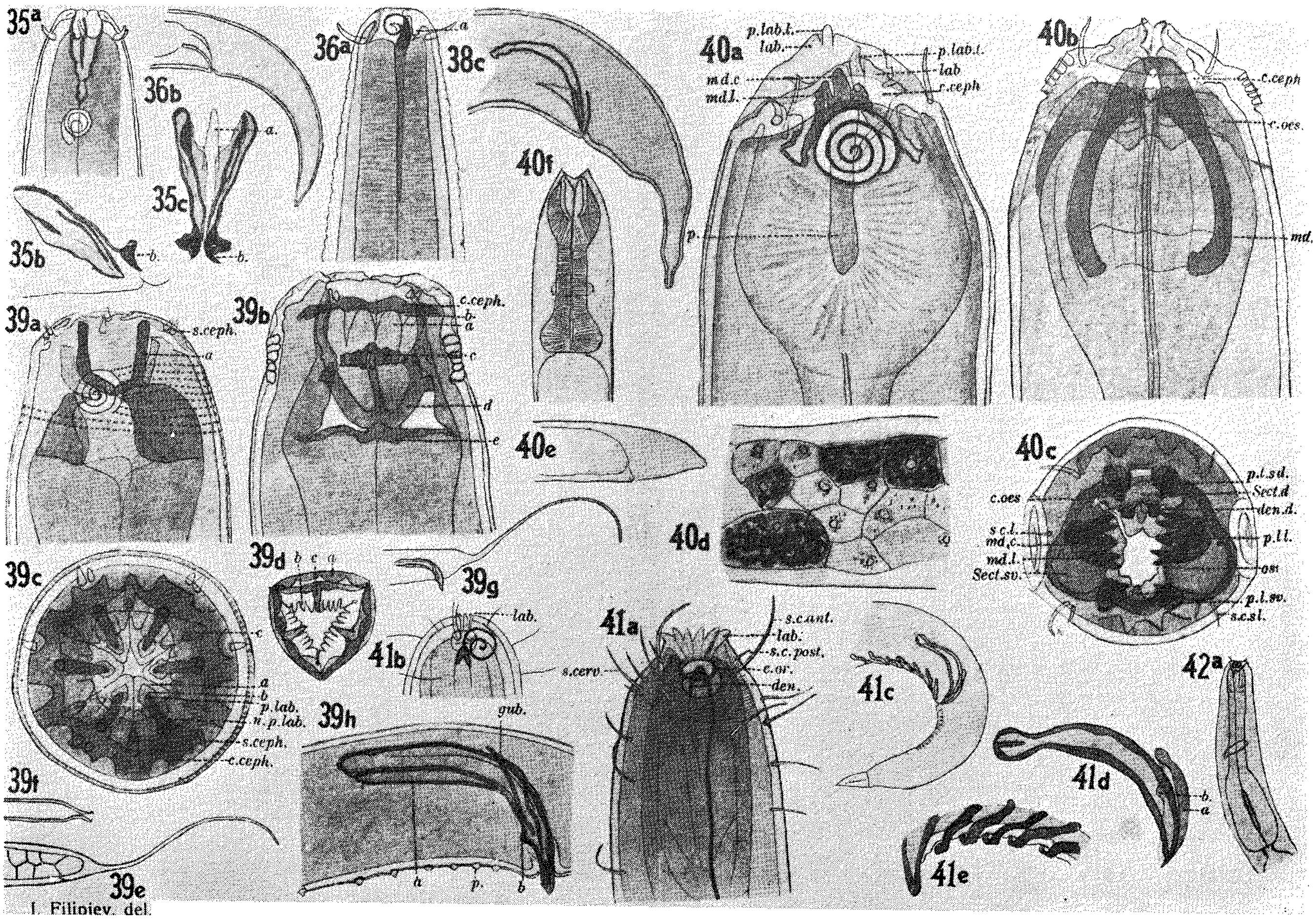
I. Filipjev. del.

TABLE 5



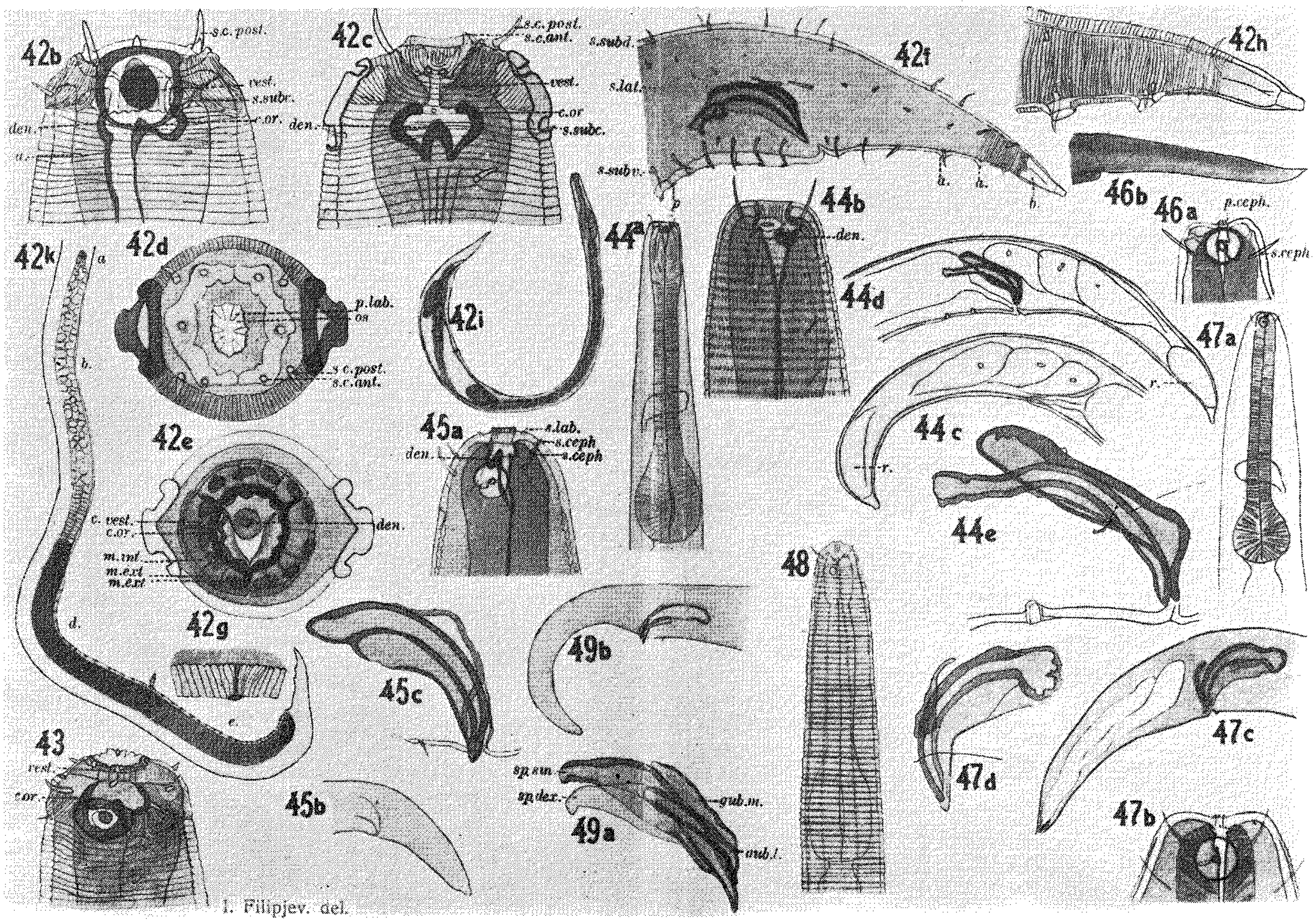
I. Filipjev. del.

TABLE 6



I. Filipjev. del.

TABLE 7



I. Filipjev. del.

TABLE 8

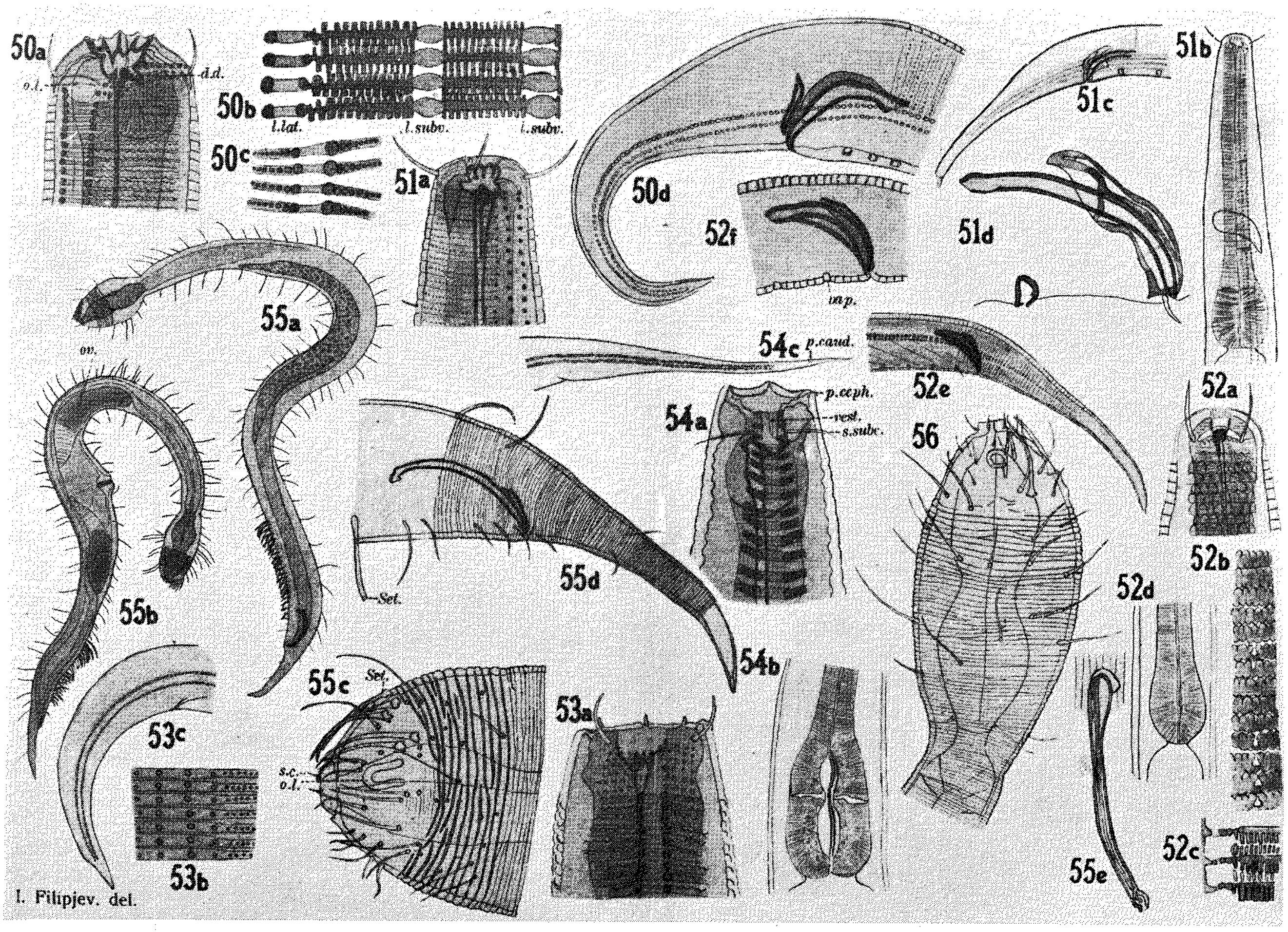


TABLE 9

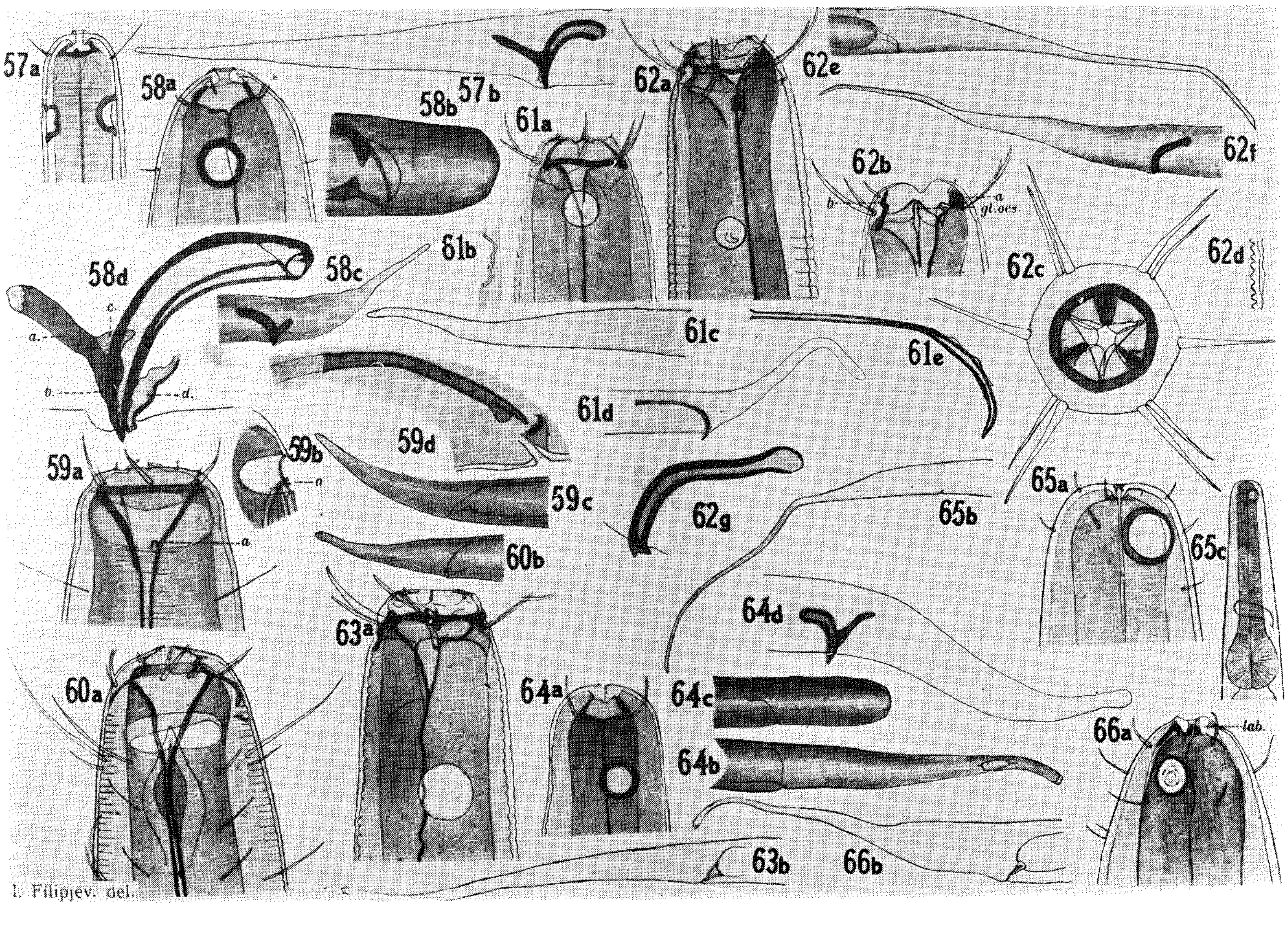
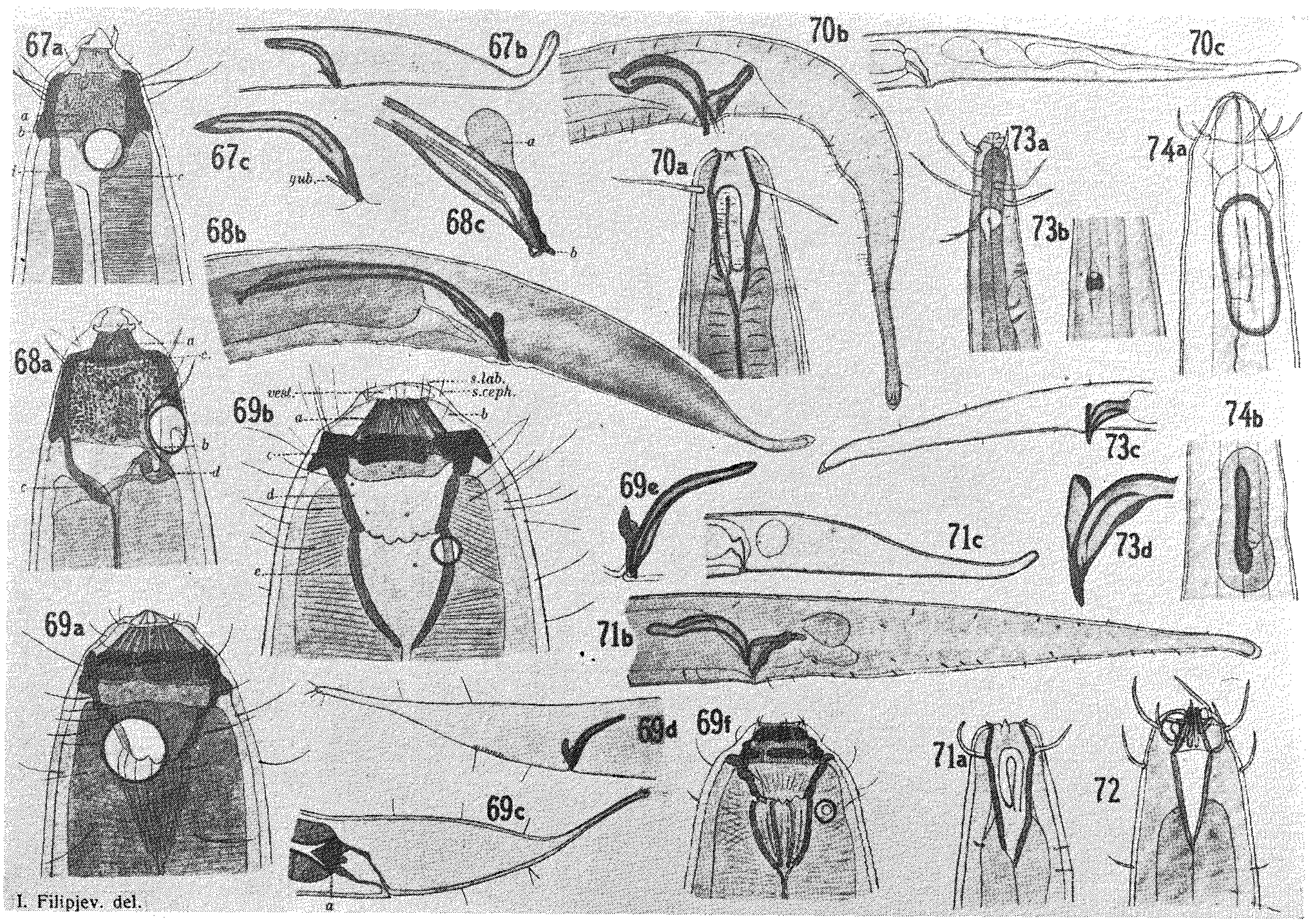
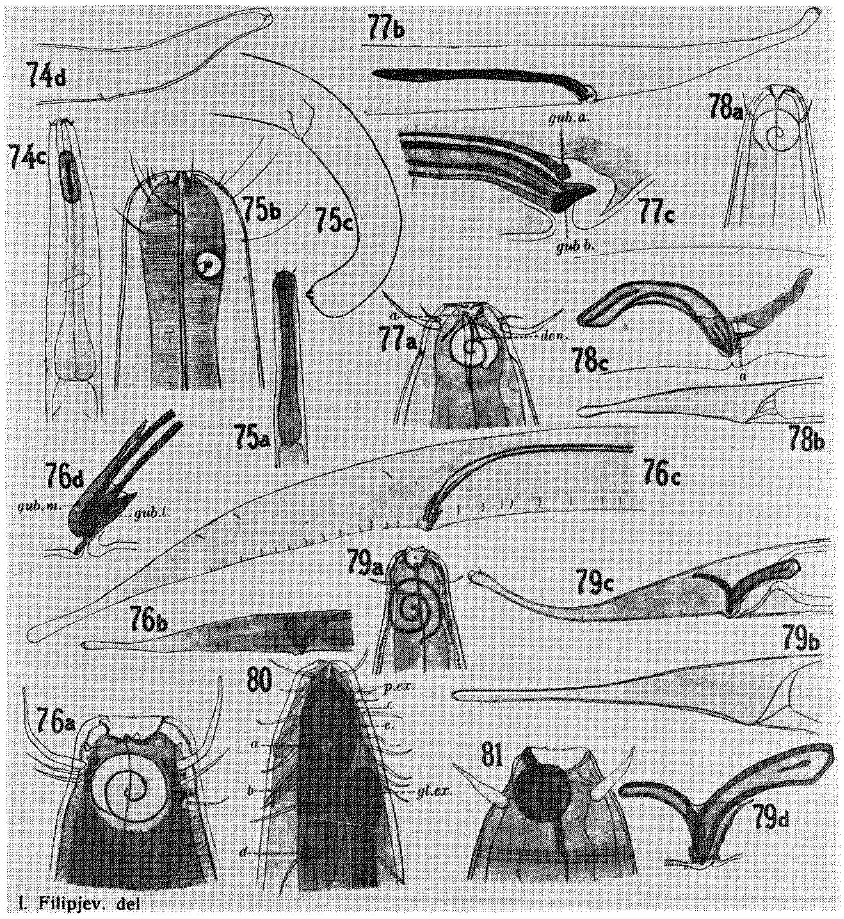


TABLE 10



I. Filipjev. del.

TABLE 11



I. Filipjev. del

# INDEX

[This index is reproduced photographically from the Russian original and covers both the present volume and Part I. The references are to Russian page numbers, which are indicated in the left-hand margin of the English text.]

Bold face entries indicate families and subfamilies.

Italics indicate synonyms of genera, families and subfamilies.

Bold face numbers indicate the page in the systematic section, where a survey of the species or references to the genus are given.

The index gives only pages with detailed information on the structure of the genus.

*Other IPST Titles of Interest to Readers of This Book—Translated from Russian*

FREE-LIVING MARINE NEMATODES OF THE SEVASTOPOL AREA
I. N. Filip’ev—*Russian Academy of Sciences—Petrograd,* 1918
IPST cat. no. 1921 272 pages

PLANT-PARASITIC NEMATODES
A. A. Paramonov—*Academy of Sciences of the USSR—Moscow,* 1962
IPST cat. no. 1930 400 pages

HELMINTHOFAUNA OF MARINE MAMMALS (ECOLOGY AND PHYLOGENY)
S. L. Delyamure—*Academy of Sciences of the USSR—Moscow,* 1955
IPST cat. no. 1886 532 pages

CONTRIBUTIONS TO HELMINTHOLOGY: PUBLISHED TO COMMEMORATE THE 60TH BIRTHDAY OF PROF. R. S. SHUL’TS
Editors: S. N. Boev and others—*The Kazakh State Publishing House—Alma-Ata,* 1958
IPST cat. no. 1929 360 pages

ORIGIN AND EVOLUTION OF PARASITISM IN THE HYMENOPTERA PARASITICA AND DEVELOPMENT OF THEIR FAUNA IN THE USSR
N. A. Telenga—*Academy of Sciences of the Ukrainian SSR—Kiev,* 1952
IPST cat. no. 5506 136 Russian pages

ESSENTIALS OF NEMATODOLOGY. VOLUME VI
K. I. Skrjabin, N. P. Shikhobalova, and I. V. Orlov—*Academy of Sciences of the USSR—Moscow,* 1957
IPST cat. no. 5509 581 Russian pages

*IPST is publishing a wide range of books in all fields of science. Full details of all books and series, including those mentioned above, will be found in the IPST GENERAL CATALOGUE which is available from booksellers specializing in scientific literature, or direct from the publishers.*

**ISRAEL PROGRAM FOR SCIENTIFIC TRANSLATIONS**
KIRYAT MOSHE, P.O. BOX 7145, JERUSALEM, ISRAEL. CABLES: MATAM

Cover designed by S. Bar-Lev
Printed in Jerusalem, Israel [5458]