THE

CAMBRIDGE NATURAL HISTORY

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VOLUME II

FLATWORMS AND MESOZOA

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THREAD-WORMS AND SAGITTA

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GEPHYREA AND PHORONIS

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PLATYHELMINTHES AND MESOZOA

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CHAPTER I

TURBELLARIA

INTRODUCTION: DESCRIPTION OF THE POLYCLAD *LEPTOPLANA TREMELLARIS*—APPEARANCE—HABITS—STRUCTURE: POLYCLADIDA—CLASSIFICATION—HABITS—ANATOMY—DEVELOPMENT: TRICLADIDA—OCCURRENCE—STRUCTURE—CLASSIFICATION: RHABDOCOELIDA—OCCURRENCE—HABITS—REPRODUCTION—CLASSIFICATION.

The Platyhelminthes, or Flat Worms, form a natural assemblage of animals, the members of which, however widely they may differ in appearance, habits, or life-history, exhibit a fundamental similarity of organisation which justifies their separation from other classes of worms, and their union into a distinct phylum. Excluding the leeches (Hirudinea), and the long sea-worms (Nemertinea)—which, though formerly included, are now treated independently—the Platyhelminthes may be divided into three branches: (1) Turbellaria (including the Planarians), (2) Trematoda (including the liver-flukes), and (3) Cestoda (tape-worms). The Mesozoa will be treated as an appendix to the Platyhelminthes.

The Turbellaria were so called by Ehrenberg[1] (1831) on account of the cilia or vibratile processes with which these aquatic animals are covered, causing by their incessant action, tiny currents ("turbellae," disturbances) in the surrounding water. The ciliary covering distinguishes this free-living group from the parasitic Trematodes and Cestodes, some of which possess such an investment, but only during their early free

[1] Hemprich and Ehrenberg, *Symbolae physicae*, Berlin, fol. 1831.

larval stage, for the short period when they have left the parental host and are seeking another (Figs. 26, 27, 42).

Some Turbellaria (Rhabdocoelida) resemble Infusoria in their minute size, shape, and movements. Nevertheless they possess an organisation of considerable complexity. The fresh-water Planarians (Fig. 14), abounding in ponds and streams, vary from a quarter to half an inch in length, and are elongated and flattened. Their body is soft, and progresses by a characteristic, even, gliding motion like a snail. The marine Planarians or Polyclads (Fig. 8) are usually broad and leaf-like, sometimes attaining a length of six inches, and swim or creep in a most graceful way. Land Planarians occur in this country (Fig. 15), but far more abundantly in tropical and sub-tropical districts, in moist places, venturing abroad at night in pursuit of prey. They are elongated and cylindrical, in some cases measuring, when fully extended, a foot or more in length, and are often ornamented with brilliantly coloured, longitudinal bands.

Turbellaria are carnivorous, overpowering their prey by peculiar cutaneous offensive weapons, and then sucking out the contents of the victim by the "pharynx." Land Planarians feed on earthworms, molluscs, and wood-lice; fresh-water Planarians on Oligochaet worms, water-snails, and water-beetles; marine forms devour Polychaet worms and molluscs. Some Turbellaria seem to prefer freshly-killed or weakly examples of animals too large to be overpowered when fully active. Certain Rhabdocoelida are messmates of Molluscs and Echinoderms, and a few others are truly parasitic —a mode of life adopted by all Trematodes save *Temnocephala*.

The Trematodes[1] may be divided into those living on the outer surface of various aquatic animals, usually fish (Ectoparasites); and those which penetrate more or less deeply into the alimentary canal or the associated organs of the host (Endoparasites). They are oval, flattened Platyhelminthes ranging from a microscopic size to a length of three feet (*Nematobothrium*, Fig. 22), and are provided with organs of adhesion by which they cling to the outer surface, or to the interior, of the animals they inhabit. Trematodes occur parasitically in all groups of Vertebrates, but, with the exception of the liver-flukes of the sheep (*Distomum hepaticum* and *D. magnum*), and of *Bilharzia haematobia* found in man (in the blood-vessels of the urinary bladder) over the greater part

[1] Τρῆμα, a hole; referring to the orifices of the suckers.

of Africa, their attacks are not usually of a serious nature. Ecto-parasitic Trematodes are *Monogenetic;* that is, their larvae grow up directly into mature forms. The Endoparasitic species, however, are usually *Digenetic.* Their larvae enter an Invertebrate and produce a new generation of different larvae, and these another. The last are immature flukes. They enter a second host, which is swallowed by the final Vertebrate host in which they become mature.

The Cestodes or Tape-worms have undergone more profound modifications both in structure and in mode of development. They are all endoparasitic, and, with one exception (*Archigetes*), attain maturity solely within the alimentary canal of Vertebrates. In length they range from a few millimetres to several metres, but this great size is attained from the need for the rapid production and accumulation of enormous numbers of eggs. The "head" or "scolex" is attached to the mucous membrane of the host by suckers or hooks, but there is no mouth nor any certain trace of a digestive tract at any stage of the life-history of Cestodes. For nourishment they absorb, through the skin, the previously-digested food (of the host) that bathes them. In a few Cestodes the body is simple and not divided into "proglottides" or generative segments, but in most cases it is jointed in such a way that the last segment is the oldest, and each contains a set of reproductive organs. The life-histories of Cestodes are most remarkable. The proglottides containing the eggs pass out of the final host along with the faeces and enter the intermediate host with the food. The larvae hatch, and boring their way into the blood-vessels, are carried by the circulation to various internal organs. Here they usually become "bladder-worms," and develop the "head" of the future sexual form. Then, if, as is usually the case, the intermediate host is preyed upon by the final host, the larval Cestodes enter the alimentary canal of the latter. The head of the larva alone survives digestion, and from it the mature worm is formed.

Of these three branches of the phylum Platyhelminthes, the Turbellaria possess features of special interest and importance. Not only do they furnish the explanation of the structure of the two parasitic groups (which have probably arisen from Turbellarian-like ancestors), but they occupy the lowest position in the whole group of worms. There are reasons for thinking that this is the simplest group of bilateral animals which adopt the habit of creeping. The Turbellaria are most closely allied to that great extinct group from which they, the Nemertinea, Rotifera, and even the Annelids, offer increasingly convincing evidence of having been derived. Many questions relating to the affinities of, or the origin of organs in, the Annelids, resolve themselves into similar questions about the Turbellaria. For these reasons, this group is here dealt with at greater length than the others, the interest of which is of a more special nature.

The history of our knowledge of the Cestodes dates back to ancient times, as the presence and effects of tape-worms early attracted the attention of physicians. Trematodes are first distinctly referred to in the sixteenth century, while Turbellaria first figure in Trembley's memoir on Hydra (1744).[1] The whole subject of the increase in our knowledge of parasitic Platyhelminthes is dealt with in the standard work, *The Parasites of Man*, by Leuckart,[2] and a complete list of references in zoological literature to Cestodes and Trematodes is to be found in Bronn's *Thierreich*.[3] O. F. Müller[4] and Ehrenberg founded our knowledge of the Turbellaria, but for a long time the group remained in a most neglected condition. In this country Montagu, G. Johnston, and in Ireland, William Thompson, discovered several marine species, one of which, *Planocera folium* (from Berwick), has not again been met with on British shores. Dalyell[5] conducted classical researches on the habits of Planarians, and Faraday[6] made interesting experiments on their power of regenerating lost parts. The credit of assigning the correct interpretation to most of the various organs of fresh-water Planarians belongs to von Baer[7] and Dugès,[8] while Mertens[9] effected a similar service for the marine forms, or Polyclads. The minute Rhabdocoels were first successfully investigated and classified by Oscar Schmidt.[10] The great work on this group is, however, the

[1] *Mémoires pour servir à l'histoire d. Polypes d'eau douce*, Leyden, 1744.

[2] *Die Parasiten des Menschen*, 1879——. Engl. Transl. by W. E. Hoyle, i. 1886.

[3] Band 4, by M. Braun. (Mesozoa and Trematoda completed; Cestoda in progress.)

[4] *Verm. terr. et fluv. . . . succincta historia*, 1773; *Zool. Danica*, 1777.

[5] *Observations on Planariae*, Edinburgh, 1813.

[6] M. Faraday, "On the Planariae," *Medical Gazette*, Feb. 1832; and in *Edinburgh New Philosoph. Journal*, vol. xiv. 1833, pp. 183-189.

[7] *Nov. Act. Acad. Caes. Leop.-Carol.* tom. xiii. 1827.

[8] *Ann. Sci. Nat.* (Zool.) I. tom. xv. 1828.; *ibid.* tom. xxi. 1830.

[9] *Mém. Acad. St. Pétersbourg*, 5th ser. tom. ii. 1832.

[10] *Die rhabdocoelen Turbellarien des Süsswassers.* Jena 1848.

monograph by von Graff.[1] A similarly comprehensive and indispensable treatise by Lang, on the Polycladida,[2] contains references to all previous publications on the group, among which the papers by Quatrefages, Johannes Müller, Keferstein, Minot, and Hallez stand out conspicuously. Moseley's work[3] on the Land Planarians of Ceylon is undoubtedly the most revolutionary paper referring to this group, and the best contribution towards elucidating the structure of the Tricladida at a time when the subject was very obscure. A monograph on Land Planarians is being prepared by von Graff.

The Turbellaria are divided into: (1) *Polycladida*, marine forms with multiple intestinal branches; (2) *Tricladida*, marine, fresh-water, and terrestrial Planarians with three main intestinal branches; (3) the *Rhabdocoelida*, as varied in habit as the Triclads, but possessing a straight and simple or slightly lobed, intestine. A detailed description of an example of the Polyclads, and then a comparative account of each division, will now be given.

Fig. 1.—*Leptoplana tremellaris* O. F. M. Seen from the dorsal surface. The alimentary canal runs down the middle line and sends branches to the margin of the body. × 6.

Turbellaria. I. Polycladida.

Description of Leptoplana tremellaris.

Appearance and Habits.—An account of the Polyclad Turbellaria may be fitly prefaced by a description of a very common representative, *Leptoplana tremellaris*, so called on account of the thin, flat body which executes when disturbed, quivering or tremulous swimming movements.

[1] *Monographie d. Turbellarien.* I. Rhabdocoelida, 1882. Die Acoela, Leipzig, 1892.

[2] "Die Polycladen," *Fauna u. Flora d. Golfes v. Neapel*, Monogr. XI. 1884.

[3] *Phil. Trans.* 1874, p. 105.

Like all Polyclads, *Leptoplana* is marine. It is probably found on all European shores, northwards to Greenland and southwards to the Red Sea, while vertically it ranges from the littoral zone down to fifty fathoms. There is, however, an apparently well-marked difference between the littoral specimens, which vary from three-quarters to one inch in length, are brownish in colour and firm in consistency, and the more delicate examples half an inch long, white with a brown tinge, which occur in deeper water.

At low water *Leptoplana* may be found buried in mud or on the under surface of stones, in pools where darkness and dampness may be ensured till the return of the tide. It is, however, by no means easy to detect and remove it from the encrusting

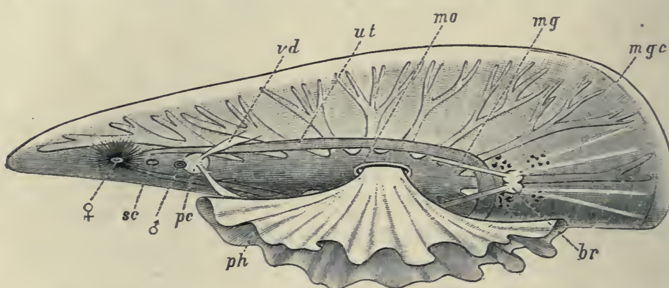

FIG. 2.—*Leptoplana tremellaris.* Three-quarters view from the ventral surface. The pharynx (*ph*) is widely protruded through the mouth (*mo*) as in the act of attacking prey. *br*, Brain with nerves, close to which are the four groups of eyes; *mg*, stomach; *mgc*, "marginal groove"; *pe*, penis; *sc*, sucker; *ut*, uterus; *vd*, vasa deferentia; ♀, female genital aperture surrounded by the shell-gland; ♂, male aperture. (Semi-diagrammatic, and × 6.)

Polyzoa, Ascidians, or Sponges with which it is usually associated. The flat, soft, unsegmented body is so closely appressed to the substratum that its presence is usually only betrayed by its movement, an even gliding motion of the mobile body, which suggested the apt name "la pellicule animée" to Dicquemare. The creeping surface is called ventral, the upper one dorsal, and as the broader end of the body always goes first, it is anterior as opposed to the more pointed posterior extremity. With a lens the characters shown in Figs. 1 and 2 may be observed. The eyes are seen as black dots near the anterior end, and are placed at the sides of a clear oval space, the brain. Along the transparent margin of the body, the ends of the intestinal branches may be seen. These ramify from a lobed stomach or main-gut, and should the specimen be mature, the "uterus" loaded with eggs forms a dark margin round the latter (Figs. 1 and 2, *ut*). The ventral surface is whitish, and through it the "pharynx," a frilled protrusible structure, may be dimly observed. The "mouth,"[1] through which the pharynx at the time of feeding

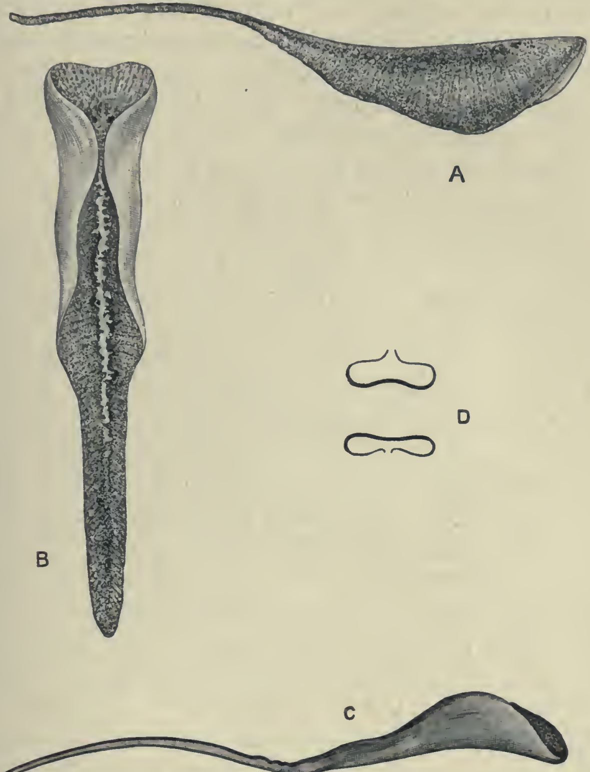

FIG. 3.—*Leptoplana tremellaris* in the act of swimming. **A,** Seen from the right side during the downward stroke (the resemblance to a skate is striking); **B**, from above, showing the upward stroke and longitudinal undulations of the swimming lobes; **C,** side view during the upward stroke; **D,** transverse sections of the body during the strokes. × 5.

is thrust out (Fig. 2, *mo*), is almost in the centre of the ventral surface. Behind this, a white, V-shaped mark (*vd*) indicates the ducts of the male reproductive organs, and still further back is the irregular opaque mark of the "shell-gland," by which the egg-shells are formed (Fig. 2, ♀).

[1] Since no food, but only the pharynx, passes through this "mouth," the term is unfortunate. Moreover the true mouth is the aperture placing the stomach in communication with the pharynx (Fig. 5, *gm*).

Leptoplana employs two kinds of movement, creeping and swimming. Creeping is a uniform gliding movement, caused by the cilia of the ventral surface, aided perhaps by the longitudinal muscular layers of this surface, and is effected on the under side of the "surface-film" of water almost as well as on a solid substratum. Swimming is a more rapid and elegant movement, employed when alarmed or in pursuit of prey. The expanded fore-parts of the body act as lobes, which are flapped rapidly up over the body and then down beneath it, undulations running rapidly down them from before backwards. The action in fact is somewhat similar to that by which a skate swims, a resemblance pointed out long ago by Dugès[1] (Fig. 3).

We have few direct observations on the nature of the food of *Leptoplana*, or the exact mode by which it is obtained. Dalyell,[2] who observed this species very carefully, noticed that it was nocturnal and fed upon a *Nereis*, becoming greatly distended and of a green colour after the meal, but pale after a long fast. Keferstein[3] noticed a specimen in the act of devouring a *Lumbriconereis* longer than itself, and also found the radulae of *Chiton* and Taenioglossate Molluscs in the intestine. That such an apparently weak and defenceless animal does overpower large and healthy Annelids and Mollusca, has not hitherto been definitely proved. Weak or diseased examples may be chiefly selected. The flexible *Leptoplana* adheres firmly to its prey, and the rapid action of the salivary glands of its mobile pharynx quickly softens and disintegrates the internal parts of the victim. The food passes into the stomach (Fig. 2, *mg*), and is there digested. It is then transferred to the lateral branches of the intestine, and, after all the nutritious matters have been absorbed, the faeces are ejected with a sudden contraction of the whole body through the pharynx into the water.

Leptoplana probably does not live more than a year. In the spring or summer, batches of eggs are laid and fixed to algae or stones by one individual, after having been fertilised by another. Young *Leptoplana* hatch out in two to three weeks, and lead a

[1] *Ann. Sci. Nat.* 1 sér. tom. xv. 1828, p. 146. "La Planaire trémellaire . . . peut parcourir . . . en faisant battre rapidement ses parties laterales à la manière des larges nageoires des Raies."

[2] *Observations on Planariae.* Edinburgh, 1813, p. 12.

[3] "Zur Anat. u. Entwickl. einiger Seeplanarien v. St. Malo," *Abh. K. Gesellschaft d. Wiss.* Göttingen, 1868.

pelagic existence till they are three or four millimetres in length. In late summer, numbers of such immature examples may be found among sea-weeds and *Corallina* in tide pools. In the succeeding spring they develop first the male and then the female reproductive organs.

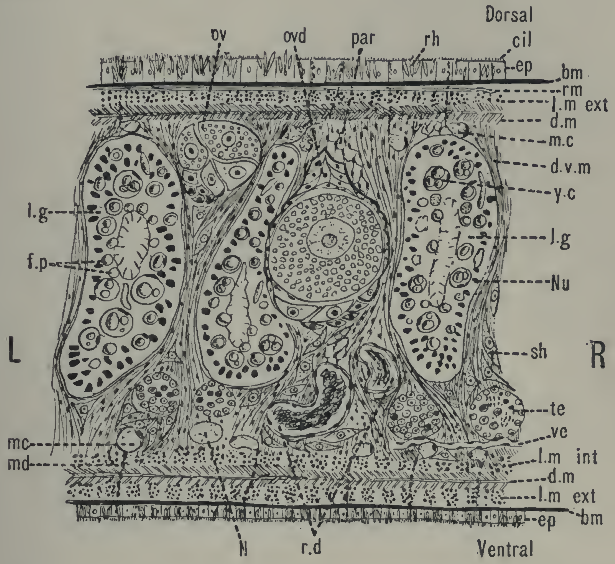

FIG. 4.—Portion of a transverse section of *Leptoplana tremellaris* in the hinder part of the body. × 100. *bm*, Basement (skeletal) membrane; *cil*, cilia; *d.m*, diagonal muscles; *d.v.m*, dorso-ventral muscles; *ep*, epidermis; *f.p*, food particles: *l.g*, lateral intestinal branches cut across; *l.m ext*, external, and *l.m int*, internal longitudinal muscle layers; *m.c*, glandular (mucous) cells; *md*, their ducts; *N*, longitudinal nerve; *Nu*, nuclei of the intestinal epithelium; *ov*, ovary; *ovd*, oviduct; *par*, cells of the parenchyma; *r.d*, vasa deferentia, with spermatozoa; *rm*, circular musculature; *rh*, rhabdites; *sh*, cells of the shell-gland; *te*, testes; *ve*, vasa efferentia; *y.c*, "yellow cells." (After Lang.)

Anatomy of Leptoplana tremellaris.—*Leptoplana* may be divided into corresponding halves only by a median vertical longitudinal plane. The body and all the systems of organs are strictly bilaterally symmetrical. Excepting the cavities of the organs themselves, the body is solid. A connective "parenchyma" (Fig. 4, *par*) knits the various internal organs together, while it allows free play of one part on another. These organs are enclosed in a muscular body-wall, clothed externally by the ciliated epidermis, which is separated from the underlying musculature by a strong membrane (Fig. 4, *bm*), the only skeletal element in the body.

Body-Wall.—The epidermis (Fig. 4, *ep*) is composed of a single layer of ciliated cells, containing small, highly refractive, pointed rods or "rhabdites" (*rh*), and gives rise to deeply-placed mucous cells (*m.c*), which are glandular and pour out on the surface of the body a fluid in which the cilia vibrate. The tenacious hold on a stone which *Leptoplana* exerts if suddenly disturbed, or when grasping its prey, is probably due to the increased glutinous secretion of these glands, aided perhaps by rhabdites, which on such occasions are shot out in great numbers. The basement membrane is an elastic skeletal membrane composed of stellate cells embedded in a firm matrix. It serves chiefly for the origin and insertion of the dorso-ventral muscles (*d.v.m*). Under the basement membrane lies a very thin layer of transverse muscular fibres (Fig. 4, *rm*), which are, however, apparently absent on the ventral surface. Then follows a stout layer of longitudinal fibres (*l.m ext*), and beneath this a diagonal layer (*d.m*), the fibres of which intersect along the median line in such a way that the inner fibres of one side become the outer diagonal fibres of the other. Lastly, within this again, on the ventral surface, is a second stout longitudinal layer (*l.m int*). The sucker (*sc*, Figs. 2 and 5) is a modification of the body-wall at that point. In addition to the dorso-ventral muscles, there exists a complex visceral musculature regulating the movements of the pharynx, intestine, and copulatory organs.

Parenchyma.—The spaces between the main organs of the body are filled by a tissue containing various kinds of cells, salivary glands, shell-glands, and prostate glands. Besides these, however, we find a vacuolated, nucleated, thick-walled network, and to this the word parenchyma is properly applied. Besides its connective function, the parenchyma confers that elasticity on the body which *Leptoplana* possesses in such a high degree. Pigment cells are found in the parenchyma in many Polyclads.

Digestive System.—The general arrangement of this system may be seen in Figs. 2, 5, and 7; and may be compared, especially when the pharynx is protruded, as in Fig. 2, with the gastral system of a Medusa. The "mouth" (there is no anus) is placed almost in the centre of the ventral surface. It leads (Fig. 7, B, *phs*) into a chamber (the peripharyngeal space) divided into an upper and a lower division by the insertion of a muscular collar-fold (the pharynx, *ph*), which may be protruded, its free lips advancing, through the mouth (Fig. 2), and is then capable of enclosing by its mobile frilled margin, prey as large as *Leptoplana* itself. The upper division of the chamber communicates by a hole in its roof[1] (the true mouth, Figs. 5 and 7, *g.m*) with the cavity of the main-gut or stomach (*m.g*), which runs almost the length of the body in the middle line, forwards over the brain (Fig. 5, *up*). Seven pairs of lateral gut-branches convey the digested food to the various organs, not directly however, but only after the food mixed with sea-water has been repeatedly driven by peristalsis first towards the blind end of the gut-branches and then back towards the stomach. Respiration is probably largely effected by this means. The epithelium of the intestine (Fig. 4, *l.g*) of a starving specimen is composed of separate flagellated cells frequently containing "yellow cells."[2] After a meal, however, the cell outlines are invisible. Gregarines, encysted Cercariae, and Orthonectida[3] occur parasitically in the gut-branches.

An **excretory system** of "flame-cells" and fine vessels has hitherto been seen only by Schultze[4] in this species, which will not, however, resist intact the compression necessary to enable the details to be determined. They are probably similar to those of *Thysanozoon* described on p. 25.

Nervous System.—The brain, which is enclosed in a tough capsule (Fig. 5, *br*), is placed in front of the pharynx, but some distance behind the anterior margin of the body. It is of an oval shape, subdivided superficially into right and left halves by a shallow depression, and is provided in front with a pair of granular-looking appendages, composed of ganglion-cells from which numerous sensory nerves arise, supplying the eyes and anterior region. Posteriorly the brain gives rise to a chiefly motor, nervous sheath (Fig. 5, *nn*), which invests the body just within the musculature. This sheath is thickened along two ventral lines (Fig. 5, *ln*) and two lateral lines (*n.s*), but is very slightly developed on the dorsal surface. Ganglion-cells occur on the course of the nerves, and are particularly large at the point of origin of the great motor nerves.

Sense Organs.—*Leptoplana* possesses eyes, stiff tactile, mar-

[1] The roof of the peripharyngeal chamber is hence known as the "diaphragm."

[2] See Brandt, *Fauna u. Flora d. Golfes v. Neapel*, Monogr. XIII. 1885, p. 65.

[3] See p. 94.

[4] *Verhandlungen d. med. Gesellschaft zu Würzburg*, iv. 1854, p. 223.

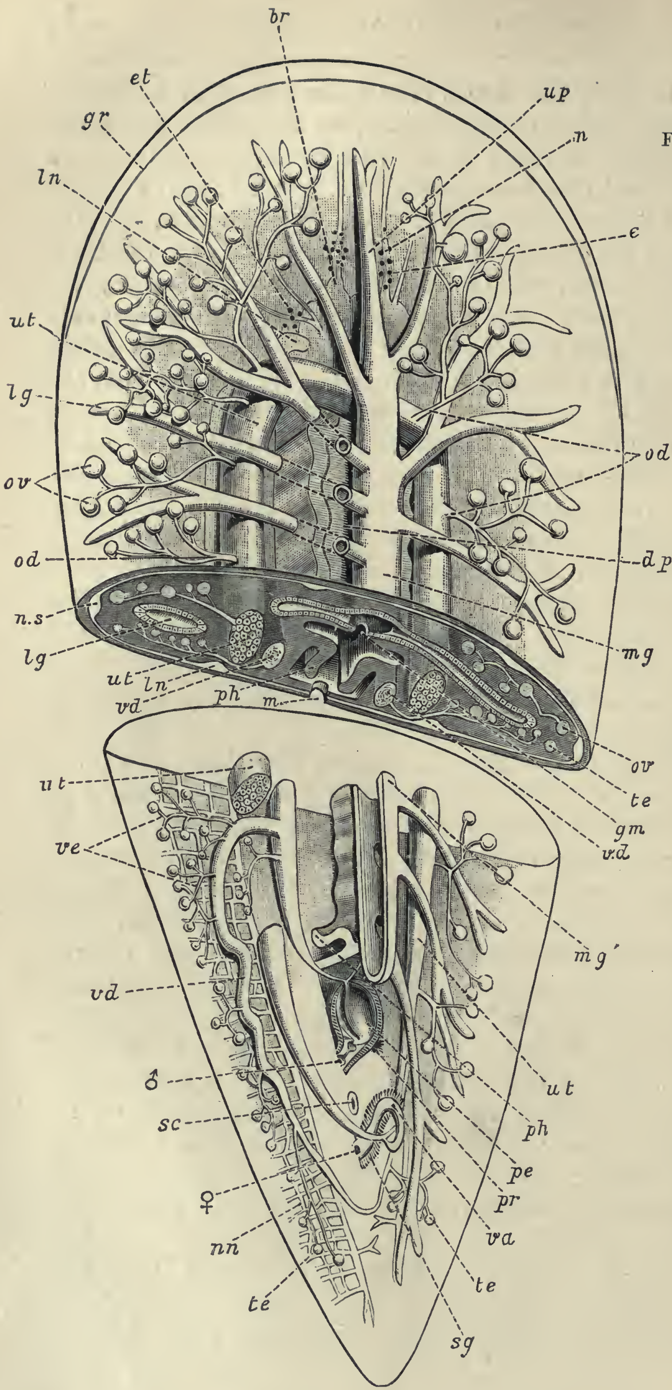

FIG. 5.—Diagrammatic view of the structure of *Leptoplana tremellaris* as a type of the Polycladida. The body is cut across the middle to show the relative position of organs in transverse section. In the posterior half the alimentary canal has been bisected and removed from the left side, to exhibit the deeply placed nervous sheath (*nn*) and the male reproductive organs. *br*, Brain; *dp*, "diaphragm"; *e*, cerebral group of eyes; *et*, tentacular eye-group; *gr*, marginal groove; *gm*, true mouth; *lg*, lateral gut-branch; *ln*, longitudinal nerve stem; *m*, external mouth; *mg*, *mg′*, main-gut, whole, and bisected; *n*, sensory nerve supplying the eyes; *nn*, nervous network lying on the ventral musculature; *n.s*, lateral nerve; *od*, oviduct; *ov*, ovary; *pe*, penis (in section); *ph*, pharynx; *pr*, prostate or "granule gland"; *sc*, sucker; *sg*, shell-gland; *te*, testes; *vp*, anterior unpaired gut-branch; *ut*, uterus; *va*, vagina (in section); *vd*, vas deferens; *ve*, vasa efferentia; ♂, male genital pore; ♀, female pore.

ginal cilia, and possibly a sense organ in the "marginal groove." The eyes, which are easily seen as collections of black dots lying at the sides of the brain, may be divided into two paired groups: (1) cerebral eyes (Fig. 5, *e*), and (2) tentacle eyes (*et*), which indicate the position of a pair of tentacles in allied forms (Fig. 8, A, *t* and B). Each ocellus consists of a capsule placed at right angles to the surface of the body in the parenchyma, below the dorsal muscles, and with its convex face outwards. It is a single cell in which pigment granules have accumulated. The light, however, can only reach the refractive rods, which lie within it, obliquely at their outer ends. These rods are in connexion with the retinal cells, and thus communicate by the optic nerve with the brain. The cerebral eyes are really paired, and are directed some upwards, some sideways, some downwards.

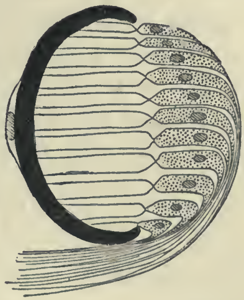

FIG. 6.—Diagram of an eye of *Leptoplana* from the tentacle group. × 600. (After Lang.)

The "marginal groove" is a shallow depression of the epidermis (Fig. 5, *gr*) lined by cilia, and containing the ducts of very numerous gland-cells. It runs almost parallel to the anterior margin of the body, a short distance from it, but we have no observations on its functions.

Reproductive Organs.—*Leptoplana* is hermaphrodite, and, as in most hermaphrodites, the reproductive organs are complicated. The male organs are the first to ripen, but this does not appear to prevent an overlapping of the periods of maturity of the male and female products, so that when the eggs are being laid, the male organs are, apparently, still in a functional state. The principal parts are seen in Fig. 5. The very numerous *testes* (*te*) are placed ventrally, and are connected with fine *vasa efferentia* (*ve*), which form a delicate network opening at various points into the two *vasa deferentia* (*vd*). These tubes, especially when distended with spermatozoa, may easily be seen (Fig. 2, *vd*) converging at the base of the penis, and connected posteriorly by a loop that runs behind the female genital pore (Fig. 5). The *penis* (*pe*) is pyriform and muscular, and is divided into two chambers, a large upper one for the spermatozoa, and a smaller lower one for the secretion of a special "prostate" gland. The apex of the penis is eversible and not merely protrusible, being turned inside out when evaginated. The *ovaries* (Fig. 5, *ov*) are numerous and somewhat spherical. They are dorsally placed, but when fully developed extend deeply wherever they can find room to do so, and they not only furnish the ova, but elaborate food-yolk in the ova, as there are no special yolk-glands. The slender *oviducts* (*od*) open at several points into the "uterus" (*ut*) (a misnomer, as no development takes place within it), which encircles the pharynx, and opens by a single duct into the *vagina* (*va*). Here the ova are probably fertilised, and one by one invested by the *shell-gland* (*sg*) with a secretion which hardens and forms a resistant shell. They are then laid in plate-like masses which are attached to stones or shells. The development is a direct one, and the young *Leptoplana*, which hatches in about three weeks, has the outline of a spherical triangle, and possesses most of the organs of the adult. After leading a floating life for a few weeks it probably attains maturity in about nine months.

Classification, Habits, and Structure of the Polycladida.

The Polyclads were so called by Lang on account of the numerous primary branches of their intestine. They are free-living, purely marine Platyhelminthes, possessing multiple ovaries, distinct male and female genital pores (Digonopora), but no yolk-glands. The eggs are small, and in many cases give rise to a distinct larval form, known as "Müller's larva" (Fig. 12). The Polyclads, with one exception,[1] fall into two sub-groups, Acotylea and Cotylea :—

Character.	Acotylea.	Cotylea.
Sucker	A sucker absent.[2]	A sucker always present (Figs. 8, D, *s*; 7, A, *sc*).
Mouth	In the middle, or behind the middle, of the ventral surface.	In the middle, or in front of the middle, of the ventral surface.
Pharynx	More or less intricately folded.	Rarely folded. Usually cylindrical or trumpet-shaped.
Tentacles	A pair of dorsal tentacles usually present.	A pair of marginal tentacles (except in *Anonymus*).
Development	Usually direct. Larva when present, not a typical Müller's larva.	Müller's larva present. Metamorphosis, however, extremely slight.

[1] *Enantia spinifera* Grff. *Mittheil. d. Naturwiss. Verein. f. Steiermark*, 1889.

[2] The sucker of *Leptoplana tremellaris* probably does not correspond with that of the Cotylea.

Fig. 8 shows that, starting with a member (A, D) of each division, in which the mouth is almost in the middle of the ventral surface, and the brain and sense organs somewhat remote from the anterior end, we find in the Acotylea a series leading to an elongated form (Cestoplanidae), in which the mouth, pharynx, and genital pores are far back near the hinder

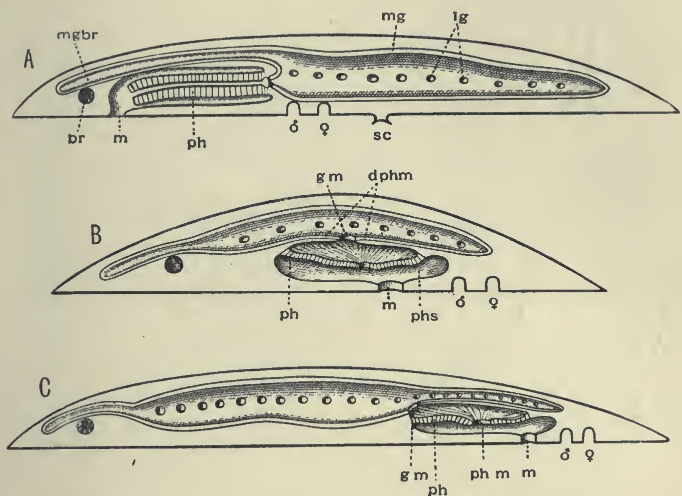

Fig. 7.—Diagrammatic vertical longitudinal sections: **A**, Of *Prosthiostomum* (type of Cotylea); **B**, of *Leptoplana;* **C**, of *Cestoplana* (types of Acotylea). (After Lang.) These figures illustrate the changes which follow the shifting of the mouth from a central position (**B**) to either end of the body. *br*, Brain; *dphm*, "diaphragm"; *gm*, true mouth; *lg*, openings of lateral gut-branches; *m*, mouth; *mg*, main-gut or stomach; *mgbr*, median gut-branch; *ph*, pharynx; *ph.m*, aperture in pharyngeal fold; *phs*, peripharyngeal sheath; *sc*, sucker; ♂, male, and ♀, female, genital aperture.

end of the body; while in the Cotylea the series leads similarly to the elongated Prosthiostomatidae, in which, however, the pharynx and external apertures are in the front part of the body. This view of the morphology of the Polyclads is due to Lang, and is based on the assumption that the more radially-constructed forms (Fig. 8, A, D) are the primitive ones.

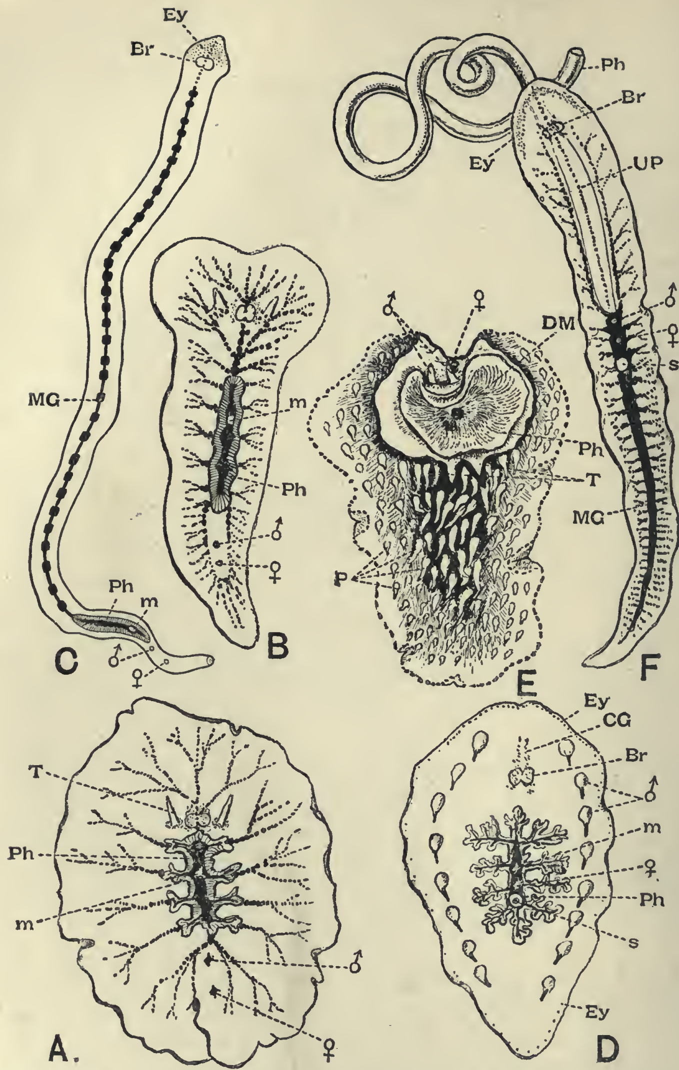

FIG. 8.—Chief forms of Polycladida: **A-C,** Acotylea; **D-F,** Cotylea. **A,** *Planocera graffii* Lang, nat. size; **B,** *Stylochoplana maculata* Stimps, × 7; **C,** *Cestoplana rubrocincta* Lang, × $\frac{4}{5}$; **D,** *Anonymus virilis* Lang, × 3, ventral surface; **E,** *Thysanozoon brocchii* Grube, nat. size; the head is thrown back and the pharynx (*ph*) is protruded. **F,** *Prosthiostomum siphunculus* Lang, × 3. *Br*, Brain; *CG*, cerebral eye group; *DM*, true mouth; *Ey*, marginal eyes; *m*, mouth; *MG*, main-gut or stomach; *P*, dorsal papillae; *Ph*, pharynx; *s*, sucker (ventral); *T*, tentacles; *UP*, dorsal median gut-branch. ♂, male, and ♀, female, genital aperture, except in **D,** where ♂ refers to the multiple penes. (After Lang and Schmidt.)

Classification of Polycladida.

ACOTYLEA.

Family.	Genus.	British Representatives.
PLANOCERIDAE. With dorsal tentacles. Mouth sub-central.	*Planocera* (Fig. 8, A). *Imogine.* *Conoceros.* *Stylochus.* *Stylochoplana* (Fig. 8, B). *Diplonchus.* *Planctoplana.*	*Planocera folium* Grube. Berwick-on-Tweed. *Stylochoplana maculata* Quatref. Among brown weeds in Laminarian zone.
LEPTOPLANIDAE. Without dorsal tentacles. Penis directed backwards.	*Discocelis.* *Cryptocelis.* *Leptoplana.* *Trigonoporus.* ? *Polypostia* (see p. 27).	*Leptoplana tremellaris* O. F. Müll. *L. fallax* Quatref. Plymouth. *L. droebachensis* Oe. Plymouth Sound. *L. atomata* O. F. Müll. Doubtful species.
CESTOPLANIDAE. No tentacles. Body elongated. Penis directed forwards.	*Cestoplana* (Fig. 8, C). In Mediterranean and on French side of the Channel.	
ENANTIIDAE. No sucker. No tentacles. Main-gut very short. External apertures as in *Euryleptidae.*	*Enantia.* Adriatic Sea.	

COTYLEA.

Family.	Genus.	British Representatives.
ANONYMIDAE. Mouth central. No tentacles. With two rows of penes.	*Anonymus* (Fig. 8, D). Naples (two specimens).	
PSEUDOCERIDAE. Marginal tentacles folded. Mouth in anterior half.	*Thysanozoon* (Fig. 8, E). *Pseudoceros.* *Yungia.*	
EURYLEPTIDAE. Tentacles usually present and pointed, or represented by two groups of eyes. Mouth close to anterior end. Pharynx cylindrical.	*Prostheceraeus.* *Cycloporus.* *Eurylepta.* *Oligocladus.* *Stylostomum.* *Aceros.*	*Prostheceraeus vittatus* Mont. On west coast. *P. argus* Quatref. Guernsey. *Cycloporus papillosus* Lang. On Ascidians in 2-30 fms. *Eurylepta cornuta* O. F. Müll. On sponges and shells, 2-10 fms. *Oligocladus sanguinolentus* Quatref. *O. auritus* Clap. Doubtful. *Stylostomum variabile* Lang.
PROSTHIOSTOMATIDAE. Tentacles absent. Body elongated. Pharynx long, cylindrical. Penis with accessory muscular vesicles.	*Prosthiostomum* (Fig. 8, F).	

Appearance and Size of Polyclad Turbellaria.—Polyclads are almost unique amongst animals in possessing a broad and thin, delicate body that glides like a living pellicle over stones and weeds, moulding itself on to any inequalities of the surface over which it is travelling, yet so fragile that a touch of the finger will rend its tissues and often cause its speedy dissolution. The dorsal surface in a few forms is raised into fine processes (*Planocera villosa*), or into hollow papillae (*Thysanozoon brocchii*), and in very rare cases may be armed with spines (*Acanthozoon armatum*,[1] *Enantia spinifera*); in others, again, nettle-cells (nematocysts) are found (*Stylochoplana tarda*, *Anonymus virilis*). Some Polyclads, especially the pelagic forms, are almost transparent; in others, the colour may be an intense orange or velvety black, and is then due to peculiar deposits in the epidermal cells. Between these two extremes the colour is dependent upon the blending of two sources, the pigment of the body itself and the tint of the food. Thus a starved *Leptoplana* is almost or quite white, a specimen fed on vascular tissue reddish. Many forms are coloured in such a way as to make their detection exceedingly difficult, but this is probably not merely due, as Dalyell supposed, to the substratum furnishing them with food and thus colouring them sympathetically, but is probably a result of natural selection.

The largest Polyclad, the bulkiest Turbellarian, is *Leptoplana gigas* (6 inches long and 4 in breadth), taken by Schmarda, free-swimming, off the coast of Ceylon. The largest European form is *Pseudoceros maximus*, $3\frac{1}{2}$ inches in length and stoutly built. A British species, *Prostheceraeus vittatus*, attains a length of from 2 to 3 inches. These large forms, especially the Pseudoceridae (pre-eminently the family of big Polyclads), are brightly coloured, and usually possess good swimming powers, since, being broad and flat, they are certainly not well adapted for creeping rapidly, and this is well shown by the way these Polyclads take to swimming when in pursuit of prey at night. The size of any individual is determined, amongst other factors, by the period at which maturity sets in, after which probably no increase takes place. Polyclads apparently live about twelve months, and mature specimens of the same species vary from $\frac{1}{2}$ inch to $2\frac{1}{2}$ inches in length (*Thysanozoon brocchii*),

[1] Collingwood, *Trans. Linn. Soc.* 2 ser. vol. i. pt. 3, 1876, p. 83.

showing that growth is, under favourable conditions, very rapid.

Habits of Polyclad Turbellaria.—Polyclads are exclusively marine, and for the most part littoral, animals. Moreover, there is no evidence of their occurrence in those inland seas where certain marine animals (including one or two species of otherwise characteristically marine Rhabdocoelida, p. 46) have persisted under changed conditions. From half-tide mark down to 50 fathoms, some Polyclads probably occur on all coasts, but as to their relative abundance in different seas we have very little accurate information. The southern seas of Europe possess more individuals and species than the northern, and probably the maximum development of the group takes place on the coasts and coral islands of the tropics.[1] No Polyclads have been taken below 60 fathoms; but their delicacy and inconspicuousness render this negative evidence of little value. Six truly pelagic forms, however, are known,[2] and these are interesting on account of their wide distribution (three occurring in the Atlantic, Pacific, and Indian oceans), and also from the distinct modifications they have undergone in relation to their pelagic existence.

Whatever may be the interpretations of the fact, Polyclads are notoriously difficult to detect, and this fact doubtless explains the scanty references to them by the older naturalists who collected even in tropical seas. Lang, who worked seven years at Naples, added to the Mediterranean fauna as many Polyclads as were previously known for all Europe, in spite of the assiduous labours of his predecessors, Delle Chiaje and Quatrefages. Again Hallez, collecting at Wimereux at low-water, obtained some twenty specimens of *Leptoplana tremellaris* in an hour, while some other collectors working by his side could only find two or three. Yet, even making allowance for the difficulty of finding Polyclads, few of them appear to be abundant.

Leptoplana tremellaris is frequently associated with colonies of *Botryllus*, and if separated soon perishes, whereas the free-living individuals are distinctly hardy (Hallez). A closely allied but possibly distinct form lives upon the surface of the Polyzoon

[1] Von Stummer-Traunfels, *Zeitschr. f. wiss. Zool.* Bd. lx. 1895, p. 689.

[2] *Planocera pellucida* Mertens, *P. simrothi* v. Grff., *P. grubei* Grff., *Stylochoplana sargassicola* Mertens, *S. californica* Woodworth, *Planctoplana challengeri* Grff., all belonging to the Planoceridae. See v. Graff, "Pelagische Polycladen," *Zeitschrift f. wiss. Zoologie*, Bd. lv. 1892, p. 190.

Schizoporella, on the French side of the Channel, and cannot long endure separation from its natural habitat, to which it is adaptively coloured. A striking case of protective mimicry is exhibited by *Cycloporus papillosus*, on the British coasts. This species, eminently variable in colour and in the presence or absence of dorsal papillae, is usually a quarter of an inch in length and of a firm consistency. Fixed by its sucker to Polyclinid and other Ascidians, *Cycloporus* appears part and parcel of the substratum, an interesting parallel to *Lamellaria perspicua*,[1] though we are not justified in calling the Polyclad parasitic. Indeed, though a few cases of association between Polyclads and large Gasteropods, Holothurians, and Echinids are known,[2] there is only one case, that of *Planocera inquilina*,[3] in the branchial chamber of the Gasteropod *Sycotypus canaliculatus*, which would seem to bear the interpretation of parasitism. The jet-black *Pseudoceros velutinus* and the orange *Yungia aurantiaca* of the Mediterranean, are large conspicuous forms with no attempt at concealment, but their taste, which is not known, may protect them. Other habits, curiously analogous with devices employed by Nudibranch Mollusca (compare *Thysanozoon brocchii* with *Aeolis papillosa*), emphasise the conclusion that the struggle for existence in the littoral zone has adapted almost each Polyclad to its particular habitat.

As regards the vertical distribution of this group on the British coasts, *Leptoplana tremellaris* has an extensive range, and appears to come from deeper to shallower water to breed.[4] In the upper part of the Laminarian zone, *Cycloporus papillosus*, and, among brown weeds, *Stylochoplana maculata* are found. At and below lowest water-mark *Prostheceraeus vittatus*, *P. argus*, and *Eurylepta cornuta* occur. *Stylostomum variabile* and *Oligocladus sanguinolentus*, though occasionally found between tide-marks, especially in the Channel Islands, are characteristic, along with *Leptoplana droebachensis* and *L. fallax*, of dredge material from 10 to 20 fathoms.

Locomotion.—Locomotion is generally performed by Polyclads at night when in search of food, and two methods, creeping

[1] *Cambridge Natural History*, vol. iii. p. 74.

[2] Lang, "*Polycladen*," p. 629.

[3] Wheeler, *Journal of Morphology*, vol. ix. part 2, 1894, p. 195.

[4] Many Nudibranchiate Mollusca undergo this change of habitat. See Garstang, *Journal of the Marine Biological Assoc.* n.s. i. No. 4, 1890, p. 447.

and swimming, are usually employed—creeping by the cilia, aided possibly, as in the case of some Gasteropod Mollusca, by the longitudinal muscles of the ventral surface; and swimming, by undulations of the expanded margins of the body. In the former case the cilia work in a glandular secretion which bathes the body, and enables them to effect their purpose equally well on different substrata. The anterior region is generally lifted up, exploring the surroundings by the aid of the tentacles, which are here usually present. The rest of the body is closely appressed to the ground.

Swimming is particularly well performed by the Pseudoceridae, certain species of *Prostheceraeus*, the large Planoceridae, some *Stylochoplana*, *Discocelis*, and *Leptoplana*, and in the same manner as in *Leptoplana tremellaris* (p. 9). In *Cryptocelis*, *Leptoplana alcinoi*, and *L. pallida*, however, the whole body executes serpentine movements like an active leech (e.g. *Nephelis*); a cross section of the body would thus present the same appearance during the whole movement. Many Polyclads, notably *Anonymus* (Lang), if irritated, spread out in all directions, becoming exceeding thin and transparent.

FIG. 9.—*Discocelis lichenoides* Mert. (after Mertens), creeping on the inner side of a glass vessel by means of the lobes of the extended and exceedingly mobile pharynx (*ph*). These lobes also serve to enclose *Crustacea* (*a*), and one lobe may then be withdrawn independently of the rest, back into the body (*b*). The brain (*br*) and shell-gland (*sg*) are shown by transparency.

Discocelis lichenoides, *Planocera graffii*, and *Anonymus virilis* have peculiar modes of progression. The first, according to Mertens, will climb up the sides of a vessel by means of the expanded lobes of the pharynx (Fig. 9, *ph*), a habit of considerable interest, since we know that certain Ctenophores—*Lampetia*, for instance—progress when not swimming on the expanded lobes of their "stomach."[1] *Planocera* and *Anonymus*

[1] Chun, "Ctenophoren," *Fauna u. Flora G. v. Neapel*, Monogr. I. 1880, p. 180.

creep by extending parts of the anterior margin and dragging the rest of the body behind. In consequence, the brain and dorsal tentacles may come to lie actually behind the middle of the body, and thus no definite anterior end or "head" advances first. Along with this curious habit it may be noticed (Lang) that the radial symmetry of the body is well marked; but even without accepting this author's suggestion of the concurrent development of a "head" with locomotion in a definite direction, the facts, whether these two forms are primitive or not, are highly interesting.

Food.—Though we are probably right in calling Polyclads a carnivorous group, the food of very few forms has been ascertained. Those which possess a large frilled pharynx (most Acotylea) probably enclose and digest large, and, it may be, powerful prey, as appears to be the case in *Leptoplana tremellaris*. *Cryptocelis alba* has been seen by Lang with the pharynx so distended, owing to a large *Drepanophorus* (Nemertine) which it contained, as to resemble a yolk-sac projecting from the under surface of an embryo. The Cotylea such as *Thysanozoon*, with a bell- or trumpet-shaped pharynx, are fond of fixing this to the side of the aquarium, but whether they thus obtain minute organisms is not clear. *Prosthiostomum* shoots out its long pharynx with great vehemence (Fig. 8, F) and snaps up small Annelids by its aid (Lang). Those Polyclads which, as *Cycloporus* and others, are definitely associated with other organisms are not certainly known to feed upon the latter, though "*Planaria velellae*" has been seen by Lesson[1] devouring the fleshy parts of its host. The salivary glands which open on the lips and the inner surface of the pharynx powerfully disintegrate the flesh of the prey. Digestion takes place in the main-gut, and the circulation of the food is accomplished by the sphinctral musculature of the intestinal branches (conf. *Leptoplana*, p. 13).

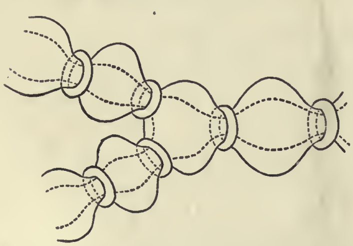

Fig. 10.—Diagram of the musculature, causing peristaltic movements of the intestinal branches of Polyclads. (After Lang.)

A distinct vent or anus is always absent. After a meal the

[1] See Lang, "*Polycladen*," p. 607.

faecal matter collects in the main-gut, and is discharged violently by the pharynx into the water. In a few species, however, the intestinal branches open to the exterior (Lang). *Yungia aurantiaca*, a large and abundant Neapolitan form, possesses such openings over the greater part of the dorsal surface; *Cycloporus papillosus* has marginal pores; *Oligocladus sanguinolentus* apparently possesses an opening at the posterior end of the main-gut; and *Thysanozoon brocchii* frequently rends at this point, in consequence of the accumulation of food.

Respiration.—The oxygen of the atmosphere dissolved in the sea-water is, in default of a special circulatory fluid, brought to the tissues of Polyclads in two ways. The ciliated epidermis provides a constant change of the surrounding water, by which the superficial organs may obtain their supply; and the peristaltic movements of the digestive system, aided by the cilia of the endoderm cells, ensure a rough circulation of the sea-water, which enters along with the food, to the internal organs. The papillae of *Thysanozoon brocchii*, containing outgrowths of the intestinal branches, are possibly so much additional respiratory surface, although still larger forms (other Pseudoceridae) are devoid of such outgrowths.

Excretion.—The excretory system of only one Polyclad (*Thysanozoon brocchii*) is accurately known. Lang, by compressing light-coloured specimens, found the three parts of the system known to occur in many Platyhelminthes: (1) the larger longitudinal canals, and (2) the capillary vessels, which commence with (3) the flame-cells in the parenchyma of the body. The mode of distribution of these parts is not, however, ascertained. The canals are delicate, sinuous, apparently intracellular tubes, coursing close to the margin of the body and sending offsets which suspend the canals to the dorsal surface, where possibly openings may occur. In dilatations of these vessels bunches of cilia, and occasionally flame-cells, are found. Usually, however, flame-cells occur at the commencement or during the course of the capillaries, which are straight, rarely branching, tubes of exceeding tenuity, and appear (Lang) to be outgrowths of the flame-cells, just as the duct is an outgrowth of a gland-cell. In fact there is little doubt that the stellate flame-cells are modified parenchymatous gland-cells, containing a lumen filled with a fluid into which a number of cilia project and vibrate synchronously. The cells excrete nitrogeneous waste substances, which are then discharged into the capillaries, whence the cilia of the main vessels drive them presumably to the exterior, though external openings of the excretory system are not known. Traces of this system have been observed in young *Leptoplana* (first by Schultze in 1854) and also in *Cestoplana.*

Sensation.—A nervous sheath, with scattered ganglion cells, everywhere underlies the musculature. It is exceedingly faintly marked on the dorsal surface, but laterally and ventrally forms a dense network with polygonal meshes. Thickenings of this sheath give rise to lateral nerves, and also to a pair of stout longitudinal nerves from which the internal organs are probably innervated. The brain, hardly distinct in pelagic Polyclads, in most forms does not differ greatly from that of *Leptoplana* (p. 13).

The sense organs of Polyclads have the form of tentacles, eyes, otocysts (in *Leptoplana otophora*), and stiff tactile cilia. The solid dorsal tentacles of Planoceridae contrast strongly with the folded or pointed hollow processes of the Cotylea. The former (Fig. 8, A, *T*) are muscular and very contractile, and are placed near the brain some distance from the anterior end. The latter are outgrowths of the front margin of the body, and are sometimes (*Yungia*) provided superficially with olfactory pits and internally with eyes and intestinal coeca.

The eyes which occur in Polyclads may be divided into (*a*) a pair of cerebral groups overlying the brain; (*b*) those embedded in the tentacles (tentacular group); and (*c*) the marginal eyes, which in *Anonymus* occur all round the margin. A complex form is sometimes assumed by the cerebral eyes of Pseudoceridae, resulting probably from incomplete fission (Fig. 11). *Leptoplana otophora* was obtained by Schmarda on the south coast of Ceylon. On each side of the brain is a capsule containing two otoliths. This is the only known case of the occurrence of these organs in Polyclads.

Reproduction.—Although Polyclads are able to repair the result of injuries to a very considerable extent, they are not known to multiply asexually. The two processes are intimately associated, but, though probably all Turbellaria can regenerate certain lost parts, asexual reproduction only occurs sporadically.

All known Polyclads are hermaphrodite. The male organs, scattered, like the testes of *Leptoplana*, over the ventral surface, develop earlier than the ovaries, though the periods of maturation overlap; hence the possibility of self-fertilisation, though remote, is still worth consideration. The genital apertures, through which, in the male, spermatozoa, and in the female, ova, are emitted, are usually situated as in *Leptoplana* (Figs. 2 and 5, ♂ and ♀). In *Trigonoporus*, a genus once found at Naples, a secondary female aperture has been discovered leading into the female genital canal[1]; and in *Anonymus*, *Polypostia*, and *Thysanozoon* (Fig. 7, E, ♂) two or more male pores and penes have been found. *Anonymus* has several penes (Fig. 7, D, ♂) arranged radially round the body. *Polypostia*, a remarkable form described by Bergendal,[2] belonging to the Acotylea, possesses

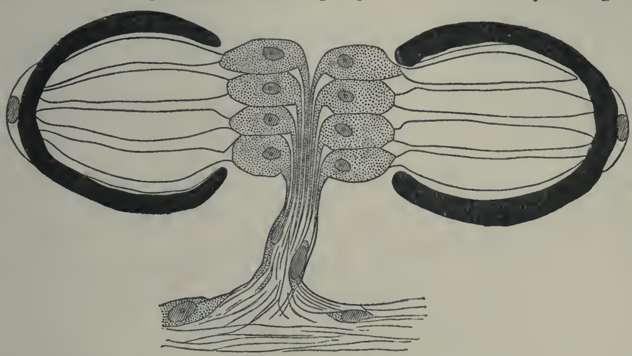

FIG. 11.—Double eye from the cerebral group of *Pseudoceros maximus*. (After Lang.)

about twenty such structures ranged round the female genital aperture. Lang, whose attention was attracted by these singular facts, made the interesting discovery that *Thysanozoon* uses its penes as weapons of offence rather than as copulating organs, burying them in the skin of another Polyclad (*Yungia*) that happened to cross its path, spermatozoa being of course left in the wound. Lang further found that *Prostheceraeus albocinctus* and *Cryptocelis alba* in this way implanted a spermatophore in the skin of another individual of the same species, and he suggested that from this point the spermatozoa wandered through the tissues till they met with and fertilised the eggs. It is now known that a similar process of "hypodermic impregnation" occurs sporadically in several groups of animals.[3]

[1] Lang, "*Polycladen*," Pl. 30, Fig. 8.

[2] *Kongl. Fysiograf. Sällskapets Handlingar*, Bd. iv. Lund, 1892-93.

[3] Whitman, *Journal of Morphology*, vol. iv. 1890, p. 361.

Nevertheless, in some Polyclads it is probable, and in *Stylochus neapolitanus* it is certain, that normal copulation takes place. The sperm-masses are transferred to a coecal diverticulum of the female genital canal, and then by a delicate mechanism, of which we know only the effects, one spermatozoon obtains entrance into one matured ovum, which differs from the ova of most Turbellaria in that it contains in its own protoplasm the yolk necessary for the nutrition of the embryo. In other words, there are no special yolk-glands. After fertilisation, the ovum in all Polyclads is coated with a shell formed by the shell-gland, which also secretes a substance uniting the eggs together. They are deposited on stones and shells, either in plate-like masses or in spirals (like those of Nudibranchs). *Cryptocelis alba* lays masses of an annular shape, with two ova in each shell, and buries them in sand.

Development.[1]—The first stages in the embryology of Polyclads appear to be very uniform. They result, in all Cotylea and in certain Planoceridae, in the formation of a Müller's larva (Fig. 12) about a couple of weeks after the eggs are laid. This larva (1-1·8 mm. long), which is modified in the Planoceridae, is distinguished by the presence of a ciliated band, running somewhat transversely round the body, and usually produced into a dorsal, a ventral, and three pairs of lateral processes. When swimming the body is placed as in Fig. 12, and twists round rapidly about its longitudinal axis by means of the strong locomotor cilia placed in transverse rows upon the processes. The cilia of each row vibrate synchronously, and recall the action of the swimming plates of a Ctenophore. It is noteworthy that whereas *Stylochus pilidium* passes through a modified or, according to some authors, a primitive larval stage, its near ally, *S. neapolitanus*, develops directly. Most

[1] A full account of Polyclad development is contained in Lang's "*Polycladen*," with references to the literature of the subject. Since the date of that work (1884) the embryology of Ctenophora has become better known, but, though the segmentation of the egg and early stages of development are very similar in both cases, the elaborate investigations of E. B. Wilson (*Journ. Morphology*, vol. vi. p. 361) show that the segmentation of Polychaet worms is again similar. The question of the affinities of the Polycladida is also discussed by Lang ("*Polycladen*," p. 642 *et seq.*). The work of the last decade has neither proved nor disproved his suggestion that the Ctenophores and Polyclads have been derived from common ancestors. On this subject the remarks made by Hatschek (*Lehrbuch d. Zoologie*, p. 319) are some of the weightiest that have appeared.

Acotylea indeed develop directly, and their free-swimming young differ from Müller's larva merely in the absence of the ciliated band and in the mode of swimming.

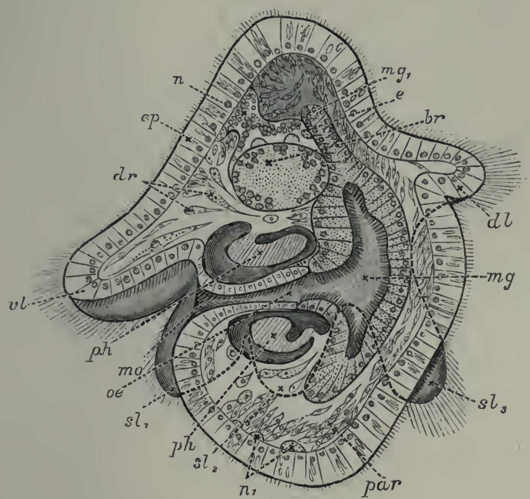

Fig. 12.—Section through Müller's larva of *Thysanozoon brocchii* (modified from Lang). The right half is seen from inside. × 150. Semi-diagrammatic. *br*, Brain; *dl*, dorsal ciliated lobe; *dr*, salivary gland-cells of pharynx; *e*, eye; *ep*, ciliated epidermis containing rhabdites; *mg*, stomach or main-gut; mg_1, unpaired gut branch over the brain; *mo*, "mouth" of larva; *n*, n_1, section of nerves; *oe*, ectodermic pit forming oesophagus of larva; *par*, parenchyma filling the space between the alimentary tract and the body wall; *ph*, pharynx lying in the cavity of the peripharyngeal sheath, the nuclei of which are visible; sl_1, sl_2, sl_3, lateral ciliated lobes of the right side; *vl* ventral ciliated lobe.

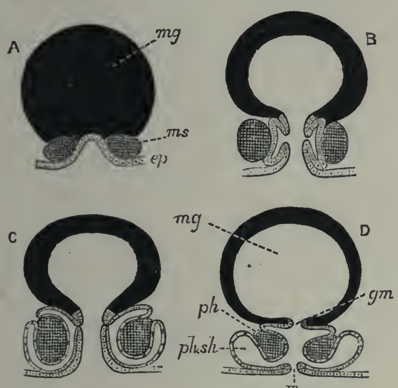

Fig. 13.—Diagrammatic transverse sections of a larval Polyclad at different stages, to illustrate the development of the pharynx. (After Lang.) **A**, Larva of the eighth day still within the shell. The main-gut (*mg*) is still solid, the epidermis is slightly invaginated, and a pair of muscular mesodermic thickenings (*ms*) are present. **B**, Young pelagic larva. The epidermic invagination has deepened and developed laterally. **C**, The lateral pouches have formed the wall of the peripharyngeal sheath, enclosing the mesodermic, muscular, thickening or pharyngeal fold (*ph*). (Compare Fig. 12.) Towards the end of larval life, when the ciliated processes (*sl*, Fig. 12) have aborted, the stage **D** is reached. By the opening outwards of the pharyngeal sheath (*ph.sh*) the two apertures *gm*, or true mouth, and *m*, or external mouth, are formed, which together correspond with the oesophageal opening of the younger larva. (Compare the transverse section in Fig. 5.)

Polyclads possess an undoubted mesoderm, which gives rise to the muscles, the pharyngeal fold, and the parenchyma. The ectoderm forms the epidermis, in the cells of which the rhabdites (Fig. 12) arise, apparently as so many condensed secretions. From the ectoderm the brain arises as two pairs of ingrowths, which fuse together, and from these the peripheral nervous system grows out. Three pigmented ectoderm cells give rise, by division, to the eyes—an unpaired cell (Fig. 12, *e*) to the cerebral group of eyes, and the other two to the marginal and tentacular groups. The copulatory organs apparently arise to a large extent as ingrowths from the ectoderm, from which the accessory glands (prostates, shell-glands) are also formed. The endoderm forms the lining of the main-gut and its branches. The pharynx is developed as in Fig. 13, which shows that the "mouth" of the young larva (C) does not correspond exactly with that of the adult (D). The salivary glands arise from ectoderm cells, which sink deeply into the parenchyma. The reproductive organs (ovaries and testes) possibly arise by proliferation from the gut-cells (Lang, v. Graff). The change from the larva to the adult is gradual, the ciliary band being absorbed and the creeping mode of life adopted.

Turbellaria. II. Tricladida.

The Triclads are most conveniently divided into three groups[1]: (i.) *Paludicola*, the Planarians of ponds and streams; (ii.) the *Maricola*, the Triclads of the sea; and (iii.) *Terricola* or Land Planarians. From the Polyclads they differ in their mode of occurrence; in the elongated form of their body and almost constant, mid-ventral position of the mouth; in possessing a single external genital pore (Monogopora); and in the production of a few, large, hard-shelled eggs provided with food-yolk.

Occurrence of the Paludicola.—The Planarians of our ponds and streams are the most familiar and accessible Turbellaria. Their elongated, flattened bodies, and gliding movements, render them conspicuous objects on the under surface of stones and on the leaves of aquatic plants, where they live gregariously. The variable *Polycelis nigra* (Fig. 14, H) is very abundant in stagnant water and slowly-moving streams, whereas its ally, *P. cornuta* (Fig. 14, G), distinguished by a pair of tentacles, is more local. *Planaria* (*Dendrocoelum*) *lactea* (A), *P. polychroa* (I), *P. torva*, and *P. punctata* are not infrequently found together, but the last

[1] Hallez, *Revue Biologique du Nord de la France*, tom. ii. 1889-90.

is at once the largest and rarest. *Planaria alpina* (Fig. 14, B)

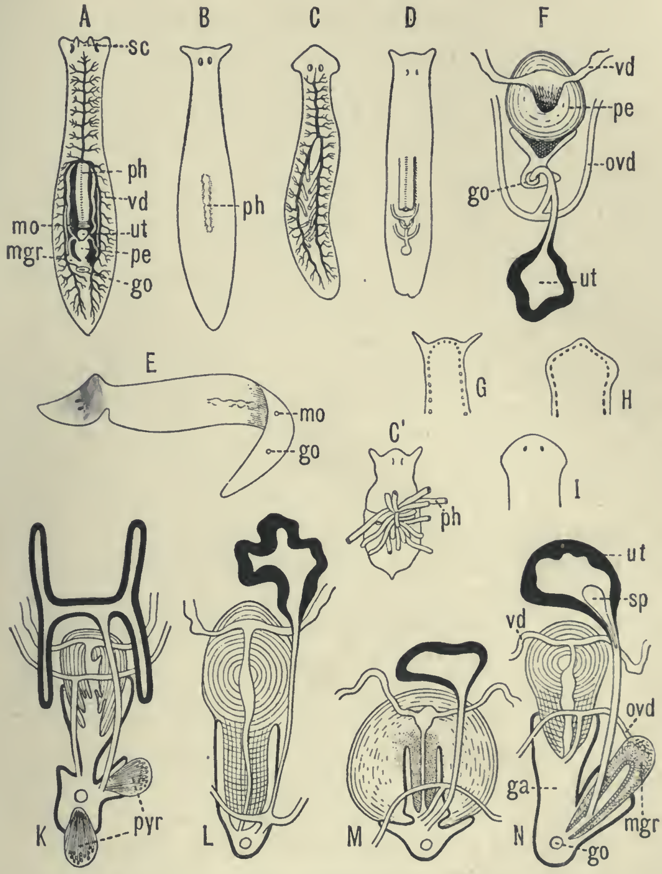

FIG. 14.—Forms of Triclads, with the distinguishing specific characters of certain British forms. **A**, *Planaria lactea* O. F. M., × 2 ; **B**, *Planaria alpina* Dana, × 4 (after Kennel) ; **C**, *Phagocata gracilis* Leidy (after Woodworth), × 6 ; **C′**, the same with the pharynges (*ph*) extruded ; **D**, *Gunda ulvae* Oer., × 4 ; **E**, *Planaria gonocephala* Dug. (after Schmidt), × 4 ; **F**, genitalia of *Gunda ulvae* (after Wendt) : **G**, head of *Polycelis cornuta* Schm. ; **H**, head of *Polycelis nigra* Ehr. ; **I**, head of *Planaria polychroa* Schm. **K** to **N** show the distinctive characters of the genital ducts in **K**, *Polycelis nigra* ; **L**, *Planaria polychroa* ; **M**, *Planaria alpina* ; **N**, *Planaria torva* Schultze (after Iijima and v. Kennel). *ga*, Genital atrium ; *go*, common genital opening ; *mgr*, "musculo-glandular organ" ; *mo*, "mouth" ; *ovd*, oviduct ; *pe*, penis ; *ph*, pharynx ; *pyr*, pyriform organs of unknown significance ; *sc*, sucker ; *sp*, spermatophore lying in (*ut*) uterus ; *vd*, vesicula seminalis. (All except **C** and **E** are found in England.)

is characteristic of cold mountain streams, but occurs down to sea-level in England, the Isle of Man, and Ireland, and from its abundance in spring water, probably enjoys a wide distribution underground. In the Swiss Alps it has been found at altitudes of over 6000 feet, at lower levels in the Rhone, and also in the Lake of Geneva. This wide distribution may perhaps be accounted for, partly, by its faculty for asexual reproduction in summer, and also, by the production, later in the year, of hard-shelled eggs which are laid loosely, not attached to stones or plants.[1] But we have no really direct evidence of the means of dispersal of this or of any of the foregoing species, although they all have a wide distribution in Europe. Of extra-European forms the accounts that exist are very fragmentary. The only indubitable diagnostic character of a Triclad is the structure of its genital ducts, and this is accurately known in only a few cases. Several species such as *Dicotylus pulvinar* (Fig. 16, B), at present known only from Lake Baikal,[2] and others (*Planaria mrazekii*, *P. albissima*) from Bohemia,[3] will doubtless be found elsewhere when they are carefully looked for. *Phagocata gracilis* is a remarkable North American form, possessing several pharynges (Fig. 14, C and C′), recalling the independent movement of the pharyngeal lobes of *Discocelis lichenoides* (Fig. 9).[4]

Occurrence of the Maricola.—Little as we accurately know of the distribution of the fresh-water Planariae, our knowledge of the occurrence of the marine forms is still more limited. *Gunda* (*Procerodes*) *ulvae* (Fig. 14, D) is the commonest European form, occurring abundantly in the upper part of the littoral zone, on the shores of the Baltic. *G. segmentata* from Messina has been carefully described by Lang,[5] but these are almost the only species of Maricola which can be accurately determined. They differ from the Paludicola in the position of the "uterus" behind the genital pore and in the absence of a "musculo-glandular organ" (Fig. 14, F). A special interest attaches to the Bdellouridae, a family containing three species, all parasitic on *Limulus* from the east coast of America. These remarkable Triclads usually have a sucker at the hinder end of the body, by which they attach themselves firmly to the cephalo-thoracic appendages and to the

[1] Voigt, *Zool. Anz.* xv. p. 238.
[2] Grube, *Archiv f. Naturgeschichte*, 38 Jahrg. Bd. i. 1872, p. 273.
[3] Vejdovsky, *Zeitschr. f. wiss. Zoologie*, Bd. lx. 1895, p. 200.
[4] Woodworth, *Bulletin Mus. Comp. Zoology, Harvard*, vol. xxi. No. 1, 1891.
[5] *Mitth. Zool. Stat. Neapel*, 1882, p. 187.

gill-plates, upon which the eggs may be found in considerable numbers. One species, *Syncoelidium pellucidum*, possesses a pair of problematical organs in the hinder part of the body, opening to the exterior ventro-laterally by a couple of chitinous mouth-pieces, but having no connexion with the genital ducts.[1]

Occurrence and Distribution of Land Planarians.—The terricolous Triclads or Land Planarians are the most interesting division of the group. Some forms, such as *Bipalium kewense*, attain large dimensions, being usually 6 to 9 inches in length, and specimens fully extended have measured 18 inches. Their bodies are frequently banded or striped with brilliant colours. *Geoplana coerulea* Mos. has a blue ventral surface and is olive green or dark Prussian blue above. *G. splendens* Dendy, is marked dorsally by three stripes of emerald green alternating with four dark brown longitudinal bands. The mode of coloration, though somewhat variable, is an important specific character. Its significance, however, is not clearly understood. The colours may be a warning signal, as some *Geoplana* at least are disagreeable to the taste of man and some birds[2]; but since Land Planarians are largely nocturnal animals, living by day under logs, banana leaves, and in other moist and dark situations, this explanation is clearly insufficient. Two *Geoplana* have been noticed by Mr. Dendy which seem to be protectively coloured. *G. triangulata* var. *australis* occurs abundantly in the beech forest in the South Island of New Zealand, and its brown back and yellow or orange ventral surface match the leaves around its haunts. *G. gelatinosa* again looks like a mere slimy patch on the rotten bark where it is found. In arid districts, during the dry season, Land Planarians burrow in the soil and form a cyst, in which they lie coiled up, after the manner of earthworms.[3] The glutinous investment of their delicate bodies forms a moist medium in which the cilia covering the body (and especially the ventral surface) may constantly and evenly vibrate, and by which they adhere firmly to their prey. In some tropical Planarians, in addition to possessing offensive properties, the mucus is so copious in amount and hardens with such rapidity, that

[1] Wheeler, *Journal of Morphology*, vol. ix. 1894, p. 167.

[2] Dendy, *Trans. Roy. Soc. Victoria* 1890, p. 65; Id. *Austral. Assoc. Brisbane*, 1895, "Presid. Add. to Sect. D," p. 15.

[3] Darwin, *Ann. and Mag. Nat. Hist.* vol. xiv. 1844, p. 241.

these Triclads may creep over bridges of it, and may even be blown from one stem or branch of a plant to another, hanging at the ends of their threads.[1]

In Europe there are only two or three indigenous Land Planarians, of which *Rhynchodemus terrestris* O. F. M. (Fig. 15, B) is the most widely distributed, and has been found in moist situations for the most part wherever it has been carefully looked for. It measures about $\frac{3}{4}$ inch in length, and is dark grey above, whitish below, and bears a pair of eyes near the anterior extremity (Fig. 15, B). *Bipalium kewense* (Fig. 15, A), which has been found in the forests of Upolu, Samoa, by Mr. J. J. Lister, has been accidentally imported, from the (unknown) districts where it is indigenous, with plants and soil to various parts of the world — England, Germany, the Cape, and also to Sydney, where it appears to have established itself. In these Bipalia living in hothouses, the genitalia never appear to attain maturity, and apparently multiple fission and subsequent reparation of the missing parts is the only mode of reproduction. *Geodesmus bilineatus* (Fig. 15, C), which has occurred at Giessen, Würzburg, and Dresden, has, in all probability, been introduced with ferns from the West or East Indies. *Microplana humicola,* described by Vejdovsky from dunghills in Bohemia, is doubtfully indigenous.

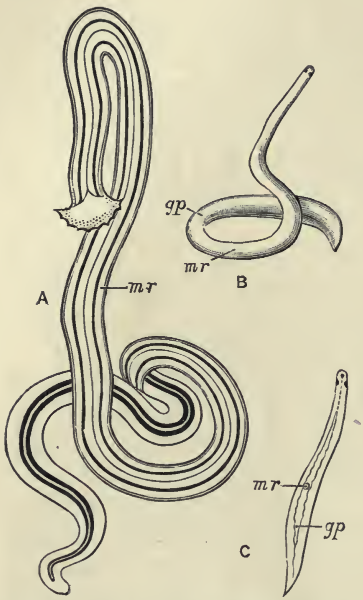

FIG. 15.—Some Land Planarians found in Europe. **A**, *Bipalium kewense* Mos. × ⅓ (after Bergendal) ; **B**, *Rhynchodemus terrestris* O. F. M., × 2 ; **C**, *Geodesmus bilineatus* Metsch., × 2½ (after Metschnikoff). *mr*, Region of mouth ; *gp*, region of genital pore.

In marked contrast with the poverty of the temperate zones in Land Planarians, is the abundance and great variety of this group in Southern Asia, South America, and especially in Australasia, where the rich Land Planarian fauna has been carefully investigated by Spencer, Dendy, Fletcher, and others, in

[1] Shipley, *Proc. Camb. Phil. Soc.* vol. vii. pt. 4, 1891 (with literature).

certain parts of Victoria, New South Wales, and New Zealand.[1] About forty species of Planarians have been discovered on the Australian continent, thirty-five of which belong to the predominant genus *Geoplana*, distinguished by the presence of numerous eyes along the border of the simple anterior extremity. Of the remaining five, four belong to the genus *Rhynchodemus*, with, lastly, the introduced *Bipalium kewense*. The distribution of any one species, however, is so limited that only three forms are common to the two former colonies; and although some of the twenty known New Zealand Planarians (chiefly species of *Geoplana*), are identical with Australian species, yet only one, or possibly two, varieties of these species are Australian also. In addition to their prevalence in Australasia, the *Geoplanidae* also occur in South America, South Africa, Japan, and the East Indies. The *Bipaliidae* are characteristic of the Oriental region, being found in China, Borneo, Bengal, and Ceylon. The *Rhynchodemidae* are a cosmopolitan family, occurring in Europe, North and South America, the Cape of Good Hope, Ceylon, the East Indies, Australia (particularly Lord Howe Island), and Samoa.[2]

Habits and Structure of Triclads.—The common *Planaria* (*Dendrocoelum*) *lactea*, which usually progresses by ciliary action, aided, it is said, by muscular contractions of the ventral surface, performs, if alarmed, a series of rapid "looping" movements, by affixing a sucker (Fig. 14, A, *sc*), placed on the under side of the head, to the substratum, and pulling the posterior end close to this. The sucker, discovered by Leydig, is even better developed in *P. punctata* (Fig. 16, A), *P. mrazekii*, and *P. cavatica*, and is an efficient adhering-organ which has probably been developed from a similar but simpler structure found in a considerable number of both fresh-water and marine Triclads (*P. alpina*, Fig. 16, E). Probably the sucker of the Land Planarian *Cotyloplana* (D) is the same structure, but the two suckers of *Dicotylus* (B) are at present unique. *Planaria dioica*, found by Claparède on the coast of Normandy,[3] is covered with minute adhesive papillae,

[1] *Trans. Roy. Soc. Victoria* from 1889 onwards. *Trans. New Zealand Institute*, 1894-95.

[2] Moseley, *Phil. Trans.* 1874, p. 105; Id. *Quart. Journ. Micr. Sci.* vol. xlvii. 1877, p. 273; Loman, *Bijdrag tot d. Dierkunde*, Aflev. 14, 1887, p. 71; Id. *Zool. Ergeb. ein. Reise in Nieder-Ost-Indien*, Hft. 1, p. 131; Beddard, *Zoogeography*, 1895, p. 53.

[3] *Beobachtungen ü. Anat. u. Entwickel. an der Küste von Normandie*, 1863, p. 18.

similar to those of certain Rhabdocoelida (e.g. *Monotus*, Fig. 19, D), enabling it to cling tightly to the *Zostera*, and so to resist the loosening action of the waves.

The movements of Land Planarians are somewhat peculiar. The ventral surface of *Bipalium* has a median groove, into which the ducts of numerous mucus-glands open. This is bordered by two ridges clothed with long and powerful cilia, which perform the chief part in propelling the animal, aided, according to Lehnert,[1] by muscular waves which pass from the

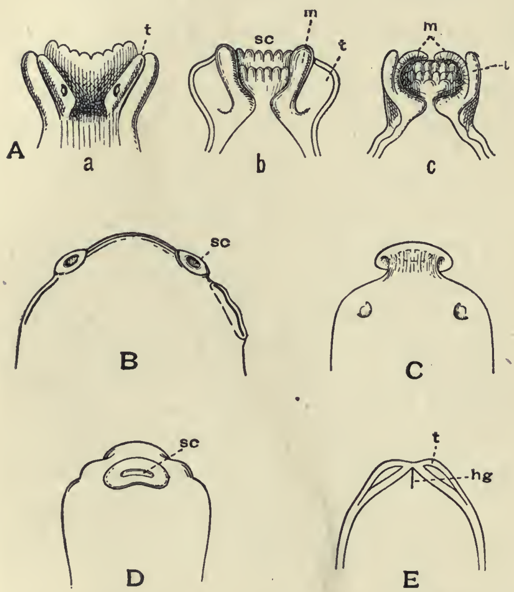

FIG. 16.—Suckers of Triclads. **A**, *Planaria punctata* Pall.; *a*, dorsal surface of head; *b*, ventral surface (freely moving) showing the sucker; *c*, sucker contracted (after Hallez): **B**, ventral surface of head of *Dicotylus pulvinar* Gr., from Lake Baikal (after Grube): **C**, dorsal surface of *Procotylea fluviatilis* Gir. (after Girard): **D**, sucker of *Cotyloplana whiteleggei* Sp. (after Spencer): **E**, ventral view of head of *Planaria alpina* Dana (preserved specimen); *hg*, adhering groove; *m*, thickened musculature forming the margin of the sucker; *sc*, sucker; *t*, tentacles.

head, backwards, *i.e.* opposite in direction to those by which a snail slides along. This observation, however, needs confirmation. The whole body executes sinuous movements, during which the crescentic head, lifted slightly above the ground (Fig. 15, A), is constantly altering and regaining its normal shape, somewhat as a *Planaria lactea* uses the lobes of its head. Further examination shows that the margin of the head of *Bipalium* is not only provided with eyes, but in addition, with ciliated, (probably) olfactory pits. Such depressions, innervated directly from the cerebral ganglia, have been found in sixteen species of *Geoplana*,

[1] *Archiv f. Naturgeschichte*, 57 Jahrg. Bd. i. Hft. 3, 1891, p. 308.

and in one or two species of *Rhynchodemus*.[1] Some Land Planarians (a species of *Rhynchodemus* from Ceylon, and a *Dolichoplana* from the Philippines) wriggle out of a box or the hand with great speed (Moseley).

The skin of Triclads is full of minute rods or rhabdites, which are shot out in great numbers when the animal is irritated, and doubtless serve an offensive purpose. The Terricola possess two kinds of these: (1) needle-like rods; and (2) in *Bipalium kewense*, flagellated structures, bent into a V-form and with a slender thread attached to one end (Shipley). In *Geoplana coerulea* these bent rods furnish the blue colour of the ventral surface. The rhabdites arise in all Triclads in cells below the basement-membrane, which they are said to traverse in order to reach the epidermis, thus differing in origin, and also in structure, from the rods of Polyclads.

Food.—Triclads are largely if not wholly carnivorous animals, feeding upon Annelids, Crustacea, Insects, Insect-larvae, and Molluscs. The mouth is usually mid-ventral or behind the middle of the body, but in the anomalous *Leimacopsis terricola* Schm. from the Andes[2] and in *Dolichoplana* it is near the anterior end. The pharynx (Figs. 17, 18, *ph*) is cylindrical or bell-shaped, exceedingly dilatable and abundantly supplied with glands and nervous tissue. It opens into the three main intestinal branches, one of which runs in the median plane forwards, the others backwards right and left, enclosing a space in which the genital ducts lie (Figs. 14, A, 17). The fresh-water Planarians prey upon Oligochaeta, Hydrophilidae (aquatic beetles), and the commoner pond-snails. *Bipalium kewense* pursues earthworms, seizes the upper surface of the anterior end by the glutinous secretion of its ventral surface, and then proceeds to envelop part or the whole of the worm within its pharynx, which is stretched as a thin skin over the body of its struggling prey (Lehnert). The tissues of the latter pass into the intestine of the Planarian, and distend it greatly. After such a meal, which lasts from one to five hours, a *Bipalium* may remain for three months without seeking food. *Geobia subterranea*, a white eyeless form from Brazil, pursues earthworms (*Lumbricus corethrurus*) in their burrows, and has been seen by Fritz Müller sucking the blood out of a young

[1] Dendy, *Proc. Roy. Soc. Victoria*, vol. iv. n.s. i. 1892.
[2] Schmarda, *Neue wirbellose Thiere*, Leipzig, 1859, I. i. p. 30.

worm.[1] *Geoplana typhlops*, a Tasmanian species, is also blind, and pursues worms, as does *G. triangulata* (Dendy). In Trinidad, von Kennel[2] observed that land-snails (Subulinae) were the food of certain Land Planarians, the name of which, however, he does not state. The pharynx was employed to suck out the soft parts of the snail even from the upper whorls of the shell.

Reproduction.—In *Planaria lactea* the numerous testes (Fig. 17, *te*) are placed both above and below the alimentary canal throughout the greater part of its course. The membrane of each gonad is continued into a minute vas efferens, which unites with those of neighbouring testes. Two vasa deferentia (*v.d*) arise thus on each side, one from the posterior, the other from the anterior testes of the body, and open into the vesiculae seminales (*v.s*), which may be seen in the living animal as tortuous whitish tubes at the sides of the pharynx (Fig. 14, A). These open into the penis (Figs. 14, A; 17, *pe*), a large pyriform organ, the apex of which, when retracted, points forwards, projecting into the penial cavity. When this apical portion is evaginated and turned inside out, it is of considerable length, and is able to pass into the long slender duct of the uterus (*ut*) of another individual. The penial sheath (*ps*) is part of the genital atrium (*gs*), which is developed as a pit from the skin, and invests the end of the genital ducts, the mouth of the pit forming the common genital pore (*go*), through which both male and female genital products are emitted.

There are two ovaries (*ov*) placed far forwards, between the third and fourth pairs of intestinal coeca. The oviducts (*ovd*) lie just over the lateral nerves, and have a slightly tortuous course, at each outward bend receiving the duct (*yo*) of a yolk-gland (*yg*), so that ova and yolk are already associated when the oviducts open by a short unpaired tube into the genital atrium. The yolk-glands develop rapidly,[3] and when fully formed are massive glands occupying the spaces between the intestinal branches and the testes which are then aborting. The so-called *uterus* (*ut*), apparently at first a diverticulum of the genital atrium, expands

[1] *Abhandl. d. Naturf. Gesell. zu Halle*, Bd. iv. 1857, p. 33.

[2] *Arb. Zool.-Zoot. Instit. Würzburg*, Bd. v. 1882, p. 120.

[3] Woodworth (*loc. cit.* p. 38) states that in *Phagocata* the yolk-glands arise by proliferation from two parovaria, placed just in front of the ordinary ovaries. Iijima, however (*Zeitschr. f. wiss. Zool.* Bd. xl. 1883, p. 454), regarded them as derivatives of the parenchyma.

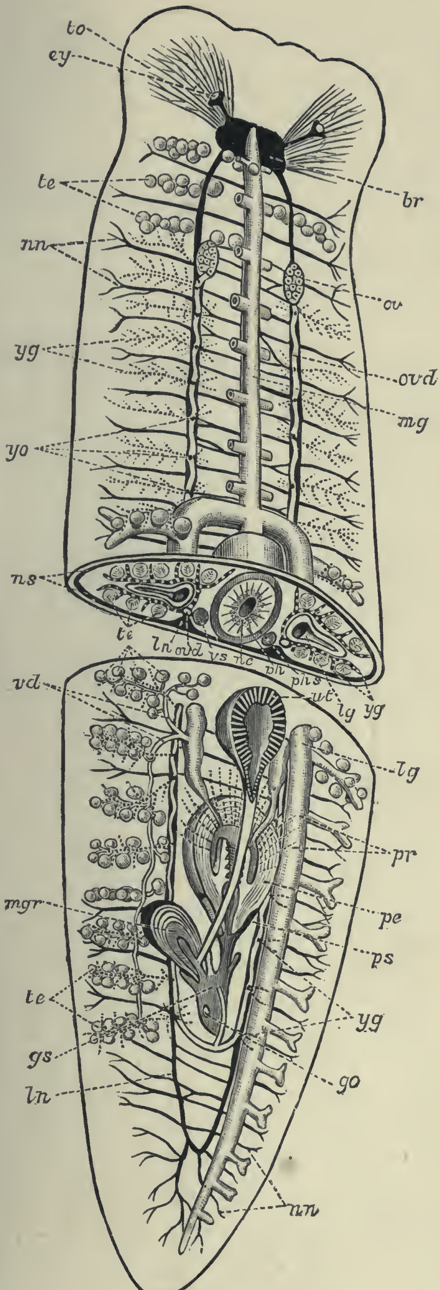

FIG. 17.—Diagrammatic view of the structure of *Planaria* (*Dendrocoelum*) *lactea.* × 7. The body has been cut across and a portion removed. In the posterior half the alimentary tract of the left side is removed and the uterus, penis, and muscular organ sliced open horizontally. The nervous system is represented by black, and the yolk-glands by dotted lines. *br*, Brain; *ey*, eye with lens and optic nerve; *go*, external genital aperture for both male and female products; *gs*, genital atrium; *lg*, paired lateral intestinal branch; *ln*, longitudinal nerve; *mg*, unpaired anterior intestine, the branches of which are cut off close to the main stem; *mgr*, eversible "musculo-glandular organ"; *nc*, nerve-cells in the pharynx; *nn*, lateral nerve-twigs; *ns*, nerve-sheath; *ov*, ovary; *ovd*, oviduct; *pe*, the eversible penis, the corrugated inner white portion of which is the apex; *ph*, pharynx; *phs*, pharyngeal sheath; *pr*, "prostate" or granule-gland (represented by dotted lines opening into the penis); *ps*, penial sheath; *te*, testes; *to*, tactile lobe of the head; *ut*, "uterus" opening into the genital atrium just above *mgr*; *vd*, vasa deferentia; *vs*, vesicula seminalis; *yg*, yolk-glands; *yo*, openings of the yolk-ducts into the oviducts.

behind the pharynx into a receptacle lined by long glandular columnar cells, which, however, are not all of the same kind. The uterine duct opens into the atrium just above the aperture of a problematical, eversible, "musculo-glandular organ" (*mgr*).

Fertilisation appears to occur in the uterus, where ova, yolk, and spermatozoa, or (in *P. torva*) spermatophores (Fig. 14, N, *sp*), are found. The formation of the cocoon in *Planaria lactea* is probably begun in the "uterus," but is undoubtedly completed in the genital atrium. In *P. polychroa*, however, the stalked cocoon is formed wholly in the "uterus." Thus we find two types of cocoons in different species of the genus *Planaria* associated with two types of reproductive organs (Hallez):—

I. Planariae in which the two oviducts open separately into the posterior part of the duct of the uterus. A musculo-glandular organ is absent. The cocoons are spherical and stalked. Examples — *Planaria polychroa* (Fig. 14, L), *P. albissima, P. gonocephala.*

II. Planariae in which the two oviducts open by means of an unpaired duct into the genital atrium. A musculo-glandular organ present (*Planaria torva* (Fig. 14, N), *P. mrazekii, P. lactea, P. cavatica*), or absent (*P. alpina,* Fig. 14, M). The cocoons are sessile.

The genitalia of the Maricola (Fig. 14, F) and Terricola do not differ very much from those of *Planaria.* The uterus (greatly reduced in the Land Planarians) lies behind the genital pore, and several ova, together with much milky yolk, are enclosed in a capsule which is formed in the genital atrium.

Asexual Reproduction.[1]—It has long been known that fresh-water Planarians have not only great powers of repairing injuries, but that they use this faculty in order to multiply by transverse fission. *Planaria alpina* and *Polycelis cornuta,* in summer, separate off the posterior part of the body, and this ultimately becomes an entire individual. *P. albissima,* and especially *P. subtentaculata,* anticipate matters so far, that before fission is complete, the new individual has a head nearly fully formed. The new organs are largely regenerated in both parent and young,

[1] The extensive literature on this subject is fairly completely summarised by Voigt in *Biol. Centralblatt,* vol. xiv. Nos. 20, 21, 1894. Faraday's observations (cf. p. 6, note 6) have been generally overlooked.

apparently by the division and specialisation of scattered embryonic cells in the parenchyma. The asexual reproduction of Land Planarians is not fully proved, though it is known that they repair injuries to the body completely, and that *Bipalium kewense* is often found in hothouses, divided into fragments which regenerate all the organs of the parent, but like the latter, do not mature their sexual organs.

Excretion.—The excretory organs of Triclads consist of flame-cells, canaliculi, and a pair of longitudinal canals, the external

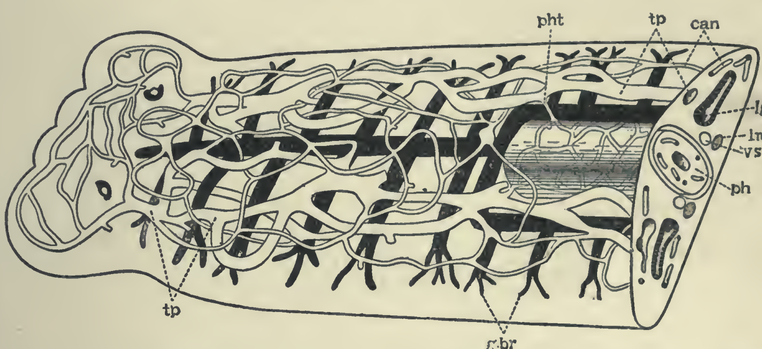

Fig. 18.—Semi-diagrammatic view of the excretory system of *Planaria lactea.* (Partly after Chickoff.) *can*, Capillary network on both dorsal and ventral surfaces ; *g.br*, branches of the intestine ; *lg*, lateral branches of the digestive system ; *ln*, longitudinal nerve ; *ph*, pharynx, with intermuscular capillary excretory network arising from the point marked *pht ; tp*, principal vessels of the excretory system, the external opening of which is not certainly known ; *vs*, vesicula seminalis.

openings of which, have not been satisfactorily ascertained. The flame-cells are difficult to detect in *Planaria lactea,* and the latest observer, Chickoff,[1] was unable to see them, although to him we are indebted for figures of this system in *P. lactea* (Fig. 18) and *P. alpina* (*P. montana*). In the latter, the flame-cells are distinct, and may open directly into the two main canals or indirectly through unbranched canaliculi. The pharynx possesses a special supply of excretory tubules communicating with the main canals. A similar system has been described and figured in *Gunda segmentata* by Lang.[2]

[1] *Archives d. Biologie*, tom. xii. 1892, p. 437.

[2] *Mitth. Zool. Stat. Neapel*, Bd. iii. 1882, p. 187.

Classification of Tricladida.

PALUDICOLA.

Family.	Genus and British Species.
Planariidae . .	*Planaria lactea* O. F. M., *P. punctata* Pall., *P. polychroa* Schm., *P. torva* M. Sch., *P. alpina* Dana.
	Polycelis nigra Ehr., *P. cornuta* Schm.
	Anocelis.
	Oligocelis. } Doubtful genera.
	Procotyla. }
	Sorocelis.
	Dicotylus.

MARICOLA.

Procerodidae . . (=Gundidae).	*Procerodes* (= *Gunda*) *ulvae* Oersted, *P. littoralis* van Beneden.
	Cercyra.
	Uteriporus.
Bdellouridae . .	*Bdelloura.*
	Syncoelidium.

TERRICOLA.

Bipaliidae . .	*Bipalium kewense* Moseley (introduced).
Geoplanidae . .	*Geoplana.*
	Geodesmus.
Rhynchodemidae .	*Rhynchodemus terrestris* O. F. M.
Belonging to undetermined Families	*Dolichoplana.*
	Polycladus.
	Microplana.
	Leimacopsis.

Turbellaria. III. Rhabdocoelida.

The Rhabdocoelida include a very heterogeneous assemblage of usually minute Turbellaria, distinguished collectively from the Polyclads and Triclads by the form of the digestive tract. This is a simple or slightly lobed sac, except in the Bothrioplanidae, which in this and many other points closely resemble the Triclads. It is to the straight, rod-like nature of the alimentary canal that the name of the group refers. The size and form of the body, and the structure of the pharynx and genitalia, vary within wide limits.

The Rhabdocoelida are subdivided into three tribes:—

(1) *Acoela,* in which a sub-central mouth and pharynx are present, but lead into the parenchyma of the body, not into an intestine with proper walls. An excretory system has not hitherto been seen. Yolk-glands are absent. An otolith underlies the brain. The *Acoela* are marine.

(2) *Rhabdocoela,* which possess a complete alimentary tract separated from the body-wall (except for a few suspensory strands) by a space or body-cavity, filled with fluid. This space is sometimes (*Vortex viridis*) lined by an endothelium of flattened parenchymatous cells. There are two compact testes, which are enclosed (as are the ovaries and yolk-glands) in a distinct membrane. An otolith is present in some genera and species. Terrestrial, fresh-water, marine.

(3) *Allococoela,* in which the body-cavity is greatly reduced. Except in the Bothrioplanidae, the gonads have no distinct membrane. Testes numerous; yolk-glands present. Marine with a few exceptions.

Occurrence and Habits of the Rhabdocoelida.—The *Acoela* are usually minute, active Turbellaria abounding amongst weeds throughout the lower half of the Littoral, and the whole of the Laminarian zone, but are most plentiful in the pools exposed during spring-tides on our coasts, especially on the shores of Devonshire. The species of *Haplodiscus,* however, and *Convoluta henseni* are modified pelagic forms found in the Atlantic Ocean.[1] *Convoluta paradoxa* (Fig. 19, B) is the commonest British species. It is from 1 to 9 mm. in length, and of a brown colour, marked above by one or more transverse white bars. The brown colour is due to a symbiotic alga, the nature of which has not been thoroughly investigated. In an allied species, however (*C. roscoffensis*), from the coast of Brittany, the alga, which is here green, has been carefully examined by Professor Haberlandt,[2] and it appears from his researches that the algae form a special assimilating tissue, enabling the *Convoluta* to live after the fashion of a green plant. At Roscoff, these elongated green *Convoluta* live gregariously in the sandy tide-pools, fully exposed to the sun's rays, and have the appearance of a mass of weed floating at the surface of the water. Access to the atmosphere and to sunlight are necessary in order to enable the assimilating tissue to form the carbohydrates, upon which this form lives exclusively. Not only has the alga itself undergone such profound changes (loss of membrane, inability to live independently after the death of the host) as to disguise its true nature (a tissue-cell derived from algal ancestors), but the *Convoluta* has also undergone con-

[1] Böhmig, *Ergebnisse d. Plankton Expedition,* Bd. ii. H. g. 1895.

[2] von Graff, *Die Acoela,* Leipzig, 1892. Appendix.

comitant changes, in form, in the loss of a carnivorous habit, and in the development of marked heliotropic movements, thus adapting itself to an holophytic or plant-like mode of nutrition. Nevertheless the Acoela, as a group, are carnivorous, feeding upon Diatoms, Copepoda, and small Rhabdocoela, the absence of a digestive tract indeed being probably more apparent than real.[1]

The *Rhabdocoela* live under varied conditions. One form, *Prorhynchus sphyrocephalus*, has been found among plants far from water in the neighbourhood of Leyden, by De Man.[2] With this exception the group is purely aquatic, and though a few genera and even individuals of the same species occur both in salt and fresh water, whole sub-families and genera are either marine or paludicolous. Among the latter, *Mesostoma, Castrada, Vortex,* and *Derostoma* are common in brooks and ponds, especially at certain times, often only for one month (May or June) in the year. Species of *Macrostoma, Stenostoma,* and *Microstoma* are also abundant in similar places. The two latter occur in chains formed by fission; but the sexual individuals (which are of distinct sexes, contrary to the usual hermaphrodite condition of Flat Worms) only appear at stated times and are not well known. A large number of genera are purely marine, and one family, the Proboscidae (distinguished by having the anterior end invaginated by special muscles and converted into a sensory organ), is entirely so. The most cursory examination of littoral weeds reveals species of *Macrorhynchus, Acrorhynchus, Promesostoma, Byrsophlebs,* and *Proxenetes,* the character of which may be gathered from von Graff's great monograph, or from Gamble's paper on the "British Marine Turbellaria."[3] Much, however, still remains to be done before we possess an adequate idea of the occurrence of this group on our coasts.

Some Rhabdocoels are parasitic. *Fecampia erythrocephala,*

[1] The development of the *Acoela* has been worked out recently by Mdlle. Pereyaslawzewa (*Zapiski Novoross. Obshch. Odessa,* 17 Bd. 1892) and Gardiner (*Journal of Morphology,* xi. No. 1, 1895, p. 155) with conflicting results. The former finds four endoderm cells, which give rise to a larval intestine. The *Acoela* are for her, *Pseudacoela.* Gardiner, on the other hand, finds no trace of an endoderm at any stage of the development of *Polychoerus caudatus.*

[2] *Tijdschr. Nederland. Dierk. Ver.* Deel ii. 1875.

[3] Von Graff, *Monographie d. Turbellarien: I. Rhabdocoeliden,* 1882. Gamble, *Quart. Journ. Microscop. Science,* vol. xxxiv. 1893, p. 433.

which occurs in the lacunar spaces and alimentary canal of young shore crabs (*Carcinus maenas*), is a white cylindrical animal $\frac{1}{4}$ inch long, with a red snout. After attaining maturity it works its way out of the crab and encysts under stones, forming a pyriform mass in shape like a "Prince Rupert's drop." Within this case the eggs develop, and the young probably emerge through the open narrow end of the hard white tube, but how they reach the crab is not known. *Graffilla muricicola* is found in the kidney of *Murex brandaris* and *M. trunculus*, at Naples and Trieste; *G. tethydicola* in the foot of *Tethys*. *Anoplodium parasiticum* occurs among the muscles which attach the cloaca of *Holothuria tubulosa* to the body-wall; and *A. schneideri* occurs in the sea-cucumber, *Stichopus variegatus*. These are truly parasitic forms, constituting a special subfamily. They have no rhabdites in the skin; the nervous system and sense-organs are only slightly developed; and the pharynx has undergone a notable reduction in relation to the simpler mode of obtaining nourishment. Other cases of association between certain Rhabdocoels (closely allied to, if not identical with, certain free-living species) and Lamellibranchs or Sea-urchins, are, however, of another kind. Thus on the gills or in the mantle cavity of species of *Mytilus*, *Cyprina*, *Tellina*, and upon the test of *Clypeaster*, such forms as *Enterostoma mytili*, *Acmostoma cyprinae*, and *Provortex tellinae* have been found. But it is probable that these Turbellaria here obtain merely a temporary

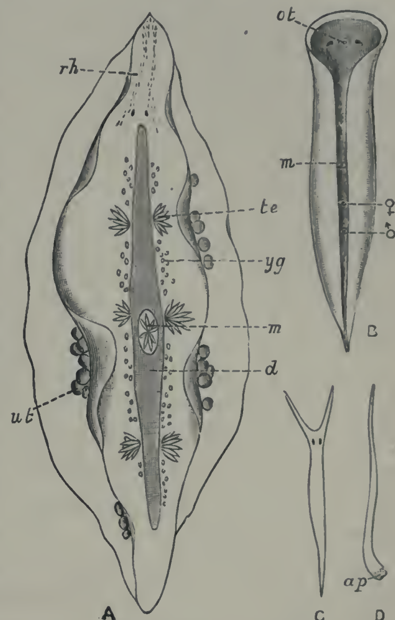

FIG. 19.—Forms of Rhabdocoelida. **A**, *Mesostoma tetragonum* O. F. M. (Rhabdocoela), ×10; **B**, *Convoluta paradoxa* Oe. (Acoela), ×10; **C**, *Vorticeros auriculatum* O. F. M., ×6; **D**, *Monotus fuscus* Oe. (Alloeocoela), ×4. *ap*, Adhesive papillae; *d*, intestine; *m*, pharynx; *ot*, otolith; *rh*, rhabdites; *te*, testes; *ut*, uterus with eggs; *yg*, yolk-glands; ♂, male, ♀, female genital pores. (**A** after Braun.)

shelter and possibly a supply of the food of the mussel or sea-urchin.

The *Alloeocoela* afford a well-established case of association. *Monotus fuscus* (Fig. 19, D), an abundant, active, elongated animal, lives on our coasts in the upper part of the littoral zone among *Patella*, *Balanus*, and sometimes *Chiton*. When the tide is low, the *Monotus*, to obtain moisture and darkness, creeps between the mantle-folds of these animals, where it may readily be found. Upon the return of the tide it leaves its retreat and creeps or swims about freely. Other Alloeocoela collect in great numbers in tufts of red-seaweeds (Florideae). By placing such tufts in vessels, the sea-water, especially as darkness sets in, begins to swarm with *Cylindrostoma 4-oculatum*, species of *Enterostoma* and *Plagiostoma*; *P. vittatum*, with three violet bands across the white body, being a particularly obvious form. *Vorticeros auriculatum* (Fig. 19, C), another abundant species, is remarkable for the long tentacles which can be completely withdrawn, and in this condition it completely resembles a *Plagiostoma*.

The presence of a species (*P. lemani*) of the characteristically marine genus *Plagiostoma*, in the Lake of Geneva, and in one or two other Swiss lakes, at depths varying from 1 to 150 fathoms, is very interesting, and is perhaps the only well-established case of the survival of a once marine Rhabdocoelid under changed conditions. *Plagiostoma lemani* is by far the biggest of the group to which it belongs, being over half an inch in length. It is usually found in fine mud, sometimes among *Chara hispida*, and has the general appearance of an inactive white slug. We are indebted to Forel and Duplessis for the discovery of this species, and also of *Otomesostoma morgiense*, a *Mesostoma* with an otolith, dredged in 10 to 50 fathoms in the Lake of Geneva, the Lake of Zürich, and found recently also by Zacharias in the Riesengebirge. The genus *Bothrioplana*, first found by Braun in the water-pipes of Dorpat, has been carefully investigated by Vejdovsky,[1] who places it in a special family, Bothrioplanidae, among the Alloeocoela. One species has recently been found near Manchester.

A comprehensive survey of the Rhabdocoelida shows that, with the chief exception of the Proboscidae, the more lowly organised forms, the Acoela and Alloeocoela, are marine, whereas the fresh-water forms are in most cases the most highly organised

[1] *Zeitschr. f. wiss. Zoologie*, Bd. lx. 1895, p. 163.

genera (*Mesostoma, Vortex*). But *Macrorhynchus helgolandicus*, though minute (1·5-2 mm. long), has a more complex structure[1] than any other species of the specialised marine genus to which it belongs, and is a remarkable instance of great complexity being associated with small size.

Reproduction. — The Rhabdocoelida present the greatest diversity in the development of the reproductive system. The Acoela and Alloeocoela have the simplest arrangement. Scattered testes, often without a distinct membrane, form the spermatozoa, which in most cases wander into parenchymatous spaces, but in *Monoporus rubropunctatus* and *Bothrioplana*, into distinct vasa deferentia. In both groups a protrusible penis opens independently to the exterior, and may be simply muscular or provided with a chitinous armature. Two ovaries are present, and the oviducts, if distinct, are continuations of the ovarian membrane. In most forms a "bursa seminalis," which receives the spermatozoa of another individual, is appended to the female genital canal. In many of the Alloeocoela, however, a portion of the ovary is sterile, and its cells, forming a yolk-gland, feed the fertile portion, the whole structure being then spoken of as a germ-yolk-gland. In many others (Monotidae) this sterile part has become an independent yolk-gland, which communicates by yolk-ducts with the oviducts. The Acoela form no egg-case, the body of the parent becoming a bag for the ova, which elaborate their own food-yolk. The Alloeocoela lay hard-shelled eggs, which are produced in *Bothrioplana* and *Automolos* by the activity and interaction of reproductive organs, resembling closely those of certain Triclads.[2]

The Rhabdocoela exhibit every stage in the development of a complex reproductive system, from the simple ovaries and testes of a *Microstoma* or *Macrostoma*, to the intricate system of ducts and glands of a *Macrorhynchus* (Proboscidae), in which there is still much to be made out. The complications of the copulatory organs chiefly arise from the way in which the spermatozoa are brought into contact with a nutritive prostatic fluid, or are formed into spermatophores; and also from the penial armature,

[1] See von Graff's *Monographie*, pl. ix.; and Jensen, *Turbellaria ad Litora Norvegiae*, Bergen, 1878, pl. iv.

[2] For the reproductive organs of Rhabdocoelida consult von Graff, *Monographie*, "Die Acoela"; and Böhmig, *Zeitschr. f. wiss. Zool.* Bd. li. 1891, p. 167.

which is often very complex, and may consist of a curved chitinoid hook or a coiled loop (*Promesostoma*), of hooks (Proboscidae), or of an intricate arrangement of plates (*Proxenetes*); or the penis may take on a complex corkscrew-like form (*Pseudorhynchus*). The (frequently armed) female genital canal usually possesses a bursa seminalis for the fertilisation of the eggs, but a receptaculum seminis or spermatheca may serve for the reception, the bursa, for the lodgment of the spermatozoa of another individual. The fertilised ovum is provided with a supply of food-yolk and with a shell, which may be formed in a special diverticulum, the "uterus." The development of these organs strains the resources of the animal to the utmost, and in some Proboscidae the alimentary canal is squeezed out and disintegrates, in order to make room for them.

A few *Mesostoma* (*M. ehrenbergii*, *M. productum*, *M. lingua*) produce two kinds of eggs—thin- and thick-shelled. The latter are laid throughout the summer, and lie dormant through winter. The young which hatch in spring out of these "winter" eggs develop rapidly, and when only 7 to 8 mm. long (*i.e.* one-third the size of the parent) already possess functional genital organs; the penis, however, is rudimentary, and incapable of being used for copulation. Hence it is probable that this stunted progeny self-fertilise their thin-shelled or "summer" eggs. After the formation of these eggs the same parent is said (Schneider[1]) to produce thick-shelled or winter eggs, but however that may be, the first young which hatch from the thin-shelled ova are produced in great numbers at a time (April to May) when food is abundant. These grow rapidly to the full size, and then having attained maturity, cross-fertilise one another's ova, which become encased in a thick brown shell; and it is these numerous "winter" eggs that lie dormant throughout the autumn and winter. Many *Mesostoma*, and practically all other Rhabdocoela, however, produce only thick-shelled eggs, and in all cases it is probable that to these many species owe their wide distribution, the exact range of which is, however, unknown, as is also the means of dispersal.

[1] *Untersuchungen ü. Platyhelminthen*, Giessen, 1873, p. 101.

Classification of Rhabdocoelida.

ACOELA.

Family.	Genus and British species.
Proporidae .	. *Proporus venenosus* O. Sch. Plymouth. *Monoporus rubropunctatus* O. Sch. Plymouth. *Haplodiscus.*
Aphanostomatidae	. *Aphanostoma diversicolor* Oe. Common. *A. elegans* Jen. Plymouth. *Convoluta saliens* Grff. Plymouth, Millport. *C. paradoxa* Oe. (Fig. 19, B). Common. *C. flavibacillum* Jen. Plymouth, Port Erin, Millport. *Amphicoerus.* *Polychoerus.*

RHABDOCOELA.

Macrostomatidae	. *Mecynostoma.* *Macrostoma hystrix* Oe. Stagnant water. *Omalostoma.*
Microstomatidae	. *Microstoma lineare* Oe. Fresh water. *M. groelandicum* Lev. Plymouth, among *Ulva.* *Stenostoma (Catenula) lemnae* Dug. Near Cork. *S. leucops* O. Sch. Common in fresh water. *Alaurina claparedii* Grff. Skye.
Prorhynchidae .	. *Prorhynchus stagnalis* M. Sch. In Devonshire rivers. *Promesostoma marmoratum* M. Sch. Common. *P. ovoideum* O. Sch., *P. agile* Lev. Plymouth. *P. solea* O. Sch. Plymouth, Port Erin. *P. lenticulatum* O. Sch. Port Erin.
Mesostomatidae .	. *Byrsophlebs graffii* Jen. Plymouth, Millport. *B. intermedia* Grff. Millport, Port Erin. *Proxenetes flabellifer* Jen. Millport, Plymouth, Port Erin. *P. cochlear* Grff. Millport. *Otomesostoma.* *Mesostoma productum* Leuck., *M. lingua* O. Sch., *M. ehrenbergii* O. Sch., *M. tetragonum* O. F. M. (Fig. 19, A). All at Cambridge. *M. rostratum* Ehr. Widely distributed. *M. viridatum* M. Sch. Manchester. *M. robertsonii* Grff., *M. flavidum* Grff. Both at Millport. *Bothromesostoma personatum* O. Sch. Preston. *Castrada.*
Proboscidae .	. *Pseudorhynchus bifidus* M'Int. Millport, St. Andrews, Port Erin. *Acrorhynchus caledonicus* Clap. Generally distributed. *Macrorhynchus naegelii* Köll., *M. croceus* Fabr. Plymouth, Millport. *M. helgolandicus* Metsch. West coast. *Gyrator hermaphroditus* Ehrbg. St. Andrews. Also common in fresh water. *Hyporhynchus armatus* Jen. Plymouth, Port Erin. *H. penicillatus* O. Sch. Plymouth.

VORTICIDAE . . . *Schultzia.*
Provortex balticus M. Sch. Generally distributed.
P. affinis Jen., *P. rubrobacillus* Gamb. Plymouth.
Vortex truncatus Ehrbg. Abundant in fresh water.
V. armiger O. Sch. Millport (fresh water). *V. schmidtii* Grff., *V. millportianus* Grff. Millport.
V. viridis M. Sch. Generally distributed.
Jensenia.
Opistoma.
Derostoma unipunctatum Oe. Edinburgh.
Graffilla.
Anoplodium.
Fecampia erythrocephala Giard. Plymouth, Port Erin.

SOLENOPHARYNGIDAE . *Solenopharynx.*

ALLOEOCOELA.

PLAGIOSTOMATIDAE . *Acmostoma.*
Plagiostoma dioicum Metsch., *P. elongatum* Gamb., *P. pseudomaculatum* Gamb., *P. sagitta* Ulj., *P. caudatum* Lev., *P. siphonophorum* O. Sch., *P. ochroleucum* Grff. All at Plymouth.
P. sulphureum Grff. Port Erin. *P. vittatum* F. and Leuck. Millport, Plymouth, Port Erin. *P. koreni* Jen. Plymouth, Millport. *P. girardi* O. Sch. Plymouth, Port Erin, Valencia.
Vorticeros auriculatum O. F. M. (Fig. 19, C). Port Erin, Plymouth. *V. luteum* Grff. Plymouth.
Enterostoma austriacum Grff. Plymouth, Port Erin.
E. fingalianum Clap. Skye, Plymouth. *E. coecum* Grff. Millport.
Allostoma pallidum van Ben. Millport.
Cylindrostoma 4-oculatum Leuck. Skye, Millport, Plymouth.
C. inerme Hall, *C. elongatum* Lev. Plymouth.
Monoophorum striatum Grff. Plymouth.

BOTHRIOPLANIDAE . *Bothrioplana.*
Bothrioplana sp. ? Manchester.
Otoplana.

MONOTIDAE . . . *Monotus lineatus* O. F. M., *M. fuscus* Oe. (Fig. 19, D). Both common littoral forms.
M. albus Lev. Plymouth.
Automolos unipunctatus Oe. Skye, St. Andrews, Plymouth.
A. horridus Gamb., *A. ophiocephalus* O. Sch. Plymouth.

CHAPTER II

TREMATODA

CHARACTERS OF TREMATODES—HABITS AND STRUCTURE OF TREMATODA ECTOPARASITICA (MONOGENEA) — LIFE-HISTORIES OF *POLYSTOMUM INTEGERRIMUM*, *DIPLOZOON PARADOXUM*, AND *GYRODACTYLUS ELEGANS* — TREMATODA ENDOPARASITICA (DIGENEA)—OCCURRENCE AND HABITS OF DIGENEA—LIFE-HISTORY OF *DISTOMUM MACROSTOMUM*—*DISTOMUM HEPATICUM* AND ITS EFFECTS—*BILHARZIA HAEMATOBIA*—BISEXUAL TREMATODES—TABLE OF HOSTS—CLASSIFICATION.

FROM the Turbellaria we now pass on to a consideration of the second great subdivision of the Platyhelminthes, the Trematodes or "flukes," of which the "liver-fluke" is the best known, since it is one of the most dangerous parasites that infest domestic animals.

It has been pointed out that the Polyclads, Triclads, and Rhabdocoels are carnivorous, and that in each of these groups sporadic cases of parasitism occur. In other words, when the prey is much larger than the Turbellarian, the latter tends to become a parasite, and we can trace the development of the parasitic habit from the gradual association of Turbellaria with Ascidians, Crustacea, Molluscs, and Polyzoa merely for protective purposes, through the adoption, not only of the body of the host for shelter, but of its flesh for food; though it is only in some Rhabdocoels (*Graffilla*, etc.) that there exists a degeneration corresponding to the easier mode of nutrition and simpler life. The Trematodes,[1] however, are wholly parasitic, either on the outer surface, the gills, or internal organs of their host, which is almost always a

[1] Compare the remarks on Trematodes, pp. 4-5.

Vertebrate. Some Trematodes lodge in the mouth; others wander down the oesophagus into the stomach or intestine, where they fix themselves to the mucous membrane. Again, others work their way into the digestive glands by the ducts, and thus become further and further removed from the external world, and more adapted to live in the particular organs of that host in which they best flourish. The most important result of the adoption of this internal habitat by endoparasitic Trematodes is, however, seen in their life-history. If a liver-fluke were to deposit its million or so of eggs in the bile-ducts of the sheep, and these were to develop *in situ*, the host could not withstand the increased drain upon its vital resources, and host and parasites would perish together. Hence it is clear that the infection of a second host by Trematodes is highly necessary, whether they be *ectoparasitic*, in which case the infection is easily effected, when two hosts are in contact, by the adult worms, as well as when they are apart, by free-swimming larvae. In *endoparasitic* Trematodes it is brought about by the migration of the young to the outer world, their entrance into a, usually, Invertebrate host and their asexual multiplication within it, and the capture and deglutition of this "intermediate host" by the final Vertebrate one. Within the latter the immature parasites find out the organ in which their parents flourished, and here they too grow and attain maturity. The chances of any one egg of an endoparasitic Trematode producing eventually an adult are, therefore, far less favourable than in the case of an ectoparasitic form. In other words, while the former must lay a great number of small eggs, the latter need only deposit a (comparatively) few large ones, and this fact has a corresponding influence on the structure of the genitalia in the two cases. The Digenea, which employ two hosts in a lifetime, have accordingly a different generative mechanism from that of the Monogenea. The great need of the latter is a powerful apparatus for adhering to the surface of the body of its host; while the adaptations which the endoparasite requires are, in addition, (1) protection against the solvent action of the glands of its host, (2) the power of firm adhesion to a smooth internal surface, and (3) the ability not only to produce a large quantity of spermatozoa and ova, but in the absence of a fellow-parasite, to fertilise its own ova; and we find these conditions abundantly satisfied.

Trematoda monogenea (*ectoparasitica*).

There are four subdivisions of the Monogenea:—

I. *Temnocephalidae,* with four to twelve tentacles, and one sucker posteriorly (Fig. 20).

II. *Tristomatidae,* with two lateral, anteriorly-placed suckers. Oral suckers are absent, a large posterior sucker is constant, and is often armed with hooks (Fig. 22, C).

III. *Polystomatidae,* with, usually, two oral suckers and a posteriorly-placed adhesive disc armed with suckers and hooks (Figs. 23 and 24).

IV. *Gyrodactylidae* (Fig. 29).

Habits and Structure of Ectoparasitic Trematodes.

I. *Temnocephalidae.*—These interesting forms, of which a good account has lately been written by Haswell,[1] occur on the surface (rarely in the branchial chamber) of fresh-water crayfish and crabs in Australasia, the Malay Archipelago, Madagascar, and Chili. Others have been found on the carapace of a fresh-water tortoise, and in the branchial chamber of the mollusc *Ampullaria* from Brazil. Wood-Mason discovered others, again, in bottles containing spirit-specimens of Indian fish. *Temnocephala* is rarely more than a quarter of an inch long, and looks like a minute Cephalopod or a broad flattened *Hydra*. By the ventral sucker each species adheres to its own particular host, the tentacles being used as an anterior sucker for "looping" movements. The food, consisting of Entomostraca, Rotifera, and Diatoms, is first swallowed whole by the large pharynx (Fig. 20, *ph*), which can be protruded through the ventrally-placed mouth, and is then received into a simple lobed intestine (*d*). The skin, especially on the surface of the tentacles, is provided here and there with patches of cilia borne by the cellular epidermis,—the only undoubted case of external cilia occurring in an adult Trematode. Minute rhabdites formed in special gland-cells, occur plentifully on the tentacles, and are another distinctly Turbellarian feature. The excretory system is peculiar (Fig. 21). Fine ducts proceed from the various organs of the body, and open to the exterior by means of a pair of contractile sacs

[1] Haswell, *Monograph of the Temnocephaleae.* Macleay Memorial Volume. Mem. iii. 1893.

placed on the dorsal surface. Each sac is a single cell, and within it not one merely, but several "flames," or bunches of rhythmically contractile cilia, are present. These are placed on the course of excessively fine canals, which perforate the protoplasm of this cell. The terminal branches of the excretory canals end in branched cells, apparently devoid of "flames."

The reproductive system is very similar to that of certain

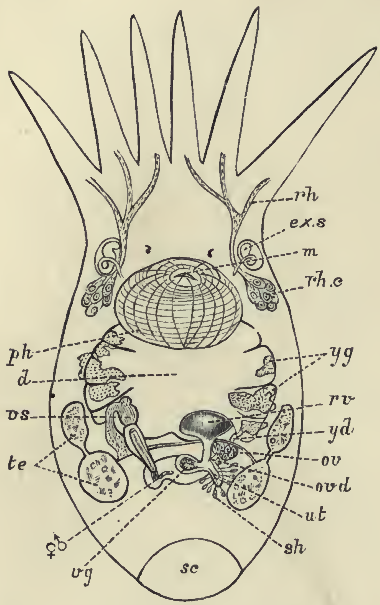

FIG. 20.—*Temnocephala novae-zealandiae* Has. × 10. Ventral view to show the digestive and reproductive systems. (After Haswell.)

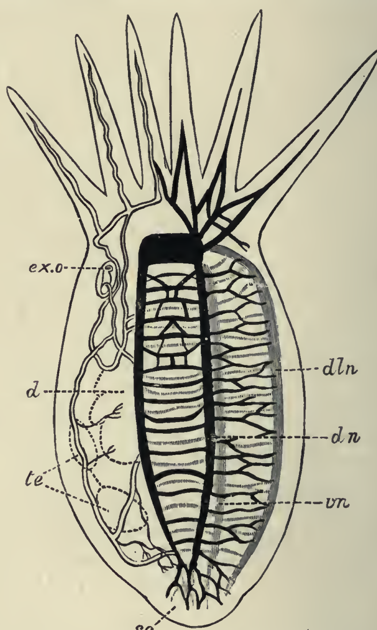

FIG. 21.—The same from the dorsal surface, to show the excretory system (double line), and the nervous system (black and shaded). (After Haswell.)

d, Intestine ; *dln*, dorso-lateral nerve ; *dn*, dorsal nerve ; *ex.o*, excretory aperture on dorsal surface ; *ex.s*, terminal excretory sac ; *m*, mouth ; *ov*, ovary ; *ovd*, oviduct ; *ph*, pharynx ; *rh*, rhabdites ; *rh.c*, cells in which the rhabdites are formed ; *rv*, yolk receptacle ; *sc*, sucker ; *sh*, shell-gland ; *te*, testes ; *ut*, uterus ; *vg*, vagina ; *vn*, ventral nerve ; *vs*, vesicula seminalis ; *yd*, yolk-duct ; *yg*, yolk-gland. ♀, ♂, common genital pore.

Rhabdocoels. An armed penis and the female genital duct open into a genital atrium, and this by a single aperture (♀, ♂, Fig. 20) to the exterior. The fertilised ovum and yolk are enclosed in a stalked shell formed in the uterus.

The interest and importance of the Temnocephalidae lies in the fact that they are almost as much Turbellaria as Trematodes.

In habits, in the character of the skin, the muscular, digestive, and reproductive systems, they find their nearest allies in Rhabdocoels (Vorticidae). But in the excretory and nervous systems, the latter composed of two dorsal, two lateral, and two ventral trunks all connected together (Fig. 21), they are Tristomid Trematodes. Thus they may fitly connect an account of the two great groups.

II. *Tristomatidae and* III. *Polystomatidae.*[1]—The members of these families are found on the body, or attached to the gills, of

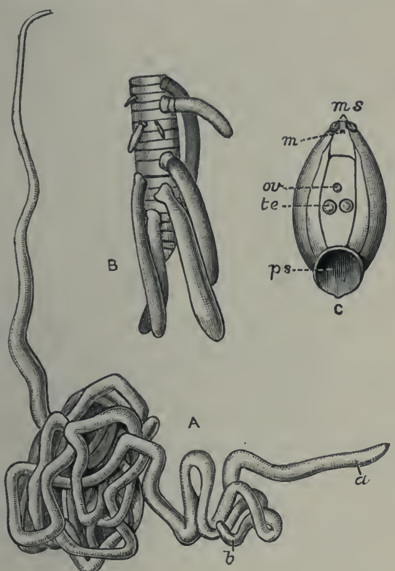

Fig. 22. — **A,** *Nematobothrium filarina* van Bened. Nat. size. Two individuals (*a* and *b*) are found together, encysted on the branchial chamber of the Tunny. **B,** *Udonella caligorum* Johns. A Tristomid, several of which are attached to the ovary of a Copepod (*Caligus*), itself a parasite on the gills of the Hake. × 8. **C,** *Epibdella hippoglossi* O. F. M. A Tristomid found on the body of the Halibut. Nat. size. *m*, Mouth; *ms*, lateral suckers; *ov*, ovary; *ps*, posterior sucker; *te*, testes. (All after P. J. van Beneden.)

fresh-water and marine fishes. The edible and inedible fish of our coasts have each their particular ectoparasitic Trematodes; while the Minnows, Sticklebacks, and Miller's Thumbs of streams and ponds are attacked by *Diplozoon, Gyrodactylus,* and other forms. The aquatic Amphibia also harbour a number. *Polystomum integerrimum* is common in the bladder of Frogs, where it leads a practically aquatic life. Other species of *Polystomum* inhabit the buccal and nasal cavities of certain Chelonia, but naturally no terrestrial Vertebrates are infested externally by these Trema-

[1] Braun, in Bronn's *Klassen u. Ordn. d. Thierreichs,* vol. iv. p. 407, gives a valuable summary of our knowledge of this group. For figures, see van Beneden and Hesse, *Mémoires de l'Acad. roy. de Belgique,* tom. xxxiv. 1864, pp. 1-169. A valuable paper (with synoptic tables) on Japanese Monogenea, by Goto, *Journ. Coll. Sci. Japan,* vol. viii. pt. 1, 1894, has recently appeared.

todes. The blood and epithelia of the host are sucked, and to this end the pharynx has frequently a chitinous armature to aid in the abrasion or inflammation of the tissues upon which the parasite feeds. In the case of a Sturgeon attacked by *Nitzschia elongata,* a Tristomid, the mouth of the host appeared to be highly inflamed by these attacks (v. Baer).

The suckers, in the two families under consideration, vary in number and complexity. There is always a powerful apparatus at the hinder end of the body securing the Trematode firmly to the slimy body or gills of its host, and, usually in the Polystomatidae, a pair of suckers at the sides of the mouth accessory to the pumping action of the pharynx. In *Axine,* and to a less extent in *Octobothrium* (Fig. 23), the suckers are strengthened by a complex hingework of chitinoid bars or hooks, which serve as insertions for the muscles of the suckers, and thus increase their efficiency.

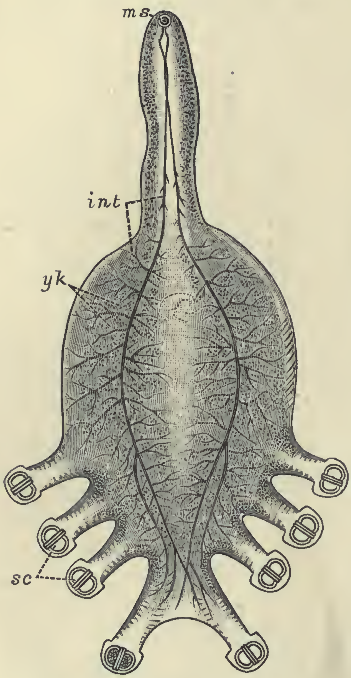

Fig. 23.—*Octobothrium merlangi* Kuhn, from the gills of the whiting. × 8. *int,* Intestine ; *ms,* mouth ; *sc* suckers with chitinoid armature ; *yk* yolk-glands. (After v. Nordmann.)

The mouth is invariably present just beneath the anterior end of the body. It leads into a muscular, pumping pharynx (Fig. 24, *ph*), and this into a bifurcated intestine which ends blindly. The two openings of the excretory system lie on the dorsal surface (as in *Temnocephala*), and the excretory canals branch through the substance of the body, ending usually in "flame-cells." The nervous system is highly developed, and resembles that of *Temnocephala* (Fig. 21) in detail. Upon the brain one or even two pairs of eye-spots are present in the larvae, and may persist throughout life. Tactile setae occur in *Sphyranura,* a parasite of the North American Amphibian *Necturus,* but a cellular epidermis is apparently rendered impossible, perhaps from the nature of the mucus in which the body is bathed, or to the attempts of the host to free itself from these parasites; and hence an investing membrane is present, which morphologically is either a modified epithelium, or a cuticle formed by the glandular secretion of the parenchyma.

The reproductive organs of the Polystomatidae may be understood from Figs. 24, 27, and 28. At the point of union of the ovi-

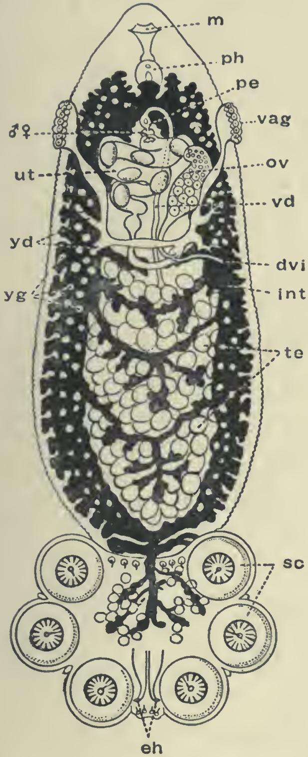

Fig. 24.—*Polystomum integerrimum* Fröh., from the bladder of the Frog, and seen from the ventral surface. The alimentary canal is black, the white dots upon it being the yolk-glands. *dvi*, Ductus vitello-intestinalis (probably homologous with the Laurer's canal or "vagina" of Digenea); *eh*, hooks of sucking disc; *int*, intestine; *m*, mouth; *ov*, ovary; *pe*, penis; *ph*, pharynx; *sc*, suckers with an embryonic hook persisting in each; *te*, testes; *ut*, uterus with eggs; *vag*, left vagina; *vd*, vas deferens; *yd*, yolk-duct; *yg*, yolk-glands; ♂ ♀, common genital aperture. (Modified from Zeller.) × 8.

duct (Fig. 28, *ovd*), the vitelline ducts (*yd*), and the commencement of the uterus (*ut*), a slender duct is given off which opens into the intestine, and is known as the "vitello-intestinal canal" (Fig. 24, *dvi*; Fig. 28, *gic*). This duct has apparently the same relations as the "canal of Laurer" of Digenea,[1] except only that the latter opens to the exterior directly. In connexion with this vitello-intestinal canal a "vagina" is present, which in *Polystomum* and most Monogenea is paired (Fig. 24, *vag*), in *Diplozoon* and in one

[1] See Leuckart, "*Parasiten*," Bd. ii. p. 238.

or two other forms, however, unpaired. The vagina receives the penis of another individual during copulation (Fig. 26), and does not appear to have an homologue in the liver-fluke or other Digenea.

Life-Histories of the Polystomatidae.[1]—*Polystomum integerrimum.* After the mutual fertilisation of two individuals, the eggs are laid in the water by the protrusion of the body of the parent through the urinary aperture of the Frog. About 1000 eggs are laid in the spring at the rate of 100 a day for ten days. After about six weeks, the larva (·3 mm. long) hatches

Fig. 25.—Eggs of Monogenea. **A**, Eggs of *Encotylabe pagelli* v. Ben.-Hesse ; **B**, eggs of *Udonella pollachii* v. Ben.-Hesse (with young forms just hatching out) ; **C**, egg of *Microcotyle labracis* v. Ben.-Hesse. (After van Beneden and Hesse.) × 50.

out, and swims about freely by means of bands of large ciliated cells (Fig. 26, A); but if it does not meet with a tadpole within twenty-four hours, it dies. Should it, however, encounter one, the larva creeps along it in a looping fashion until it approaches the opercular spout, or opening of the branchial chamber, on the left side; into this it darts suddenly, fixes itself, and throws off its cilia. Here it remains eight or ten weeks, feeding, increasing in size, and forming the suckers from behind forwards.

[1] Zeller, *Zeitschr. f. wiss. Zool.* xxii. 1872, pp. 1, 168 ; also Bd. xxvii. 1876, p. 238 ; xlvi. 1888, p. 233.

At the time of the tadpole's metamorphosis, the young *Polystomum* works its way down the pharynx into the oesophagus and along the intestine, till it reaches and enters the opening of the bladder. Three years afterwards it becomes mature.

Sometimes, however, *Polystomum* experiences another fate. The larvae settling down on the external gills of a young, recently-hatched tadpole, and obtaining a richer supply of blood than in the previous case, grow far more rapidly, so that in five weeks they are mature, although still in the branchial chamber of the tadpole. They do not then wander into the alimentary canal, but usually, having discharged their eggs, die at the time of the tadpole's metamorphosis. Still more interesting, however, is the difference between the genitalia in these and in the normal *Polystomum*. In contrast with the latter, these possess (1) one testis and a rudimentary penis; and their spermatozoa differ in structure and shape from those of the normal *Polystomum*. (2) The vaginae are absent, a fact connected with the absence of a functional copulatory organ. (3) In compensation for the loss of these, a duct connects the single testis and the point of union of oviduct and yolk-ducts, and by this self-fertilisation occurs. (4) The uterus is absent; the "ootype" or duct into which the shell-gland opens, communicating directly with the exterior. In (1) and (4) these aberrant *Polystomum* resemble *P. ocellatum*, from the Tortoise *Emys europaea*.

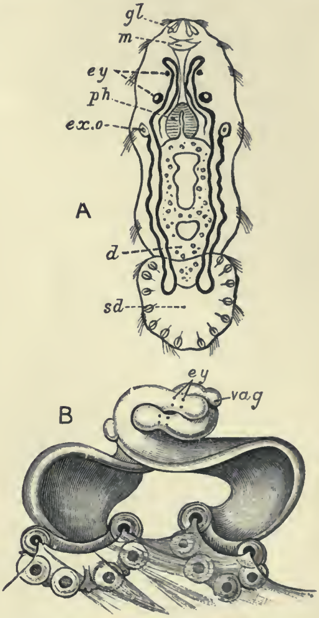

FIG. 26.—*Polystomum integerrimum.* **A**, Free-swimming larva, seen from the ventral surface. × 80. **B**, Two mature individuals in mutual coition attached to the bladder of a Frog. × 5. (After Zeller.) *d*, Intestine; *ex.o*, excretory pore, dorsal in position, seen here by transparency; *ey*, eye-spots; *gl*, frontal glands; *m*, mouth; *ph*, pharynx; *sd*, adhering disc; *vag*, vagina.

Diplozoon paradoxum.—The life-history of *Diplozoon* is unique. For whereas the larvae of most animals grow up, each into a single adult, in *Diplozoon*, of the few larvae that

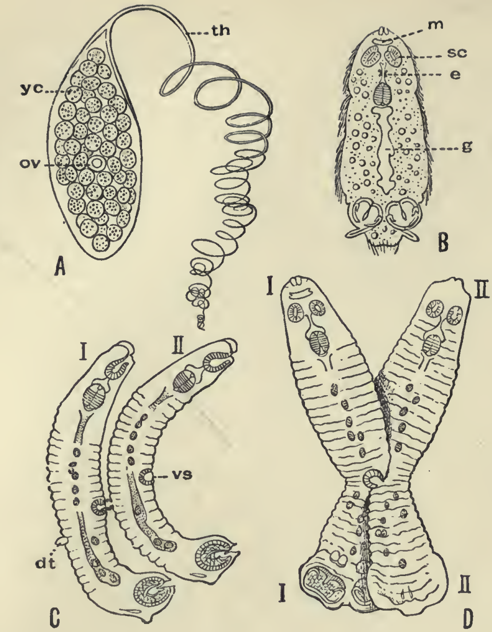

Fig. 27.—**A**, Egg of *Diplozoon paradoxum* v. Nord., consisting of a shell enclosing *ov*, the actual ovum, surrounded by *yc*, the yolk-cells; **B**, larva just hatched (× 125); **C**, two *Diporpa* (I and II) about to unite; **D**, conjugation in progress but not yet complete. *dt*, Dorsal papilla; *e*, eye; *g*, intestine; *m*, mouth; *sc*, ad-oral sucker; *th*, spirally-wound thread attaching the egg to the gill of the Minnow; *vs*, ventral sucker; (in D) I, I, one *Diporpa*, ventral view; II, II, the other, dorsal view. (After Zeller.)

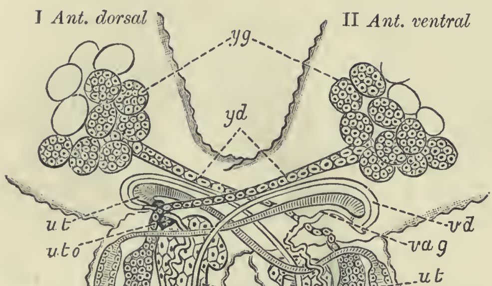

Fig. 28.—Hinder part of the body of *Diplozoon paradoxum*. The fusion of the two *Diporpa*, where they come into contact, is now complete. They now cross each other like an X, and are twisted, so that *Diporpa* I, in front of the point of fusion, is seen from the dorsal surface; behind, from the ventral surface; and the reverse is the case with *Diporpa* II. The compound animal is seen from the opposite surface to that shown in Fig. 27, D. The digestive and excretory organs are omitted. (After Zeller.) I *Ant. dorsal*, dorsal surface of *Diporpa* I, facing the anterior end; I *Post. ventral*, ventral surface of *Diporpa* I, posterior end; and similarly for II *Ant. ventral* and II *Post. dorsal*. *d*, Piece of the intestine showing opening of, *gic*, vitello-intestinal canal; *ov*, ovary; *ovd*, point of union of female genital ducts; *sc*, suckers; *te*, testis; *ut* (in *Diporpa* I), "ootype" or chamber into which shell-glands open. This is continuous with the uterus (*ut*) of *Diporpa* I; *uto*, ventral opening of uterus; *vag*, vagina, with *vd*, vas deferens, permanently inserted into it through the genital pore; *yd*, yolk-ducts; *yg*, yolk-glands.

survive the dangers of their free-swimming existence, only those become mature which conjugate permanently with another individual. But although there are thus only half as many adult *Diplozoon* as there were conjugating larvae (or *Diporpa*, as they were called when they were considered distinct forms), yet the total number of eggs produced is probably as great as if each larva became individually mature.

Diplozoon paradoxum lays its eggs on the gills of the Minnow, which it frequently infests in great numbers. The ovum divides rapidly at the expense of the yolk-cells, and in a fortnight a larva (·2 mm. long) of the shape and complexity shown in Fig. 27, B, hatches out, which, however, succumbs if it does not meet with a Minnow in five or six hours. Should it survive, a dorsal papilla, a median ventral sucker, and a second pair of posterior suckers develop. Thus the *Diporpa* stage is attained. These *Diporpa* may acquire a third and even a fourth pair of suckers, and continue to live three months, but they only develop and mature their reproductive organs, if each conjugates with another *Diporpa* (Fig. 27, C, D), and this only occurs in a small percentage of instances. Each grasps the dorsal papilla of the other by its own ventral sucker, thus undergoing a certain amount of torsion. Where the two bodies touch, complete fusion occurs, and, as shown in Fig. 28, the united *Diporpa* (or *Diplozoon*, as the product is now called) decussate, each forming one limb of the X-shaped *Diplozoon*, within which the two sets of complex genitalia develop (Fig. 28).

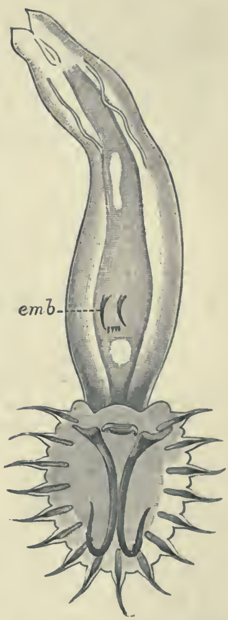

FIG. 29.—*Gyrodactylus elegans* v. Nord., from the fins of the Stickleback. (After v. Nordmann.) × 125. *emb*, Embryo.

IV. *Gyrodactylidae.*—*Gyrodactylus* (Fig. 29), the structure of which is in many ways peculiar, produces one large egg at a time. An embryo, in which the large and smaller hooks of the adhesive disc can be seen (*emb*), develops from this egg while still within the body of the parent, and may give rise to yet another generation within itself. The details of the process have not, however, been well ascertained.

Trematoda digenea (*endoparasitica*).

Occurrence and Habits of Digenea.—Endoparasitic Trematodes have been found in almost all the organs of Vertebrate hosts excepting in the nervous, skeletal, and reproductive systems. The alimentary canal, however, is the most usual habitat. From the buccal cavity to the large intestine, or even to the cloaca, its different regions are the resorts of various Trematodes. No Digenea have been found in the mouth, pharynx, or oesophagus of Mammals; but in Birds, Reptiles, Amphibia, and especially in Fishes, these parts are largely affected. It is a striking fact that Trematodes should occur in the stomach of (chiefly) large predaceous fishes, such as the Pike, Sharks, the Angler-fish, and others, considering the powerful digestive action of the gastric juice of these carnivores. The peculiar nature of the defence which must be employed by the parasites against this digestive action, becomes still more marked when it is considered that if a Trematode normally living in the stomach of one host be transferred to that of another, it is usually speedily digested, as is shown (p. 65) in the case of *Distomum macrostomum*. From these considerations the suggestion has been made that the cutaneous secretions of these Trematodes must act, not only as a protection against digestive or other ferments, but that the action in each case must be a specific one (Frenzel, Braun).

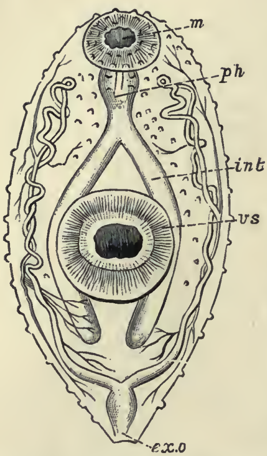

Fig. 30.—*Distomum luteum* v. Baer (immature), to show the arrangement of the excretory vessels. × 50. *ex.o*, Excretory aperture by which the terminal contractile duct opens—the finer vessels end in flame-cells; *int*, intestine; *m*, mouth-sucker; *ph*, pharynx; *vs*, ventral sucker. (After la Valette.)

It is, however, in the small intestine that most Trematodes occur, as the examination of the common Frog[1] will readily demonstrate. Both this and the edible Frog are attacked by a dozen Distomatidae, only a few of which, however, are common

[1] An excellent and beautifully illustrated account, by Looss, of the Distomatidae of Frogs and Fishes may be found in Leuckart and Chun's *Bibliotheca Zoologica*, Heft 16, 1894.

to both hosts, and a number of Holostomatidae also pass a stage of their development within these Amphibia. Some idea of the extent to which animals, whose habits lead to infection, may be attacked by Trematodes (to say nothing of Cestodes and Nematodes, which often occur also) may be gathered from the fact that in dissecting a black stork, Nathusius found several hundred *Holostomum excavatum* and about a hundred *Distomum ferox* in the small intestine, twenty-two *D. hians* in the oesophagus, five others in the stomach, and one *D. echinatum* in the intestine. Snipe, Woodcock, Sandpipers, Dunlin, Gulls, Bittern, Geese, and Wild Ducks are, to mention a few cases, greatly infested by members of this group.

The following Trematodes have occurred in man[1]:—

Distomum hepaticum Abild.
„ *lanceolatum* Mehlis.
„ *conjunctum* Cobbold.
„ *spathulatum* Leuckart (= *D. sinense* Cobb., *D. japonicum* R. Blanch.).
„ *rathouisi* Poir. (probably = *D. crassum* Busk, *D. buskii* Lank.).
„ *heterophyes* v. Sieb.
Distomum pulmonale Bälz (= *D. ringeri* Cobb., *D. westermanni* Kerb.).
„ *oculi humani* Ammon (= *D. ophthalmobium* Dies.).
Monostomum lentis v. Nord.
Amphistomum hominis Lewis and M'Connell.
Bilharzia haematobia Cobb.

Life-histories of the Digenea.—The classification of Trematodes according to their life-histories, expressed in the divisions Monogenea and Digenea, though a very useful one, breaks down entirely in the case of certain forms. Thus the life-history of *Gyrodactylus* is probably digenetic rather than monogenetic. *Aspidogaster conchicola*,[2] which lives in the pericardial cavity of the fresh-water mussel (possibly the only case of a Trematode becoming normally mature in an Invertebrate host, since other species of *Aspidogaster* live in Chelonia), produces larvae which enter another *Anodonta* and develop directly into the sexual form. In other words, *Aspidogaster*, though structurally a digenetic form, possesses a life-history which is direct and simple, *i.e.* monogenetic.

The Holostomatidae, which live in birds of prey and aquatic birds, give rise to eggs from which a minute larva escapes. The fate of this aquatic larva is not directly known,

[1] Leuckart, *Parasiten d. Menschen*, "Trematoden," 1892-94; R. Blanchard, *Traité d. Zool. médicale*, i. 1889; H. B. Ward, *Report for* 1894 *of Nebraska State Board of Agric. Lincoln*, U.S.A. 1895, p. 225.

[2] Huxley, *Anat. of Invert. Animals*, 1877, p. 194.

but in all probability after entering a host (Fish, Amphibian, Mollusc), it undergoes a gradual change into what has long been known as a *Tetracotyle,* from the frequent presence of four (sometimes only three) adhering organs. Fig. 31 exhibits a species which is abundant in the lens and vitreous humour of the eye of the Perch. Its further history is not known, but presumably the Perch is presently devoured by the final host in which the *Diplostomum* attains maturity. Thus the Holostomatidae are "metastatic" (Leuckart), their (probably) direct development requiring the presence of two hosts.[1]

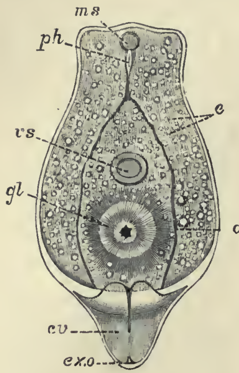

Fig. 31.—*Diplostomum* (*Tetracotyle*) *volvens.* (After v. Nordmann.) × 130. *cv,* Contractile excretory vesicle; *d,* intestine; *e,* calcareous bodies in excretory tubules; *ex.o,* excretory aperture; *gl,* glandular adhesive body; *ms,* oral sucker; *ph,* pharynx; *vs,* ventral sucker.

The other Digenea, the life-histories of which are known, belong to the Distomatidae and Amphistomatidae, and we may distinguish the steps by which the complex life-history of the liver-fluke (*Distomum hepaticum*) has been brought about, by a consideration of that of *Distomum macrostomum.*

Distomum macrostomum.—This form occurs in the intestine of several common Passerine birds. It is remarkable not only for the large oral sucker, but also on account of the position of the common genital pore at the hinder, and not as usual, at the anterior, end of the body (Fig. 32, A). The eggs pass out through this pore, and are discharged with the bird's excrement. Should a certain snail (*Succinea putris*) happen to rasp off the epidermis of a leaf upon which the faeces have fallen, the eggs are swallowed and a minute active larva is set free (Fig. 32, B). This penetrates through the thin wall of the digestive tract of the snail, and passing into the connective tissue, throws off its cilia and assumes the shape of Fig. 32, C. This *sporocyst,* as the larva is now termed, grows rapidly in all directions (Fig. 32, D) at the expense of the snail's tissues, until it becomes impossible to separate parasite and host completely. Those branches which

[1] Braun, Bronn's *Thierreichs,* Bd. iv. p. 792; Leuckart, *Parasiten d. Menschen,* 11 Abth. p. 158; Brandes, in *Spengels Zool. Jahrb. Syst. Abtheil.* Bd. v. 1890, p. 849; v. Nordmann, *Mikr. Beitr.* i. Berlin, 1832.

lie superficially in the cephalic region of the snail become greatly swollen, cylindrical, and contractile. They are banded with green and white, ornamented with red terminal spots, and pulsate rapidly. Hence these fertile branches of the sporocyst (which in this condition was known as *Leucochloridium paradoxum*, Fig. 33, B) naturally attract the attention of insectivorous birds, which peck off the tentacles of the snail, and with it the swollen sporocyst-branch. A sphincter muscle closes the cut end of the fertile sac when the bird's bill nips it off. The sac contains large numbers

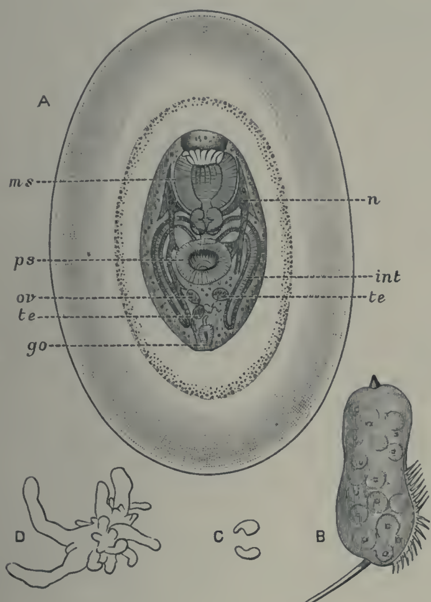

FIG. 32.—Life-history of *Distomum macrostomum* Rud. **A**, Immature *Distomum* (really a tailless *Cercaria*) found in the swollen terminal parts of *Leucochloridium* (Fig. 33, B) and enclosed in two protective membranes, × 40 ; **B**, larva which hatches out of the egg of *D. macrostomum*, × 125 ; **C**, the metamorphosed larva (sporocyst) fourteen days after having entered *Succinea putris*, and pierced through its intestinal wall ; **D**, actively growing sporocyst. (After Heckert.) *go*, Genital aperture ; *int*, intestine ; *ms*, mouth sucker ; *n*, nervous system ; *ov*, ovary ; *ps*, ventral sucker ; *te*, testis.

of young *D. macrostomum* (Fig. 32, A), produced by the division of embryonic cells of the larva (Fig. 32, B), which are apparently blastomeres of the egg reserved for this future use. It is a remarkable circumstance that the old bird itself is immune from infection, and if it swallows these young Distomes, they are digested. Should, however, the snail's tentacle and its contents be offered as food to the nestlings, their weaker digestive powers merely set the Distomes free from the protective membranes (Fig. 32, A), and thus the Blackcaps, Sparrows, and other birds infested by *D. macrostomum* have acquired the parasite when they were nestlings by the unintentional agency of their parents.[1] The snail regenerates its lost tentacles only for the sporocyst to again bud off fertile branches into them.

The egg of this Distome thus gives rise to a larva which enters the tissues of one particular Mollusc. Here it becomes a branched sporocyst within which the sexual worms are formed,

FIG. 33.—**A**, *Succinea putris*, infested by **B**, *Leucochloridium paradoxum*, or the fully-formed sporocyst of *Distomum macrostomum*. (After Heckert.) **A**, Natural size; **B**, × 7.

apparently each from a single embryonic blastomere ("Keimzelle"), by a process comparable with the development of a parthenogenetic ovum, and the whole cycle has been termed *Alloiogenesis, i.e.* alternation of sexual and parthenogenetic generations (Grobben).[2] Leuckart [3] and Looss,[4] however, consider that what was once a metamorphosis of an individual (as in the

[1] Heckert, *Bibliotheca Zoologica* (Leuckart and Chun), Heft 4, 1889. I am not aware that *Leucochloridium* has been noticed in England.

[2] "Heterogamy" usually means the alternation of bisexual and unisexual generations (e.g. *Rhabdonema nigrovenosum*), but is, unfortunately, also used in the sense of Alloiogenesis, as defined above. See Grobben, *Arbeit. Zool. zoot. Ints. Wien*, Bd. iv. 1881, p. 201.

[3] *Parasiten*, Bd. i. Abth. II. p. 152.

[4] *Festschrift f. Leuckart*, Leipzig, 1892, p. 167.

Holostomatidae) has now become, by maturation of the Cercaria in the comparatively modern warm-blooded bird, a metamorphosis extending over two or more generations.

Distomum (*Fasciola*) *hepaticum*—The liver-fluke of the Sheep, which produces the disastrous disease, liver-rot, has a distribution as wide as that of a small water-snail, *Limnaea truncatula*, the connexion between the two being, as Thomas[1] and Leuckart discovered, that this snail is the intermediate host in which the earlier larval, sporocyst, and redia stages are passed through, and a vast number of immature flukes (Cercariae) are developed. These leave the snail and encyst upon grass, where they are eaten by the sheep. Over the whole of Europe, Northern Asia, Abyssinia, and North Africa, the Canaries, and the Faroes, the fluke and the snail are known to occur, and recently the former has been found in Australia and the Sandwich Islands, where a snail, apparently a variety of *Limnaea truncatula*, is also found.[2] Over these vast areas, however, the disease usually only occurs in certain marshy districts and at certain times of the year. Meadows of a clayey soil, liable to be flooded (as in certain parts of Oxfordshire), are the places where this *Limnaea* occurs most abundantly, and these are consequently the most dangerous feeding-grounds for sheep. The wet years 1816, 1817, 1830, 1853, and 1854 —memorable for the occurrence of acute liver-rot in England, Germany, and France—showed that the weather also plays a considerable part in extending the suitable ground for *Limnaea* over wide areas, which in dry years may be safe pastures. In 1830 England lost from this cause,[3] one and a half million sheep, representing some four millions of money, while in 1879-80 three millions died. In 1862 Ireland lost 60 per cent of the flocks, and in 1882 vast numbers of sheep perished in Buenos Ayres from this cause. In the United Kingdom the annual loss was formerly estimated at a million animals, but is now probably considerably less. After infection during a wet autumn, it is usually in the succeeding winter that the disease reaches its height.

[1] *Quart. Journ. Micros. Sci.* vol. xxiii. 1883, p. 90.

[2] The intermediate host in the Sandwich Islands is said to be *Limnaea peregra*. See Lutz, *Centralbl. f. Bakter.* xi. 1892, p. 783.

[3] The mortality in wet years, however, is said to be largely due to pulmonary inflammation. This and other causes of death are not always discriminated in the returns.

The symptoms of "rot" appear about a month after infection, more acutely in lambs than in sheep, and again, less in oxen than in sheep. At first, death may result from cerebral apoplexy, but if the first few weeks are passed through, a pernicious anaemia sets in, the sheep are less lively and fall at a slight touch, the appetite diminishes, and rumination becomes irregular. The conjunctiva is of a whitish-yellow colour, the dry, brittle wool falls off, and there is sometimes fever and quickened respiration. In January, about three months after infection, the wasting, or fatal, period sets in. Oedemas or swellings, usually visible before, become larger at the dependent parts of the body, a large one in the submaxillary region being especially well marked, and this is considered one of the most characteristic symptoms ("watery poke"). Through this period few of the infected sheep survive, but should they do so, the flukes begin to migrate, though some remain much longer within the liver. Migration is effected through the bile-duct into the duodenum and outwith the faeces, in which the altered remains of the *Distomum* are sometimes scarcely recognisable. Under these circumstances (or owing to death of the fluke *in situ*) the sheep recover more or less fully.

The preventive measures seem to be: (1) Destruction of the eggs and of the manure of rotten sheep; (2) slaughter of badly fluked sheep; (3) adequate drainage of pastures; (4) an allowance of salt and a little dry food to the sheep; and (5) dressings of lime or salt on the ground to destroy the embryos.[1]

Distomum hepaticum, contrary to most Trematodes, enjoys a wide range of hosts. Man himself occasionally falls a victim; thus in Dalmatia, in the Narenta Valley, the disease is endemic but slight in its effects. The horse, deer, camel, antelopes, goat, pig, rabbit, kangaroo, beaver, and squirrel have all been known to harbour this fluke occasionally. In the Italian deer-parks at Mandria a large species, *D. magnum*, decimated the herds some years ago; and this species, probably imported from Italy, is now almost as dangerous a parasite on the western plains of the United States as *D. hepaticum*.

Bilharzia haematobia.[2]—This formidable parasite was discovered by Bilharz in 1853 in the veins of the bladder of patients

[1] See Thomas, *Quart. Journ. Micros. Science*, xxiii. 1883. Neumann, *Parasites of Domesticated Animals*, translated by Fleming, 1892.

[2] Leuckart, *loc. cit.*; Looss, *Archiv f. mikroskop. Anatomie*, Bd. xlvi. 1895, p. 1.

at the Cairo Hospital, and is remarkable from its abundance on the east coast and inland countries of Africa from Egypt to the Cape, as well as in the districts bordering Lake Nyassa and the Zambesi river, while westwards it occurs on the Gold Coast. Mecca is a source of infection whence Mohammedans carry the disease to distant places. In Egypt about 30 per cent of the native population is affected by the serious disease known as Haematuria, resulting from the attacks of *Bilharzia*, so that, of the many scourges from which in Africa man suffers, this one is perhaps the most severe.

The worm is found usually in couples, which have been proved to be male and female individuals (Fig. 34), often in considerable numbers in the veins of the pelvic region, chiefly the veins of the bladder and of the large intestine, and it is tolerably certain that *Bilharzia* enter these vessels from the portal vein. Their long slender bodies enable them to penetrate into the finer vessels, which get partially or entirely choked up, and the circulation accordingly impeded. But the most serious consequences are observed in the urinary bladder. The mucous membrane is swollen and inflamed here and there, chiefly on the dorsal surface, the capillaries appear varicose and covered with mucus, mixed with blood-extravasations in which *Bilharzia*-eggs are noticeable. The eggs also cause numerous swollen knots in the submucous tissue. Should the disease not pass beyond this stage (and such is usually the case, especially in South Africa), a temporary haematuria ensues. The urine, which is only expelled with great effort, accompanied by intense pain, is mixed with blood, mucous clots, and masses of *Bilharzia*-eggs, from which some of the embryos have already hatched out. The symptoms, however, may gradually pass away, and a more or less complete recovery accomplished. The disease may indeed be of a far less severe character, and may not interfere with the usual occupations of the patient; but, on

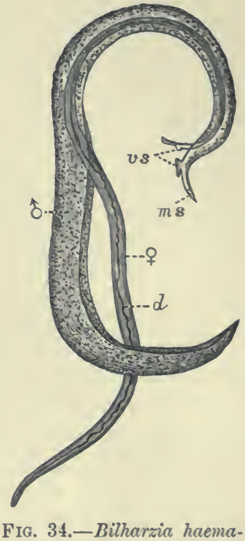

FIG. 34.—*Bilharzia haematobia* Cobb. × 10. The female (♀) lying in the gynaecophoric canal of the male (♂). *d*, Alimentary canal; *ms*, oral sucker of male; *vs*, ventral suckers. (After Leuckart.)

the other hand, a far more extensive thickening of the wall of the bladder sometimes occurs; hard masses of eggs, uric acid crystals, and other deposits, may lead to the formation of stones, degeneration of the substance of the ureter, and eventually to that of the kidney itself. The stone, indeed, has long been known to be a prevalent disease in Egypt, and it is now known to arise from concretions formed round masses of *Bilharzia* eggs. From the portal vein, again, other *Bilharzia* may gain access to the rectum, or the liver, and it has also been found in the lungs, and may give rise to most serious complications, if indeed the patient lives.

How infection occurs is a question to which at present no satisfactory answer can be made. The attempt to introduce embryos of *Bilharzia* into the common fresh-water animals of Alexandria has hitherto proved fruitless (Looss[1]), although there seems little doubt that the comparative immunity of Europeans from the disease is in some way owing to their drinking purer water than the natives. Possibly, as Leuckart suggests, the embryo becomes a sporocyst in man himself, somewhat as *Taenia murina* is known to develop in the rat without an intermediate host.[2] The immense numbers of the parasite in one host would then readily receive an explanation.

A *Bilharzia*, possibly *B. haematobia*, was found by Cobbold in the portal vein of *Cercopithecus fuliginosus*; and *B. crassa* infests the cattle of Egypt, Sicily, and certain parts of India, but does not produce haematuria.

Of the other Trematodes of man and domestic animals there is not room to speak fully. *Distomum pulmonale*, which occurs in the lungs of the cat, tiger, and dog, as well as in man, is especially common in Japan, China, Corea, and Formosa. *D. sinense* and *D. rathouisi* have been also found in inhabitants of these countries.

Bisexual Trematodes.—Zoologically, *Bilharzia* is interesting from its bisexual condition. It is not, however, the only bisexual Trematode. In cysts in the branchial chamber of Ray's bream, *Brama raii*, two worms are found, which are probably the slender male and the swollen female of the same species (*Distomum okenii*). The only doubt that can arise proceeds from the tendency in all Trematodes for the male organs to ripen before

[1] In Leuckart, *Die Parasiten d. Menschen*, pp. 521-528, 1894. [2] Cf. p. 89.

the female organs. Until we certainly know that the swollen egg-bearing form (♀) does not arise from a previously male form (♂), the case is open to suspicion. Since, however, Kölliker[1] never found intermediate hermaphrodite conditions, this *Distomum* may be almost certainly regarded as of distinct sexes. *Didymozoon thynni* (*Monostomum bipartitum*), from cysts on the gills of the Tunny (*Thynnus*), is another case. Two slender worms flattened posteriorly, come together, and the body of one becomes folded to receive that of the other. They fuse completely except for a small lateral opening through which the anterior parts of both worms may freely protrude. The enclosing individual contains a coiled uterus filled with eggs, and is the female, whereas the smaller individual never possesses eggs, and is probably the male.[2] *Nematobothrium* (Fig. 22, A), which occurs also in the Tunny, in the form of two immensely long individuals intricately wound about each other in a cyst, is, however, not bisexual.

FIG. 35.—*Distomum okenii* Köll. Showing male and female as they occur together in the branchial cavity of *Brama raii* (Ray's bream). (From Bronn, after Kölliker.) Nat. size.

Table of Digenetic Trematodes and their Life-Histories.[3]

Species.	Final host.	Host into which the larva enters, and in which Cercariae are eventually formed.	Host into which the Cercariae migrate and encyst; eaten by final host.
Diplodiscus (*Amphistomum*) *subclavatus* Göze	*Rana, Bufo, Triton*	Smaller species of *Planorbis* and *Cyclas*	Insect-larvae, *Rana, Bufo*, but frequently omitted
Distomum advena Duj. (*D. migrans* Duj.)	*Sorex araneus*	Not known	*Limax*
D. appendiculatum Rud.	*Clupea alosa*	Not known	*Lucullus acuspes, Centropages hamatus* (Copepoda)
D. ascidia v. Ben.	Species of Bats	*Limnaea stagnalis* *Planorbis corneus*	*Ephemera, Perla, Chironomus plumosus*
D. atriventre Weinl.	Frogs and Toads of N. America	*Physa heterostropha*	Not known
D. brachysomum Crepl.	The Dunlin (*Tringa alpina*)	Not known	*Anthura gracilis*
D. caudatum v. Linst.	Hedgehog (*Erinaceus europaeus*)	*Helix hortensis*	

[1] See Braun. Bronn's *Klassen u. Ordnungen d. Thierreichs*, vol. iv. p. 572.

[2] Braun, *loc. cit.* p. 573.

[3] Taken largely from Braun, *Ibid.* pp. 864-866, where the literature of the subject is referred to fully.

Species.	Final host.	Host into which the larva enters, and in which Cercariae are eventually formed.	Host into which the Cercariae migrate and encyst; eaten by final host.
D. clavigerum Rud.	*Rana*	*Limnaea ovata*, *Planorbis corneus*	Not known
D. cygnoides Zed.	*Rana*	*Pisidium*, *Cyclas*	*Limnaea* sp. (*Cercaria macrocerca* Fil.)
D. cylindraceum Zed.	*Rana*	*Limnaea ovata*	*Ilybius fuliginosus*
D. dimorphum Dies.	*Ardea*, *Ciconia* (Brazil)	Not known	Different species of Fishes
D. echinatum Zed.	*Cygnus*, *Anser*, *Anas*	Species of *Limnaea*	Species of *Limnaea*, *Paludina vivipara*
D. endolobum Duj.	*Rana*	*Limnaea stagnalis*	*L. stagnalis*, *Gammarus pulex*, larvae of *Limnophilus rhombicus*
D. globiporum Rud.	*Perca fluviatilis*	Not known	*Limnaea stagnalis*, *L. ovata*, *Succinea pfeifferi*, *S. putris*, *Physa fontinalis*, *Planorbis marginatus*
D. hepaticum Abild.	Sheep, Oxen, Man, etc.	*Limnaea truncatula*	Omitted
D. hystrix Duj.	*Lophius piscatorius*	Not known	Marine Fishes
D. macrostomum Rud.	Warblers, Tits, Woodpeckers, etc.	*Succinea putris*	Omitted
D. militare v. Ben.	Common Snipe	*Paludina vivipara*	*P. vivipara*
D. nodulosum Zed.	*Perca fluviatilis*	*Bithynia tentaculata*	*Cyprinus*, *Acerina cernua*
D. ovocaudatum Vulp.	*Rana esculenta*	Species of *Planorbis*	Probably omitted. (*Cercaria* known as *C. cystophora* Wag.)
D. retusum Duj.	*Rana*	*Limnaea stagnalis*	*L. stagnalis*, larvae of Phryganeidae
D. squamula Dies.	Polecat	Unknown	*Rana temporaria*
D. signatum Duj.	*Tropidonotus natrix*	Unknown	*Rana*
D. trigonocephalum Rud.	Badger, Polecat	*Paludina vivipara*	Unknown
Gasterostomum sp.	Dogfish, Rays	*Ostrea edulis*, *Cardium rusticum*, *C. edule*	*Belone vulgaris*
G. fimbriatum v. Sieb.	*Perca*, *Esox*	*Unio*, *Anodonta* (*Cercaria* known as *Bucephalus polymorphus*)	*Leuciscus erythrophthalmus*
G. gracilescens Rud.	*Lophius piscatorius*	Unknown	Species of *Gadus* (e.g. *G. aeglefinus*), *Molva*, *Lophius*
Monostomum flavum Mehl.	*Anas*	*Planorbis corneus*	Omitted

Classification of Trematodes.—We have seen (p. 63) that it is hardly possible to carry out fully the division of Trematodes into Monogenea and Digenea. Nevertheless, pending further investigation on the doubtful points, this classification may still be used. Monticelli[1] has proposed the main divisions of a new classification, which has been also adopted by Braun, and is based on the nature of the suckers. These divisions are indicated below in brackets.

A. **Monogenea** v. Ben. (Heterocotylea Mont.).
1. Fam. Temnocephalidae Hasw.
Gen. *Temnocephala* Hasw.
2. Fam. Tristomatidae Tschbg.
Sub-Fam. 1. Tristomatinae Mont.
Gen. *Tristomum*, *Nitzschia*, *Epibdella*, *Trochopus*, *Acanthocotyle*, *Phyllonella*, *Placunella*, *Encotylabe.*
Sub-Fam. 2. Monocotylinae Tschbg.
Gen. *Pseudocotyle*, *Calicotyle*, *Monocotyle.*
Sub-Fam. 3. Udonellinae v. Ben.-Hesse.
Gen. *Udonella*, *Echinella*, *Pteronella.*
3. Fam. Polystomatidae Tschbg.
Sub-Fam. 4. Octocotylinae v. Ben.-Hesse.
Gen. *Octobothrium*, *Pleurocotyle*, *Diplozoon*, *Anthocotyle*, *Vallisnia*, *Phyllocotyle*, *Hexacotyle*, *Platycotyle*, *Plectanocotyle*, *Diclidophora.*
Sub-Fam. 5. Polystomatinae v. Ben.
Gen. *Polystomum*, *Onchocotyle*, *Erpocotyle*, *Diplobothrium*, *Sphyranura.*
Sub-Fam. 6. Microcotylinae Tschbg.
Gen. *Microcotyle*, *Gastrocotyle*, *Axine*, *Pseudaxine.*
4. Fam. Gyrodactylidae v. Ben.
Sub-Fam. 7. Gyrodactylinae Par. et Per.
Gen. *Gyrodactylus*, *Dactylogyrus*, *Tetraonchus*, *Diplectanum.*
Sub-Fam. 8. Calceostominae Par. et Per.
Gen. *Calceostomum*, *Anoplodiscus.*
5. Fam. Aspidobothridae Burm. (= Aspidocotylea Mont.).
Gen. *Aspidogaster*, *Platyaspis*, *Cotylogaster*, *Macraspis.*

B. **Digenea** v. Ben. (Malacocotylea Mont.).
6. Fam. Holostomatidae Brandes (= Metastatica Leuckart).
Gen. *Diplostomum*, *Polycotyle*, *Hemistomum*, *Holostomum.*
7. Fam. Amphistomatidae Mont.
Gen. *Amphistomum*, *Diplodiscus*, *Gastrodiscus*, *Homalogaster*, *Gastrothylax*, *Aspidocotyle.*
8. Fam. Distomatidae Mont.
Gen. *Distomum* (and sub-genera), *Rhopalophorus*, *Koellikeria*, *Bilharzia.*
9. Fam. Gasterostomatidae Braun.
Gen. *Gasterostomum.*
10. Fam. Didymozoontidae Mont.
Gen. *Didymozoon*, *Nematobothrium.*
11. Fam. Monostomatidae Mont.
Gen. *Monostomum*, *Notocotyle*, *Ogmogaster*, *Opisthotrema.*

[1] *Festschr. f. Leuckart*, 1892, p. 134.

and with those of the head. Each joint contains at first male genitalia comparable with those of a Trematode; then the female organs develop, and finally self-fertilisation follows. The Cestodes feed through their skin, probably by the aid of fine protoplasmic processes, which penetrate the tough investing membrane and absorb the already digested food which bathes them. When a proglottis of *Calliobothrium* is approaching maturity it separates from the parent, the broken ends of muscles, nerves, and excretory vessels speedily heal, and it is now capable of continued growth and of fairly active movement if it remains in the intestine of the host. According to van Beneden, it may even attain a size equal to, or exceeding, that of the whole parent or "strobila."[1] These considerations led Leuckart, von Siebold, P. J. van Beneden, and others, to Steenstrup's conclusion that a jointed tape-worm is really a colony composed of two generations—the head and neck derived from the larva, and the proglottides produced by the segmentation of the neck.[2] This view of the colonial nature of jointed Cestodes was generally adopted from 1851 to 1880. During the last fifteen years, however, the varied interpretations of the facts of the ontogeny of this group have led some authors to adopt the monozootic view (that a Cestode is one individual), others are still of the older opinion, and Hatschek (*Lehrbuch*, p. 349) and Lang take up intermediate positions. Lang considers that the formation of the joints of a tapeworm from a small fixed "scolex," is not only largely comparable with the strobilation of a *scyphistoma* and the consequent formation of a pile of medusae, as in the life-history of *Aurelia*, but

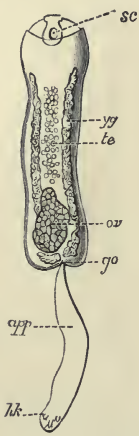

FIG. 37.—*Archigetes sieboldii* (*appendiculatus*), from the coelom of *Tubifex rivulorum*. × 40. *app*, Persistent larval appendage; *go*, genital pore; *hk*, persistent larval hooks; *ov*, ovary; *sc*, sucker; *te*, testes; *yg*, yolk-glands. (After Leuckart.)

[1] The mature proglottis of *Calliobothrium eschrichti* is 8-9 mm. long, whereas the strobila only measures 4-5 mm. in length. Species of *Phylliobothrium*, *Anthobothrium*, and *Tetrarhynchus* show a similar but not an equal contrast between the size of the parent and proglottis (P. J. van Beneden, "Les Vers Cestoides," *Nouv. Mém. de l'Acad. Roy. d. Belgique*, tom. xxv. 1850).

[2] The difficult question of the nature of the Cestode body and Cestode larvae is adequately discussed by Braun, *loc. cit.* p. 1167.

that both processes have arisen from the power of regenerating the necessary organs in each of the new segments. The result in both cases is the rapid formation of a number of joints, which gradually separate from the parent, to carry the eggs and young to new stations. Just as some Coelenterata (*Lucernaria*) may be regarded as not having advanced much beyond a scyphistoma stage, so there are unisegmental Cestodes (e.g. *Archigetes*, Fig. 37) which have remained as a slightly altered but sexual scolex, directly comparable with a Trematode, and, as all authors are agreed, representing one generation only. Such monozootic forms are now classed as a special family, the Cestodaria or Monozoa, of which *Caryophylleus mutabilis*, from the intestine of various Cyprinoid fish, is the most abundant representative, while *Amphiptyches* (*Gyrocotyle*) *urna*, from *Chimaera monstrosa* of the northern hemisphere, is paralleled by *A. rugosa*, found in *Callorhynchus antarcticus* of the southern seas.

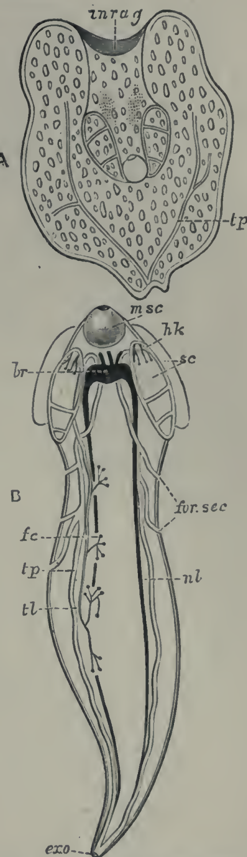

FIG. 38.—*Scolex polymorphus* Rud. (larva of *Calliobothrium filicolle* Zschokke), from the muscles of *Apogon*, a Mediterranean fish; also found in many Invertebrates (e.g. *Sepia*). **A**, Inverted scolex, with calcareous bodies; **B**, everted older larva. *br*, Brain; *exo*, terminal excretory aperture; *fc*, flame-cells; *for.sec*, secondary excretory pores; *hk*, hooks of the adult Cestode; *inrag*, pit at the bottom of which the head is developed; *msc*, anterior sucker; *nl*, lateral nerve; *sc*, suckers; *tl*, *tp*, lateral and main excretory vessels. (After Monticelli.)

Occurrence of Cestodes.—The distribution of Cestodes and their larvae is analogous to that of the digenetic Trematodes, although the absence of an alimentary canal limits the habitat of the mature worms to certain sites, such as the blood-vessels, the lymphatic and coelomic spaces, and the digestive system, where their body may be bathed by a nutritive fluid. Almost all groups of Vertebrates are attacked by Cestodes. Those of fishes, and particularly of Elasmobranchs, are distinguished by certain structural and developmental features; those of birds by others; those of mammals, by a third set of characters. The young stages of the Cestodes of Sharks and Rays occur encysted in the body-cavity, or in the pyloric appendages, of Teleosteans, which probably swallow them along with those invertebrate animals upon which they prey. The larvae of the Cestodes of carnivorous mammals or piscivorous birds, live respectively in herbivores and fishes, but how the latter are infected we know in very few instances. Cestode larvae are known to occur in many Invertebrates, and occasionally are taken free swimming in the sea, presumably crossing from one host to the next. Ctenophores, Siphonophores, Copepods, Ostracods, Decapods, various Molluscs especially Cephalopods, Earthworms, and other Annelids, are the intermediate hosts of these larvae (see Fig. 38), the fate of which, however, has been determined in but few cases.

Occurrence of Cestodes in Man.[1]—Tape-worms, either in the adult or larval stages (bladder-worms), have, from ancient times, been known to occur in man, and in the animals that serve him as food. Until comparatively recent times, however, the true nature of these parasites, and particularly of "hydatids" (cystic larvae), was unrecognised. Up to the seventeenth century the larvae were regarded as abscesses or diseased growths of the affected organs, and it was only at the close of that century that their animal nature was even suggested. Even at the beginning of the nineteenth century, three modes of origin of Cestodes—by "generatio aequivoca" from the tissues of the body, or by the union of previously distinct proglottides, or again by metamorphosis of free-living worms drunk with water by cattle or birds (as Linnaeus suggested)—were still variously held, at a time when Malpighi, Pallas, and Goeze had recognised the true connexion between the cystic and segmented states of *Taenia crassicollis* (the cat tape-worm), and when Goeze had seen the eggs of *Taeniae*, and Abildgaard[2] had even conducted the first helminthological experiments (conversion of the larval *Schistocephalus*, Fig. 40, into the adult form).

Generally speaking, "a tape-worm" in Western Europe will prove to be *Taenia saginata* Goeze (the beef tape-worm, Fig. 39, A),

[1] Leuckart, *Die Parasiten d. Menschen* [English trans. by W. E. Hoyle]; Blanchard, *Traité de Zoologie médicale*, 1893.

[2] For a full account of the history of this subject see Leuckart, *Parasiten d. Menschen*, p. 28; Braun, *loc. cit.* Bd. iv. p. 929 *et seq.*; Huxley, *Collected Essays*, vol. viii. p. 229.

exceedingly prevalent also in the East, and indeed cosmopolitan, occurring wherever the infected flesh of the ox is eaten in a raw or half-cooked state. Its attacks are fortunately not usually severe. *Taenia solium* Rud. (the pork tape-worm) is found wherever the pig is kept as a domestic animal, and has consequently a world-wide distribution. Its size (6-9 feet long) and powers of adhesion would alone render *T. solium* a formidable parasite. But the danger of its presence in the body of man, or in the flesh of pigs, lies in the fact that the larva or bladder-worm (known as *Cysticercus cellulosae*) can live in the most varied organs. Thus if by accident a mature proglottis be eaten, the embryos escape, bore their way into the wall of the stomach, and entering the portal vein, may reach in time the muscles, the brain, the eye, or even the heart itself, and attain the cystic condition. Even more disastrous may be the result, should some ripe joints of a mature worm work their way from the intestine back towards the stomach. Should this happen (and though it has not been directly proved, the possibility is to be reckoned with), the result would be the release of vast numbers of embryos capable of inflicting fatal injury on the host. An abnormal *Cysticercus* of this species is probably the *Taenia* (*Cysti-*

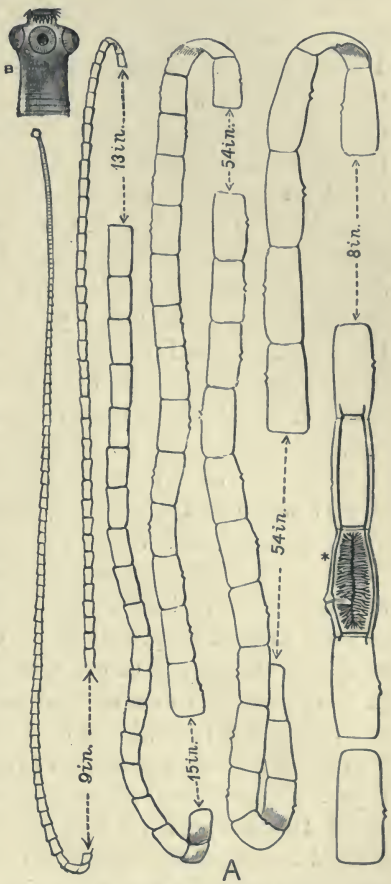

FIG. 39.—**A**, *Taenia saginata* Goeze. Nat. size. (From a specimen in the Cambridge Museum.) The approximate lengths of the portions omitted in the drawing are given. At * (after Leuckart) the branched uterus and the longitudinal and transverse excretory vessels are shown. The genital apertures are seen as a lateral opening on each of the larger proglottides. **B**, Head (scolex) of *T. solium* Rud. × 12. (After Leuckart.)

cercus) *acanthotrias* Weinl. (see, however, Leuckart, *loc. cit.* p. 711).

Taenia (*Hymenolepis*) *nana* v. Sieb.[1] is found in man in Egypt, Italy, England, Servia, Argentine Republic, and the United States. Though small ($\frac{3}{4}$-1 inch long), its numbers usually excite digestive and nervous disorders of considerable severity, more serious, indeed, than those caused by the commoner tape-worms. *H. diminuta* Rud. (*flavopunctata* Weinl.), normally found in Rodents, has been rarely recorded in man. *Taenia* (*Dipylidium*) *caninum* L. (= *T. cucumerina* Bloch = *T. elliptica* Batsch), the commonest parasite of pet cats and dogs, and *T.* (*Davainea*) *madagascariensis* Davaine, have occasionally been recorded from infants and young children. But the attacks of these species are insignificant in comparison with those of the cystic stage (*Echinococcus polymorphus*) of a tape-worm (*T. echinococcus* v. Sieb.) which lives when mature in the dog.

Echinococcus is most frequent in Iceland, where it affects 2 to 3 per cent of the population, and a still larger proportion of sheep; while in Copenhagen, Northern Germany, some districts of Switzerland, and Victoria it is not uncommon, but is frequently found during *post-mortem* examinations when no definite symptoms of its presence had been previously noticed. *Echinococcus* [2] varies greatly in size, form, and mode of growth, but is distinguished in the formation not of one scolex only, as in the *Cysticercus*, but in the production of a number of vesicles, usually from the inner wall. Within these, large numbers of scolices may be developed. The whole organism continues to swell by the formation of a watery liquid within it, and if its growth be rapid the fluid tension may cause the rupture of the enclosing connective-tissue capsule formed around the parasite, at the expense of the host, and the protrusion of the daughter vesicles. It is the consequent injury to the surrounding organs of the host, at this critical stage, often only reached after the lapse of several years, that occasions serious or even fatal results. Zoologically, *Taenia echinococcus* and *T. coenurus* are interesting, since they exhibit an indubit-

[1] By Grassi this form is considered identical with *T. murina.* The latter species is known, from this author's researches, to develop in rats without migration into an intermediate host. Should Grassi's synonymy prove correct, the presence of large numbers of this tape-worm in man would readily receive its explanation.

[2] Leuckart, *loc. cit.* p. 752 *et seq.*

able alternation of asexual generations in the larval state, with a sexual adult stage.

Bothriocephalus latus Brems., the broad tape-worm, which attains a length of 20-30 feet, or even more, occurs in man endemically in the eastern Baltic provinces, certain parts of Switzerland, generally throughout Russia (especially near Kasan), in North America, and commonly in Japan,—that is, in districts where the population partake largely of pike or other fish in a raw or partially-cooked state. Elsewhere it occurs sporadically, and in Munich, where it was unknown before 1880, its presence has been traced to emigrants from infected districts, who settled on the shores of the Starenberger Lake, from which Munich was supplied with fish. How the pike, the usual but not invariable intermediate host, becomes infested (and its musculature is frequently riddled with the larvae) we do not accurately know, but some Invertebrate, the prey of the pike, is probably the first host into which the free-swimming ciliated larva (Fig. 42) finds its way. In Greenland, *B. cordatus* is very common in the dog, and probably also in man, though few cases have been recorded. *B. mansoni* Cobb. (= *B. liguloides* Leuck.) was, till recently, known only in the larval state from China and Japan. Iijima, however, has found older specimens in the latter country. *B. cristatus* Dav. is a species founded somewhat doubtfully on two fragments found, one in a child, the other in a man, in France.

Occurrence of Cestodes in Domestic Animals.[1]—Among domestic animals, the dog is, undoubtedly, the most frequently attacked by Taeniae. Six species of *Taenia* (*T. serrata, marginata, coenurus, echinococcus, krabbei,* and possibly *T. serialis*), *Dipylidium caninum* (the commonest form), *Mesocestoides lineatus,* and three or four species of *Bothriocephalus* have been found in the dog. The table of life-histories (p. 83) shows that sheep, rabbits and other Rodents serve as the intermediate hosts, in which the cystic stages of the species of *Taenia* are found. Hence the prevalence of *T. serrata* in a given locality is connected with the abundance there of the rabbit and hare, in which the larva (*Cysticercus pisiformis*) occurs. *Bothriocephalus cordatus* develops from the young stage present in the fish which the Icelanders give to their dogs. In Iceland and certain parts of

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Australia *T. echinococcus* infests one-third to one-half the number of dogs examined; a fact connected with the frequency of *Echinococcus* in man in these countries.

In sheep the most noteworthy and dangerous parasite is *Coenurus cerebralis* (or the cystic stage of the dog-taenia, *T. coenurus*), which gives rise to the disease known as "gid" or "staggers." It is found in various parts of the brain or spinal cord, and the symptoms differ according to the position of the parasite. If this presses upon one hemisphere the sheep describes circles and finally falls: if on the optic lobes, the eyes are affected: if the pressure affects the cerebellum the movements of the sheep are uncertain and incoordinated. Four or six weeks after the appearance of the symptoms, death results from cerebral paralysis, or from general debility, and the loss of sheep incurred by this disease (happily less frequent in England than formerly) has been calculated by Youatt at a million for France annually; at 35 per cent of the flocks for England in bad seasons; and about 2 per cent for Germany. Besides sheep, which are most subject to "gid" during their first year, various ruminants —Goat, Ox, Moufflon, Chamois, Roe, Antelope, Reindeer, Dromedary—are attacked in the same way. A similar form, *Coenurus serialis* Baill., is common in the wild rabbit in this country, and in Australia in the hare and squirrel. It forms large swellings in the connective tissue of various parts of the body, but usually does not affect the health of the host. It is not known in what carnivore *Taenia serialis* Baill. normally occurs. Experiments have, however, shown that it develops rapidly in dogs.

The preventive measures which are steadily diminishing the prevalence of the Cestode parasites in man in some parts of Western Europe cannot be dealt with here, but it may be noticed that the Jewish observance with regard to swine is the surest preventive measure against taeniasis and trichinosis. Careful inspection of meat and general cleanliness, are the leading measures that in these hygienic matters secure the greatest immunity from disease.

Table of the Life-Histories of the principal Cestodes of Man and the Domestic Animals.

Cestode.	Final host.	Larva.	Intermediate host.
Taenia serrata Goeze	Dog	*Cysticercus pisiformis* Zed.	Rabbit, Hare, Mice (liver and peritoneum)
T. marginata Batsch	Dog, Wolf	*Cyst. tenuicollis* Rud.	Monkeys, Ruminants, Ungulates (in peritoneum)
T. saginata Goeze (= *T. mediocanellata* Küch.)	Man . . .	*Cyst. bovis* Cobb.	Ox, Giraffe (in muscles)
T. solium Rud.	Man . . .	*Cyst. cellulosae* Rud. (? *Cyst. acanthotrias* Weinl.)	Pig, Man, Monkeys, Bear, Dog, Cat, Black Rat (in various organs)
T. crassicollis Rud.	Cat and other Felidae, Stoat	*Cyst. fasciolaris* Rud.	Rat, Mouse, Bat (liver)
T. coenurus Küch.	Dog, Arctic Fox	*Coenurus cerebralis* Rud.	Brain of Sheep, Ox, Goat, Dromedary, Camel, Antelope, Horse
T. serialis Baill.	? Dog . . .	*Coenurus serialis* Baill.	Rabbit (connective tissue)
T. echinococcus v. Sieb.	Dog, Dingo, Jackal, Wolf	*Echinococcus polymorphus* Dies. (incl. *E. multilocularis* found in Man)	Man, Monkeys, many Carnivores, Rodents, Ungulates, Ruminants, and Marsupials; also in Turkey and other birds
Moniezia expansa Rud.	Sheep, Ox, Goat, etc.	Unknown	
Thysanosoma fimbriata Dies.	Sheep, Cervidae .	Unknown	
Stilesia globipunctata Riv.	Sheep . . .	Unknown	
Anoplocephala perfoliata Goeze	Horse . . .	Unknown	
Dipylidium caninum L. (= *Taenia cucumerina* Bloch = *T. elliptica* Batsch)	Man, Dog, Cat	Cysticercoid larva (Fig. 43), *Cryptocystis trichodectis* Vill.	Body-cavity of *Trichodectes* and *Pulex* of Dog
Hymenolepis murina Duj.	Mouse, Rat	*Cercocystis* Vill.[1] (develops in parental host)	Usually absent
H. nana v. Sieb.	Man . . .	Unknown	
H. diminuta Rud. (= *Taenia flavopunctata* Weinl.)	Man, Mouse, Rat	*Cercocystis* Vill.	Meal-moth, *Asopia* (*Pyralis*) *farinalis;* also certain Orthoptera and Coleoptera

[1] For description of the *Cercocystis*-larva see Villot, *Ann. Sci. Nat.* (*Zool.*) (6), xv. 1883, Art 4; and compare Leuckart's criticism of this paper, "*Parasiten*," p. 979.

Cestode.	Final host.	Larva.	Intermediate host.
Drepanidotaenia gracilis Zed.	Duck, Goose, Wild Duck	*Cercocystis* Vill.	The Ostracods *Candona rostrata* and *Cypris compressa*, and also *Cyclops viridis*
D. anatina Krabbe	Duck . . .	,, ,,	*Cypris incongruens*, and also Perch
D. setigera Fröh.	Goose . . .	,, ,,	*Cyclops brevicaudatus*
D. infundibuliformis Goeze	Common Fowl .	,, ,,	House-fly
Dicranotaenia coronula Duj.	Duck . . .	,, ,,	*Cypris ovum*
Davainea proglottina Dav.	Fowl . . .	,, ,,	? *Limax cinereus*, *L. agrestis*
D. madagascariensis Dav.	Children . .	Unknown	
D. friedbergeri v. Linst.	Pheasant . .	Unknown	? Ants
Mesocestoides lineatus Goeze	Dog . . .	Unknown	
Bothriocephalus latus Brems.	Man, Dog, ? Cat	Plerocercoid, *i.e.* solid, elongate larva, with no bladder	Probably first enters an Invertebrate host, which is eaten by Pike, Perch, Trout, etc.

Structure and Development of Cestoda.[1]—Of the unsegmented Cestodes, *Caryophyllaeus mutabilis*, from the intestine of carp and other Cyprinoid fishes, is the most easily accessible form.

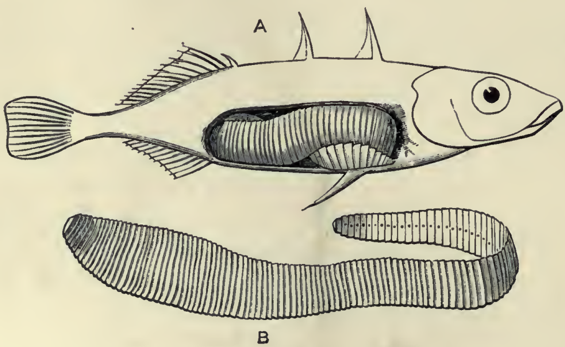

FIG. 40.—**A**, Stickleback (*Gasterosteus aculeatus*) infested by an advanced larva of *Schistocephalus solidus* Crepl. **B**, The larva. All × 1½. (From specimens in the Cambridge University Museum.)

Triaenophorus nodulosus, which is very useful for the study of the excretory system, occurs mature in the pike. In the body-cavity of the Stickleback (Fig. 40) a large, broad, yellow worm may sometimes

[1] Moniez, "Sur les Cysticerques," Paris, 1880; *Id.* "Sur les Cestodes," 1881; Zschokke, "Recherches sur la structure anatomique et histologique d. Cestodes," Genève, 1888.

be found, the larva of *Schistocephalus solidus* Crepl., which occurs in the intestine of Terns, Storks, Mergansers, and other birds. Species of *Ligula* are found in the same birds. The intestine of a *Lophius* or *Cyclopterus* ("lump-fish") contains, usually, the early and intermediate stages of various Cestodes, while the alimentary canal of Elasmobranchs often contain many peculiar Tetrarhynchidae and other forms. For the study of development, the *Taenia anatina* from the duck may be used. The ripe proglottides are collected, and the eggs placed with *Cypris ovum* in an aquarium, with the probability that some of the embryos will enter the Ostracod, and the peculiar Cysticercoid may be bred.[1] *Cysticercus pisiformis* and *Coenurus serialis*, which occur commonly in rabbits, are also suitable objects for examination.

A Cestode such as *Echinobothrium* (Fig. 36) is divisible into head and proglottides. Moniez has suggested that the head is really the morphologically hinder end of the body, in which case the formation of proglottides would closely resemble the mode of segmentation of an Annelid larva. The close similarity, however, between the Cysticercoid larva (Fig. 43, F) and the Cercaria of a liver-fluke, seems to show that the anterior end is the same in both cases, and since it bears the central part of the nervous system, we may reasonably call it the "head." Moreover the hinder end of a Platyhelminth usually possesses the chief excretory pore. Another difficulty is the determination of dorsal and ventral surfaces. Authors are agreed,—on the analogy of Trematodes, in which the testes are usually dorsal and the ovaries ventral,—that the dorsal and ventral aspects of a Cestode are determined by the position of these organs, although the often radially formed "head," the lateral or superficial position of the genital apertures, and the variability of these features, render it a matter of considerable doubt whether "dorsal" and "ventral" are more than useful conventional terms. The suckers and hooks are borne on a muscular cap, the "rostellum," which is only slightly developed in the *Ichthyotaeniae*. The body is solid, and is divisible into an outer muscular coat—enveloped in a (possibly epidermal) investing membrane—and an inner parenchymatous tissue containing the chief part of the excretory, nervous, and reproductive systems. One or two pairs

[1] Schmidt, *Archiv f. Naturgeschichte*, Jahrg. lx. Bd. 1, 1894, p. 65.

of longitudinal excretory vessels are present, usually connected by transverse ducts and opening by a single terminal pore. Occasionally a regularly paired arrangement of lateral or secondary pores is present (Figs. 38 and 41, *for.sec*). Flame-cells occur at the end of the fine tubules (Fig. 38), and the whole system is well developed, but may undergo degenerative changes in the older proglottides. The central nervous system varies according to the degree of differentiation of the rostellum; and, owing to the difficulty of staining the nerves and the contradictory statements of authors, we do not yet possess a fully reliable account of the nervous system even of the commoner Taeniae. Free nerve endings and other sensory terminations have been recently

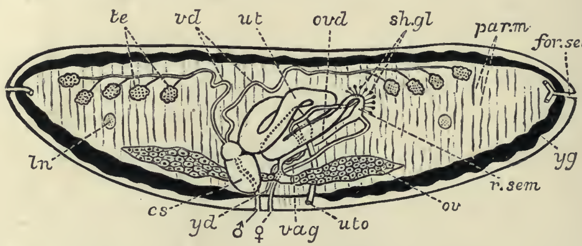

Fig. 41.—Diagrammatic transverse section of *Schistocephalus solidus* Crepl., from the Wild-duck, illustrative of the Cestodes with uterine aperture (*uto*). × 12. *cs*, Cirrus-sac; *for. sec*, one of the paired lateral openings of the excretory vessels; *ln*, longitudinal nerve; *ov*, ovary; *ovd*, oviduct; *par.m*, parenchymatous muscles; *r.sem*, receptaculum seminis; *sh.gl*, shell-gland; *te*, testes; *ut*, uterus; *uto*, uterine pore; *vag*, vagina; *vd*, vasa deferentia; *yd*, yolk-duct; *yg*, yolk-glands (black); ♂, male, ♀, female genital aperture. (After Riehm.)

stated to exist in the cuticle of Cestodes and Trematodes. If true, this would tend to show that the parasitic mode of life of these animals demands a complex nervous system comparable with that of the Turbellaria.

The reproductive organs, unlike the preceding systems, are discontinuous from one proglottis to the next. The male and female organs and their mutual connexions, especially in the unsegmented Cestodes, may be compared in detail with those of Trematodes, but the difference between the arrangement of the generative organs of various Cestodes is very great.[1] The penis (Fig. 41, *cs*) is evaginated through the male pore (Fig. 41, ♂), and inserted far into the vagina (♀, *vag*) of the same or another

[1] For example, the genitalia in *Dipylidium caninum* are duplicated in each proglottis. Other differences are noted in the following table (pp. 89-90).

segment of the tape-worm. From this fact and the anatomical relations of the vagina, it is becoming increasingly probable that the so-called uterus of Trematodes is an organ corresponding to the vagina of Cestodes, and not to the uterus of Cestodes. The latter opens to the exterior in *Schistocephalus*, *Bothriocephalus*, and some other Cestodes of fishes by a special pore (Fig. 41, *uto*). Through this, some of the eggs (which in these genera give rise to ciliated larvae) are enabled to escape, and need not wait for the detachment of the proglottis, as must happen in the Taeniidae, where the uterus is closed. This uterus, a true physiological one, is probably the homologue of the "canal of Laurer" ("Laurer-Stieda canal," or "vagina") of Trematoda. The fertilised

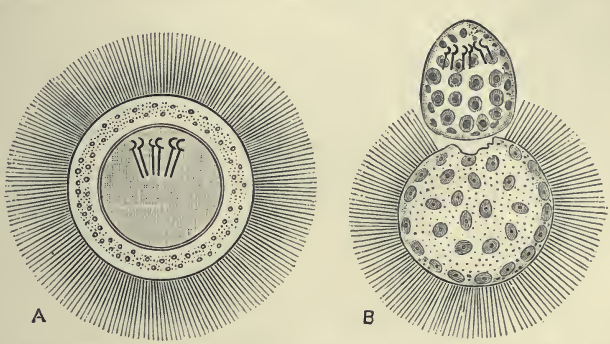

FIG. 42.—**A**, Free-swimming, six-hooked larva of *Bothriocephalus latus* Brems. (the broad tape-worm of Man), still enclosed in a ciliated (possibly cellular) double membrane or mantle. In this condition it may continue to live in water for a week or more, but eventually throws off its ciliated coat (as in **B**) and commences to creep about vigorously by the aid of its hooks, in search of its first host, which is at present unknown. (After Schauinsland.) × 600.

ovum and yolk are brought together into the "ootype," where the shell-gland forms the egg-shell around them (Fig. 41, *sh.gl*), and the egg is then passed into the uterus. The ovum segments to form a minute six-hooked larva, which may (Bothriidae, Fig. 42) or may not (Taeniidae) be ciliated. Thus in *Taenia serrata* the proglottides are shed with the faeces of the host (dog), and they protect the young from the desiccating influence of the surroundings. If inadvertently eaten by a rabbit along with herbs, the proglottis and larval envelope are digested, and by its six hooks the tiny larva bores through the gastric wall into the portal vein, and so into the liver. Here the hooks are thrown off, and the solid mass of cells becomes vacuolated. At one pole an invagi-

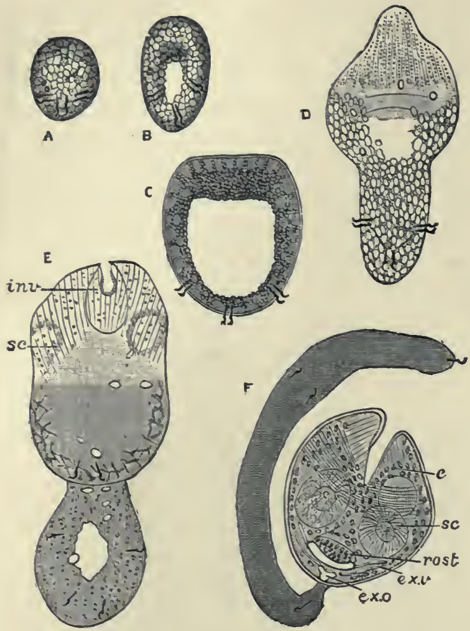

FIG. 43.—Stages in the development of *Dipylidium caninum* L. (= *Taenia elliptica* Batsch, *T. cucumerina* Bloch), the commonest of the Dog-Taeniae; compare Fig. 44. **A**, Six-hooked larva (now often spoken of as an "Onchosphaera"); **B**, larva elongating; formation of a central lacuna; **C**, larva further advanced; **D**, distinction between body and tail is visible; **E**, invagination of the rostellum is commencing; **F**, Cysticercoid larva with four suckers, invaginated rostellum, and excretory vessels. *c*, Calcareous concretions in cells of the larva; *ex.o*, excretory aperture; *ex.v*, excretory vessels; *inv*, invagination commencing; *rost*, rostellum; *sc*, suckers. (After Grassi and Rovelli; highly magnified.)

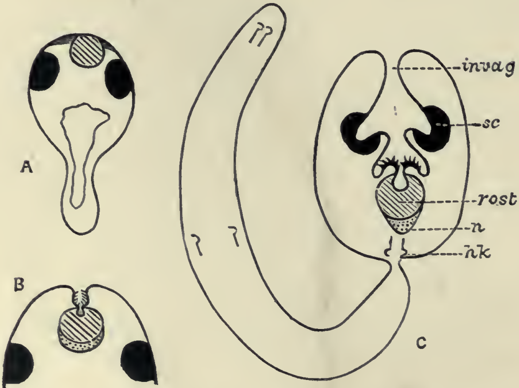

FIG. 44.—Schematic longitudinal sections through the larvae of *Dipylidium caninum* L. All these stages are passed in the body-cavity of the Dog-flea (*Pulex serraticeps*). (Compare Fig. 43 for further details.) **A**, Six-hooked larva with developing rostellum (shaded) and suckers (black). In this species the invagination (**C**, *invag.*) occurs after the formation of these organs, and not, as in most Taeniae, before it. **B**, Invagination commencing; the hooks are developing above the rostellum, while beneath it the nervous system (dotted) is seen. **C**, The invagination has now carried the suckers inwards. The tail has become distinct, and the whole larva at this stage is known as a Cysticercoid. *hk*, Larval hooks; *invag*, mouth of the invagination; *n*, central nervous system; *rost*, rostellum and hooks; *sc*, suckers, of which only two can be seen in a longitudinal section; four are really present. (After Grassi and Rovelli.)

nation occurs, at the bottom of which the rostellum, suckers, and hooks are gradually formed, but inside out as compared with the head of the *Taenia serrata*. At this stage the larva (*Cysticercus pisiformis*) has usually issued from the liver and attached itself to the omentum. The invagination projects into the cavity of the bladder, within which a watery fluid accumulates. Thus the "bladder worm" is formed, the head of which is evaginated if the larva be introduced into the digestive system of a dog. The bladder and neck of invagination are digested, while the head, protected by these, remains, and forms the neck, from which the proglottides are afterwards segmented off. In *Taenia* (*Hymenolepis*) *murina* the whole development may take place in the parental host, the larva living in the villi, the adults in the cavity of the same rat's intestine (Grassi). The different forms of Cestode larvae depend largely upon the presence and degree of development of the caudal vesicle or bladder, which in *Scolex polymorphus* (Fig. 38) (the young stage of *Calliobothrium filicolle* Zsch.) is practically absent. If the bladder be small, the larva is known as a Cysticercoid. For example, the common *Dipylidium caninum*, which lives in the dog, has such a larva, the development of which is explained and illustrated by Figs. 43 and 44. The bladder becomes exceeding capacious in *Coenurus* and *Echinococcus*.

Table for the Discrimination of the more usual Cestodes of Man and Domestic Animals.[1]

I. Scolex in most cases with hooks ; uterus with a median and lateral branches ; yolk-glands simple, median ; genital pore single ; dorsal excretory vessel narrower than the ventral, without a circular commissural trunk ; eggs without pyriform apparatus (processes of the ovarian membrane) . . . Gen. TAENIA L. (s. str.)
  A. Genital ducts pass on the ventral side of the nerve and of the two longitudinal excretory vessels . . *T. crassicollis* Rud.
  B. Genital ducts pass between the dorsal and ventral longitudinal vessels.
    a. Nerve present on dorsal side of genital ducts.
      α. Head armed . . . . . *T. solium* Rud.
      β. Head unarmed . . . *T. saginata* Goeze.
    b. Nerve on ventral side of genital ducts.

[1] See Stiles, *Centralbl. f. Bakt. u. Parasitenkunde*, 1893, xiii. p. 457 (conf. note, p. 90).

DOG-TAENIAE[1]

- Head armed; genital pore marginal and
  - Single
    - Many proglottides; strobila several centimetres long; small hooks with guard.
      - Bifid hooks, which are
        - 230μ-260μ long[2]; genital pore very distinct . *T. serrata* Goeze.
        - 136μ—157μ long; genital pore not very salient *T. serialis* Ball.
      - Entire large hooks, which are
        - 180μ-220μ long; length of mature segments double their width *T. marginata* Batsch.
        - 150μ-170μ long; length of mature segments treble their width *T. coenurus* Küch.
    - 3-4 segments; a few mm. long . *T. echinococcus* v. Sieb.
  - Double and bilateral . . . *Dipylidium caninum* L.
- Head unarmed; two genital pores on ventral surface . *Mesocestoides lineatus* Goeze.

II. Scolex without hooks; one or two transverse uteri present; one or two genital pores and yolk-glands, the latter never median; genital ducts pass on the dorsal side of the nerve; eggs with pyriform apparatus.

A. One transverse uterus present.

a. Uterus with bullate egg-sacs; pyriform apparatus without horns; genital ducts between dorsal and ventral vessels THYSANOSOMA Dies.

α. Head large (1·5 mm.); square lobed testes in median field; posterior margin of segments fimbriated; genital pore double *T. fimbriata* Dies.

β. Head small; no fimbriae; pore rarely double . *T. giardii* Riv.

b. Uterus without saccular dilatations; segments short, thick, and slightly imbricate . . ANOPLOCEPHALA E. Blanch.

HORSE-TAENIAE.
- α. Head very large
  - No posterior lobes *A. plicata* Zed.
  - Four posterior lobes *A. perfoliata* Goeze
- β. Head small, without posterior lobes *A. mamillana* Mehl.

B. Two uteri and two genital pores present; horns of pyriform apparatus well developed; genital ducts pass on the dorsal side of the longitudinal vessels . . . . MONIEZIA R. Bl.

a. Interproglottidal glands[3] arranged in linear series (*planissima* group) . . *M. planissima* S. and H. *M. benedeni* Mz. *M. neumani* Mz.

b. Interproglottidal glands saccular (*expansa* group) *M. expansa* Rud. *M. oblongiceps* S. and H. *M. trigonophora* S. and H.

c. Interproglottidal glands absent (*denticulata* group) *M. denticulata* Rud. *M. alba* Perr.

C. Uterus single or double, without spore-like egg-sacs; eggs with a single shell; genital pores irregularly alternate; strobila narrow; testes absent from median part of the field . STILESIA Raill.

[1] Taken from Neumann, *Parasites of Domesticated Animals*, 1892, p. 448.

[2] $\mu = \frac{1}{1000}$ millimetre.

[3] For a description of these glands, and for further diagnostic details and literature, see Stiles and Hassall, *U. S. Department of Agriculture, Bureau of Animal Industry*, Bulletin 4, 1893.

a. A transverse uterus in middle part of median field ; head 2 mm. diameter . . . . *S. centripunctata* Riv.
b. Two lateral uteri in each segment ; head less than 1 mm. in diameter . . . . *S. globipunctata* Riv.

III. Scolex almost invariably provided with hooks ; genital pores on left border of segment ; eggs with three shells but no cornua. Segments broader than long ; posterior angles salient. HYMENOLEPIS Weinl.
a. Scolex with a single series of 24-30 hooks, each 14-18μ long *H. nana* v. Sieb. *H. murina* Duj.
b. Scolex very small, unarmed . . *H. diminuta* Rud.

IV. Scolex provided with two elongated muscular pits. Body segmented ; three genital apertures in middle of ventral surface BOTHRIOCEPHALUS Rud.
Body 2-20 metres in length . *B. latus* Brems. *B. cristatus* Dav. (doubtful species). *B. cordatus* Leuck. *B. mansoni* Cobb. (= *B. liguloides* Leuck.)

Classification of Cestodes.—The following classification, which, so far as the Taeniidae are concerned, follows that employed by Railliet, Blanchard, and most recent writers, includes only a few representative genera :—

1. Fam. CESTODARIIDAE Mont. (MONOZOA Lang).
   Gen. *Caryophyllaeus, Archigetes, Gyrocotyle, Amphilina.*
2. Fam. BOTHRIOCEPHALIDAE.
   Sub-Fam. 1. Bothriocephalinae. Gen. *Bothriocephalus, Schistocephalus, Triaenophorus* (= *Tricuspidaria*).
   Sub-Fam. 2. Ligulinae. Gen. *Ligula.*
   Sub-Fam. 3. Solenophorinae. Gen. *Solenophorus, Duthiersia.*
   Sub-Fam. 4. Diphyllinae. Gen. *Echinobothrium.*
3. Fam. TETRARHYNCHIDAE.
   Gen. *Tetrarhynchus.*
4. Fam. TETRAPHYLLIDAE.
   Sub-Fam. 1. Phyllobothrinae. Gen. *Phyllobothrium, Echeneibothrium,* etc.
   Sub-Fam. 2. Phyllacanthinae. Gen. *Calliobothrium, Anthobothrium,* etc.
5. Fam. TAENIIDAE.
   Sub-Fam. 1. Cystotaeninae. Gen. *Taenia* s. str.
   Sub-Fam. 2. Anoplocephalinae. Gen. *Moniezia, Thysanosoma, Stilesia, Anoplocephala.*
   Sub-Fam. 3. Cystoidotaeninae. Gen. *Dipylidium, Hymenolepis, Drepanidotaenia, Dicranotaenia, Echinocotyle, Davainea.*
   Sub-Fam. 4. Mesocestoidinae. Gen. *Mesocestoides, Dithyridium.*
   Sub-Fam. 5. Ichthyotaeninae. Gen. *Ichthyotaenia, Corallobothrium.*

CHAPTER IV

MESOZOA

DICYEMIDAE — STRUCTURE — REPRODUCTION — OCCURRENCE : ORTHONECTIDAE — OCCURRENCE — STRUCTURE : TRICHOPLAX : SALINELLA.

THE Mesozoa are an obscure group, the position of which in the animal kingdom is still doubtful. The name Mesozoa was given to the group by its discoverer, E. van Beneden,[1] as he concluded that they were intermediate between the Protozoa and the higher Invertebrates. Recent authors, however, have called attention to the resemblance existing between them and the "sporocysts" of Trematodes, and though we still are ignorant of certain important points in their life-histories, the Mesozoa are most conveniently (and probably rightly) considered as an appendix to the Platyhelminthes.

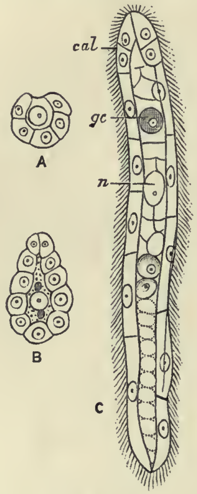

FIG. 45.—**A, B, C**, Stages in the development of the vermiform larva in *Dicyema typus* van Ben. (After Ed. van Beneden.) *cal*, "Calotte"; *gc*, germinal cell; *n*, nucleus of endodermal cell.

The animals composing this group are minute and parasitic, and are composed of a small number of cells. They may be divided into two families: the *Dicyemidae*, which occur exclusively in the kidneys of certain Cephalopods (cuttle-fish); and the *Orthonectidae*, which live in the brittle-star *Amphiura squamata*, the Nemertine *Nemertes lacteus*, or the

[1] Ed. van Beneden, *Bull. Acad. Roy. Belgique*, 1876, p. 35.

Polyclad *Leptoplana tremellaris*. In addition to the undoubted Mesozoa, certain anomalous forms—*Trichoplax adhaerens* and *Salinella salve*—may be referred to this group.

Dicyemidae.—If the kidney of *Eledone moschata*, a Cephalopod common on our south-western shores, be opened, a number of fine, yellowish, hair-like filaments may be seen attached at one end to its inner surface, floating in the fluid contained in the renal cavity. These may be *Dicyemennea eledones* Wag., although another form, *Dicyema moschatum* Whit., also occurs in the same host. *D. eledones* (Fig. 46) is 7 to 9 mm. long, transparent, and is composed of one large inner cell with a simple nucleus (Fig. 46, *n.end*), and of an outer layer of ciliated cells, nine of which form the "calotte" or pole by which the animal is attached. Within the former (endodermal) cell the formation of urn-shaped "infusoriform embryos" takes place (B and C), the fate of which is not known, but they are possibly the males. The individual which produces these larvae is called a "Rhom-

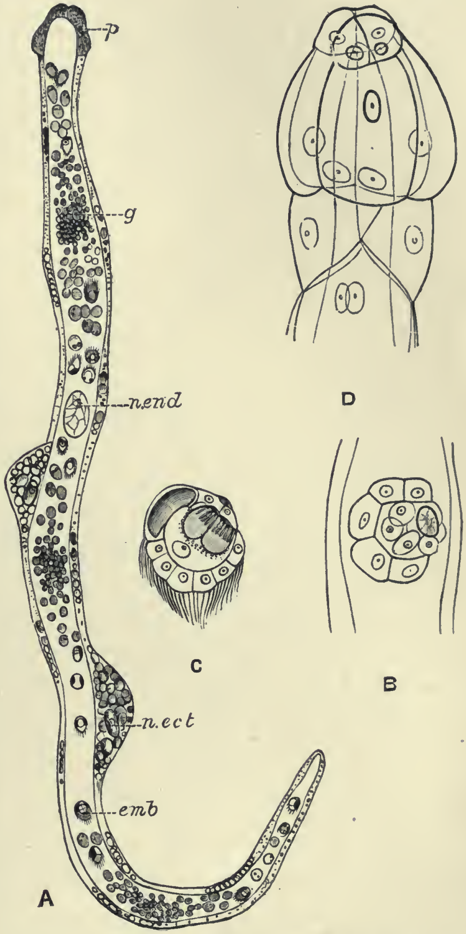

Fig. 46.—*Dicyemennea eledones* Wag., from the kidney of *Eledone moschata*. **A**, Full-grown Rhombogen with infusoriform embryos (*emb*); **B**, one of the latter developing; **C**, fully formed; **D**, calotte, composed of the upper nine cells shown in the figure. (After Ed. van Beneden and Whitman.) *emb*, Infusoriform embryo; *g*, part of endoderm-cell where formation of these embryos is rapidly proceeding; *n.ect*, nucleus of ectoderm-cell; *n.end*, nucleus of endoderm-cell; *p*, "calotte."

bogen." Other individuals which produce a more elongated larva ("vermiform larva," Fig. 45) are called "Nematogens," and Whitman has described a third kind, which produce first infusoriform, and then vermiform, larvae (Secondary Nematogens).[1]

The occurrence of the known species of Dicyemids (a group which has not been investigated on our coasts) is as follows:—

Species.	Host.
Dicyema typus van Ben.	*Octopus vulgaris.*
D. clausianum van Ben.	*O. macropus.*
D. microcephalum Whit.	*O. de Filippi.*
D. moschatum Whit.	*Eledone moschata.*
D. macrocephalum van Ben.	*Sepiola rondeletii.*
D. truncatum Whit.	*Rossia macrosoma, Sepia elegans, S. officinalis.*
D. schultzianum van Ben.	*S. biseralis, Octopus vulgaris.*
Dicyemennea eledones Wag.	*Eledone moschata, E. aldrovandi.*
D. mülleri Clap.	*E. cirrosa.*
D. gracile Wag.	*Sepia officinalis.*
Conocyema polymorphum van Ben.	*S. officinalis, Octopus vulgaris.*

Orthonectida.[2]—Two species of Orthonectids are fairly well known, *Rhopalura giardii* Metschn. from *Amphiura squamata*, and *R. intoshii* Metschn. from *Nemertes lacteus.* The latter appears to be very rare, the former occurring in 2 to 5 per cent of the number of hosts examined. The parasites occur in a granular "plasmodium," the nature of which is uncertain. Metschnikoff regards it as formed by the Orthonectids, and he considers that the cellular envelope, by which it is sometimes enclosed, is developed from the neighbouring tissue of the host. These granular, sometimes nucleated, plasmodial masses, which can perform active amoeboid movements in sea-water, occur attached to the ventral part of the body-cavity of *Amphiura*, and between the gut-branches and body-wall in *Nemertes.* Should these hosts be infected by great numbers of the Orthonectids, their sexual organs degenerate (as is the case with pond-snails attacked by sporocysts[3]), and it is possible that the remains of these organs may constitute the "plasmodia" (Braun).

[1] Whitman, *Mittheil. Zool. Stat. Neapel*, Bd. iv.; see also Braun, in Bronn's *Thierreich*, Bd. iv. p. 253.

[2] Braun, *loc. cit.* p. 281 (with literature).

[3] Giard, "La Castration parasitaire," *Bull. Sci. d. France et de Belgique*, 3 sér. i. 1888, p. 12.

Rhopalura giardii is of distinct sexes. Either males or females are found in one *Amphiura*. Two kinds of females, flattened unsegmented, and cylindrical segmented forms, are known. They consist of a ciliated ectodermal layer enclosing an endodermal mass of eggs, between which is a fibrillar layer usually considered to be of a muscular nature. The cylindrical female gives rise to eggs which develop, probably exclusively, into

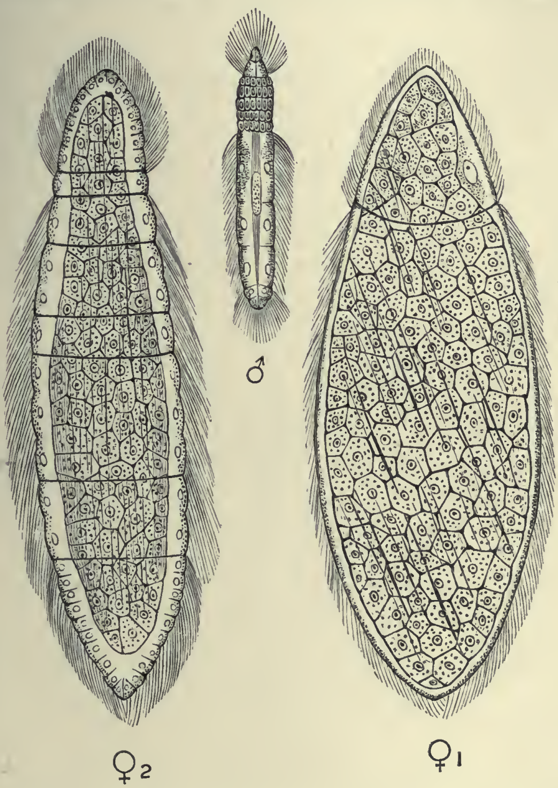

FIG. 47. — *Rhopalura giardii* Metschn. (from the brittle-star *Amphiura squamata*). ♂, Full-grown male (× 800); ♀$_1$, flattened form of female (× 510); ♀$_2$, cylindrical female (× 510). (After Julin.)

males. The flattened female produces eggs from which females alone arise, though the origin of the two forms of this sex is not well ascertained. The males contain spermatozoa which fertilise the eggs of the cylindrical female, whereas the ova of the flat form probably develop parthenogenetically.

Trichoplax.[1]—This anomalous animal has only been found in aquaria, originally in the marine aquarium at Graz by

[1] Schulze, *Abh. Akad. Berlin*, 1891, p. 1.

Schulze. It has the appearance of a large, flattened, ciliated *Amoeba* (1·5-3 mm. in diameter), but is distinguished by its structure. The upper surface is composed of a flattened epithelium. The lower surface is made up of cylindrical ciliated cells, which pass imperceptibly into the branched cells, embedded in a hyaline matrix, which compose the middle layer of the body. No distinct organs, and beyond simple fission, no mode of reproduction, have been observed. One species, *T. adhaerens,* is known, but has never been met with in a free state.

Salinella.[1]—This is another aquarium-animal, found by Frenzel in the Argentine, in an artificial saline solution with which he filled some aquaria. It measures ·2 mm. in length, and has a somewhat flattened, barrel-shaped appearance. A single layer of ciliated cells bounds a central cavity opening at each end. Fission, and conjugation followed by encystment, have been observed. One form, *S. salve,* is known from salines taken from Cordova.

[1] *Arch. Naturg.* lviii. 1891, p. 66.