

Studies on Sponges.

By

Dr. G. C. J. Vosmaer,

Assistant at the Zoological Station. Naples.

II. On the supposed difference between *Leucandra crambessa* H. and *aspera* (O. S.) H., with an attempt to explain it.

With Plates 28 and 29.

HAECKEL described in his well-known Monograph¹ two species of his genus *Leucandra*, which show however, as I hope to prove, so many transitions that there can be little doubt that both are but varieties. A glance on HAECKEL's figures of *L. aspera* (O. S.) H. and *L. crambessa* H. compared with his descriptions makes one think that both species are easily to be distinguished one from another. But if one sees a great quantity of specimens, it becomes clear that it is often not so easy to determine them. HAECKEL has known this too, as he (l. c. II. p. 182) remarks that there are what he calls »transitorische Varietäten« from *L. crambessa* H. to *L. aspera* (O. S.) H. I never understood these transitory varieties. If two species vary so strongly as to show forms which are between the two, this fact proves that they are what we call varieties of one species: and we do not want the new idea of transitory varieties. Every body now is convinced that species are not constant, and that it is difficult in many cases at least to circumscribe them. In fact we only give specific names for our own practical use, because Nature never makes such sharp distinctions. But if this is so we must try to make our system in such a way as to give us a clear idea of the genealogical relations and thus try to find a practical way.

Sponges vary perhaps more than any other group of animals, and thus we are obliged to be content in using the idea »species« in a very

¹ E. HAECKEL, Die Kalkschwämme. Bd. I—III. Berlin 1872.

wide sense, otherwise, as has been said so often, we should want names for nearly every individual. HAECKEL himself was conscious of this, but he took a way that had too many side-paths.

In order to give a clear view of the principal differences HAECKEL gives of the two species he mentions, I will put his diagnoses one next to the other.

Leucandra crambessa H.

»Dermalfäche fast glatt oder anliegend behaart.

Gastralfäche kurz-stachelig.

Hauptmasse des Skeletts aus regulären und subregulären Dreistrahlern (IV. und V. Gr.) gebildet.

An der Gastralfäche sagittale Vierstrahler mit kurzem Apical-Strahl.

In der äußeren Hautfläche (nicht über diese vorragend) liegen ohne Ordnung zerstreut spindelförmige Stabnadeln (I. Gr.).

Diese colossalen Stabnadeln sind 6—10mal so dick, als die kleinen Dreistrahler und Vierstrahler.«

Leucandra aspera (O. S.) H.

»Dermalfäche borstig-stachelig.

Gastralfäche stark dornig.

Hauptmasse des Skeletts aus subregulären und irregulären Dreistrahlern (IV. Gr.) gebildet.

An der Gastralfäche sagittale Vierstrahler mit starkem Apical-Strahl.

Colossale spindelförmige Stabnadeln (I. Gr.) ragen weit über die Dermalfäche vor; andere sind oft auch im inneren Parenchym zerstreut.

Dieselben sind 4—6mal so dick, als die Dreistrahler, und stehen bald dünner, bald dichter, oft in Bündel vereinigt, von der Dermalfäche schief ab.«

The roughness of the outside, owing to the gigantic rods (»colossale Stabnadeln«) apparently is considered by HAECKEL as the principal thing. In order to make the difference greater he says in his diagnosis of *L. crambessa* that the rods do not project the surface, but in his description we find the following remarkable contradiction: »Eigentlich liegen sie« (the rods) »nicht völlig in der Hautfläche, sondern gegen die Längsachse der Person mit der inneren aboralen Spitze etwas geneigt, so dass die äußere orale Spitze etwas vorsteht« (l. c. II. p. 184). So the difference between the two so-called species is a quantitative one. The same is true with regard to the length of the »Apical-Strahl« of the tetrascetes, as well as the diameter of the gigantic rods.

In the Naples Zoological Station I studied a rather large number of specimens of both sponges. Very big specimens from the »Porto mercantile«, were often brought to me and the well-known conservator SALVATORE LOBIANCO told me that those Sponges were sent to different Museums as *L. aspera* (O. S.) H. I do not know who introduced this name for them but a few sections taught me that it was not *L. aspera* in the sense HAECKEL takes it¹. One may call those specimens *L. cram-*

¹ I feel obliged to say that I am by no means responsible for the determination of Sponges, sent from the Station to different Museums etc.

bessa H. or give it a new name but it is not the old *L. aspera*. I however consider all these together as varieties of one species, for which then the name *aspera* should have priority. According to POLÉJAEFF's new system in which however the old generic names are kept as far as possible, the Sponges under description belong to *Leuconia*.

How much the Sponge which HAECKEL called *L. aspera* varies in external appearance one may see on his plate (l. c. III. taf. 35). On Plate 28 I have illustrated several other varieties. Partly one would call them *L. aspera*, partly *crambessa*, partly perhaps give them new names. Of all these as well as of typical specimens of *aspera* and *crambessa* the anatomy does not show constant differences valuable enough to account for species.

As for the external appearance I have observed that there are all desirable transitions between the rather compressed thin walled var. *crambessa* and the more or less round var. *typica*. The diagrams of macroscopical sections on Plate 28 may clear this up. It is evident that the flatness of the former is not constant as HAECKEL says (l. c. II. p. 183)¹. The gigantic rods are not always so frequent as is figured on HAECKEL's Plates. As a rule we find them stronger, more frequent and farther protruding in the var. *typica*, a little thinner, rarer and less protruding in the var. *crambessa*. As a rule the walls of the former are also thicker but the correlation is not always so strongly marked out. Fig. 3 on Plate 29 is taken from a section of a colony showing partly very flat and rather smooth individuals, which show very plainly the shape of a cocks-comb given by HAECKEL as characteristic for *L. crambessa*, partly however also conical individuals with circular section and projecting spicules. Sometimes the surface is quite smooth and then you may see here and there big spicules glistening in the light but lying parallel to the surface, sometimes the surface seems to be smooth if you touch it moving the finger in an »oral« direction, however it appears to be rough if moving in the opposite way. But there are also specimens to be found in which many rods protrude as far as in the typical *L. aspera*. HAECKEL says that in the latter the angle between the rods and the axis of the Sponge is 45°. As shown in fig. 3 (Plate 29) there the angle is about 45° also. In the variety *typica* however this angle may become greater the size varying also immensely. According to HAECKEL *L. aspera* varies between 10 and 40 mm (»solitäre Form«)

¹ »Der Körper der Personen ist nämlich ganz constant blattförmig zusammengedrückt«

and *L. crambessa* between 50 and 70 mm. Fig. 1 on Plate 28 is an »individual« of a colony measuring 210 mm. The specimen in fig. 2 was still somewhat longer.

The second point in HAECKEL's diagnosis regards the apical ray of the tetrasceles. Also this factor is by no means constant as I often saw long rays in flat specimens (Pl. 29 fig. 3). Finally there is supposed to be a difference in the shape of the tri- and quadriradiates, being in *crambessa* more regular than in *aspera*. Nobody of course would consider this alone of specific value and thus we may declare them all for varieties of one species. It is too well known that an accurate anatomical account, as we want it now, is not to be found in the »Monograph«. I gave something of it in a previous paper on *L. aspera*¹, and now only have to add that the canal-system of all the varieties is identical in main points. I will speak hereafter about some modifications.

Having stated now that *Leuconia aspera* (O. S.) Vosm. shows a polymorphosis as is hardly known in any other Calcareous Sponge² it will be of some interest to look out for its reason. The variety *typica* is as a rule small, thick-walled and rough; the variety *gigantea* is large, rather thin-walled and smooth. Between these extremities there is a variety *crambessa* which is characteristic by its flatness and its shape, being ramified or lobed, often resembling very much a cocks-comb. But there are very many transitions. Fig. 4 on Plate 28 shows a very flat specimen which may be called *gigantea*, although the typical variety of that name (fig. 1 and 2) is not at all so flat and about three times as big. In fig. 1 the specimen has a rather even surface, in fig. 2 it is overloaded with cylindrical or conical protuberances. In fig. 5 these are flat, and the Sponge-body itself is more or less elliptical (on sections). In fig. 2 both are elliptical or circular. In how far the wideness of the individuals of one colony vary may be seen in fig. 6. The varieties *typica* and *crambessa* live under circumstances that seem to be the same. Both are fixed on stones; both live in a depth of about 1 meter. Why, we ask of course, is one variety flat and rather smooth, the other thick and rough? The big variety *gigantea* however is always found attached to the keel of vessels. I consider this fact to be of great importance for the solution of our question. Sponges are all fixed animals. The only way for them of providing themselves with the wanted nourishment is

¹ VOSMAER, Über *Leucandra aspera* H. Tijdschr. Ned. Dierk. Ver. Bd. V. p. 144—166.

² POLÉJAEFF (Voyage of the Challenger. Vol. VIII. Part XXIV. *Calcareae*. p. 54) described something of this sort in his *Leuconia multiformis*.

to keep up the current of water and with it the food, as they do by means of the flagellated collar-cells. The more new water comes in contact with those cells which take in the food-particles the more fully the Sponge may develop itself. Now it is evident that those specimens which hang on the keel of vessels and are thus dragged through the water as the vessel moves must, at least may be in a favourable condition for their development. I have therefore no doubt that the (passive) movement through the water is the origin of its gigantic size. As I was occupied, some years ago, in studying the oyster-culture in Holland at Bergen-op-Zoom and Yerseke I found Calcareous Sponges (for the first time on our coasts) in the tanks where the young oysters are kept. These animals are carefully spread on a kind of framework, which is left swimming in the water. On the same framework and on the little oysters, hanging downwards as they grow through the meshes a great quantity of Sycons were to be found. These Sycons belong to HAECKEL's *Sycandra ciliata* and *coronata*¹ and reach an enormous size. As the water in the big tanks is changed, I believe twice a day, so also this circumstance may be a favourable factor for the size of the Sponges. Not only do they develop rather well in the tanks as regards the size, but they seem also to grow very quickly. As people believe that these Sponges are dangerous for the oysters so every week or every fortnight the frames are lifted and those Sycons are taken away which by their size attract notice. I saw often specimens of about 65 mm. Supposing that these people only take away specimens of more than 30 mm, then even we may say that the Sycons grow from 30 to 65 mm (in length) in half a month.

Returning to our *Leuconia aspera* we have more questions to solve. Why is the roughness in the typical *L. aspera* gone? There may be two reasons for this. In the first place it is possible that the augmented pressure and friction of the water diminished the angle which the rods make with the axis of the Sponge. But another explanation may be given still. According to the most recent investigations it is highly probable that in Sponges the cells of the surface as well as those ectodermic cells which line the subdermal cavities, if present, and the inhalant canals take in food-particles. If this is true it is of great importance for fixed animals to keep hold of the food that comes in their neighborhood, and thus the protruding spicules may have the function, at least partly,

¹ I believe that both are identical and shall call them *Sycon ciliatum* (Fabr.) Lbkn.

to do this. Sponges with many protruding spicules are nearly always covered with sand-particles and all kinds of detritus, which probably serves as food. But this arrangement is of course not so important if the animals every moment come into new water, and thus have much chance of finding sufficient food. A remarkable fact is that in those specimens where the gigantic rods do not protrude much, very thin, short rods do so. These are so thin that they are more or less flexible; besides they are short and thus the pressure and friction of the water has less influence. In what measure these minute rods may be more favourable for the keeping of food in the modified condition of the Sponge, I for the moment cannot decide.

To solve these questions time and experiments are wanted. One of the great advantages of Zoological Stations is that just here and only here such biological problems can be worked out. In many groups of animals we may begin to do so; with regard to Sponges however we must proceed with great care. There is still too much systematic confusion, owing to the fact that even the simplest anatomical details are unknown. First of all a natural system, based on anatomy and not on the occurrence of certain spicules alone, is to be made. We first must learn a little in what measure the principal anatomical details are similar enough to enable us to bring certain Sponges into one species. Then we ought to make experiments with it and see under which circumstances they vary and then perhaps we may give some explanation. Without careful examination of different specimens of the *Leuconia* above mentioned, I never would have taken them as belonging to the same species. Once having seen this, one inquires what has produced the changes and may perhaps find a reason; as I have just been doing.

Now we can return to our first question, about the difference between the varieties *crambessa* and *typica*. *Leuconia aspera* var. *crambessa* probably is an offspring of the var. *gigantea* but fixed again on not moveable objects. They have still more or less the shape of *gigantea* and though as a rule rather smooth, they are never so much so as the big ones. But their size is considerably reduced, because they are no more in the favourable condition of being moved. This is of course a hypothesis, but a hypothesis which explains something and may be proved or rejected by experiments.

Thus the diagnosis of *Leuconia aspera* must be as follows.

Leuconia with three kinds of spicules: rods, triradiates and quadriradiates. Ordinary rods much thicker and longer than the rays of the tri- and quadriradiates. The latter form a more or less distinct gastric

layer. The peripheral skeleton consists of triradiates (occasionally also a few quadriradiates) and gigantic rods, sometimes with thin acerates.

Leuconia aspera var. *typica* is characterised by its extremely rough surface and thick walls. Cloacal-cavity as a rule circular in section.

Leuconia aspera var. *gigantea* is characterised by its gigantic size, its smooth surface and rather thin walls. Cloacal-cavity sometimes circular, very often however elongated elliptical in section. Thin slender acerates often present.

Leuconia aspera var. *crambessa* is characterised by its flatness and its shape, resembling a cocks-comb (or a cabbage, HAECKEL). Surface smooth, here and there a little rough; walls thin. Slender acerates often present.

Of course more varieties will be found. For the moment I do not think it wise to make more than the three mentioned. As I often said, in cases where specimens do not show distinctly the characters of the varieties, it is better to call them simply *Leuconia aspera* (O. S.) Vosm.

III. On Haeckel's entogastric septa.

HAECKEL has found that in some Calcareous Sponges the cloacal-cavity (»Magenhöhle« H.) instead of being a more or less equal tube, shows irregular membranes which divide the tube into entogastric septa as he calls them. He found them in Ascons, Sycons and Leucons, and first (Prodromus) considered them of great systematic value, erecting several genera for those Sponges which possessed them. In his Monograph however he had given it up and considered the absence or presence of the entogastric septa of little systematic value, as he made only varieties on it.

In *Leuconia aspera* var. *gigantea* I found those septa often, but by no means always very strongly developed. In normal specimens the wall of the Sponge is more or less equal in thickness as sections show easily. In some specimens however we see that here and there the inner (cloacal) side is thicker than in other places forming finally a kind of septum at about right angles to the wall. Now these septa often fuse together till they finally give to the Sponge-wall the appearance of the intestines of so many animals (figs. 6, 7 Pl. 2S). In the figs. 1 a, 2 a, 4 a, and 8 I have given illustrations of the greater or smaller development of these irregularities, seen on transverse sections. Fig. 8 is a

section through a whole colony and may show how far the septa vary in one animal. The canals and lacunae formed by the anastomosis of the septa thus are morphologically quite another thing than those large excurrent ones. The latter develop as ramifications, »Ausstülpungen« of the main excurrent one growing into the Sponge-mass, the former on the contrary are remains of the original wide cloacal-cavity. In flat specimens I now and then saw membranes crossing the cloaca and thus uniting both sides of it (fig. 8 Pl. 28), but I never saw this happen in a way as HAECKEL illustrates of his *Leucetta pandora* (l. c. III. fig. 3 b, c T. 22).

HAECKEL considers the entogastric septa as »Brutkapseln« or »Fruchtbehälter«. I can hardly believe they have this function. Which advantage the Sponge may have of it I do not know. If we may hold on POLÉJAEFF's opinion that also the entodermic epithelium cells take in food, the advantage would be that the surface which is able to do so, is enlarged in proportion to the mesoderm. That an overdevelopment of the septa may lead to lipogastria seems to be clear.

Histologically the septa possess the same elements as the inner parts of the Sponge-body. They consist of connective tissue lined with flat epithelium. Canals and ciliated chambers are frequent in them, as well as tri- and quadriradiates, the latter lining the cavities in the same way as they, in normal cases do the cloacal tube (fig. 2 Pl. 29). According to their morphological value we never see the flagellated chambers opening directly into them, but by means of the ordinary wide canals, described by me some years ago.

IV. On the relation between certain Monactinellidae and Ceraospongiae.

In his paper on the Monactinellids¹ VON LENDENFELD states that there is a very close relation between the »echten hornlosen Renieriden« and the so-called Ceraosponges. There cannot be any reasonable doubt that it is true that there are innumerable transitions between both groups. In this point we agree perfectly. But then VON LENDENFELD says²:

¹ Zool. Anzeiger. 1884. No. 164.

² l. c. p. 203.

»Unsere Schwämme weisen darauf hin, dass die hornfreien Monactinelliden die Endglieder einer Reihe darstellen, die von den Hornschwämmen ausgeht.« Unfortunately this author does not give any proof for this hypothesis and therefore it may be asked why? Why do not on the contrary the Hornsponges descend from those Monactinellids? Although it is not yet proved that all the siliceous spicules in Sponges take their origin in cells, as far as we know now, this is highly probable, and what is stated for the spicules in certain groups of Siliceous Sponges may be safely generalised over the other groups. Accepting that the spicules always develop in cells, we may say that those cells represent an older modification of ordinary connective-tissue-cells than those which produce the spongin-fibres. In the oldest Sponges, the Hexactinellids, we find no trace of spongin neither in recent not in fossil specimens. It is not made out whether Ceraosponges exist in fossil state, but at any rate they are younger than Hexactinellids and do not appear before Monactinellids. This is one of the reasons why it seems to me more probable that the reverse from what VON LENDENFELD says, is true. Another argument lies in the canalsystem. All those Monactinellid Sponges which are closely allied with the Ceraosponges possess a canalsystem that is less developed than that of numerous Hornsponges. I never found a system of canals and canaliculi as complicated as it is in some Aplysinids; it belongs always to my third type. And even if one shall find once a canalsystem of the fourth type or any other complication in subdermal cavities or oscules or whatever, the great majority is very simply organised.

VON LENDENFELD gives new arguments in favour of the Ceraosponges being closely related with Monactinellids. Till now however it is not made out that the substance which sticks together the spicules of many *Chalineae*, *Renieridae* etc. is really to be compared with the substance of the hornfibres. I think SOLLAS and RIDLEY were the first who tried to investigate this point¹. RIDLEY observed the substance in question in polarizing light »in order to discover, if possible, some real difference in optical properties between ordinary sarcode and keratose«. He found that »the horny matter, mounted in balsam, of *Tuba*, *Rhizochalina oleracea*, *Hircinia lingua* and *Euspongia virgultosa* polarizes light, while that of *Chalina finitima* does not«. The substance of the latter he called »pseudo-keratose«. This proves 1^o that the horny matter

¹ SOLLAS in Ann. and Mag. (5.) Vol. IV. p. 48. — RIDLEY in Journ. Linnean Soc. Vol. XV. (1881) p. 481.

not always polarizes light and 2^o that true keratose or spongin seems to occur as well in *Ceraospongiae* as in *Chalineae* etc. I have studied many Sponges in polarizing light and have had the same result. I found that light was polarized by the spongin of the following Sponges: *Euspongia officinalis* (strongly), *Cacospongia cavernosa* O. S., *Aplysina aërophoba* Ndo., *Velinea gracilis* Vosm., *Ectyon* (strongly), *Reniera cratera* O. S. (feebly), *Reniera filigrana* O. S. (feebly), *Clathria coralloides* O. S., *Cl. ulmus* Vosm., *Cl. elegans* Vosm. (all strongly), *Axinella polypoides* (feebly), *Pachychalina*, *Cribrochalina variabilis* Vosm. On the other hand I could not see any trace of it in *Aplysilla sulfurea* F. E. S. and *Siphonochalina coriacea* O. S. The fact that I found the horny substance in a typical Renierid (*R. cratera* O. S.) polarizing light struck me rather. I therefore renewed my investigations on this Sponge, and I found that the »Kitt-Substanz« not only in the point just mentioned agreed with true spongin, but that also the same granulous matter occurred, lying in »Kuppen« (SCHULZE) one above the other, just as SCHULZE and VON LENDENFELD described it in some Hornsponges (Pl. 29 fig. 4). In preparations macerated by means of boiling corrosive sublimat, a method that I can strongly recommend for isolating Sponge-cells, this is to be seen very distinctly. In the same preparation I saw cells which resembled so much the Spongoblasts of *Euspongia*, that I am very much inclined to believe that also in *Reniera* the spongin is formed in the same way as in *Euspongia*. Unfortunately I till now, have not been able to make really good sections of *R. cratera* O. S. and I have not found those cells in situ as SCHULZE illustrates of *Euspongia*. But I think there can be but little doubt that they occur.

According to what I said above we may suppose that some mesoderm-cells of siliceous Sponges gradually changed into real spongoblasts.

Probably certain qualities of the seawater or in general the locality where the Sponge grows is favourable to a strong development of spongin-fibre, and so more and more the latter may prevail and the spicules remain in the background, till finally under circumstances very favourable for one, very unfavourable for the other, true Hornsponges have been formed.

It is true that my suggestion is a hypothesis also, but I have given some arguments in favour of it, a fact which cannot be stated of VON LENDENFELD'S.

Naples. Aug. 4.

Explanation of the Plates.

Plate 28.

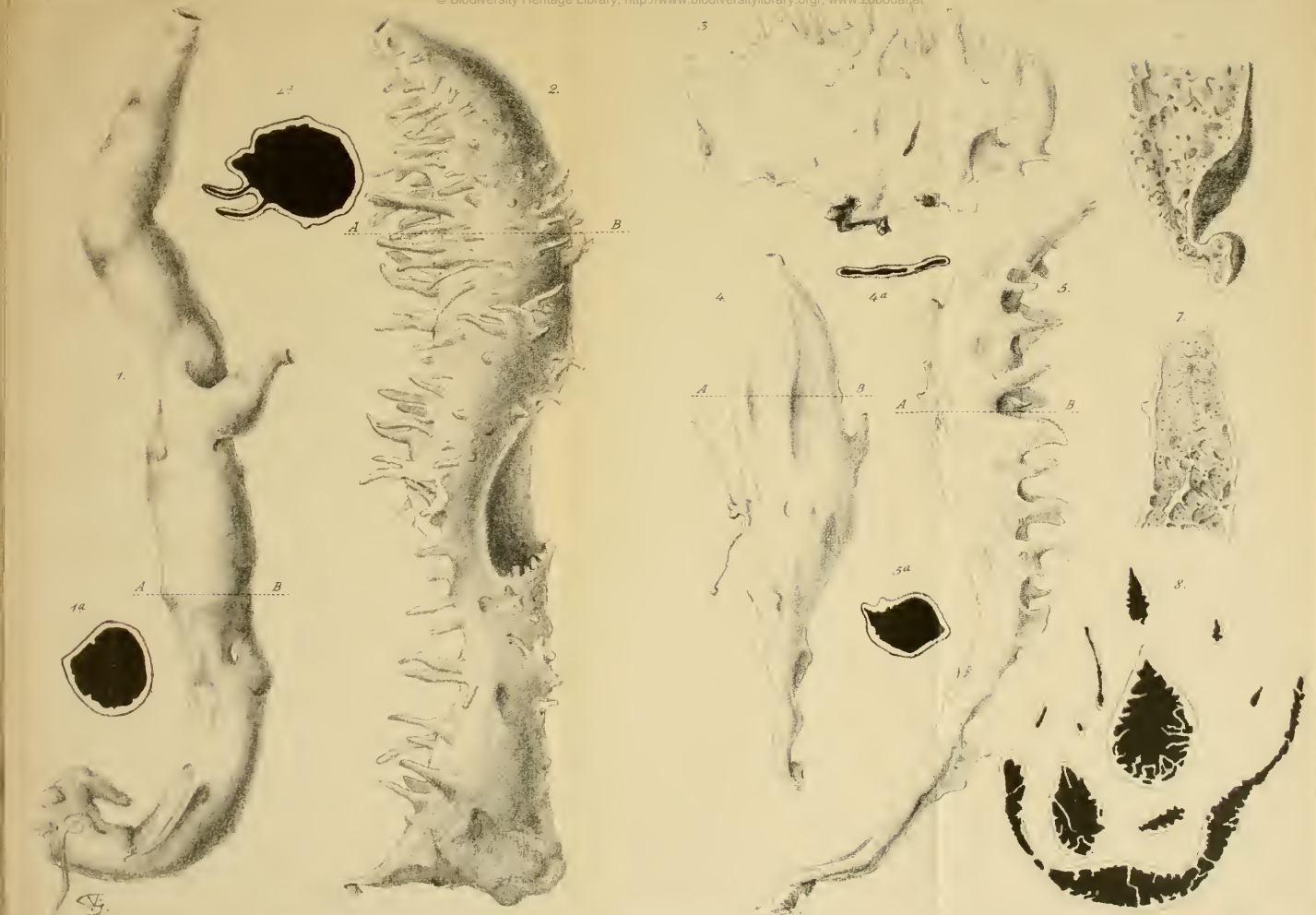
(The figures are all drawn after specimens, preserved in spirit, in natural size.)

- Fig. 1. *Leuconia aspera* var. *gigantea*.
 Fig. 1a. " " " " Section through *A B* fig. 1.
 Fig. 2. " " " " With numerous appendages.
 Fig. 2a. " " " " Section through *A B* fig. 2.
 Fig. 3. *Leuconia aspera* var. *crambessa*, showing here and there transitions (in shape) to var. *gigantea* and (in its spicules) to var. *typica*.
 Fig. 4. *Leuconia aspera* var. *gigantea*. Small very flat specimen.
 Fig. 4a. " " " " Section through *A B* fig. 4.
 Fig. 5. *Leuconia aspera*. Transition between var. *crambessa* and var. *gigantea*.
 Fig. 5a. " " " " Section through *A B* fig. 5.
 Fig. 6. *Leuconia aspera* var. *gigantea*. Longitudinal section through the base, showing the entogastric septa.
 Fig. 7. *Leuconia aspera* var. *gigantea*. (Other specimen.)
 Fig. 8. " " " " Section at right angles through a colony.

Plate 29.

(I used Microscop HARTNACK; Cam. luc. of ZEISS-OBERHÄUSER.)

- Fig. 1. *Leuconia aspera* var. *gigantea*. Section at right angles to the axis, showing the anastomoses of the septa, and the rather thin Sponge-wall. *cl.c.* = cloacal-cavity. $\times 4/3$.
 Fig. 2. The same. Part of the wall and entogastric septa, which form the pseudo-canals, *ps.c.* — *cl.c.* = cloacal-cavity. H. II. Cam. luc. Proj. obj. stage.
 Fig. 3. *Leuconia aspera* var. Longitudinal section, showing gigantic rods; one protruding at an angle of about 45° , another totally immersed in the wall. H. IV. Cam. luc. Proj. obj. stage.
 Fig. 4. *Reniera cratera* O. S., showing the structure of the spongin-substance. After a sublimat-preparation. H. VII. Cam. luc. Proj. obj. stage.





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