OBSERVATIONS ON SPONGES.

BY

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I. NUTRITION.

In 1856 Carter stated (p. 242) that in Spongilla the pores of the investing membrane „admit currents of water, as proved by the presence of particles of carmine; which particles were found to have been taken into the bodies of the sponge-cells and so-called 'zoosperms'." Lieberkühn published in the same year his observations, likewise on Spongilla, and independently from Carter arrived at about the same conclusions. „Um die Aufnahme von Substanzen durch die Spongillen zu beobachten, wurde der Flüssigkeit, in der sie sich befanden, Carmin zugesetzt; es drangen in mehreren Fällen die rothen Körnchen in eine oder zwei Oeffnungen ein, welche in einiger Entfernung von der kegelförmigen Erhebung lagen, und färbten fast die ganze Spongille roth; viele der rothen Körnchen steckten im Innern der Schwammzellen selbst, was sich beim Zerreissen der Spongille unter Anwendung starker Vergrösserungen leicht nachweisen liess" (1856 p. 497). Both Carter and Lieberkühn published new observations in the next year. Carter put young small specimens of Spongilla in a watch-glass with water to which carmine was added. The particles of carmine are rapidly sucked in through the pores, „not vortically but directly" (1857 p. 27), and traversing the cavities and canals, finally come into the „ampullaceous sacs, where they remain a quarter of an hour or more" (p. 28). Carter states that he has seen particles enter a flagellated chamber by an aperture. When „the

aperture happens to be on one side of the sac (viz. the flagellated chamber), the particles may be seen to pass through it into the interior, and generally to adhere to the first part with which they come into contact, when they are instantly enclosed by the spongecell on which they impinge" (p. 28). This happens after the manner of an Amoeba (p. 26). He found that in isolated choanocytes the flagellum was producing a current towards the body of the cell „on either side of the cilium, by which the particles may be seen to be thrown almost point-blank on its surface, and at the same time caught up. . . and rapidly passed into the interior. Hence we may easily conceive the united effort of all the ciliated sponge-cells in the ampullaceous sacs being sufficient to produce a considerable current into its interior, and thus to catch the particles which are passing through the afferent canals" (p. 30). Carter believed that „there was no direct communication between the afferent canals, or the ampullaceous sacs, and the efferent canals" (p. 29), but that the vacuoles of the cells discharge the water with the particles into the efferent system of canals. „When we consider the powerful organ which the contracting vesicles of all the ampullaceous cells together must form for effecting this function, it does not seem unreasonable. . . to conclude that the currents, both afferent and efferent, of the sponge may be produced in this way" (p. 30). Lieberkühn described similar observations on Spongilla. He says (1857 p. 384): „Die einströmenden Karminkörnchen dringen schnell in die Kanäle hinein und bleiben in grösserer oder geringerer Entfernung von der Eingangsöffnung plötzlich in kugelförmigen Räumen stecken; diese kugelförmigen Räume sind die Wimperorgane." Lieberkühn found that part of the particles were enclosed in the tissue of the sponge, part of them however simply passed the flagellated chambers and by an opening (which Carter could not find) came into the efferent canals. Lieberkühn does not tell us which cells take in the particles. He remarks (p. 387): — ....„es gleitet ein Theil in die eigentliche Gewebsmasse des Körpers hinein und bleibt von Zellen rings umgeben lange Zeit darin zurück, nur bisweilen kamen Fälle vor, wo innerhalb der Zellen selbst Karminkörnchen zu stecken schienen zwischen Kernen und Zellenwand, den Kern rings umgebend. Beim Zerreissen solcher Spongillen liessen sich immer Zellen auffinden, in denen Karminkörnchen sassen. Es ist jedoch schwierig zu entscheiden, ob die Zellenwand in solchen Fällen unversehrt war." Apparently Lieberkühn considered it a rather risked suggestion that an uninjured sponge-cell could swallow foreign particles. When

he describes the disintegration of an Infusorian in the parenchyme of the sponge, Lieberkühn compares the phenomenon with what he had observed in Actinophrys sol, absorbing an Infusorian. But the comparison is only made between digestion in one *organism* and in another. He does not speak of an intracellular digestion; it even follows from his description that there can hardly be thought of such a thing.

Carter in later years often returned to the question. In 1870 in describing his observations on marine sponges, he plainly says (p. 334): — „Thus it is proved that the ampullaceous sac is the eating-organ in Spongilla and in the marine sponges, both calcareous and siliceous, generally."

According to Haeckel (1872 I p. 372) „die Aufnahme fester und geformter Körperchen durch die Geisselzellen (ist) durch zahlreiche Fütterungs-Experimente mit Carmin- und Indigo-Körnchen festgestellt, welche Bowerbank, Lieberkühn und Carter bei Spongilla, Sycandra und anderen Schwämmen angestellt haben." Haeckel says he has repeated these experiments with various sponges, and he confirms them. But Metschnikoff (1879 p. 371) declares that Haeckel came to quite other results than Lieberkühn, while he himself stands on the side of the last named author. The fact is, that neither Haeckel nor Metschnikoff can be said to have quite the same views as Lieberkühn. Lieberkühn did not say that the choanocytes engulf particles; he has only said, with much reserve, that he found carmine within cells. In this respect Haeckel and Lieberkühn differ in opinion. Nevertheless Lieberkühn has stated, as we have seen, that carmine enters the flagellated chambers and remains there partly, whereas Metschnikoff wrote: — „Die Wimperkörbchen, resp. deren Zellen, bleiben.... für gewöhnlich leer.... Es stellt sich also heraus, dass bei einigen Schwämmen die Rolle der Nahrungsaufnahme ausschliesslich von Mesodermelementen ausgeführt wird" (p. 373).

After Metschnikoff von Lendenfeld has argued against the opinion of Carter and Haeckel that nutritive particles were first swallowed by choanocytes. True, Lendenfeld found carmine in choanocytes, but he believes these cells to have taken the carmine from other cells in order to expel them from the sponge body; he declares the choanocytes to be excretory cells. „Nach diesen Beobachtungen möchte ich es als erwiesen annehmen, dass bei Aplysilla violacea kleine organische Körper von den ektodermalen Plattenzellen des Subdermalepithels aufgenommen und den amöboiden Zellen, welche darunter liegen, übergeben werden. In diesen Zellen werden die

aufgenommenen Körper verdaut, und es wanderen die amöboiden Zellen mit den unverdauten Resten zu den Geisselkammern, übertragen die Auswurfstoffe auf die Kragenzellen und diese stossen dieselbe aus" (1883 p. 253).

These statements found a favourable reception with Poléjaeff who, however, did not enrich our knowledge with new observations. A year afterwards von Lendenfeld says: — „I think that my scientific colleagues universally agree to my statement that the nourishment is absorbed in the canals and not in the ciliated chambers" (1884 p. 437).

But von Lendenfeld changed his opinion a few years afterwards and now defends the opposite opinion with as much ardour. „Obwohl an den Kanalwänden der gefütterten Spongien einzelne Karminkörnchen haften bleiben, so ist doch klar, dass die Kragenzellen es sind, welche das im durchströmenden Wasser enthaltene Material normalerweise aufnehmen" (1889 p. 674). And further on he says: — „von den Kragenzellen werden die aufgenommenen Substanzen theilweise verdaut und in mehr oder minder assimilirtem Zustande den Zellen der Zwischenschicht übergeben, welche den Transport der Nahrungsstoffe besorgen."

After these statements von Lendenfeld certainly cannot be said to belong to the adversaries of Carter, Lieberkühn and Haeckel; and thus a strong argument is taken from Poléjaeff, who wrote that the opinions of various authors „are so very conflicting." (1884 p. 14). The authors quoted by Poléjaeff as contradicting the views of Carter c. s. are Keller, Metschnikoff, Krukenberg and Vosmaer. Keller speaks of amoeboid sponge cells, which are able to *transport* nutritive particles, absorbed by choanocytes. „Physiologisch wären also die Wanderzellen die Vermittler oder Zwischenträger, welche die von Geisselzellen der Wimperkörbe aufgenommene und assimilirte Nahrung übernehmen" (1878 p. 572). Krukenberg (1879) investigated whether in the body of sponges occur tryptic or peptic enzyms. This question ought to be well distinguished from the other one, viz. whether the choanocytes swallow food particles, or whether this is effected by other cells. The only author, quoted by Poléjaeff who could be said to agree more or less with Metschnikoff, was one of us, Vosmaer. „De dieren werden in afzonderlijke bakjes met karmijn en andere kleurstoffen gevoederd, om kort daarna mikroskopisch te worden onderzocht. Het bleek ook mij ten duidelijkste dat de kraagcellen zoowel als de zoogenaamde amoeboïde cellen gretig voedsel (hier de korrels karmijn enz.) tot zich nemen. Intusschen schijnt het voedsel in de kraagcellen slechts

korten tijd te blijven, daar verreweg de meeste karmijnkorrels in de amoeboïde cellen gevonden werden" (1881). The last sentence involves that food-particles are first seen in choanocytes, before they appear in parenchyme cells.

Bidder states in 1888: — „In Leuconia aspera I find that carmine granules are taken in freely by the collared cells, not appearing in the mesoderm, and only infinitesimally in the other epithelia." In 1895 the author confirms (p. 29) his former statements.

Taking thus all in account, we see that Metschnikoff [1]) is the only author who admits that particles entering with the water through the pores of the sponge, are not swallowed by the cells of the flagellated chambers but by cells of the „mesoderm." Metschnikoff's supposition is based on his observation that particles of carmine were abundantly found in cells of the parenchyme and little or not at all in choanocytes. Moreover he often found in the former cells foreign corpuscles like sand, diatoms etc.; and he observed living „mesoderm"-cells engulfing little corpuscles, e. g. chlorophyll-granules.

Now it is beyond doubt that the cells of the parenchyme which, when alive, generally show vivid amoeboid movements, that these cells are apt to absorb little particles, in the way of an Amoeba. But this is not the cardo questionis. If Metschnikoff says (p. 373): — „Es stellt sich also heraus dass bei einigen Schwämmen die Rolle der Nahrungsaufnahme ausschliesslich von Mesodermelementen ausgeführt wird" we must answer that this sentence is in direct contradiction with the careful observations of Carter and Lieberkühn, made on the very same object, viz. Spongilla. And his sentence is not proved by the fact that the cells of the parenchyme can act as phagocytes. It is merely based on the absence of carmine in the flagellated chambers.

According to our own researches the absence or the rarity of carmine particles in choanocytes of carmine-fed sponges, does not prove that these cells do not swallow particles. It became obvious to us that in Metschnikoff's experiments a large factor is omitted, viz. time. Still, it is clear that we have to take this factor into account. Several authors have stated that the choanocytes, after having absorbed particles of carmine or indigo, give off these particles to other cells. Vosmaer, as we have seen, came to the conclusion that the carmine remained only a very short time in the choanocytes. Master-

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[1]) Topsent (1888. p. 122—123) is of Metschnikoff's opinion; he does not give, however, further evidence. Our arguments against Metschnikoff are at the same time applicable to Topsent.

man (1894) does not believe that the choanocytes, loaded with carmine, give it to the cells of the parenchyme, but that they lose their flagellum and collar after feeding and move as amoeboid cells into the parenchyme. The open places, according to this author, are filled by cells of the parenchyme, which thus move towards the flagellated chambers, develope a flagellum and a collar, becoming in this way transformed into choanocytes. We have never met with anything like this in our preparations. But even if it were true, it could easily happen to find the flagellated chambers some time after feeding, without carmine. This would at any rate not prove that carmine was not originally captured by choanocytes.

We have made a series of experiments in feeding Spongilla lacustris and Sycon ciliatum with carmine; the former we also fed with milk. The animals were left for some time in water with carmine or milk; a slight current of air was led through the water in order to keep the fluid sufficiently oxygenated. They were either killed immediately, or placed back into pure water, and killed afterwards. For killing we used 1 % osmic acid; sections were made in paraffine, but always controlled by maceration preparations. [Cf. for these methods our paper of 1893].

In sponges which had been for half an hour to two hours in water with carmine or milk, we found both in sections and in macerations of Spongilla as well as of Sycon a considerable quantity of carmine in the choanocytes, while in the pinacocytes and in the cells of the parenchyme particles were seen here and there, but in a considerably smaller quantity than in the choanocytes. In Sycon the choanocytes were pretty well regularly loaded with carmine, throughout the whole sponge. Not so in Spongilla. Here we observed, that, often already with a low power, some of the flagellated chambers were conspicuous by their red tinge, while in other chambers the particles could only be made visible by using homogenous immersion (Zeiss). If the sponge had remained for hours (to 24 hours) in the carmine, there was more carmine in the cells of the parenchyme than in the choancytes. If, after a stay of many hours in carmine, the sponge was placed back into in pure water for some hours, the carmine was abundantly found in the cells of the parenchyme and hardly at all in the choanocytes.

Feeding with milk had about the same results. A Spongilla was put in milk-water; a piece of it was killed by osmic acid after $1^1/_4$ hour; a second piece after 3 hours; a third after 17 hours. They were all macerated afterwards in water. In the isolated choanocytes of the first piece the number of fat-globules was con-

siderably larger than in the cells of the parenchyme. In the second piece there were more globules in the parenchyme cells than in the choanocytes, and in the third piece the relation was still more in favour of the parenchyme cells. Still, there were in all three cases choanocytes in which 10—20 fat-globules could be found. On the whole we got the impression that the globules in the parenchyme cells were larger than those of the choanocytes. But the contrary was observed too.

Many authors have remarked that carmine is no food for a sponge, and that therefore the conclusions drawn from such experiments as above described were of little value. We therefore tried to experiment with corpuscles which might be used as food, e. g. bacteria. We did, however, not succeed in this respect. Notwithstanding the fact that the bacteria we added to the water, were cultivated from the water wherein the Spongillae lived and that we made cultures aerobian as well as anaerobian, the influence they had on the sponge was always fatal, if a large quantity was added to the water. If the sponge was investigated soon after administering bacteria, very few of these were found in the sponge cells, even often less than under normal conditions. It seems probable to us that the sponge in such a case had shut its pores. Thus no new bacteria could enter, while those once in the body were digested and therefore indistinguishable. After remaining for one or two days in bacteria-water the sponges died. Perhaps it would be possible, after repeated research, to find an organism which, in large quantities, could easily be digested by sponges. In such a case one could follow the alterations of the particles in the cells of the sponge. As yet we abstain from speculations with respect to the further destiny of the particles absorbed by choanocytes. But we believe we are entitled to say that the choanocytes really are the organs by which particles suspended in the water, passing the canals, are captured and thus brought into the tissue of the body. Carter and Lieberkühn have shown that these particles are sucked in through the pores and transported to the flagellated chambers. We will see that here the regular current at once changes into a very irregular movement. The particles are moved to and fro in the flagellated chamber, and though they partly leave the chamber through the apopyle, a number will, however, arrive within the collars of the choanocytes. The protoplasma of these cells then seizes the particles in order to give them off again to the cells of the parenchyme. This does not prevent that now and then particles can be seized by cells lining the canals; but this will always be

of less importance. Metschnikoff's opinion that the flagellated chambers were not the real „eating organs", as Carter expressed it, is not sufficiently supported by his observations.

It is obvious that the flagellated chambers could not act very well as organs for catching particles, suspended in the water, if this were continuously streaming instead of irregularly whirling. One of the chief objections Poléjaeff has against considering the choanocytes as able to catch particles, lies in the way this author believes the water to move in the flagellated chambers. In Sycon e. g. he supposes a rapid current in the axis of the chamber, towards the cloaca, and a slow somewhat vortical movement at the sides, in the immediate neighbourhood of the choanocytes. Particles, therefore, entering with the water through the prosopyles, have more chance, according to Poléjaeff, to pass rapidly in the axis of of the chamber towards the apopyle and to leave the chamber, than to be seized by a choanocyte. Yet, the supposition of Poléjaeff is not based on observation, but is merely the result of reasoning. Poléjaeff did not take into consideration that the flagella of Sycon are exceedingly long, reaching far into the lumen of the chambers. Add to this that the water enters by several prosopylae all around the wall of the chamber, and it will become easy to understand that circumstances are indeed very unfavourable to a rapid and regular current. Moreover we did observe certain facts in our sections of carmine fed Sycons, which can hardly be explained in another way than by accepting a slow whirling movement in the chambers. We found, that not only a large quantity of carmine was enclosed within the choanocytes, but that in the lumina of the chambers clods of detritus were often mixed with carmine. These clods were many times larger than the prosopylae. Consequently they could not have entered the chambers through the prosopylae, but must forcibly have been formed within the chambers. This fact suggests a whirling movement of the fluid in the chambers. A regular water current through the axis of the chamber would certainly have prevented the formation of clods loaded with carmine.

If we thus find an irregular whirling movement highly probable in the large pouch-shaped chambers of Sycon ciliatum, how much the more so in those sponges which, like Spongilla, possess small spherical or sub-spherical chambers not regularly arranged around a central tube (cloaca) as in Sycon, but dispersed everywhere in the parenchyme. We can hardly accept a regular current in those chambers even with the most perfect coordination of the flagella.

Carter and Lieberkühn acurrately described the movement of particles in the chambers, observed in living animals.

According to our own observations the movement of the flagella is exactly such as to produce an irregular whirling motion of the water. The water is so to say stirred in the flagellated chambers, in order to bring particles, suspended in it, as much and as surely as possible into contact with the choanocytes. Lendenfeld says (1889, *a*, p. 754): — „it appears that the cilia in the entodermal collar-cells move pendulum-like, backward and forward, similarly to the cilia of the polyciliar epithelium-cells in the respiratory tracts and other parts of vertebrates." In spite of this assertion, which indeed does not rest on observation, we believe that there is no question of coordination, nor any faint similarity with ciliated epithelia of vertebrates.

We need not wonder at hardly finding any statements concerning the way in which the flagella move. In most sponges the flagellated chambers are too small for accurate observations on the movement of the flagella. In some sponges the chambers can be more or less isolated; but we have then still to look through the wall of the chamber if we want to study the flagella. And if we open such isolated chambers, then of course so much is destroyed by this rough method that we may not draw conclusions from what is then actually observed to what happens in the uninjured condition. It is therefore better to study such sponges as Sycon ciliatum, which possess large flagellated chambers radially arranged. Still better is Leucosolenia, where almost the wole internal surface is provided with choanocytes.

The descriptions of the movement of the flagella which we find in previous papers are either too superficial or, if the authors go into details, they are wrong, with exception of Bowerbank, who in 1862 has already given very accurate descriptions. In speaking of the flagella of „Grantia compressa" he says: — „their motions are not synchronous, each evidently acts independently of the others" (1862 p. 806 and 1864 I p. 129). Our observations are in perfect accord with these statements of Bowerbank. The English spongiologist says further: — „the upper portion of the cilium was thrown gently backward towards the surface of the sponge, and then lashed briskly forward towards the osculum, and this action was steadily and regularly repeated." In this respect we cannot agree with Bowerbank.

Bidder observed about the motion of the flagella in Sycon compressum (1895 p. 17): — „The movement is certainly asym-

metrical, with a longer rest on one side than on the other. In several cases it was also certain that the motion lay entirely in one plane." We will see below that we differ from this opinion.

At first we saw the motions of the flagella only in Sycon ciliatum. A portion excised from the wall of a flagellated chamber was observed in sea-water. We saw the flagella move as irregularly as possible. But we were afraid of drawing conclusions from such preparations, as the portions were only small and it was possible that the choanocytes were hurt. Afterwards we could investigate living Leucosoleniae. A piece of about 1 qcm. was cut from a tube and then split open quickly and immediately observed. The piece was covered with a cover-glass; but this could hardly harm the choanocytes, as it was carried by the apical rays of the tetrasceles. The preparations were observed with Zeiss's homog. imm. 1.40, 3; Oc. 12. It was evident then that the flagella were beating quite independently from each other, all in different directions. The movement of each flagellum was not always in the same plane, and one moment it was stronger in one direction, another moment stronger in another. Sometimes a flagellum was stretched for a while almost horizontally. It happened also that one or more flagella were motionless, in order to beat again vividly a few moments afterwards. Every now and then flagella crossed, without ever becoming entangled. Particles, suspended in the water were whirling about, never carried forward. In short, the aspect of the motion was absolutely different from what is observed in ciliated membranes of higher animals. There was no trace of a coordination of neighbouring cells.

We have seen that this mode of motion cannot be but advantageous for capturing particles by the choanocytes. This is not only the case for choanocytes forming flagellated chambers, but eminently so for those lining the cloacae of Leucosolenia. If all the flagella lashed briskly towards the osculum, the particles, entered through the pores, would be directed chiefly towards the axis of the tube and rapidly removed through the osculum. On the contrary the movement of the flagella has the effect that particles can easily reach the collars and thus come into contact with the protoplasma of the choanocytes.

Moreover it seems possible to us, to explain by the irregular motion of the flagella, the regular current through the canals of the sponge, as this is so often observed, and so carefully studied by Grant. Pieces of the wall of Leucosolenia, after fixation in osmic acid or alcohol, were stained in various ways and mounted in different media. In such preparations the pores were always

visible. In somewhat macerated preparations [1]) it was distinctly seen that the pores in Leucosolenia (botryoides?) were short canals which had their greatest diameter in the middle. The diameter on the dermal side, as well as that on the cloacal side was less. It must be said that the dermal aperture was smaller than the cloacal one. Bidder (1891) and Minchin (1892 and 1898) have made these pores an object of careful observation. Both spongiologists came to the conclusion that it are intracellular canals; they admit a high degree of contractility in such „pore-cells". It is certainly not impossible that these cells during the manipulations for fixation have time enough to contract at least partly [2]). It is therefore possible that in the active, living state the pore is cylindrical, or even that the dermal aperture is the larger one and consequently the pore funnel-shaped, with the mouth of the funnel externally. Minchin has given in a previous paper (1892 Pl. X fig. 1) an illustration of pores in Leucosolenia, where the dermal opening is larger than the cloacal one, and we have seen exactly such things in some of our sections of Sycon ciliatum. But even if the cloacal (internal) aperture of the pore is not smaller than the dermal (external) one, it seems to us that in the living sponge the water would find more resistance in flowing out from the chamber through a pore than it finds in streaming in. For we found that in carefully mounted preparations where all the choanocytes remained fixed in their place, these cells surround the pores closely and are placed, not exactly perpendicular on the wall, but somewhat oblique, so as to narrow the cloacal opening of the pore. Pl. I, fig. 6—9. We found this to be the case in a flat, stretched piece of Leucosolenia. Their position must be all the more oblique in the living state if the wall is of course not flat but concave. If therefore in the cloaca the pressure of the water becomes higher, the collars of the choanocytes will become somewhat inflated and the pore will be narrowed. If, on the contrary in the cloaca the pression of the water in the neigbourhood of a pore is lessened, water can easily flow in through the pores; the choanocytes with their collars thus act as valves. Now by the irregular motion of the flagella the pressure on the wall of the tube, which by the spicules is kept rigid, is continually changing. If the pressure becomes higher, this is of little effect, but if the pressure becomes less, water will flow in through the pores, as

[1]) It is often an advantage to treat the osmium-preparations with water. A certain number of choanocytes are then loosened and washed away.

[2]) In our preparations the dermal aperture is larger in the specimen treated with osmic acid than in those killed with alcohol.

long as they are open. The sponge will thus suck in water, which will leave the body again through the osculum. Around the osculum we find, at least in several species of Leucosolenia, a remarkable contrivance. Lieberkühn writes about „Grantia botryoides" (which is a Leucosolenia): — „Kurz vor dem Rande der Ausströmungsöffnungen hört der Wimperbezug mit gerader oder welliger Abgrenzung auf...." (1865 p. 735). Minchin has observed the same detail, and the species of Leucosolenia we could study all show that the cloaca in the neighbourhood of the osculum is destitute of choanocytes. Such portions of the cloacal tube, where an irregular motion of the water by the flagella is thus excluded, must act as chimneys. It is noteworthy that the sieve-like membrane described by Minchin (1892 p. 253), occurs exactly on the limit between the part with choanocytes and that without them, and does not prevent in any way the water flowing out, while it has the advantage that it does prevent intruders to enter.

Yet, this chimney, even if strengthened by long spicula, is of but small efficiency, being at any rate rather short. We ought not to forget, however, that sponges like Leucosolenia which possess but little parenchyme in comparison to their volume, do not want a very strong current.

It is, however, quite another thing if the sponge is more complicated. In sponges with a canal-system of the second type (Vosmaer 1880 p. 72), like e. g. Sycon, the chimney is of much more importance. Here we find a central wide tube with a multitude of radial, pouch-shaped outgrowths. The central tube is lined with pinacocytes; its free aperture (osculum) is generally strengthened by special spicula, often forming a rigid tube. The radial outgrowths are the flagellated chambers, which show several pores and one (larger) mouth into the cloaca. The shape of the pores, (in higher forms the prosopylae) agrees with that of the pores in Leucosolenia. It is certainly a remarkable fact that the aperture at the top of the chamber is much larger than the pores at the side; at the top the chamber is much more concave than at any other place, and so the pore can be larger without danger for the direction of the water-current. On the other hand those distal pores are frequently surrounded by long spicula, which are arranged so as to prevent the entrance of too large particles or ennemies. The water in the chambers, kept in continual irregular movement by the flagella, cannot escape through the pores, but may easily pass through the wide apopyle. Through the pores of the chamber water flows easily in. Water will thus continually pass from

the chambers into the cloaca; here it will escape in the direction of minor resistence, viz. towards the osculum. Thus in the central tube the water will obtain a certain velocity, which, once established, acts as the flying-weel of an engine. Obviously the absence of flagella in the central tube is of great advantage. Every irregularity *here* would only diminuish the effect of the flying-weel. We know that the velocity of the water at the osculum is rather considerable. But as the quantity which escapes form the osculum in a second must forcibly be equal to what in the same time is thrown into the cloaca by the whole set of chambers, the velocity of the water in these chambers must be small, because the diameter of the osculum is enormously less than the sum of the diameters of the chambers taken together.

In sponges which possess a canal-system of the third type we see, in general, a richer development of connective tissue. The mass of the sponge becomes larger in comparison to the surface. Instead of large cylindrical flagellated chambers we find more or less spherical chambers, in which the walls are more curved, where thus the choanocytes work still better as valves. The water comes from wide lacunae into the flagellated chambers through especial pores, prosopylae. The apopylae are always larger than the prosopylae. The external surface of the sponge is perforated by numerous pores, through which the water is sucked in by the motion of the flagella. Oscular tubes which can work as chimneys are generally well developed. Often the oscula are elevated above the surface of the sponge. This arrangement will certainly be advantageous for a regular current, but as Grant has already shown, it is not indispensable (1825 p. 331). The excurrent apertures are always less in number and larger in size than the incurrent apertures. The effect will be that the velocity of the water at the oscula is greater than at the pores and many times greater than the velocity with which the water flows through the flagellated chambers.

In sponges with a canal-system of the fourth type, the mass is still more predominant over the surface. The water enters the body through pores and is led by cylindrical tubes into the flagellated chambers. In these inhalant canals, which ramify under sharp angles, the water will certainly not find much resistance. Thus, even if the power of sucking of the flagellated chambers be little, it will be sufficient to introduce the water through the pores. Now the shape of the flagellated chambers is very remarkable. They are generally pear-shaped, as Schulze has shown e. g. for Chondrosia,

Oscarella and others. The consequence of a motion of the flagella in these chambers will obviously be that the water will flow in the direction of the pointed end of the chamber. In the opposite direction a current is hardly possible, as the choanocytes around the mouth of the prosodus will again work as valves. Schulze says of Chondrosia reniformis (1877 p. 107—108): — „Die eigenthümliche, im Allgemeinen als birnförmig zu bezeichnende Gestalt der ganzen Geisselkammer erscheint hauptsächlich dadurch bedingt, dass die prismatischen Kragenzellen je einer Kammer *nicht* sämmtlich streng radiär gerichtet sind, und so eine vollständige Hohlkapsel formiren, sondern, dass sie nur die äusseren, d. h. die dem zuführenden Canälchen zugewandten drei Viertheile der Kammerwand einnehmen, während die innere, direct in das abführende Canälchen sich fortsetzende Partie der Geisselkammer der Kragenzellen *entbehrt*, statt dessen von flachen, platten Zellen ausgekleidet zu sein scheint, und sich in der Regel wie ein trichterförmig ausgezogenes oder richtiger *trompetenförmig gestaltetes* Endstück darstellt."

In Chondrosia and other sponges of this fourth type, we find still another remarkable contrivance. We there find a large number of pores on the surface of the sponge, each of which is the beginning of a narrow cylindrical canal. A group of these short canals unite into a wider cylindrical canal, which runs through the ectosome in order to ramify again and to give rise to a number of prosodi. This arrangement has the advantage that the water, with food particles suspended in it, is sucked in at a surface much larger than corresponds with the diameter of the main incurrent canal. On the other hand it is thus prevented that too large particles could block the way.

The explanation we have tried to give of the regular current through the body of the sponge as caused by an irregular motion of the flagella, involves that the current must be in *one* direction. It could not be sustained if Miklucho-Maclay (1868) and Haeckel (1872) were right in their statements that the current can be reversed. We believe, however, that it may be doubted indeed whether a true reversal of the water current exists in sponges. Many observers, like Grant, who certainly must be ranged under the first authorities with respect to accuracy of observation and to amount of experience, never saw a reversal of the current. If water be observed to flow out from an aperture, which on an other occasion sucked in, one is *not* entitled to conclude to a total reversal of the current. Bowerbank gives a very remarkable instance (1857

p. 443). He found in „Hymeniacidon caruncula" oscula of different size, large and small ones, from which the water ceased to flow out if it were not changed after some time, as was generally done. One day he observed the following striking facts. „At 10 o'clock I put fresh sea-water to the sponge, and within a minute the ex-current action was apparent at both the large groups of oscula, and in a few minutes became in full vigour. The central smaller single osculum was perfectly closed, and not the slightest appearance of it was to be detected with a 2-inch lens. The action in the two groups of oscula continued in full force until half-past 12, when the group at the small bend had ceased to act and the smaller oscula of the group had contracted to about half their full diameter. I placed a drop of water charged with indigo immediately above this osculum, and watched the effect with a 2-inch lens, and was surprised to find that its action was reversed, and the molecules of indigo passed into it with a considerable degree of rapidity. I repeated the application of the drops of water charged with indigo several times, and the result was the same. Occasionally the ex-current action was resumed for an instant, and a large molecule of indigo would be expelled, but the next moment the in-current action would be resumed. At half-past 1 I repeated the application of the drops of water charged with indigo with the same result, when it suddenly broke forth again into strong ex-current action, elevating the surface of the water immediately above it in the usual manner, and continued thus to act. The reversal of the action in the osculum in this instance was apparently effected bij the vigour of the action in the other group of oscula; the wole of these organs being more or less connected, not only by the intermarginal canals, but also by the general system of interstitial canals of the mass of the sponge." Bowerbank gives an explanation of the phenomenon, without accepting a total reversal of the current. In fact, if in a system of tubes, internally connected, the velocity of the current in some branches accidentally becomes very great, fluid can then be sucked in from other branches. Bowerbank's words seem to have a much higher value than all that is written in favour of a so-called real reversal of the current.

Another argument against our explanation could be furnished by the so-called „astomie" (Schmidt 1870 p. 10) or „lipostomy" (Haeckel 1872 I p. 267). Taken in the sense Schmidt and Haeckel have used the word, lipostomy is certainly far from an established fact. Since it is certain that sponges can shut their pores as well

as their oscula, the great value Schmidt and Haeckel attach to „lipostomy", ought to be given up. It would be easy enough to quote a number of instances to prove that Schmidt and Haeckel were entirely wrong. It will be sufficient to mention the case Minchin gives of Leucosolenia clathrus, a sponge of which Haeckel declares that it occurs only as Auloplegmaform, i. e. without osculum (1872 II p. 31). Minchin has clearly proved (1892) that Leucosolenia clathrus shows distinct oscula, if the sponge be only observed in the normal healthy condition. It seems to us therefore that the „reversal of the current" and the „lipostomy" are by no means obstacles to our views.

On the other hand it is clear, according to our opinion, that if the in-current or the ex-current apertures, or both be shut, the current is at once stopped without causing dangerous differences of pressure in the body of the sponge. If the current were caused by a well-organised coordination of the flagella, moving the water in a distinct direction, there would result considerable differences of pressure the moment that pores or oscula were closed. And this might easily damage the delicate tissues of the sponge. In order to avoid this, a tolerably highly developed nervous system would be demanded, by which a stimulus at the surface of the body could be transported to all the flagellated chambers, causing the flagella to stop their motion. According to our views, however, the flagella can go on lashing if, at some danger, the pores or oscula are closed; no damage is to be feared. If the apertures at the surface of the sponge close the current will stop, because there is too much resistance as well in the excurrent as in the in-current canals. And the variation in pressure within the chambers, caused by the motion of the flagella, is so small that a current can only be established if the afflux is free and especially if the efflux is secured by a certain velocity produced by the chimneys.

We have in sponges an example of the height and fitness of organisation, which can be obtained in Metazoa, without any coordination, by a mere appropriate arrangement of cells, which are differently developed according to their function. And yet, the evolution is soon limited, because the cells of the organism are not connected in a way so as to enable them to conduct stimuli from one cell to another, in other terms because they are destitute of the principle, the significance of which culminates in nervous tissue.

II. ON ESPERELLA AEGAGROPILA (Johnst.) Tops.

Halichondria aegagropila.

1842 Johnston pp. 119—120, 248, 258. Pl. XI, fig. 1—2.
1846 Scouler p. 117.
1848 Gray p. 11.
1862 Bowerbank p. 755; Pl. XXVII, fig. 10.
1866 Bowerbank p. 352.
1866 Schmidt p. 18.
1867 Gray p. 533.
1874 Bowerbank p. 209.
1874 (a) Carter pp. 101, 105.
1875 Carter p. 197.
1880 Vosmaer p. 142.

Desmacidon aegagropila.

1864 Bowerbank pp. 75, 273. Pl. XIII, fig. 264.
1866 Bowerbank p. 352—354.
1867 Gray p. 533.
1868 Bowerbank p. 129.
1868 Wright p.
1869 (a) Norman p. 262.
1870 Schmidt p. 77.
1874 Bowerbank pp. 163—164, 274. Pl. LXIII, fig. 8—14; Pl. LXXXIII, fig. 23.
1875 Carter p. 197.
1880 Vosmaer p. 142.
1880 Waller p. 103.
1882 Bowerbank-Norman pp. 180, 181. [D. aegagrophilus].
1894 Hanitsch pp. 179—180.
1894 (b) Topsent pp. 25, 26.

Hymeniacidon subclavata.

1866 Bowerbank p. 209—210.
1868 Gray p. 163.
1870 Schmidt p. 76.
1874 Bowerbank p. 93. Pl. XXXVII, fig. 9—13.
1880 Vosmaer p. 142.
1882 Bowerbank-Norman p. 92 [Hym. subclavatus].
1882 Carter p. 293.
1894 Hanitsch p. 177.
1894 (b) Topsent pp. 20, 23.

Hymeniacidon floreum.

1866 Bowerbank p. 190—193.
1867 Gray p. 537.
1868 Gray p. 163.
1868 Wright p.
1869 (a) Norman p. 331 [Hym. floreus].
1870 Schmidt p. 76.
1874 Bowerbank p. 94.
1880 Vosmaer p. 142.
1882 Bowerbank-Norman p. 162.

Hymeniacidon macilenta.

1866 Bowerbank p. 176—177.
1867 Gray p. 537.
1868 Gray p. 163.
1870 Schmidt p. 76 [Hym. macilentus].
1871 Carter p. 276.
1874 Bowerbank p. 84. Pl. XXXIII, fig. 7—13.
1880 Vosmaer p. 143.
1880 Waller pp. 98—100, 102, 104. Pl. V, fig. 1.
1882 Bowerbank-Norman p. 83 [Hym. macilentus].
1882 Carter p. 294.
1894 Hanitsch p. 177.
1894 (b) Topsent p. 18, 20.

Isodictya aegagropila.

1866 Schmidt p. 20.

Aegogropila varians.

1867 Gray p. 533.
1882 Bowerbank-Norman p. 180 [Aegagropila].

Carmia floreum.

1867 Gray p. 537.
1882 Bowerbank-Norman p. 162.

Carmia macilenta.

1867 Gray p. 537.
1871 Carter pp. 276, 283; Pl. XVII, fig. 8.
1882 Bowerbank-Norman p. 83.

Esperia aegagropila.

1868 Wright p.
1874 Carter p. 209.
1874 (a) Carter pp. 101—105, 110. Pl. P, X. 1—16.
1874 (b) Carter pp. 323, 332, 333, 405. Pl. XXI, fig. 25—26.
1874 (c) Carter p. 456—457.
1880 Vosmaer p. 142.
1882 Bowerbank-Norman p. 180 [E. aegagrophila].

Raphiodesma floreum.

1874 Bowerbank p. 94. Pl. XXXVII, fig. 14—19.
1880 Vosmaer p. 142.
1880 Waller p. 101.
1882 Bowerbank-Norman p. 162.
1882 Carter p. 289, 293.
1894 Hanitsch p. 177.
1894 (b) Topsent pp. 20, 24.

Desmacidon similaris.

1874 Bowerbank pp. 312, 319—321. Pl. LXXXIX, fig. 14—20.
1880 Vosmaer p. 143.
1880 Waller p. 103.
1882 Bowerbank-Norman p. 179.
1894 Hanitsch p. 181.
1894 (b) Topsent pp. 20, 27.

Raphiodesma sordida.

1874 Bowerbank pp. 224, 230—236. Pl. LXXVI, fig. 13—19.
1880 Vosmaer p. 146.
1880 Waller pp. 99, 101—104.

1882 Bowerbank-Norman p. 163 [R. sordidum].
1882 Carter p. 294 [R. sordidum].
1894 Hanitsch p. 180.
1894 (b) Topsent pp. 20, 26.

Esperia macilenta.

1880 Vosmaer p. 143.
[1882 Carter p. 294].

Esperia sordida.

1880 Vosmaer p. 146.
1892 Delage pp. 367—377, 436—449. Pl. XVII—XIX.

Raphiodesma minima.

1880 Waller pp. 102, 104. Pl. V. fig. 2—7.

Esperia florea.

1882 Bowerbank-Norman p. 162.
1882 Carter pp. 289, 290.

Esperia subclavata.

1882 Bowerbank-Norman p. 92.

Desmacidon macilentus.

1882 Bowerbank-Norman p. 83.

Esperella aegagropila.

1890 Topsent pp. 201, 204.
1891 Topsent p. 528.
1894 Hanitsch pp. 179, 180, 190.
1894 (b) Topsent pp. 8, 20, 23—26.
1896 Topsent pp. 114, 123.

Esperella macilenta.

1890 Topsent pp. 201, 204.
1891 Topsent pp. 528, 537.
1894 Hanitsch pp. 177, 190.
1894 (a) Topsent p. 44.
1894 (b) Topsent pp. 8, 11.
1894 (c) Topsent p. XXXVI.
1896 Topsent p. 114.

Esperella sordida.

1890 Topsent pp. 201, 204.
1891 Topsent pp. 528, 537.

1892 Topsent p. 93.
1893 Maas p. 352.
1894 Hanitsch pp. 180, 190.
1894 (e) Topsent p. XXXVI.
1897 Topsent pp. 426, 450—460.

Esperella hamata.

1892 (a) Topsent p. XXI.
1894 (e) Topsent p. XXXVI.
1896 Topsent p. 123.

Esperella mollis.

1892 (a) Topsent p. XX.
1894 (e) Topsent p. XXXVI.

Esperella albicans.

1892 (a) Topsent p. XXI.
1894 (e) Topsent p. XXXVI.

Esperella similaris.

1894 Hanitsch pp. 181, 190.
1894 (e) Topsent p. XXXVI.

Esperella florea.

1894 Hanitsch pp. 177, 190.

Esperella subclavata.

1894 Hanitsch pp. 177, 190.

The first who described our sponge was Johnston, calling it Halichondria aegagropila (1842). It would hardly be possible to recognise it, where it not that Bowerbank and Carter completed Johnston's descriptions and illustrations. Johnston only mentions styles or tylostyles; Bowerbank found that the sponge possesses, in addition to these, anisochelae, sigmata and toxa; accordingly he brought it to his genus Desmacidon. Carter studied a „type specimen in the Johnstonian Collection, British Museum" of Halichondria aegagropila, which he arranged under the genus Esperia. If we compare the figures given both by Bowerbank and Carter [Pl. III fig. 26, 27, 33, 46, 76—78] and calculate the sizes of the microscleres, we find that according to Bowerbank the anisochelae are 22.6 μ. and the sigmata 54.8 μ.; according to Carter however 34 μ. for the former, 84 μ. for the latter and 164 μ. for the toxa. This is rather a great difference;

but the relative sizes between anisochelae and sigmata are in both cases pretty well the same viz. 2 : 5. This relation is more important than the absolute size, though even this is by no means thouroughly constant for all the varieties of E. aegagropila, as we will see afterwards.

Johnston's Halichondria aegagropila was arranged by Bowerbank, as we have said, under his genus Desmacidon. Subsequently it was brought by Schmidt (1866) to Isodictya [1]), by Wright (1868) to Esperia, by Topsent (1890) to Esperella. We need not discuss here why neither Halichondria, nor Desmacidon, nor Isodictya, nor Esperia can be used; we refer to the Porifera in „Bronn's Klassen und Ordnungen des Thierreichs." Remains thus Esperella as the generic name for Johnston's Halichondria aegagropila.

One of us suggested (Vosmaer 1880 p. 142) that Hymeniacidon subclavata Bwk. and Hym. floreum Bwk. are nothing else than varieties of E. aegagropila. Indeed if we compare the descriptions and illustrations of Bowerbank [Pl. III fig. 30, 36, 79—81] we cannot find any *specific* difference. The same may be said of the size of the anisochelae and sigmata. In Hym. subclavata they are stated to be respectively 21.6 μ. and 54.2 μ.; in E. aegagropila 22.6 μ. and 54.8 μ. In Hym. floreum they are somewhat larger viz. 37.7 μ. and 83 μ.; but Carter found, as we have seen, 34 μ. and 84 μ. in an original Johnstonian specimen of E. aegagropila. Bowerbank mentions toxa in his Desm. aegagropila, though he found them „rarely" (1866 p. 352); he does not mention these microscleres in Hym. subclavata nor in Hym. floreum. Now Carter states (1882 p. 289): — „in my mounted fragment of the type specimen of Esperia (Raphiodesma, Bk., 1870) florea, there is a tricurvate which no doubt belongs to the species" . . . and (ibid. p. 293): — „of the British species of Esperia represented by Dr. Bowerbank, viz. Hymeniacidon subclavata . . . . and Raphiodesma floreum . . . . both on valves of Pecten, the inequianchorates appear to be alike, although the skeletal spicules are so far different in the illustrations that the former is simply acuate, i. e. without terminal inflation, and the latter sub-pinlike; but this difference, as I have said before, is not of much specific value, as it is not more persistent than the absence or presence of the tricurvate, which also, as before mentioned, exists in *my* mounting of the latter." Carter concludes therefore that Hym. subclavata and floreum are but one species. Our previous view about the identity of these

[1]) Misprint?

two with E. aegagropila is thus supported by new observations of Carter, though this author does not mention the latter name.

Of course Carmia floreum (Bwk.) Gray, Raphiodesma floreum (Bwk.) Bwk., Esperia florea (Bwk.) Bwk. Norm., and Esperella florea (Bwk.) Han. are nothing but other names for Hymeniacidon floreum Bwk., like Esperia subclavata (Bwk.) Bwk. Norm. and Esperella subclavata (Bwk.) Han. are such for Hymeniacidon subclavata Bwk.

Waller identified (1880 p. 102), Hym. macilenta Bwk. with Raphiodesma sordida Bwk. Carter (1882 p. 294) considers both as varieties of E. floreum: — „the spiculation of Hymeniacidon macilenta, Bk.... obtained from the most insignificant „fragments" in point of size, of which „the largest piece only slightly exceeded an inch in length, and was about three lines in width".... such as I have often found here (Budleigh Salterton) about the roots of Laminaria digitata, seems to me but a variety of Esperia (Raphiodesma) florea, in which all three of the flesh-spicules are present, viz. inequianchoreate, bihamate, and tricurvate"... Finally Topsent (1894 b. p. 20) is the third to discover that there is no *specific* difference between Hym. macilenta Bwk. and Raphiodesma sordida Bwk. We have therefore a good chance that they really are identical. In comparing again the descriptions and illustrations of these sponges with those of the above mentioned so called species [Pl. III figs. 28, 29, 31, 32, 45, 47, 49, 68, 69, 72—75] we cannot help coming to the conclusion that they are all the same as E. aegagropila. The same may be said of Desm. similaris Bwk., which was considered by one of us (Vosmaer 1880 p. 143) as a variety of Hym. macilenta, a view with which Topsent (1894 b. p. 20) agreed. Carmia macilenta (Bwk.) Gray, Esperia macilenta (Bwk.) Vosm., Esperella macilenta (Bwk.) Topsent are of course nothing more than other names for Hym. macilenta Bwk.

Likewise Esperia sordida (Bwk.) Vosm. and Esperella sordida (Bwk.) Topsent are identical with Raphiodesma sordida Bwk., and Esperella similaris (Bwk.) Han. equal to Desmacidon similaris Bwk.

It seems to us that Raphiodesma minima of Waller must be cancelled as a species. The author states himself that this sponge „is but little removed from R. sordida, and but for the absence of the tricurvate and bihamate spicules, and the possession of long hair-like acerate spicules in the membranes, as it were in substitution, might easily be pronounced to be the same." Some of the figures Waller gives of his „hair-like spicules" indeed resemble very long and slender toxa, such as both Bowerbank and Carter have seen too. As to the absence of sigmata („bihamates") Waller writes

(p. 102) that they are „often sparsely distributed in R. sordida." If we then consider that the author's single specimen measured 6 mm. by 3 mm, („$^1/_4$ in. by $^1/_8$ in.") and was studied in the dried state, we must conclude that R. minima is but a variety of R. sordida, i. e. of Esperella aegagropila.

Topsent gave (1892, a. p. XXI) short descriptions of three new species of Esperella viz. E. hamata, mollis and albicans. Two years afterwards however the author states (1894 e. p. XXXVI) that E. mollis and E. albicans are mere varieties of. E. hamata. The latter is said to differ from E. macilenta „par la longueur exagerée de ses toxes." If we know that, according to Bowerbank himself the toxa of his Hym. macilenta can reach 333 μ., while in Topsent's sponge the largest toxa measure only 265 μ., we fail to find sufficient differences between E. hamata and E. macilenta. Esperella hamata Tops. is therefore nothing else than another variety of E. aegagropila (Johnst.) Tops.

In order to facilitate the reader to judge the above questions of synonymy, we give here a tabular view of the most striking and most valuable characters of the sponges, described as different species, but, according to us to be considered as mere varieties of E. aegagropila. In this tabular view we have only inserted such characters as may be of any specific value, and only those authors who contributed new facts in this respect.

Date.	Name.	Author.	Height.	Colour.	Styles and Tylostyles.	Anisochelae.	Sigmata.	Toxa.
1842	Halich. aegagropila	Johnston	2.5 cm.	earthy brown	(tf) ac. f tr. ac.			
1866	Desmac. aegagropila	Bwk.	2.3 mm.—1.25 cm.	red; brick-red.	(tf) ac. f tr. ac. 260 μ.	22.6 μ	54.8 μ	rare
1874	Esperia aegagropila	Carter				34 μ	84 μ	164 μ
1882	Desmac. aegagrophilus.	Bwk. Norm.	1.25 cm.					
1866	Hymeniac. subclavata.	Bwk.	1.4–1.8 mm.	flesh-red	(tf) ac. f tr. ac.	21.6 μ	54.2 μ	
1866	Hymeniac. floreum	Bwk.	less than 0.5 mm.		(tf) ac. f	37.7 μ	83 μ	
1882	Raphiodesma florcum	Carter						present
1866	Hymeniac. macilenta	Bwk.	1.42 mm.	scarlet	(tf) ac. 273 μ	34 μ	93 μ	333 μ
1871	Carmia macilenta	Carter		red; yellow	(tf) ac. f 305 μ.	48.5 μ	83 μ	27.7-41.6 μ
1874	Desmacid. similaris	Bwk.	coating		tf. ac.	37.7 μ	56 μ	180 μ
1882	Desmacid. similaris	Bwk. Norm.		scarlet				
1874	Raphiodesma sordida	Bwk.	0.95 mm.	orange; dark red.	(tf) ac. (tf) ac. f	33.3 μ	63.6 μ	180 μ
1880	Raphiodesma minima	Waller						
1892	Esperella hamata	Topsent	revêtante	jaunâtre	tf. ac.	33 μ	140 μ	265 μ
1892	Esperella mollis	Topsent		rouge-brique	tf. ac.	30 μ	60 μ	200 μ
1892	Esperella albicans	Topsent		blanche	tf. ac.	33 μ	74 μ	130 μ

The specimens of E. aegagropila which were at our disposal all covered the shells of young oysters. They formed thin crusts, generally not more than 0.5 or 1 mm. thick. This is considerably less than in the specimens of Johnston and Bowerbank. They often covered the shells entirely, growing even over the free borders. If new layers of shell are formed, the sponge immediately covers them. Hence in sections there can be found shell-layers in the middle of the sponge body. Such preparations remind us of sections Cliona. There is however a fundamental difference. In Cliona the portions of shell are actually isolated by the boring of the sponge; in Esperella aegagropila the shell-portions only *seem* to be isolated. In complete series of sections it becomes clear that isolated fragments of shell are not present. We have never observed anything like a boring, and we therefore believe the sponge to be in so far quite harmless to the oysters. We will see that there are still other arguments to be found to consider our sponge harmless. — The colour is bright yellow or orange in the living sponge. In spirit this colour is dissolved at once. By and by the sponge turns greenish in spirit. Taken out of the water the sponges have a slimy appearance. On the surface one often sees with the naked eye branching figures; in the main branches of these figures dark points are visible, giving the impression of pores [Pl. I fig. 1]. By sufficiently magnifying such a place, it becomes evident that these pseudo-apertures are in fact lacunae covered by a membrane in which there are or there are not apertures visible [Pl. I fig. 12]. These apertures are of very different size, according to their state of expansion. We will see that they belong to the excurrent system.

The incurrent apertures, which we will simply call pores as long as it is not settled whether they are stomata or stomions (Vosmaer 1892 p. 242) are a good deal smaller than the apertures mentioned above. They too vary in size; of course they can be quite shut, and then they are not visible. These pores [Pl. I fig. 10] lead into wide lacunae, the subdermal cavities [Pl. I fig. 3]. From here the water passes to other lacunae or wide canals, which ramify and penetrate in the sponge towards the base of the crust, gradually becoming narrower, but still wide enough to communicate with a number of flagellated chambers by means of generally more than one prosopyle. The chambers are sub-spherical and with their wide apopylae they communicate with the excurrent canals. The canal-system is therefore distinctly eurypylous. The canals in which the chambers debouch, unite in order to terminate either into wide cavities [Pl. II fig. 1] or into more or less cylindrical wide canals

[Pl. I fig. 3]. The latter run parallel to the surface of the sponge and give rise to the branching figures, mentioned above and illustrated in fig. 1 on Pl. I. They are covered with the dermis, which is perforated by the exhalant apertures. The two main canals in fig. 1 are the ultimate excurrent canals, and are equivalent to cloacae. They only differ in shape from the cloacae in other sponges. The cloacae are generally more or less cylindrical tubes. In Esperella aegagropila it are gutters. In stead of opening with a wide mouth (osculum) we find the gutter covered with a perforated membrane; the perforations are nothing else than the excurrent apertures. If this be true, these apertures have the morphological value of proctions (Vosmaer 1892 p. 242).

Our specimens of the sponge being so very thin, it is possible to study the anatomy in toto-preparations. It is easy enough to cut out pieces of 4.5 by 2 cm. and to detach these from the shell. Such pieces were stained with picro-carmine, and after dehydration cleared with cedar-oil and mounted in balsam. As the lacunae and canals are very wide and numerous, there is not much left for the tissues. In fact the whole body consists of a network of trabeculae and plates, containing the flagellated chambers. This is best seen in toto-preparations, combined with thick sections [Pl. I figs. 3 and Pl. II fig. 2]. On the whole we thus find an arrangement resembling that of Esperella fibrexilis, described and figured by Wilson (1894). Still, there are certain differences. Wilson states that the „dermal membrane.... is.... found to be everywhere perforated by closely set pores." In our specimens of E. aegagropila the pores are by no means numerous. But this difference is of course of little value, since we know that in every sponge pores are easily shut. Wilson found further that in E. fibrexilis the oscula are „few in number, and are distributed over the surface with entire irregularity. They are not seated on elevations, and are inconspicuous." We find in E. aegagropila that there are plenty of excurrent apertures in the membrane covering the cloacae. It seems to us not improbable that part of the pores of Wilson are in fact excurrent apertures, at least those which are lying next to the „oscula" as e. g. in his figure 6 on Pl. XIV. Sometimes an excurrent canal opens directly [Pl. II fig. 1]. Such exhalant apertures are sometimes a little elevated. But the elevation is little and not visible to the naked eye.

The skeleton of Esperella aegagropila is formed by bundles of tylostyles. The bases of the bundles are found exactly at the base of the sponge-crust. It is perhaps worthy of note that on the places where bundles of tylostyles arise, the underlaying shell is somewhat

depressed [Pl. I fig. 11]. They grow nearly vertically, thus forming with the oyster-shell angles of about 90°. Sometimes the direction is more an oblique one. Each bundle gives off branches, generally at very sharp angles; but, as the bundles follow the trabeculae or the walls of main canals, the angles sometimes become obtuse. Near to the dermis each branch terminates into elegant tufts, the spicula of which project generally beyond the surface of the sponge [Pl. I fig. 3]. As a rule the bundles are not anastomosing; but a few horizontal spicula are sometimes found to unite two bundles. Each bundle consists at its base of about 12 spicula. The bundles are distributed relatively regularly, something like trees in a wood. This comparison is especially true for the walls of the main excurrent canals, which are all lined by bundles. Seen from above — a birds-eye view on toto-preparations — we have the perfect picture of a little wood with lanes. The bundles of spicula then represent the trees, planted regularly along the lanes, while the spaces between are more irregular, exactly as in a wood [Pl. I fig. 4]. In the dermis and through the whole parenchyme are dispersed various skeletal elements: tylostyles, anisochelae, sigmata and toxa. None of these kinds of spicula is very abundant. Bowerbank says of Desmacidon aegagropila that the „dermal membrane (is) spiculous;" of Hymeniacidon subclavata, H. macilenta and Desmacidon similaris he says that it is „abundantly spiculous." On the other side he states of Hym. floreum that it is „sparingly furnished with spicules." We consider these differences simply as variations; perhaps it are individual differences. Bowerbank says himself that the „retentive spicula" of Desmacidon aegagropila are „sometimes few in number, at others remarkably abundant" (1866 p. 352).

The tylostyles possess more or less developed heads, as can be seen on Pl. III fig. 15—23. Generally the head is not much developed and in some specimens we find several transitions to styli. In other specimens, however, the heads are strongly marked out, [Pl. III figs. 21, 22 and 24]. The same variability is observed by previous authors. We have copied the figures of Bowerbank and Carter on Pl. III figs. 1—14. As a rule, the tylostyles (or styles) are slightly fusiform [Pl. III fig. 23].

The sigmata are still more variable, as well in size as in shape. We find small and thin sigmata [Pl. III fig. 40—42], as wel as stout forms [figs. 37 and 39]. In fig. 38 we give an illustration of an intermediate form. Whether there is any relation between the thin small forms and the larger ones, we cannot say; it seems

to us not very probable that there is any. About the relation between thin sigmata and anisochelae we will speak in the next chapter.

The toxa are the least variable in our specimens; but neither size nor shape are wholy constant [Pl. III fig. 50—53].

As to the anisochelae, we find an amount of variations. Still, as is generally the case in Esperella, the most frequent forms are the extremes in size, while the intermediate forms are less abundant. If we look at the illustrations Bowerbank, Carter and Waller give of the anisochelae of the so called species aegagropila, macilenta, sordida etc. [Pl. III fig. 67—78] we certainly see great differences. But if we compare them with our own illlustrations of the anisochelae of E. aegagropila [Pl. III fig. 54—66] it will become obvious that the differences in the figures of the above named authors, are not greater, and do not furnish arguments for distinguishing so many species. It is not easy to make out the exact shape of these spicules, because even the larger forms are comparitively small in E. aegagropila. We give two illustrations in figs. 43 and 82, seen with high power and carefully drawn with the camera. We observe a striking difference in size and shape of the alae and the rostrum. Figures given by other authors are generally on a scale too small to judge them properly. We must therefore not attach too much value to them. Further details about the anisochelae in general are given in the next chapter.

Many authors state to have found in E. aegagropila and other species of this genus, „gemmules". These „gemmules" we found also in our specimens (dredged in September). Wilson studied them in E. fibrexilis and remarked that „the formation of gemmules in large numbers is associated with a certain degeneration of the normal sponge structure" (1894 p. 287). We can confirm this for E. aegagropila. Before the „gemmules" are formed the mass of the parenchyme is a good deal larger than afterwards. The canals and lacunae are very wide near the free surface; but such very wide canals never penetrate deeply into the sponge, as, in ramifying they soon become narrower [Pl. II fig. 1 and 2]. In specimens, or regions of the same specimen, where „gemmules" are formed, the whole tissue is loosened and the canals grow wider. [Pl. I fig. 3]. By-and-bye the flagellated chambers diminish and finally almost disappear. While there is originally a large number of flagellated chambers, these organs are very scanty in regions where „gemmules" develop. [Pl. II fig. 3]. In our specimens we got the impression that the formation of „gemmules" starts at the base

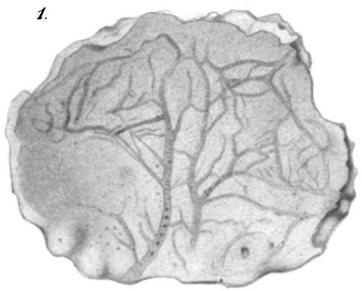
of the crust, gradually proceeding in regions nearer the free surface. The degeneration of the sponge-body follows this course. Even if this process of degeneration has gone as far as in fig. 2 Pl I, we observed that the dermis was quite uninjured, consisting of at hin layer of parenchyme, covered on both sider with pinacocytes. On the other hand we found in specimens without „gemmules" that there is another layer of pinacocytes at he base of the crust, being everywhere into contact with the shell [Pl. II fig. 2 and 3].

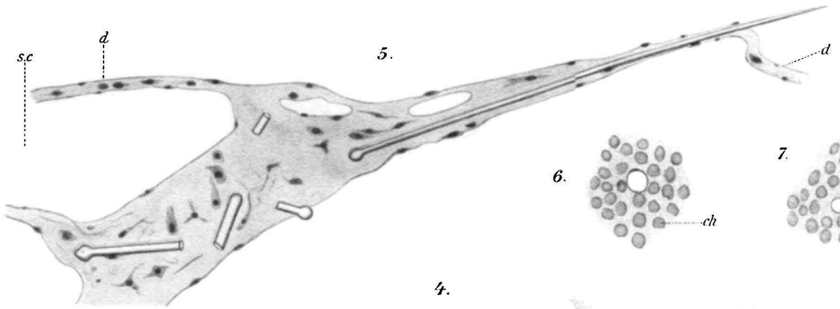
As we do not yet possess a sufficiently complete series of stages of development of the „gemmules" we shall for the present not enter into the question whether Wilson's statements about Esperella fibrexilis are applicable to our sponge. It seems to us, however, settled that, after the formation of gemmules, the mother-sponge entirely degenerates and finally dies of. Herein lies another reason for considering E. aegagropila as harmless to the oysters. The proprietor of the tanks in which we found our sponge told us that the sponge disappeared spontaneously.

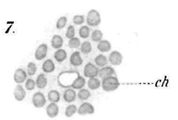
III. ON ANISOCHELAE AND ISOCHELAE.

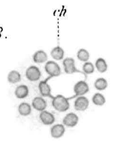
The spicula which are especially characteristic for Esperella and allied genera, belong to the „anchorates" of Bowerbank (1858 p. 303). Schmidt called these anchorates „Haken" or „Doppelhaken" (1862 p. 9), those of Esperella „hakenförmigen oder pantoffelförmigen Körperchen" (1862 p. 53). Kölliker calls them „Anker" or „Doppelanker" (1864 p. 56). But Schmidt uses the name „Haken" also for the well-known C- or S-shaped spicula, and Kölliker employes the term „Anker" likewise in two significations. It was therefore a good plan of Ridley and Dendy to propose a new name, viz. *chelae* (1887 p. XIII); this word is now generally accepted, with exception of Levinsen who makes a fundamental distinction between „chelae" and „anchorae" (1894 p. 16). We shall see in how far this distinction is right, but it seems to us at any rate very unfortunate to divide the chelae of Ridley and Dendy, which are equal to the anchorates of Bowerbank into „chelae" and „anchorae". This can but create confusion. We take the term chelae in the general sense, as Ridley and Dendy proposed.

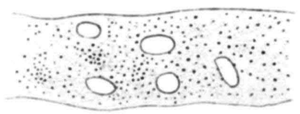
Bowerbank (1858 p. 303) makes two primary divisions of his anchorates — equi-anchorates, „when both terminations are produced to an equal extent", and inequi-anchorates, „when the distal termination is largely and fully developed, while the proximal one is, comparatively, produced to a very limited extent". According to the shape of the terminations Bowerbank calls the anchorates bidentate, tridentate or palmate. He remarks however that these „forms are in truth but different degrees of development of the normal palmate form". We need not take into consideration the form which Bowerbank calls „bidentate", since Carter (1871 p. 277) suggested,

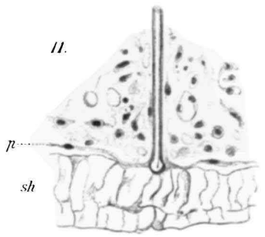


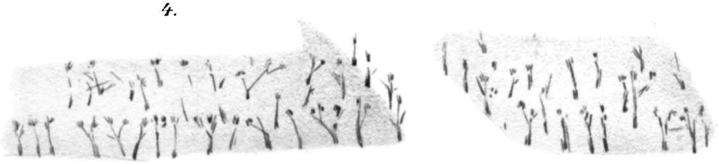


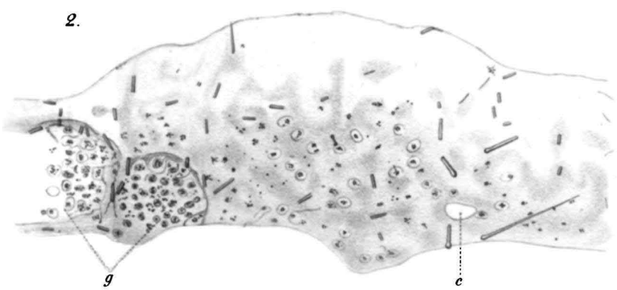


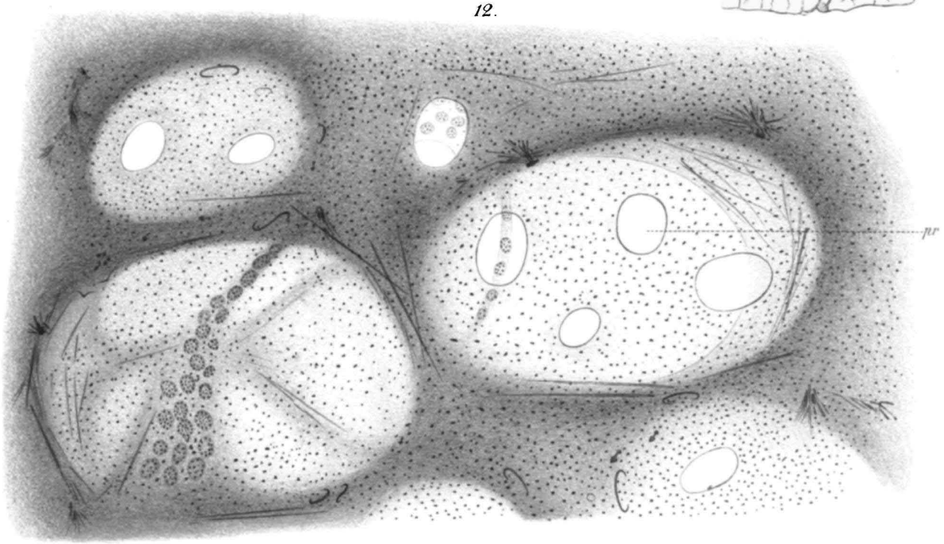












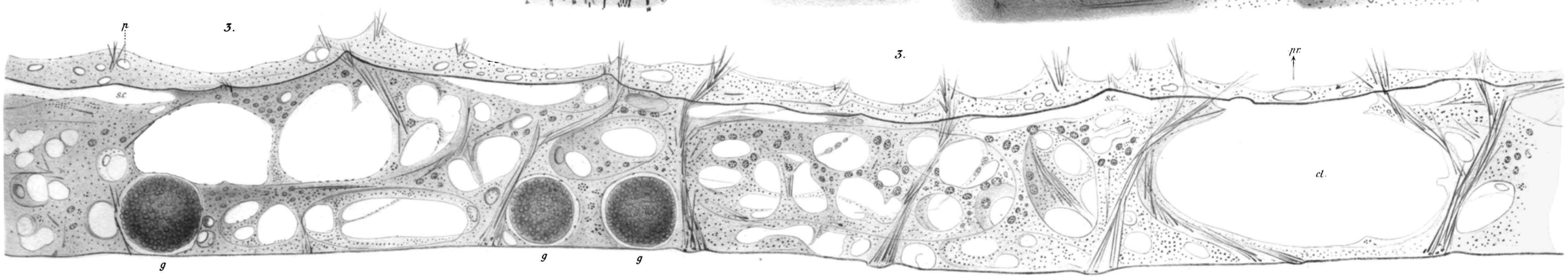


Fig 1 Hanau, cet. Vosmaer fec.
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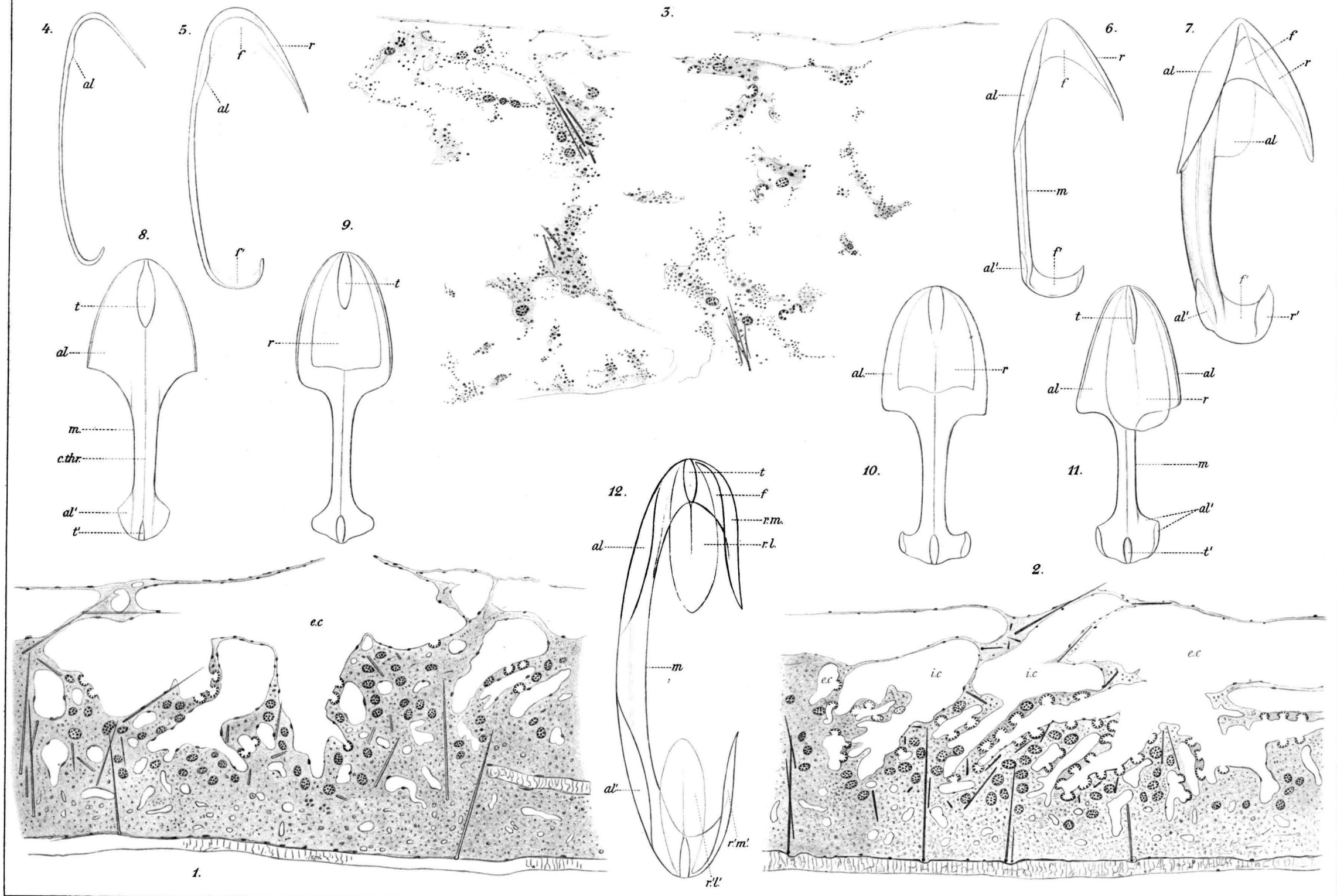

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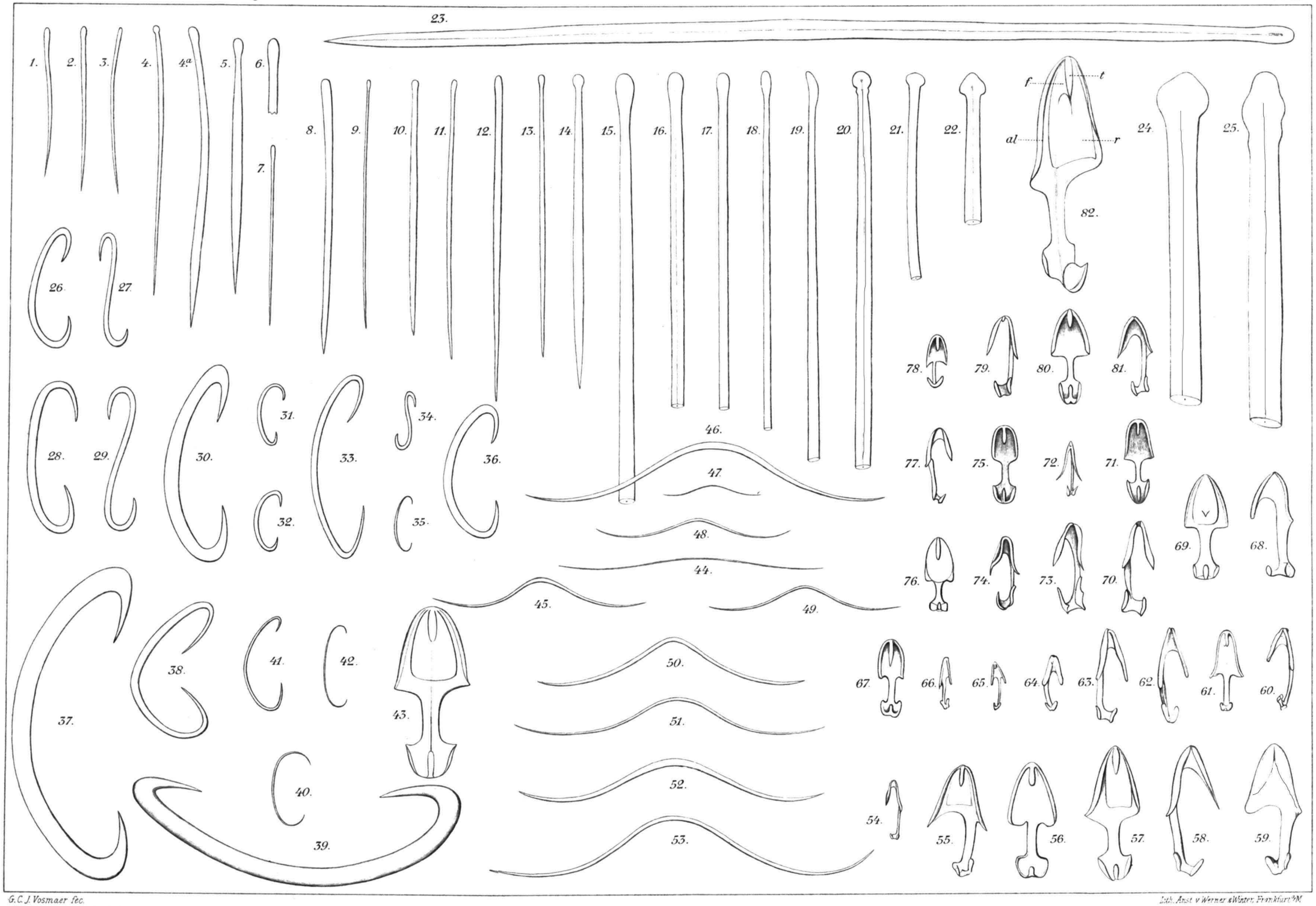

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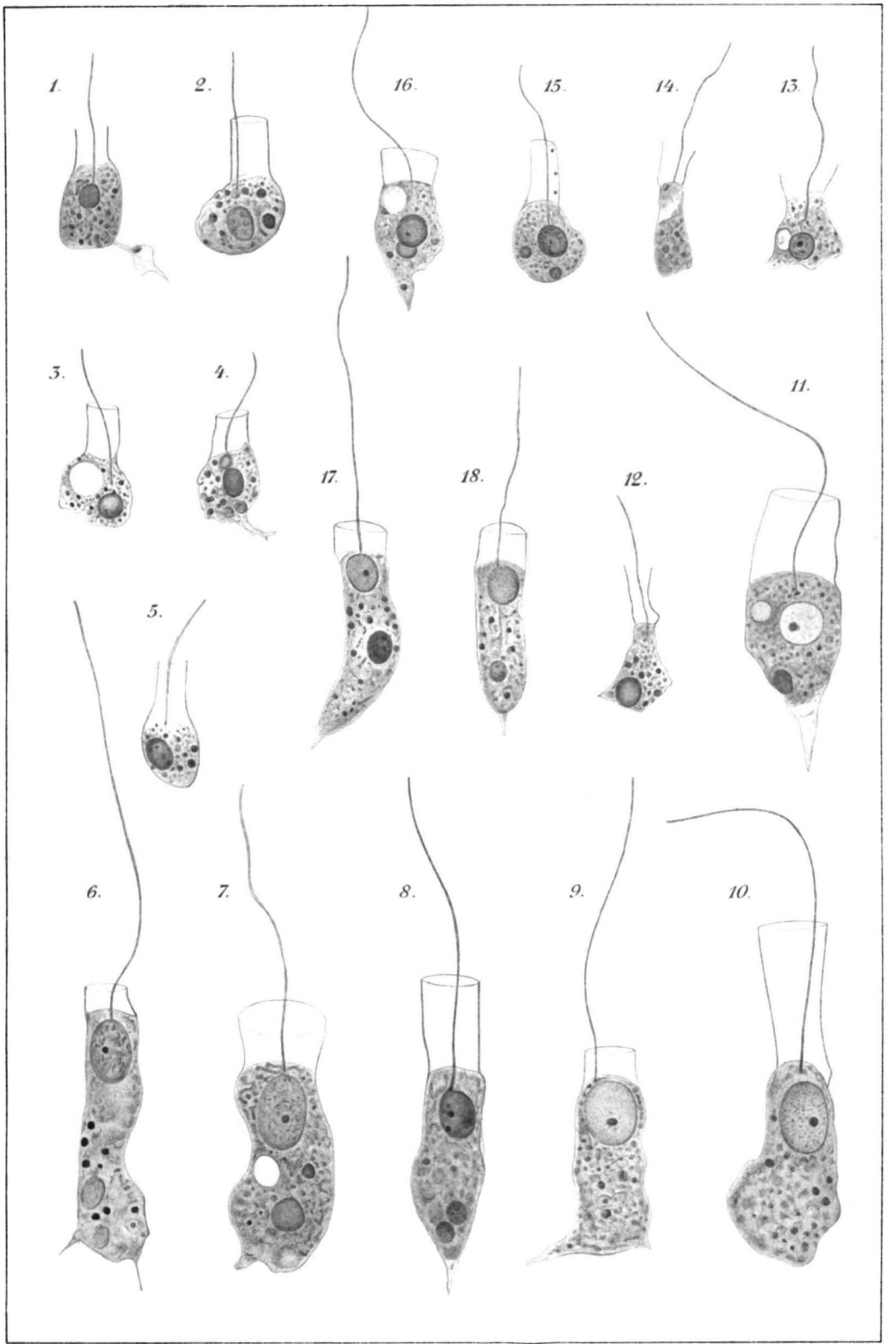

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VERHAND. KON. AKAD. V. WETENSCH. (2e Sectie) DL. VI.

and Ridley and Dendy (1887 p. XIII) further elucidated that this „bidentate" form does not in reality exist. The latter authors consider the tridentate and palmate forms as two modifications of the same principle. They call the recurved processus of the shaft „the teeth, or, when they are broad and much expanded, the palms" (1887 p. XIX). Against this view Levinsen (1894 p. 16) objects. „Inter spicula ab autoribus recentioribus nomine chelarum designata. . . formas duas bene distinctas adhuc commixtas discernere possumus: unidentatas (chelas mihi) et pluridentatas (anchoras mihi)". The fundamental difference is that in the „chelae" the axial part remains single, while in the „anchorae" it splits up into three (or more) parts. If this be true the „chelae" are monaxons, the „anchorae" tetraxons.

Before we can discuss this question, we shall have to consider first such spicula which, according to Levinsen as well as to others, possess only one axis. Such spicula are the well-known anisochelae of Esperella. Bowerbank has figured them very well indeed, but his explanations are wrong. Oscar Schmidt was the first to observe that the medial recurved process has thin *broad* expansions, united to the axis. „Sie haben einen stielförmigen Mittelkörper, welcher in zwei Endplatten übergeht. Die am oberen oder Handgriffende des Stieles ist kleiner, ihre Seitentheile sind wenig umgebogen und sie ist nur zu einem kurzen Haken zurückgekrümmt. Die untere Endplatte hat die Form eines Grabscheites, wenn man sie von oben betrachtet; im Uebrigen wiederholen sich an ihr die Bildungen, wie am anderen Ende, was am klarsten bei Esperia massa hervortritt. Die Platte, welche den Widerhaken bildet, und deren Contouren man in der Ansicht von oben oft kaum bemerkt, ist mit der untern Platte durch eine Querwand verbunden, die an dem oberen Ende als eine blosse Krümmung des Stielkörpers erscheint und nur bei Esperia massa auch hier mehr ausgeprägt ist" (1862 p. 53). Thus, according to Schmidt, the shaft terminates at both ends into a plate or blade, and these plates recurve. According to Carter, however, we have to distinguish not two plate-like parts but three, viz. a medial one and two lateral ones. „With reference to the anchorates in detail, it will be observed that they have respectively three flukes or arms . . ., that the two lateral ones are winged on to the shaft . . ., and that the central one is expanded into a petaloid form . . . . supported inferiorly by a falcate web-like septum which connects the median line of the middle fluke with this end of the shaft. A similar condition exists in the foot; but here the alae are united to the sides of the middle fluke, by which the

space between the falcate septum and the alae, on either side, is converted into holes like nostrils" (1871 p. 277). As far as we can understand Levinsen [1]), this author agrees with Carter in the description of the anisochelae of Esperella. As to the terminology Levinsen calls „alae" what Carter calls „lateral flukes", while the „middle fluke" of Carter is named „rostrum" by Levinsen. Sollas represents the shape as follows: — „Take a hen's egg as the model of a scleroblast, draw round it a broad meridional band, interrupted only on one side, for 30° above and below the equator; this will represent a truly C-shaped spicule". The back of the C he calls „tropis", the points „prorae". From this shape the various chelae can be derived. „Now broaden out the prora on the eggshell into oval lobes.... and from each pole draw a lobe midway between the prora and the tropis.... and a common form of anchorate.... results (1887 p. 417). Wilson arrived at a similar interpretation. He states (1894 p. 284) „that the blade of the shovel is not flat, but is a figure of three dimensions". Obviously the author was unaware of the fact that this statement was not in need of a proof. But he proceeds — „if an oval body should be divided by a transverse plane, passing through a point on the equator and a point on the opposite surface somewhat nearer one of the poles, two parts would be obtained, of which the smaller would roughly correspond in shape with the blade of the shovel... The wall of the oval is thickened all round.... the thickening being greatest near the apex and gradually decreasing towards the equator. A special thickening produces a tooth.... on the ventral surface of the blade. The handle of the shovel is directly continuous with the dorsal surface of the blade, and its apex is divided into three small sharp-pointed lobes, one ventral, two lateral".

We have tried to settle the question by carefully observing the anisochelae of several species of Esperella with homog. imm., and by making wax-models after our observations.

The anisochelae originates from a C-shaped spicule, as we will show afterwards. Let us call the main part of the C manubrium and the recurved hooks hami, (Bowerbank 1858 p. 304). Each hamus very soon grows out into a very thin, slightly curved blade, called by Levinsen „*rostrum*". The extremities of the manubrium produce lateral wing-like expansions, *alae* (Levinsen 1886 p. 335).

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[1]) Both papers of Levinsen are unfortunately written in the Danish language; there is however in the paper from 1894 a short latin summary.

These alae follow the curvature of the manubrium; but, in growing out laterally, they also curve towards the rostrum. This curvature is not always developed to an equal extent. It varies in different species; even in one and the same specimen it is not always the same. It is however always stronger than the curvature of the rostrum. In Esperella syrinx the alae are slightly curved at their origin; the blade here makes an angle of about 70° with the median plane of that part of the manubrium. At some distance from the manubrium they bend rather abruptly. The transverse section of an ala is therefore generally not a part of a circle. In the concavity formed by the extremity of the manubrium and the hamus (or origin of the rostrum) a falcate blade is visible, thus strengthening buttress-like the connection between the rostrum and the manubrium. Carter has named this piece „*falx*". Where it is connected with the manubrium, it is thicker than where it is united with the hamus or rostrum. The falx is a very thin plate at its free concave border. It gradually increases in thickness towards the place where it is united with the manubrium and the rostrum. All these details of course can be best seen at the larger part of the anisochela. But there is no fundamental difference between the larger (distal) and the smaller (proximal) portion of the spiculum. Carter (1871 p. 277) says that the alae of the proximal part „are united to the sides of the middle fluke, by which the space between the falcate septum and the alae, on either side, is converted into holes like nostrils". We could not find this in Esperella aegagropila, nor in E. syrinx.

It is obvious that in looking at such a spiculum from the ventral or form the dorsal side, one will see the falx in optical transverse section. It is this what Carter called „tubercle". Wilson states (1894 p. 284), as we have seen, that the „wall of the oval", i. e. the alae and the rostrum, is thickened all round, „the thickening being greatest near the apex and gradually decreasing towards the equator". According to us this is not so. On the contrary we are of opinion that the alae are only thickened along the manubrium, but for the rest posses pretty well the same thickness. The „special thickening (which) produces a tooth.... on the ventral surface of the blade is nothing else than the tubercle of Carter, i. e. an optical illusion. Levinsen (1894 p. 16) quite correctly observed: — „Axis dentis cum axi manubrii lamina horizontali compressa (falci Carter) conjuncta est quae tamen crassitudine increscit ubi manubrium et dentem attingit (tuberculum)." According to Wilson's description is the rostrum shorter than the alae. It is possible that

this is so in Esperella fibrexilis, but it is surely not so in E. syrinx and in all the other species we have observed. The rostrum often *seems* to be shorter, but after careful examination this always turned out to be only an effect of perspective.

Having thus described the adult anisochela of Esperella syrinx, let us now consider the way how it developes from a C-shaped spiculum. Bowerbank has already given us an excellent description (1858 p. 304—305; reprinted 1864 p. 47—48). „The first condition in which we detect them is in the form of an exceedingly slender and elongated simple bihamate spiculum, which is readily distinguished from the true bihamate form by the straightness of the shaft, the comparative shortness of the hami, and the obtuseness of their terminations.... We next find the same form increased in strength, and with slight lateral fimbriae near each end of the shaft at the commencement of the hami.... In a more advanced state we find a regularly curved extension of the fimbriae, slightly so at one extremity of the shaft, and considerably so at the other; and as the development progresses, the curves of the fimbriae are extended in an outward direction, and become angular; the extremities of the hami expand laterally and assume a foliated appearance, as seen in the distal or larger end especially...." In Esperella syrinx we observed the same mode of development. The youngest stage we found in our preparations was a very thin rod, recurved at both ends, in fact a C-shaped spiculum (Pl. II fig. 4). The diameter of the manubrium and of the hami is considerably less than it is in the full-grown spiculum, but their respective lengths are pretty well equal to those of the adult spicules. It must be remarked at once that full-grown anisochelae are by no means equal in length. Generally we find in Esperellae anisochelae of a certain size and in addition to these another, much smaller set. This great difference in size is not what we consider for the present. We only mean such differences as are overlooked in observing a preparation with a low power. If we make camera-drawings of such spicula seen with a power of 1000 or more, we discover that there exists a certain variation in size. We are therefore not allowed to draw the conclusion that a spiculum as figured on Plate II fig. 5 originated from a shorter C-shaped spiculum, e. g. as figured in fig. 4. It seems to us more probable that the length of the manubrium i. e. the distance between the curved ends remains the same. In other terms that the length of an anisochela in the stage of fig. 4 will nearly be the length of the full-grown specimen. Not so with regard to the diameter of the manubrium. As we have no reason to admit a growth by intus-

susception, the increase must come by apposition. Now there is no hindrance to this with respect to the diameter of the manubrium. In fact we see that in such young stages as in fig. 4 the diameter both of the manubrium and of the hami is a good deal smaller than in the next stages, and still more so than in the full-grown spicula. It is worthy of note that the diameter of the manubrium of adult anisochelae is less subject to variation than its length is. This follows immediately from our supposition about the growth of the spiculum. At a very early period the falces appear (fig. 5) and simultaneously the hami flatten in order to form rostra; finally we observe at this stage the beginning of the alae. Sometimes however we met with spicula in which the falces could not yet be seen, while the alae at the distal part were unmistakably present as very small wings. This was e. g. the case in the spiculum fig. 4. The manubrium now thickens, while the alae, the rostra and the falces grow larger. These certainly grow thicker too, but they remain plates, and the rostra are always thinner than the alae or falces. Ridley and Dendy, Levinsen and Wilson agree with Bowerbank that the anisochelae originate from C-shaped spicula. The first named authors herewith justify their placing the chelae in the group of the „hooked forms." Not only can we confirm this but we can give a new strong argument in favour of it. This lies in the fact that the anisochelae of Esperella syrinx are twisted. Certainly they are not twisted so strongly as many sigmata, but a slight torsion we often unmistakably observed. In fig. 11 e. g. the tuberculum of the proximal part was lying exactly in the direction of the axis of the manubrium. The rostrum of the distal part was not lying quite symmetrically. The falx near to the rostrum was in one plane, that near to the manubrium in another, as could plainly be seen in turning up and down the micrometer screw. We have therefore the right to say that chelae not only can be derived from spicula which have the shape of C, but indeed from spicula known as sigmata.

We have seen that Levinsen finds a fundamental difference between such spicula as he calls „chelae" and such as he calls „anchorae". On page 16 of his paper from 1894 he writes: — „In chelis dens singulus in anchoris autem dentes 3—7 inveniuntur. Carter, Ridley et Dendy igitur alas manubrii chelarum, quae modo expansiones laterales manubrii sunt et quibus pars axialis, falx et tuberculum desunt cum dentibus lateralibus anchorarum tridentarum injuria comparant". On Plate II fig. 12 we have given an illustration of an isochela which Levinsen certainly will consider as

„anchora". It shows, in addition to small alae, three recurved parts at each end of the manubrium. Each of these processus are petaloid and are connected with the end of the manubrium by distinct falces. It seems to us, however, not necessary to explain this by accepting that the manubrium splits up into three recurved axes. If this were true, the spiculum should be a tetraxon and the sponges possessing such spicules could certainly not remain in the same genus, or even family, with others in which the axis remains single. Indeed this would create rather a revolution in our systematics. But Levinsen has not given the proof that his „dentes" are really axial parts of the spiculum. This proof would be given if in the „dentes" were found ramifications of the centralthread or so-called axial canal. As long as this is not stated to be present and we can explain the shape of the spiculum in a simpler way, we prefer to do the latter. We believe that spicula such as those of fig. 12 can be as well explained in the following manner. The true alae are very insignificant; the rostrum on the contrary is strongly developed. In the anisochelae of Esperella syrinx the greatest breadth of the rostrum was less than that of the alae taken together. In the isochelae like that of Myxilla barentsi it is quite the reverse. Now suppose that the rostral plate instead of remaining simple is cut out, so as to form a figure like a leaf with incisures, and suppose that the three (or more) parts become each strengthened by a falx, we have then before us the spiculum in optima forma. As a rule the rostra are very thin; it is therefore not so easy to fix their outline with certainty. But it would be worth while to especially study the rostra of various sponges, in order to see in how far transitions can be shown to exist between such forms as in Esperella syrinx and such as in Myxilla barentsi. We have distinctly seen in Esperella syrinx that in one and the same specimen the shape is not always absolutely the same (cf. fig. 9, 10, 11). We sometimes in fact observed the first indications of incisions (fig. 9 and 10).

IV. THE CHOANOCYTES.

In order to study the structure of the choanocytes the best way is, according to our experience, to bring a small piece of the sponge into 1% osmic acid for an hour, after which it is macerated in destilled water. Generally the cells can be easily isolated after 24 hours. But sponges, treated with osmic acid can remain in water for weeks or even months, without any apparent change of the cells. If to the drop of water in which the cells are isolated for microscopical research, a trace of methylene blue be added, the whole cell is stained; the nucleus generally darker than the cytoplasma, but often not as dark as enclosed granules. The collar and the flagellum always stain fainter.

In 1893 we have figured choanocytes of Spongilla lacustris and Halichondria panicea, treated in the above way. In this paper we give illustrations of the choanocytes of Esperella aegagropila, Cliona celata, Sycon ciliatum and Leucosolenia [bothryoides?] [Pl. IV]. Dendy has quite correctly observed (1891 p. 8) that Haeckel's statements about the uniformity in structure of the choanocytes are entirely wrong. Indeed there is rather a great diversity in appearance. Sollas attached so much value to the fact that in Calcaria the choanocytes are larger than in other sponges, that he divided (1886 p. 13) the Porifera in two primary classes, Megamastictora and Micromastictora, according to the relative size of the collared cells. But apart from the size, we observed certain differences between the choanocytes of Calcaria and those of Incalcaria. Whereas the choanocytes of Sycon and Leucosolenia possess as a rule an elongated cylindrical shape, we found that in the choanocytes of all the other sponges we investigated length and breadth were less different. We noticed however, that within one and the same species neither size nor shape were

quite constant. This is especially striking in Cliona celata [Pl. IV, fig. 12—16]. The base of the choanocytes is sometimes very irregular and can terminate in one or more pointed processus. — The cytoplasma makes the impression to be coarsely granulated. In almost every choanocyte we found enclosed granules of various size, staining deeply with methylene blue or sometimes with osmic acid. These granules are probably for the greater part taken in from the cavity of the flagellated chambers. Sometimes we saw bacteria of the same shape as those which were lying between the isolated cells. In Spongilla lacustris we found granules, which were green during life, and dark olive-coloured in osmic preparations. We could not settle whether they really belong to the choanocyte like the well-known pigments in the choanocytes of Oscarella, Aplysina and so many others. — We generally found vacuoles in the protoplasma of the collared cells; but neither the quantity, nor the size, nor the position were always the same. In Spongilla lacustris we found almost always a vacuole near the base of the collar, but its presence was nevertheless not constant. [Cf. our paper on Sollas's membrane, 1893 Pl. II figs. 1—6].

The nucleus is in the species we have investigated spherical or ellipsoidical. The relative position of the nucleus seems rather constant in the same species. In Spongilla lacustris it lies always near the base of the cell; in Sycon ciliatum and Leucosolenia [botryoides?] always near the base of the collar [Pl. IV, figs. 6—11, 17—18]. In Cliona celata and Esperella aegagropila the position of the nucleus is less constant [Pl. IV fig. 12—16 and 1—5], but more often near the base of the cell, than near the base of the collar. The greatest variability in position we found in Halichondria panicea [Cf. our paper 1893, Pl. II fig. 7—8]. A nucleolus is generally visible as a dark stained spot. The structure of the nucleus we could not make out; this can not surprise in fixations with osmic acid only.

The flagellum is a thin, perfectly cylindrical thread, which in our sponges could be traced partly within the cytoplasma, as is shown for cilia in ciliated cells by Engelmann. In the figures we have given in 1893, this is only drawn in the isolated choanocyte of Halichondria panicea, and not in those of Spongilla lacustris. We have since convinced ourselves by the study of a large number of choanocytes of this sponge, that the flagellum here likewise enters the cytoplasma. As a rule it can be followed till near the nucleus [Pl. IV]. The deeper the nucleus lies in the cell, the farther can the flagellum be traced; it has in the cell and beyond it the same diameter. We did not succeed in determining the exact place where

the thread terminates in the granular cytoplasma. We can therefore not say with Bidder that „the flagellum is firmly and intimately connected with the nuclear membrane" 1895 (p. 20).

The length of the flagellum varies considerably in different sponges, but in the same species the variations are comparatively small. [Cf. tabular view on p. 42]. In Sycon ciliatum and Leucosolenia the flagella are much larger than in the siliceous sponges we studied in this respect. On the other hand in Sycon and Leucosolenia the length of the collar compared with that of the whole cell, is shorter than in the other sponges. Very frequently we found such extremely low collars as in figs. 6 and 9. Extremely high collars as in figs. 10 and 11 were rare in Sycon, and never found in Leucosolenia, whereas in Spongilla, Halichondria and Esperella, as a rule. the length of the collar by far exceeded the diameter. The shape is generally more or less cylindrical but not unfrequently we found the diameter at the distal part larger than at the proximal part; and still such cells made the impression of being perfectly well preserved. In cells which had been for a long time in water, we found folds, generally in longitudinal direction. In preparations stained with methylene blue, such folds appeared as blue stripes. We are bound to say that we believe it possible that such stripes did mislead Bidder, where he described in Sycon compressum the collar as made up of parallel rods (1895 p. 14). We have never seen such a structure of the collar in the very best preserved cells. Bidder found, to our great satisfaction, that our method for making paraffine-sections could give good results. But he has overlooked, we believe, that where for certain questions it is necessary to make sections, it is for others better to use other methods. We wrote in 1893 (p. 54): — „Imbedding in paraffin, cutting and all what is annex, even if done with the utmost care, does harm something." We are still convinced of the truth of this statement. Since Bidder has formed his opinion on the structure of the collar only from paraffine sections, and has not isolated them by maceration, we find no sufficient support for the opinion that the collar should not be a hyaline, very thin membrane.

As to the „iris" and „pupil" of Bidder (1895 p. 19) we regret to be obliged to say that we consider this likewise as an artefact. We never observed such a contrivance in our preparations. The English spongiologist draws attention to the ring we have figured in the collars of Spongilla [1893, Pl. II fig. 5 and 6]. We have often seen this ring, but only in Spongilla. In spite of much trouble we have given ourselves to explain such figures, we did not suc-

ceed. The thin line, which was always visible as a circle arround the collar, seemed to us too regular to consider it as a transverse fold. We have considered the possibility that the cytoplasma might have retracted, and left a remnant, but we failed in finding reasonable arguments in favour of this view. Certainly it is not the optical section of a diaphragm, as Bidder suggests.

We have seen in the first chapter that some authors are of opinion that the choanocytes are able to retract the flagellum and the collar, or that they can lose these organs completely in order to be transformed into amoeboid cells. But in our preparations we have never met with uninjured cells which could possibly be considered as intermediate stages between a normal choanocyte and a normal cell of the parenchyme.

Sizes of choanocytes. Measures given in μ.

Name.	Specimen.	Height.		Total.	Breadth.		Length of flagell.	Size of nucleus.
		body.	collar.		body.	collar.		
Sycon ciliatum.	α	20	5	25	10	6.9	40	6.9 × 4.7
" "	β	21.9	9	30.9	6.9	5	40	4.7 × 4.1
" "	γ	19	13.7	32.7	10.6	5	37.5	6.9 × 5
" "	δ	17.5	3.1	20.6	7.5	5	41.3	6.3 × 5
" "	ε	18.8	8.8	27.6	9.4	8.1	41	4.2 × 4.2
" "	ζ	24.4	2.5	26.9	6.9	5	44	6.8 × 3.7
" "	average	20.3	7.0	27.3	8.55	5.5	40.6	6 × 4.5
Leucosolenia [botryoides?]	α	17.5	3.75	21.25	5	5	20	3.7 × 3.1
"	β	19.9	3.1	23	5	5	31	3.75 × 3.1
"	average	18.7	3.43	22.13	5	5	25.5	3.7 × 3.1
Esperella aegagropila.	α	8.1	4.1	12.2	6.3	3.4	11.2	2.2 × 1.8
" "	β	6.2	3.75	9.95	6.2	3.75	11.2	
" "	γ	7.5	6.2	13.7	7	3.75	12.5	
" "	δ	6.2	5.3	11.5	5.3	4.1	13.1	
" "	ε	6.2	5	11.2	6.3	3.1	11.2	
" "	average	6.9	4.9	11.7	6.2	3.6	11.8	
Cliona celata.	α	7.4	3.1	10.5	6.2	3.75	16.2	2.5 × 2.5
" "	β	8.75	5.6	14.35	5.6	2.2	12.4	2.2 × 2.2
" "	γ	8.7	3.75	12.45	3.75	2.5	15	
" "	δ	7.5	5.6	13.1	6.3	3.1	14.3	
" "	ε	11.2	3.1	14.3	6.2	5	22	
" "	average	8.7	4.2	12.9	5.6	3.3	16	

Technical Note.

If we are convinced, that for studying histiological details of the sponge-cells, the best method is to properly isolate the cells in the way we have described, there remain nevertheless several questions which can only be solved by making thin sections. The spicula are herefore often a great obstacle. We decalcified calcareous sponges after fixation and hardening in alcohol (with dialisator!), in an alcoholic solution of picric acid. We can recommend this method. The siliceous sponges were always cut with the spicula [1]), and it is not so difficult to get series of 5 μ., without too much injuring the tissues. There is however another difficulty, and this is that the great quantity of pieces of spicula prevent the paraffine sections of sticking properly to the glass. In bringing the sections from alcohol into water, they often get loose from the slide [2]). We can therefore recommend the following trick. The paraffine sections are stretched on tepid water and then brought on the cover-glass or on the slide. After having been *thoroughly dried* a drop of a very weak solution of traumaticine is poured over it and the preparation is again dried. The chloroforme of the traumaticine dissolves pretty well the paraffine and extremely minute dots of getah-percha are covering here and there the section, enough to fix it, but not too much to prevent staining — at least if one has not used a too concentrated solution and has poured off the superfluous fluid. In order to dissolve the last traces of the paraffine the preparation is treated with petroleum-ether. For the rest the preparation is treated in the usual way.

The only drawback of this trick is, that the preparations cannot very well be mounted in water or glycerine, because the dots of getah-percha are in that case inconvenient. In Canada balsam, however, they completely disappear.

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[1]) We could no more make use of the methods recently published by Rousseau.

[2]) Notwithstanding Bidder's remark we consider „staining on the slide" a very valuable method.

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Explanation of the Plates.

All the figures are drawn with a camera of Abbe-Zeiss. We made use of Zeiss new apochromatic lenses 16,0; 4,0 and oil-imm. 3—1,40; eye-pieces 4, 6 and 12.

Plate I.

Fig. 1—5. Esperella aegagropila.

1. Surface view; spirit. Natural size.
2. Section at right angles to the surface. At the left hand side two „gemmules" (*g*). The flagellated chambers have disappeared; one canal (*c*) is still provided with pinacocytes. On the free surface are likewise pinacocytes present. × 140.
3. Vertical section through a portion of the specimen drawn in fig. 1. The drawning is partly done with the camera, partly it is a combined figure from a section and a toto-preparation. *p.* pores; *s. c.* subdermal cavity; *g*, „gemmule"; *pr.* proction; *cl.* cloaca. × 140.
4. Birds-eye view of a portion with main excurrent canals, showing the arrangement of the bundles of tylostyles. × 16.
5. Transverse section of the dermis (*d*), covered on both sides with pinacocytes. A tylostyle is projecting beyond the surface. *s. c.* subdermal cavity. [Cf. fig. 2 on Pl. II, from which it is a part.] × 530.

Fig. 6—9. Pores of Leucosolenia.

6—8. Seen from the cloacal side. In figs. 6 and 7 more or less contracted, in fig. 8 expanded. Some of the choanocytes overlap the entrance; *ch* nuclei of the choanocytes. × 530.

9. Seen from the dermal side; the larger opening is on the cloacal side. × 530.

Fig. 10—12. Esperella aegagropila.

10. Surface view of the dermis with pores. × 140.
11. Section of basal portion, showing a layer of pinacocytes (*p*), covering the oyster-shell (*sh*). × 530.
12. Surface view of a portion of the membrane covering a cloaca, with several proctions (*pr*). Under the dermis trabeculae with flagellated chambers are visible. In the dermis tylostyles, sigmata and anisochelae. × 140.

Plate II.

Fig. 1—3. Esperella aegagropila.

1. Vertical section through normal crust; *e. c.* excurrent canal. × 140.
2. Id. *e. c.* excurrent canals; *i. c.* incurrent canals. × 140.
3. Vertical section through a degenerating specimen; a few flagellated chambers are left; the canals are wide lacunae without epithelium. The dermis intact. × 140.

Fig. 4—11 Anisochelae of Esperella syrinx.

4. Young stage of development (sigma-stage). The alae (*al*) begin to appear, side view. × 1600.
5. Older stage; *r.* rostrum; *f. f'* falces; *al.* ala. Side view. × 1600.
6. Still older stage. The manubrium is thicker. Central thread conspicuous. The alae of the proximal part appear (*al'*). Side view. × 1600.
7. Fullgrown anisochela. Letters as in fig. 4—6. Side view. × 1600.
8. Young anisochela. No rostrum visible, probably because of extreme thinness. *t.* tuberculum; *al.* ala; *m.* manubrium; *c. thr.* central thread; *al'.* ala of the proximal part. Ventral view. × 1600.
9. Another specimen at about the same stage of development. It corresponds to fig. 6. Ventral view. × 1600.
10. More advanced stage. Dorsal view. × 1600.
11. Nearly fullgrown specimen. Letters as in fig. 8. Ventral view. × 1600.

Fig. 12. Myxilla barentsi Vosm. Side view of one of the large isochelae *al.* ala; *t.* tuberculum (= optical section of the falx of one of the lateral blades of the rostrum); *f.* falx, *r. m.* median blade of rostrum; *r. l.* one of the

lateral blades of the rostrum. (Only one lateral blade is figured in order not to obscure the drawing). *m.* manubrium. × 1600.

Plate III.

Fig. 1—3. Halichondria aegagropila. After Johnston (1842).
„ 4—4*a*. Desmacidon aegagropila, × 250. After Bowerbank (1874).
„ 5. Raphiodesma minima, × 200. After Waller (1880).
„ 6. Carmia macilenta, × 500. After Carter (1871).
„ 7. Hymeniacidon macilenta, × 150. After Bowerbank (1874).
„ 8—9. Hymeniacidon subclavata, × 250. After Bowerbank (1874).
„ 10—11. Raphiodesma floreum, × 250. After Bowerbank (1874).
„ 12. Desmacidon similaris, × 250. After Bowerbank (1874).
„ 13—14. Raphiodesma sordida, × 250. After Bowerbank (1874).
„ 15—22. Esperella aegagropila, × 1080.
[15—18 specimen α; 19 specim. β; 20—22 specim. γ; 21 specim. δ.]
„ 24—25. Esperella aegagropila, × 1600. [specim. ε].
„ 26—27. Desmacidon aegagropila, × 530. After Bowerbank (1874).
„ 28. Carmia macilenta, × 500. After Carter (1871).
„ 29. Raphiodesma sordida, × 530. After Bowerbank (1874).
„ 30. Raphiodesma floreum, × 530. After Bowerbank (1874).
„ 31—32. Hymeniacidon macilenta, × 150. After Bowerbank (1874).
„ 33. Esperia aegagropila, × 500. After Carter (1874 *a*).
„ 34—35. Desmacidon similaris, × 250. After Bowerbank (1874).
„ 36. Hymeniacidon subclavata, × 530. After Bowerbank (1874).
„ 37—42. Esperella aegagropila, × 1080.
[37 specim. ζ; 38, 41 specim. α; 39, 40, 42 specim. β.]
„ 43. Esperella aegagropila, specim. β. × 1400.
„ 44. Rahiodesma minima, × 200. After Waller (1880).
„ 45. Hymeniacidon macilenta, × 150. After Bowerbank (1874).
„ 46. Esperia aegagropila, × 500. After Carter (1874 a).
„ 47. Carmia macilenta, × 500. After Carter (1871).
„ 48. Desmacidon similaris, × 250. After Bowerbank (1874).
„ 49. Raphiodesma sordida, × 250. After Bowerbank (1874).

Fig. 50—66. Esperella aegagropila, × 1080.

„ [50, 59, 62, 64, 65 and 66 specim. δ; 51, 52 specim. η; 53, 56 and 60 specim. α; 54, 57, 58, 61 and 63 specim. β; 55 specim. ζ].

„ 67. Raphiodesma minima, × 333. After Waller (1880).

„ 68—69. Carmia macilenta, × 500. After Carter (1871).

„ 70—71. Desmacidon similaris, × 530. After Bowerbank (1874).

„ 72—73. Raphiodesma sordida, × 530. After Bowerbank (1874).

„ 74—75. Hymeniacidon macilenta, × 530. After Bowerbank (1874).

„ 76—77. Esperia aegagropila, × 500. After Carter (1874 a).

„ 78. Desmacidon aegagropila, × 530. After Bowerbank (1874).

„ 79. Hymeniacidon subclavata, × 530. After Bowerbank (1874).

„ 80—81. Raphiodesma floreum, × 530. After Bowerbank (1874).

„ 82. Esperella aegagropila, specim β. × 1400.

Plate IV.

Fig. 1—5. Choanocytes of Esperella aegagropila. Osmic acid 1%, water, methylen blue. × 1600.

„ 6—11. Choanocytes of Sycon ciliatum. Osmic acid, water. × 1600.
6. Methylen blue; mounted in acetas kalicus.
7, 9, 10, 11. Methylen blue; mounted in water.
8. Saffranine; mounted in water.

„ 12—16. Choanocytes of Cliona celata. Osmic acid, water. × 1600.

„ 17—18. Choanocytes of Leucosolenia (botryoides?). Osmic acid; water; methylen blue. × 1600.

(30 Augustus 1898).