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XXVII.—*On the* Calcispongiæ, *their Position in the Animal Kingdom, and their Relation to the Theory of Descendence.* By Professor ERNST HÄCKEL*.

I. THE POSITION OF THE CALCISPONGIÆ IN THE ANIMAL KINGDOM.

1. *The Primitive Form of the Spongiæ.*

The results of the examination of the comparative anatomy and developmental history of the Calcispongiæ (in the second section of this volume) not only furnish us with a satisfactory insight into the organization of this group of animals and of the Sponges in general, but, by comparison with the lower states of development of the higher animals, they lead us to general reflections which throw a new light upon the natural system, the genealogical tree of the animal kingdom.

In the first place, by our morphology of the Calcispongiæ the opinion entertained by most spongiologists is confirmed—namely, that they form a unitarily organized group, which, by its most important characters, belongs to the class of Sponges, but occupies within this an independent position. In the natural system we can express this relation by dividing the whole class of Sponges into three principal sections or subclasses, namely :—I. Gelatinous Sponges (*Myxospongiæ*), II. Fibrous Sponges (*Fibrospongiæ*), and III. Calcareous Sponges

* Translated by W. S. Dallas, F.L.S., from a separate copy of the last two chapters of the first volume of Prof. Häckel's monograph of the Calcispongiæ (Berlin, 1872), communicated by the Author.

(*Calcispongiæ*)*. The Myxospongiæ are characterized by the complete absence of a skeleton, the Fibrospongiæ by their partly horny, partly siliceous, fibrous skeleton, and the Calcispongiæ by their calcareous (not fibrous) skeleton.

The comparative anatomy and ontogeny of the Sponges allow us to assume with tolerable certainty that all the different forms of this class originate from a single common stock form, a *primitive sponge* (*Archispongia*) †. That all the various Calcispongiæ may be deduced without any difficulty in the most natural manner from a common stock form, *Olynthus*, has already been satisfactorily proved; the ontogeny of the Calcispongiæ leaves no doubt upon this point. Oscar Schmidt has also shown that the united horny and siliceous sponges (our *Fibrospongiæ*) must all have descended from a common stock form, which we will denominate *Chalynthus*; and we shall certainly not be far wrong if we assume that the common root of both groups is to be sought in the skeletonless group of the Myxospongiæ; for, as in all other organisms, so also in the Sponges, the formation of the skeleton is to be regarded phylogenetically as a secondary, and not as a primary act of organization. We should therefore have to derive the Fibrospongiæ and Calcispongiæ from the common stock group of

* The class of Sponges has hitherto been usually divided, after Grant's example (1826), in accordance with the three different modes of formation of their skeleton, into the three subclasses of the Horny Sponges (*Ceratospongiæ*), Siliceous Sponges (*Silicispongiæ*), and Calcareous Sponges (*Calcispongiæ*). Oscar Schmidt has shown, however, that the separation of the Horny and Siliceous Sponges is untenable, because the two groups are interwoven with each other most multifariously, and stand in the closest polyphyletic connexion (Algier. Spong. 1868, p. 35). I therefore propose provisionally to unite the two groups in the division of the Fibrous Sponges (*Fibrospongiæ*), because in the dried state both exhibit the characteristic *fibrous texture*, of which both the Calcispongiæ and the Myxospongiæ are quite destitute. The establishment of the Gelatinous Sponges (*Myxospongiæ*—the best-known representative of which is *Halisarca*) as a distinct third group seems, upon phylogenetic grounds, unavoidable.

† The conviction of the *monophyletic origin* of the whole class of Sponges becomes more and more firmly established the further we penetrate into their study. On the other hand, the assumption of a *polyphyletic* origin, which, on one's first superficial acquaintance with the sponges, seems to possess the most claim to confidence, loses more and more in probability the further we penetrate. Moreover Oscar Schmidt, who of all spongiologists undoubtedly possesses the most comprehensive view of the whole great form-series of this class, and who, by virtue of his clear understanding of the theory of descendence, is most justified in pronouncing judgment upon this question, derives all the various groups of sponges from a common stock group, which he denominates *Protospongiæ* (Atlant. Spong. 1870, p. 83; "The Natural System of Sponges," Mittheil. des naturwiss. Vereins für Steiermark, Bd. ii. Heft 2, 1870).

the Myxospongiæ; and it is among these last that the common stock form of all Sponges, the *Archispongia*, is to be sought*.

As, owing to the soft nature of their bodies, no fossil remains of the extinct Myxospongiæ could be preserved, we must refer, with respect to their organization, to their few living representatives; and among these *Halisarca* is at present the only accurately known form. This genus is also recognized by O. Schmidt as that which comes nearest to the common stock form of the whole class, his "*Protospongia*." He remarks (*l. c.* p. 34), "that the Halisarcinæ realize in the simplest manner the scheme of the sponges cannot be disputed." Nevertheless I must dispute the truth of this remark. I have examined two different species of *Halisarca* alive, namely the colourless *Halisarca Dujardinii*, on the Norwegian coast (in Bergen), and the violet *Halisarca lobularis*, on the coast of Dalmatia (in Lesina). As regards their anatomical characters, I found both to agree essentially with the representation which Lieberkühn has given of the former. The soft, gelatinous, amorphous body consists of a lump of nucleiferous sarcodine (*syncytium*), and is permeated by branched canals, which are inflated in all parts into numerous spherical or ellipsoidal flagellate chambers (the ciliary apparatus, "*Wimper-Apparate*," of Lieberkühn). Consequently the gastro-canal system is constructed on the Leucon type; and if we remove by acid the calcareous spicules from a Leucon with a racemose system of branching canals (*e.g. Leucortis pulvinar*), we obtain a sponge-body which, in essential points, resembles *Halisarca*.

But both the Leucon type and the Sycon type undoubtedly descend from the simpler Ascon type; and in accordance with this we must seek also for the Halisarcinæ a much more simply organized stock form, standing in the same relation to the Ascontes as the Halisarcinæ to the Leucontes. In order to obtain the picture of this hypothetical stock form we need only to remove, by means of acid, the calcareous spicules from

* Fritz Müller, whose instructive work 'Für Darwin' has in so high a degree advanced the comprehension of the causal nexus between ontogeny and phylogeny, in a memoir "On *Darwinella aurea*, a Sponge with stelliform horny spicules," expresses the supposition that the calcareous spicules of the Calcispongiæ on the one hand, and on the other the siliceous spicules of the Silicispongiæ, may have originated from a common horny stock form; the former by the calcification, the latter by the silicification of the original horny spicules (Archiv für mikrosk. Anat. 1865, p. 351). Although this hypothesis seems to be in accordance with our assumption above, it is nevertheless incorrect, as in the Calcispongiæ the "horny foundation" of the Fibrospongiæ never occurs.

the primitive Ascon form, *Olynthus*. This skeletonless stock form actually realizes "the scheme of the sponges in the simplest manner," and is to be regarded as the original stock form, not only of the Halisarcinæ, but also of all other sponges; it is the *Archispongia* of our monophyletic genealogical tree.

This *Archispongia*, the common stock form of all sponges, is a simple thin-walled sac of a cylindrical, ellipsoidal, or rounded elongate form, a uniaxial, unsegmented person, which is attached by one (the aboral) pole of the longitudinal axis, and at the other (the oral) pole opens by an orifice (*osculum*). The thin wall of the sacciform body consists of two lamellæ or leaves. The outer or *dermal lamina* (the *exoderm*) is composed of a simple layer of non-vibratile cells (which have either remained independent or coalesced into a syncytium); the inner or *gastral lamina* (the *entoderm*) consists of a simple layer of vibratile flagellate cells, of which, at the attainment of sexual maturity, some are converted into sperm-cells and others into ovi-cells. The thin body-wall is from time to time traversed by unstable simple holes or pores; and then water enters through these pores into the cavity of the sac (the stomachal cavity), and escapes again from the mouth-orifice in consequence of the movement of the flagella*.

2. *The Spongiæ and the Protozoa.*

The wearisome disputes as to the position of the Sponges in the animal kingdom, which have continued even till the present day, ought to be finally settled by the morphology of the Calcispongiæ. Every zoologist who recognizes *developmental history* as the "true light-bearer" of systematic zoology, must admit that by the ontogeny of *Olynthus* the very near relationship of the *Ascontes* and the *Hydroida* is proved. But before I enter into further details upon this subject, I must say a few words upon the supposed relationship of the Sponges and Protozoa which has hitherto been accepted by most zoologists †.

* Whether the simplest sponge-forms, corresponding with the picture of *Archispongia*, still exist is not known. Possibly a very near ally is the singular sponge which Bowerbank has described as *Haliphysema Tumanowiczii* (Brit. Spong. vol. ii. p. 76, fig. 359), and which Carter regards as a Polythalamian (*Squammulina*). I suspect, on the contrary, that it is a very simple Myxospongia, which, like *Dysidea*, forms for itself a skeleton of foreign bodies (spicules of other sponges, spines of Echinoderms, &c.), but in other respects has the simple structure of *Olynthus*.

† The multifarious older opinions as to the position of the Sponges in the system of the animal kingdom are brought together in Johnston's 'History of British Sponges' (1842, pp. 23–75, history of discoveries as

I have already shown that the prevailing error as to the near relationship of the Sponges and Protozoa originated for the most part from a false conception of their conditions of individuality. Because the morphontes (morphological elements) of the first order which form the sponge-organism, the flagellate and amœboid cells, exhibit a relatively high degree of physiological individuality, and because the *personality* of the sponges built up of these (the morphon of the third order) was not recognized, the former have been regarded as the "true individuals" of the sponge. I have already (1869) refuted this error by demonstrating the homology of the sponge-person with the Acaleph-person, and the composition of the wall of its stomachal cavity of two laminæ (entoderm and exoderm).

This demonstration has been repeatedly attacked during the last two years, and indeed especially by Carter, James-Clark, Saville Kent, and Ehlers. The attacks of Carter and of James-Clark, neither of whom has any conception of the essence of the cell-theory, have already been refuted. The attacks of Saville Kent* are incapable of refutation, and indeed do not need any, simply because the author neither understands the arguments brought forward by me, nor is in general sufficiently acquainted with the structure and development of the Sponges and Zoophytes. Evidently Saville Kent (of the Geological Department, British Museum) does not possess even the small measure of zoological knowledge which might be expected from a geologist who works at palæontology. He does not even know the difference between homology and analogy, between the morphological and physiological significance of an organ. He regards the differentiation of such notions as quite superfluous. Comparative anatomy and ontogeny seem not to exist for Saville Kent; and as my whole demonstration rests upon the basis of the latter, of course he cannot comprehend it. Ray Lankester has taken the thankless trouble to attempt to communicate to this geologist some of the elementary pieces of preliminary knowledge which are necessary for the discussion of such questions of comparative

to the nature of Sponges), and in a recently published memoir by Pagenstecher, "Zur Kenntniss der Schwämme" (Verhandl. der naturhist. Vereins zu Heidelberg, 1872); see also my memoir on the organization of the Sponges &c. (1869, Jenaische Zeitschr. Bd. v. p. 307; transl. in Ann. & Mag. Nat. Hist. 4th ser. vol. v. pp. 1 & 107). The later spongiologists, especially Bowerbank, Carter, Lieberkühn, O. Schmidt, and Kölliker, almost unanimously refer the sponges to a place among the Protozoa, where they are appended sometimes to the Amœbæ, sometimes to the Rhizopoda, and sometimes to the Flagellata.

* Ann. & Mag. Nat. Hist. 1870, 4th ser. vol. v. pp. 204–218.

anatomy*; but it is evident from the naïve reply of the latter that this well-meant endeavour was in vain †.

The objections which Ehlers ‡ has made against my theory I cannot refute, because his conception of the sponge-organism is completely different from mine. I cannot by any means conceive a sponge without any internal cavity and without two essentially different cell-formations (the flagellate cells of the entoderm and the non-ciliated cells of the exoderm). Ehlers, on the contrary, assumes two different primary groups of sponges, namely "*Spongiæ holosarcinæ*, with a dense tissue without a canal-system, and *Spongiæ cœlosarcinæ*, which develop body-cavities" (*l. c.* p. 555) §. He derives the latter from the former, and thinks that the *Protospongiæ* conceived by O. Schmidt as the hypothetical stock group of all Sponges were "holosarcine sponges, with a simple, not differentiated tissue." Unfortunately we can by no means understand from Ehlers's memoir what he really regards as the characteristic "tissue" of the sponges. The word "cell" occurs nowhere in the whole memoir. It would almost appear, however, that by "tissue" Ehlers understands the "hardened sarcode" or the so-called horny substance of the keratose sponges. Of the supposed new form of sponge (*Aulorhipis elegans*), upon which Ehlers founds his whole argument, he knows nothing except the horny skeleton, no trace of soft parts. But this horny skeleton, which encloses foreign bodies, is *a solid cord*, attached to a worm-tube at one end, and the dichotomously divided branches of which spread out like a fan in one plane. It is very probable that this skeleton does not belong to a sponge at all. But should it be the product of a sponge, at

* Ann. & Mag. N. H. 1870, 4th ser. vol. vi. p. 86. † Ibid. p. 250.

‡ "*Aulorhipis elegans*, eine neue Spongien-Form," Zeitschr. für wiss. Zool. Bd. xxi. 1871, p. 540, pl. 42.

§ The body-cavities of the sponges are placed by Ehlers in two different divisions. He calls "that great cavity of a sponge which has originated by the development of a section of the *cœlenteric* space a *megacœlon*, and its orifice a *megastoma*; but the inner space, which has originated by the equal participation of the whole *tissue of the sponge*, a *cœloma*, and its entrance a *cœnostoma*." According to my notion, the cavity which Ehlers indicates as a *megacœlon* with a *megastoma* will generally correspond with the *stomach* (*gaster*) with the *mouth-opening* (*osculum*). On the other hand, the cavity which Ehlers names *cœloma* will generally represent that part of the intercanal system which I have named *pseudogaster*, and the *cœnostoma* of the former the *pseudostoma* of the latter. It is, however, quite incomprehensible how Ehlers can regard the cavities of the sponges as partly cœlenteric and partly non-cœlenteric, seeing that his entire memoir is directed against the cœlenteric interpretation of the canal-system of the sponges, and at its close he expressly says:—"According to my conception, it is no longer open to discussion that the Sponges have no close relationship to the Cœlenterata."

any rate only the developmental history and the anatomy of the soft parts could furnish information upon this peculiar structure. It seems rather a bold thing to found an entirely new theory of the organization of sponges upon this skeleton alone, and upon its supposed relationship to the fossil *Stromatopora*. In any case this whole theory is completely irreconcilable with the facts contained in this monograph.

3. *The Sponges and the Acalephæ.*

In order to recognize the true relationship of the sponges to other groups of animals we must, of course, start from the simplest and least differentiated forms of the class, from *Olynthus*, and from the *Archispongia*, which differs therefrom by the want of calcareous spicules. When we seek for the nearest relations of these latter in other classes of animals, it is evident that, above all other animals, the simplest forms of the Acalephan group come into the foreground. But amongst all the known Acalephæ the two freshwater inhabitants of this group, *Hydra* and *Cordylophora*, are those which exhibit the most primitive conditions of organization, and which must stand nearest to the original stock form of this group. I cannot, therefore, but notice it as an extremely fortunate coincidence that two memoirs have just appeared, which diffuse the clearest light in every direction over these exceedingly important animal forms—namely, the excellent monographs of *Hydra* by Nicolaus Kleinenberg * and of *Cordylophora* by Franz Eilhard Schulze †. Both works are admirable in their kind, being distinguished equally by acute observation and by sagacious reflection. The monograph on *Cordylophora* is perhaps of more importance for our comparison with *Olynthus*, because this polyp has evidently, in its ontogeny, better preserved the original phylogeny of its ancestors than *Hydra*, which is also, in other respects, variously and peculiarly modified in consequence of special adaptations. On the other hand, the monograph of *Hydra* is of more importance by reason of the far-reaching philosophical explanations appended to it, and especially of the extremely important reflections upon the germ-lamella theory. Both monographs merit the highest recognition, especially because zoological literature is at present flooded with worthless and unconnected fragments, and on account of the rarity of exhaustive and complete monographic works which furnish a permanent gain to science ‡.

* *Hydra*, eine anatomisch-entwickelungsgeschichtliche Untersuchung. With 4 plates. Leipzig, 1872.

† Ueber den Bau und die Entwickelung von *Cordylophora lacustris*. With 6 plates. Leipzig, 1871.

‡ If I here bring only *Hydra* and *Cordylophora* into consideration among the Acalephæ (the Cœlenterata in the narrower sense), this is

If we compare the coarser and finer structural characters of *Hydra* and *Cordylophora*, as these appear to be established by the extremely careful histological investigations of Kleinenberg and F. E. Schulze, with the corresponding structural characters of *Olynthus*, we cannot but be astonished at the remarkable agreement which is manifested even in the finer details. This agreement appears most striking when we consider the *Olynthus* with *closed pores*, or *Prosycum*, or if we leave out of consideration the calcareous spicules, the group-peculiarity of the Calcispongiæ, and take, instead of *Olynthus*, the *Archispongia* (which differs only by the absence of spicules). As essential agreements of structure between *Hydra* and *Cordylophora* on the one hand, and *Prosycum* and the *Archispongia* on the other, we have:—1, the simple stomachal cavity with a buccal orifice; 2, the composition of the thin stomachal wall of two laminæ, the vibratile entoderm and the non-ciliate exoderm; 3, the composition of the entoderm of flagellate cells.

On the other hand, we have as essential differences:—1, the constitution of the exoderm, the cells of which in *Hydra* and *Cordylophora* develop urticating capsules and neuro-

because, of all the *accurately known* forms of this group, I regard them as the simplest and most primitive, and as most nearly approaching the unknown common stock form of the whole group, the hypothetical *Archydra*. It is true that in 1870 Richard Greeff described, under the name of *Protohydra Leuckarti*, a form apparently still simpler—namely a hydroid polype *without tentacles*, and which is said to propagate by mere transverse division (Zeitschr. für wiss. Zool. 1870, Bd. xx. p. 37, pls. 4, 5). Greeff represents it as "a marine stock form of the Cœlenterata," as an "undoubtedly completely developed and mature, but asexual animal form, propagating by transverse division." But from his whole representation it seems to me, on the contrary, to follow indubitably that here we have to do with an imperfectly developed hydroid form, which will subsequently become sexually differentiated. It would be contrary to all analogy that an animal form so highly differentiated, which in its essential anatomical structure seems to agree exactly with *Hydra*, and differs therefrom only by wanting tentacles, should propagate merely asexually by *transverse division*. The question would be very different if *Protohydra* propagated asexually only *by spores* (or single separated cells). At any rate Greeff's assumption that *Protohydra*, which was observed "for a couple of months" in an oyster-park at Ostend, is undoubtedly an independent hydroid form is quite unjustified. Greeff says, "On a careful examination of its whole habit, its structure, and movements, and taking into consideration its transverse division, and above all the long period of observation, all notions that it is a developmental form of an Anthozoon or any other form of animal, or of a hydroid polype developed and mature in its asexual stage, must disappear." These arguments, however, prove nothing at all; and these rejected notions will only be clearly established in the mind of an unprejudiced reader by Greeff's own representation. So long as the developmental history of *Protohydra* is completely unknown, we need take no notice of this hydroid form.

muscular processes, whilst in *Olynthus* (and *Archispongia?*) they coalesce to form the syncytium; 2, the circlet of tentacles of the former, which is wanting in the latter; 3, the different origin of the sexual organs, in the former in the exoderm, in the latter in the entoderm. This last difference appears to be of great importance. But even within the group of the Acalephæ, according to the statements of many observers, the sexual cells originate in some in the exoderm, in others in the entoderm. I shall revert to this, particularly, hereafter. On the other hand, the want of the circlet of tentacles in the Sponges is of no significance, as even in the Hydroida this does not appear at first, and is wanting in many Hydroid forms (Siphonophora). The difference in the formation of the exoderm appears to be of more importance; but even this is to be regarded as a secondary histological differentiation of the two divergent groups.

At any rate, these differences in anatomical structure between the simplest Hydroida and the simplest Sponges appear of quite subordinate significance, when we place in the opposite scale the weight of the above extremely important and essential agreements. This weight, moreover, is considerably augmented if we compare the ontogeny of the two groups. *Hydra* itself does not come first into consideration in this case, because its primitive ontogeny appears evidently to be strongly modified, and effaced and falsified by secondary adaptations. On the contrary, the ontogeny of *Cordylophora*, which perfectly agrees with that of *Olynthus* (see Schulze, *l. c.* pp. 38–41, pl. v. figs. 1–8), is of the greatest importance. The planula, which originates from the morula, and the planogastrula, which originates from the planula, are perfectly similar in the two animals; even the minute structure of the two layers of cells, or germ-lamellæ, which bound the stomachal cavity of the ovate ciliated larva is in striking agreement—the small, slender, cylindrical flagellate cells of the exoderm, and the large, non-ciliate, rounded-polyhedral cells of the entoderm*.

From this perfectly accordant ontogeny and anatomy of *Olynthus* and *Cordylophora* follows with perfect certainty that conception of the position of the sponges in the animal kingdom which I put forward in 1869 in my memoir "On the

* It is true that in *Cordylophora*, the breaking out of the stomachal cavity and the formation of the mouth-aperture takes place only after the planogastrula has attached itself, and passed into the Ascula-form; but even in many constantly astomatous sponges the gastrula appears not to be developed, and the planogastrula becomes directly converted into the *Clistolynthus*, whilst in *Olynthus* it passes previously into the gastrula.

Organization of the Sponges, &c.," in the following words :—"We should therefore have to divide the stem or phylum of the Zoophytes (*Cœlenterata* s. *Zoophyta*) into two primary groups (sulphyla or cladi)—1. Sponges (*Spongiæ* s. *Porifera*), and 2. Nettle-animals (*Acalephæ*, s. *Cnidæ*, s. *Nematophora*). The latter would divide into the three classes of the Corals, Hydromedusæ, and Ctenophora." But, with reference to the biogenetic fundamental law and the accordant ontogeny of the Calcispongiæ and Hydroida (*Olynthus* and *Cordylophora*), we shall have further to extend this view of the immediate relationship of the Sponges and Nettle-animals to the following proposition :—*Sponges and Acalephæ are two diverging branches of the Zoophyte stem, which have developed themselves from the common stem form of the Protascus.* This *Protascus* is still represented by the transitory young form of the *Ascula* *.

As regards the differences between the Sponges and Acalephæ, I regard the want of tentacles in the former as quite unessential. They are wanting also in many Acalephæ (*e. g.* many Siphonophora and Antipathidæ). On the other hand, in some sponges incipient tentacle-formation seems to occur, as, for example, in *Osculina polystomella* (O. Schmidt, Algier. Spong. 1868, pl. i. figs. 6, 7). What is the condition of the antimer-formation in this and other siliceous sponges requires closer investigation. Certainly the figure which O. Schmidt gives of the fissures surrounding the stomachal cavity in some forms of *Osculina* reminds one strongly of the Corals ; and his fig. 4, pl. i. (*l. c.*), might actually pass as the transverse section of an octonary Alcyonarian. In other siliceous sponges also the stomachal cavity appears to be divided into compartments by radial septa (of various number) ; and these may be referred to differentiation of antimera. As, however, antimer-formation is wanting to many Hydromedusæ, we must not lay too much weight upon this.

The *urticating organs* have hitherto appeared to form one

* The genealogical connexion of the Sponges and Acalephæ is consequently to be sought only down at the root, where, on the one hand, *Archispongia*, the stock form of the Sponges, and on the other *Archydra*, the stock form of the Acalephæ, have developed themselves from the common *Protascus* form ; whereas the near relation of the Sponges to the Corals, to which I formerly gave particular prominence, is to be understood only as an analogy, not an homology. I thought at that time that I found in the radiate structure of the Sycones an essential morphological point of comparison with the Corals ; but the developmental history of the radial tubes of the Sycones, with which I only became acquainted subsequently, has convinced me that these are not homologous with the perigastric radial chambers of the Corals.

of those histological characters which with most certainty separated the Acalephæ from the Sponges. Until recently the proposition was current that all Acalephæ possess urticating organs, and all Sponges are destitute of them. But Eimer* has lately stated that he has found urticating cells also in several species of siliceous sponges (Renierinæ). Consequently this differential character also seems to lose its value. There would consequently remain as the sole differential character between Acalephæ and Sponges, the *pore-structure* of the latter, on account of which Grant named them *Porifera*. But, in my previous memoir on the organization of the sponges, I have already pointed out that in many Acalephæ cutaneous pores also occur, which open into the gastro-canal system, and allow water to penetrate into it from without. In the Medusæ such aquiferous apertures have been described by various authors. In the Corals, cutaneous pores, which introduce water from without into the ramifications of the gastro-canal system, appear, from the observations of Milne-Edwards, Kölliker, and others, to be very widely diffused. Still it is very remarkable that these pores appear to be wanting precisely in the lowest Acalephan forms, the Hydroida. Thus, even if we suppose the two lines of the Sponges and Acalephæ to separate before the common root, we should have to regard the pore-formation in the two groups as analogous and not as homologous formations, or, more strictly expressed, as *homomorphous* but not *homophylous* structures†. At any rate, however, the boundary between the lower Acalephæ (Hydroida) and the lower Sponges appears at present to be so effaced that, at the moment, we cannot establish any single *generally applicable* differential character between the two groups of the Zoophyta.

4. *The Stem of the Zoophytes* (*Zoophyta or Cœlenterata*).

In order to facilitate the comprehension of the preceding and following observations, I must here insert a few words as to my conception of the zoophytes in general. In the older zoological systems the animals which are now usually denominated *Cœlenterata* are mixed with other lower animals in the section of the Zoophyta, established by Wotton as early as 1552. After Lamarck (1814) and Cuvier (1819) it is well known that the Hydroida, Medusæ, and Corals were generally placed, together with the Echinodermata &c., in the extremely unnatural division of the radiated animals (*Radiata* or *Radiaria*),

* Archiv für mikr. Anat. Bd. viii. 1871, p. 281.

† I call *homophyly* the real phylogenetically founded homology, in opposition to *homomorphy*, which is destitute of genealogical foundation.

a group which is now maintained only by Agassiz among zoologists of repute. In 1847 Frey and Leuckart separated the Polypes and Acalephæ of Cuvier from the Echinodermata, and united them under the name of Cœlenterata*. Almost at the same time Huxley also recognized the necessity for this separation, and proposed the denomination *Nematophora* for the united Acalephæ and Polypes, on account of their urticating organs †. At first Leuckart grasped the notion of the Cœlenterata in a narrower sense (for the three classes Ctenophora, Acalephæ, and Polypi). Subsequently (1854) he appended the Sponges also as most nearly allied to these three classes ‡. Instead of the denomination *Cœlenterata*, which is now very generally diffused in Germany, I employ the older denomination *Zoophyta*, which is still the one more generally used in England and France, for the following three reasons:—

1. The denomination *Zoophyta*, which was introduced into systematic zoology by Wotton as early as 1552, is nearly three hundred years older than the name Cœlenterata. It is true that the division *Zoophyta* in Wotton's sense and that of his successors includes not only the Cœlenterata (Sponges and Acalephæ), but also many other invertebrate animals. But exactly the same objection might also be raised, and with much more reason, against the denomination *Vermes*. The primary division of the animal kingdom which we now generally name the phylum of the Vermes, includes only a very small part of the mass of invertebrate animals which Linnæus and his school embraced in the class Vermes; in the 'Systema Naturæ' all the Invertebrata, except the Arthropoda, are called *Vermes*.

2. The denomination *Cœlenterata* of Frey and Leuckart has at present become indefinite and ambiguous, because by it most zoologists understand only the nettle-animals (Hydromedusæ, Ctenophora, and Corals), whilst Leuckart himself also referred the Sponges to it. This ambiguity is got rid of by our giving the name of *Zoophyta* to the Cœlenterata in the broader sense (including the Sponges), whilst we name the Cœlenterata in the narrower sense (after the separation of the Sponges) Acalephæ. Even Aristotle included under the idea of the Acalephæ or Cnidæ (*ἀκαλῆφαι, κνῖδαι*) the two primary types of this group, the adherent Actiniæ and the free-swimming Medusæ. The zoology of a later period was wrong in understanding only the Medusæ under the name of Acalephæ.

* Beiträge zur Kenntniss wirbelloser Thiere, 1847, pp. 38, 137.
† Report Brit. Assoc. for 1851, note p. 80.
‡ Arch. für Naturg., Jahrg. xx. 1854, Bd. ii. p. 472.

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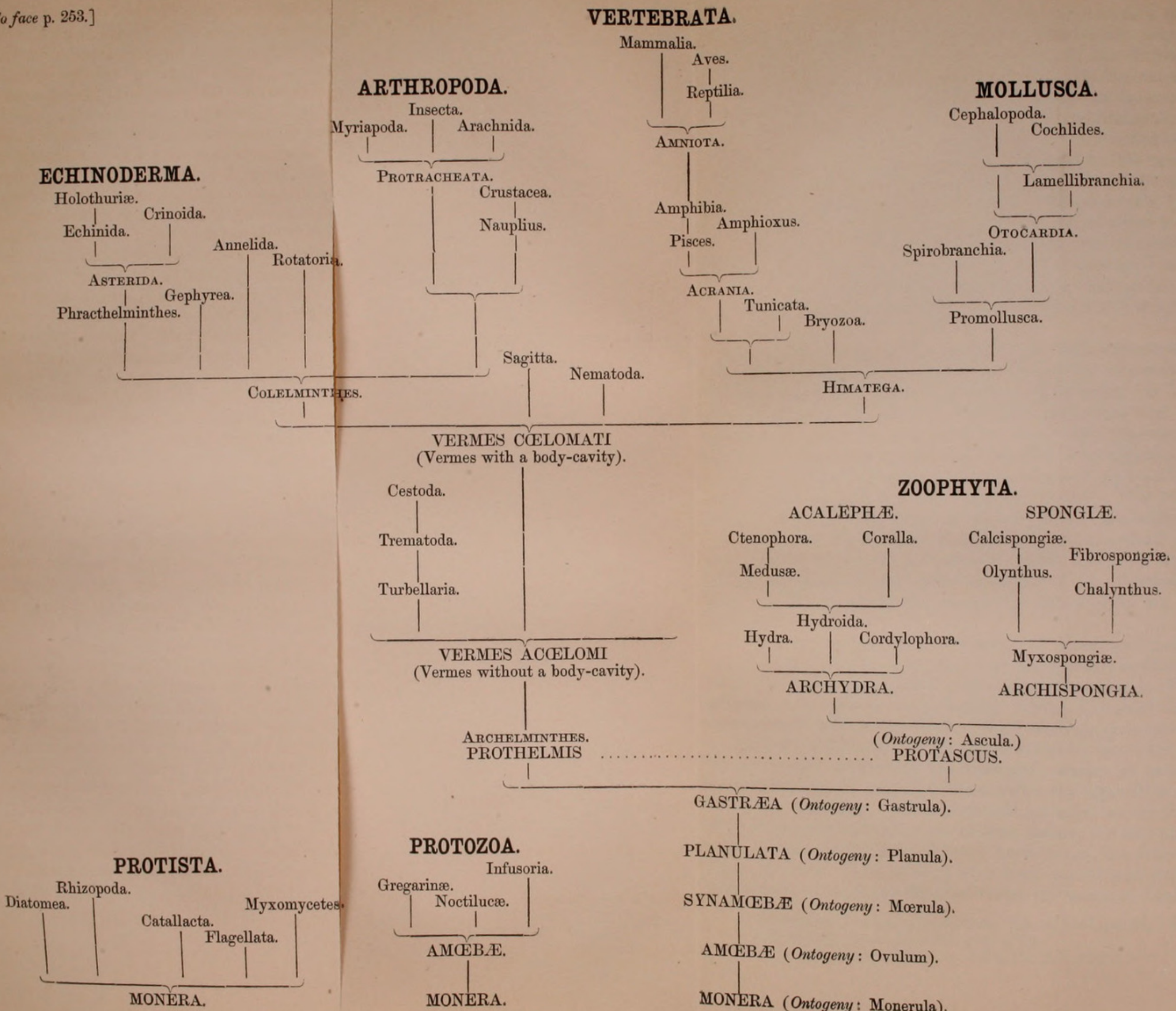
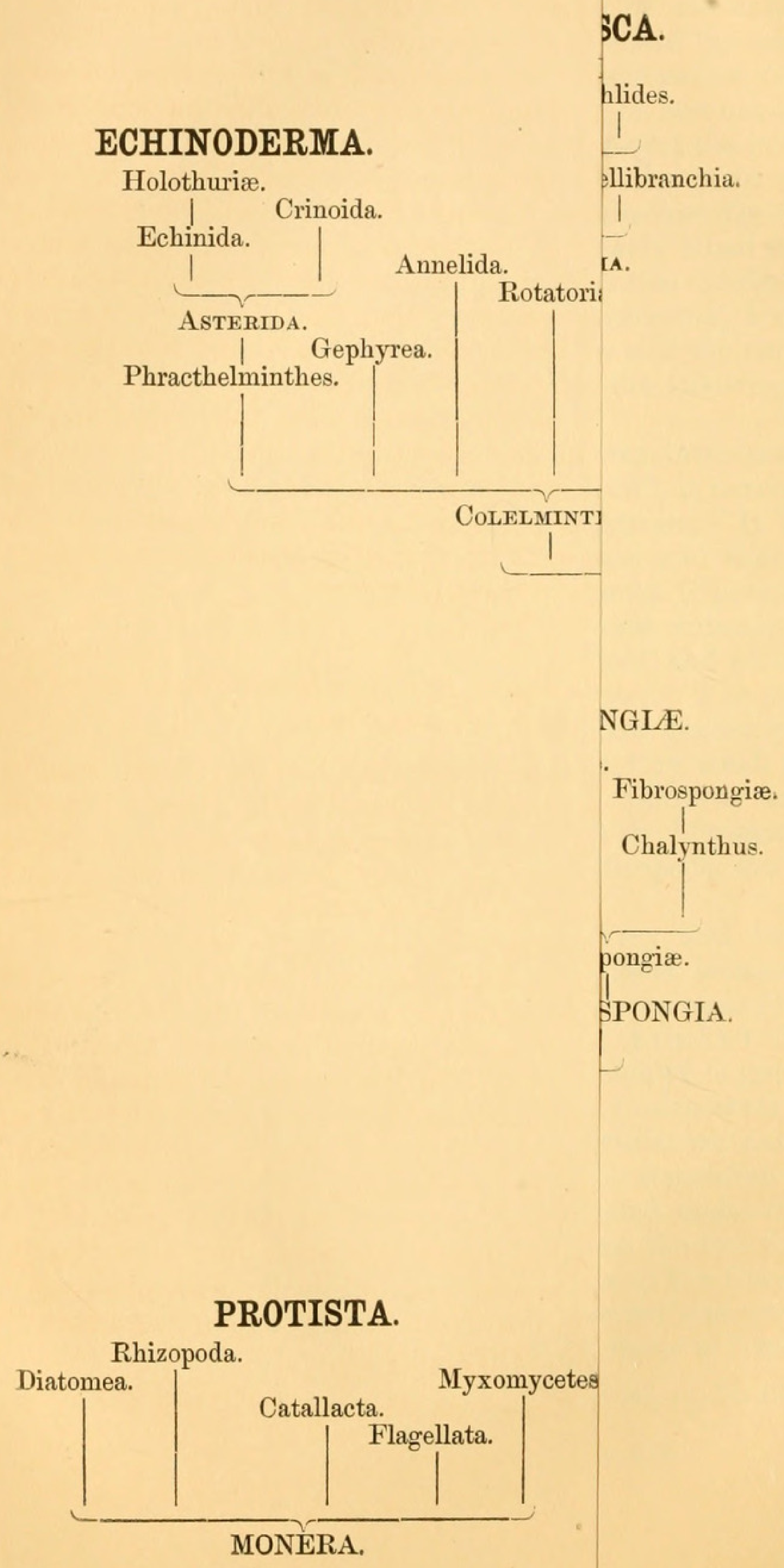

VERTEBRATA.
Mammalia.
Aves.
Reptilia.
AMNIOTA.
Amphibia.
Amphioxus.
Pisces.
ACRANIA.
Tunicata.
Bryozoa.
ARTHROPODA.
Insecta.
Myriapoda.
Arachnida.
PROTRACHEATA.
Crustacea.
Nauplius.
MOLLUSCA.
Cephalopoda.
Cochlides.
Lamellibranchia.
OTOCARDIA.
Spirobranchia.
Promollusca.
ECHINODERMA.
Holothuriæ.
Crinoida.
Echinida.
Annelida.
Rotatoria.
ASTERIDA.
Gephyrea.
Phracthelminthes.
Sagitta.
Nematoda.
COLELMINTHES.
HIMATEGA.
VERMES CŒLOMATI
(Vermes with a body-cavity).
Cestoda.
Trematoda.
Turbellaria.
VERMES ACŒLOMI
(Vermes without a body-cavity).
ARCHELMINTHES.
PROTHELMIS
ZOOPHYTA.
ACALEPHÆ.
SPONGLÆ.
Ctenophora.
Coralla.
Medusæ.
Calcispongiæ.
Fibrospongiæ.
Olynthus.
Chalynthus.
Hydroida.
Hydra.
Cordylophora.
Myxospongiæ.
ARCHYDRA.
ARCHISPONGIA.
(Ontogeny: Ascula.)
PROTASCUS.
GASTRÆA (Ontogeny: Gastrula).
PLANULATA (Ontogeny: Planula).
SYNAMŒBÆ (Ontogeny: Mœrula).
AMŒBÆ (Ontogeny: Ovulum).
MONERA (Ontogeny: Monerula).
PROTOZOA.
Infusoria.
Gregarinæ.
Noctilucæ.
AMŒBÆ.
MONERA.
PROTISTA.
Rhizopoda.
Diatomea.
Myxomycetes.
Catallacta.
Flagellata.
MONERA.

To face p. 253.]



ECHINODERMA.
Holothuriæ.
Crinoida.
Echinida.
Annelida.
Rotatori
Asterida.
Gephyrea.
Phracthelminthes.
Colelminti
SCA.
hlides.
llibranchia.
IA.
NGLÆ.
Fibrospongiæ.
Chalynthus.
pongiæ.
SPONGIA.
PROTISTA.
Rhizopoda.
Diatomea.
Myxomycetes
Catallacta.
Flagellata.
MONERA.

In our sense the Acalephæ coincide with the *Nematophora* of Huxley, and include as three classes the Hydromedusæ, Ctenophora, and Corals (or Anthozoa). The denomination is the more suitable, as, in fact, the urticating organs seem to form the most constant distinction between the Sponges and Acalephæ.

3. Above all, I reject the denomination *Cœlenterata*, because I conceive this group of animals in quite a different sense from Leuckart. This author from the first regarded the central cavity and its ramifications not as a *stomach*, but as a *body-cavity*; and he has also recently (1869) expressly opposed the notion "that the internal apparatus of cavities in them represents in its morphological significance the body-cavity of other animals." I, on the contrary, share in the views of Gegenbaur (1861), Noschin (1865), Semper (1867), and Kowalevsky (1868), that the Cœlenterata (both Acalephæ and Sponges) *possess no body-cavity at all*, and that their internal system of cavities is rather homologous with the intestinal cavity of other animals. This opinion appears to me to be phylogenetically of the greatest importance for the comprehension of the homologies of the animal stem; and it stands in the fullest agreement with the germ-lamella theory.

5. *The Germ-lamella Theory and the Genealogical Tree of the Animal Kingdom.*

Among the phylogenetic questions which have been brought into the foreground of philosophical zoology by Darwin's epoch-making reform of the theory of descendence, one of the most difficult and obscure, but also one of the most interesting and important, is the question of the *blood-relationship of the types or phyla*, the great primary divisions of the animal kingdom, which, since the time of Von Baer and Cuvier have passed as entirely separate and independent unities. In 1866, in my general phylogeny *, I made the first attempt to answer this question, and indeed so far that I assumed the common derivation of the whole animal kingdom from a single stock form, but at the same time regarded the types of the Vertebrata, Mollusca, Arthropoda, Echinodermata, and Vermes as narrower genealogical unities, which were united only at the root. I have also endeavoured to prove this connexion more clearly, and to render it more precise in detail, by the demonstration of intermediate forms, in my 'Natürliche Schöpfungsgeschichte' (1868, pl. 3; 3rd edit., 1872, p. 449).

* Generelle Morphologie, Bd. ii. pp. 408–417, pl. 1.

Within about a year (1867) my phylogenetic hypotheses received a welcome confirmation by the important embryological investigations of Kowalevsky, which made their appearance in the interval. This meritorious naturalist, who for the first time attacked the most difficult questions of comparative ontogeny at their root, and who, by his brilliant discoveries as to the identical ontogeny of *Amphioxus* and the Ascidia, bridged over the greatest gap hitherto existing within the animal kingdom, showed at the same time that in the most different groups of animals the primordial course of development of the embryo is the same, and especially that the *germ-lamella theory*, previously firmly established only among the Vertebrata, also applies to the Invertebrata of the most various groups*. In a more detailed memoir which has recently appeared, these views are further developed†.

That the primordial germ-lamellæ of the higher animals are to be compared with the two permanent formative membranes of the Acalephæ or Nematophora (the *entoderm* and *exoderm*) was shown as early as 1849 by Huxley‡, the discoverer of those membranes. In Kleinenberg's thoughtful and suggestive monograph of *Hydra*, this comparison is more closely demonstrated, and at the same time employed in favour of the view of the monophyletic origin of the animal kingdom.

The anatomy and developmental history of the Calcispongiæ, as described by me, have furnished proof that the sponges also belong to the circle of this stock-relationship, and that indeed in them the two primordial germ-lamellæ are retained through life in the purest and simplest form. The development of the Calcispongiæ from the *Gastrula* is of decisive significance for this theory. *I regard the Gastrula as the most important and significant embryonic form in the whole animal kingdom.* It occurs among the SPONGES (in Calcispongiæ of all the three families), the ACALEPHÆ (*Cordylophora*, Medusæ, Siphonophora, Ctenophora, Actiniæ), the VERMES (*Phoronis*, *Sagitta*, *Euaxes*, *Ascidia*, &c.), the ECHINODERMATA (Asterida, Echinida), the MOLLUSCA (*Lymnæus*), and the VERTEBRATA (*Amphioxus*). Embryonic forms which may be derived without difficulty from the gastrula also occur among the ARTHROPODA (Crustacea and Tracheata). In all these representatives of the most various animal stocks

* Entwickelungsgeschichte des *Amphioxus lanceolatus*, 1867 (Mém. de l'Acad. de St. Pétersb. tome xi. no. 4).

† Embryologische Studien an Würmern und Arthropoden, 1871 (ibid. tome xvi. no. 12).

‡ "On the Anatomy and Affinities of the Medusæ," Phil. Trans. 1849, p. 426.

the gastrula possesses exactly the same structure. In all, its simple, rounded elongate, uniaxial body contains a simple central cavity (stomachal cavity), which opens by an orifice at one pole of the axis. In all the thin wall of the cavity consists of two layers of cells or lamellæ :—an inner lamella of larger, darker cells—the entoderm, gastral lamella, inner, trophic or vegetative germ-lamella; and an outer lamella of smaller, generally vibratile, paler cells—the exoderm, dermal lamella, external, sensorial or animal germ-lamella. *From this identity of the gastrula in representatives of the most various animal stocks from the Sponges to the Vertebrata I deduce, in accordance with the biogenetic fundamental law, a common descent of the animal Phyla from a single unknown stock form,* Gastræa, *which was constructed essentially like the gastrula**.

6. *The Body-cavity and Intestinal Cavity of Animals.*

If the preceding comparisons are correct, and consequently the two primordial germ-lamellæ are homologous throughout the animal kingdom from the Sponges to the Vertebrata inclusive, it follows immediately and as a matter of course that *the Zoophyta or Cœlenterata cannot possess a body-cavity,* and that all the internal cavities of their body (leaving out of consideration the intercanal system of certain sponges) belong to the gastro-canal system, and are parts or diverticula of the intestinal cavity. *All these gastro-canals are originally lined by the entoderm, the gastral lamella, or intestino-glandular lamella,* as is the case with the intestinal canal and its appendages in all the higher animals. Perhaps it will be of

* Only the Protozoa are excluded from this common descent. For them I assume for the most part an independent polyphyletic descent, especially for those so-called " Protozoa " which might equally well be regarded as plants or animals, and are therefore best grouped as neutral Protista. Other Protozoa undoubtedly belong partially to the direct progenitors of the Gastrula, as especially the Amœbæa and Monera. The scruples which may arise against the homology of the gastrula in all the different animal stocks I will refute elsewhere. The most important objection seems to consist in the fact that the Gastrula is supposed to originate in two perfectly different ways from the Morula :—sometimes (in the Sponges, Hydroida, some Vermes, &c.) by *the central excavation of the Morula, and the breaking through of the stomachal cavity thus formed;* sometimes (in other Vermes, Ascidia, Echinodermata, *Amphioxus*) by the formation of a *germinal vesicle* (*Blastosphæra*), a hollow sphere, the wall of which consists of a layer of cells, and *by the inversion of this germinal vesicle into itself.* This difference, which is apparently so essential, requires, however, to be more accurately investigated with regard to its meaning and diffusion; and as it occurs in very nearly allied forms of the same stock (*e. g.* the Hydroida and Medusæ), I regard it (supposing it to be real !) as quite unessential, originating by secondary counterfeiting of the ontogenesis. In both cases the result is exactly the same.

advantage, in order to express this thoroughgoing homology, to designate the primordial rudiment of the intestine, such as persists through life in the simplest form in *Olynthus* and *Hydra*, as the *primitive intestine* (*Urdarm*, *progaster*), and its orifice as the *primitive mouth* (*Urmund*, *prostoma*), especially as, according to Kowalevsky's statements, this primordial mouth-opening appears (at least in many animals) to represent not the future permanent mouth, but the future anus.

The true body-cavity, which is usually termed the *pleuro-peritoneal cavity* in the Vertebrata, and for which we propose instead of this sesquipedalian term the more convenient denomination *cœloma* (*κοίλωμα*, a cavity), occurs only among the higher animal stocks, the Vermes, Mollusca, Echinodermata, Arthropoda, and Vertebrata. As the ontogeny of the Vertebrata shows us, this cœloma always originates between the inner and outer germ-lamellæ, by a splitting of the middle germ-lamella into a cutaneous and an intestinal fibro-lamella. Now, as the middle germ-lamella is entirely deficient in the Sponges, no cœloma can occur in them. It is equally absent in the Acalephæ, although in these a middle germ-lamella (mesoderm, or muscular lamella) is already developed. It is therefore of great importance to our monophyletic theory of descent that *the lowest Vermes* (Turbellaria, Trematoda, Cestoda, &c.) *are also entirely destitute of a cœloma*, which is only developed in the higher Vermes (*Vermes cœlomati*), from which it has been inherited by all the four higher stocks. The Vermes without a body-cavity (*Vermes acœlomi*) are *in this respect* "*Cœlenterata.*"

The true body-cavity, or cœloma, therefore, can never, like the intestinal or stomachal cavity, be enclosed by the entoderm. Leuckart certainly says expressly (even in 1869), "The body-cavity of the Cœlenterata is not situated between the exoderm and entoderm, but is enclosed by the latter;" but this very statement proves that Leuckart's conception of the "Cœlenterate type" is quite erroneous. Neither can the body-cavity ever communicate directly with the stomachal cavity or the intestinal cavity, as is said to be the case with the Cœlenterata in the writings of Leuckart and many other authors. The anatomy and ontogeny of the cœloma, or pleuroperitoneal cavity, in all the higher animals shows rather that this *true body-cavity is from the first commencement a perfectly distinct cavity*, quite independent of the intestinal tube, which is never connected with it. The buccal opening never leads into the true body-cavity; and when Leuckart and others conceive of the intestinal or stomachal cavity of the Cœlenterata as a "body-cavity," they ought, to be consistent, to call its aperture not a buccal orifice, but a *porus abdominalis.*

In the case of these and of many other difficult morphological conditions, the true and correct conception comes at once in its full power when we consider them in the light of the theory of descent. The first organ which the primordial, multicellular *Synamœba* must have formed for itself on the commencement of organological differentiation was the *intestine.* The inception of nutriment was the first requirement. In this way was produced the *Gastræa*, the whole body of which is still intestine, as in the *Protascus*, and as in *Olynthus* and *Hydra* (in the latter leaving out of consideration the tentacles). It was only much later, after the production of the middle germ-lamella, that the true body-cavity was formed in the latter (by the splitting of the mesoderm, the solid cell-mass between exoderm and entoderm). In it fluid accumulated—the first *blood.* In all animals which have a true body-cavity this is filled either with blood or lymph (therefore communicating directly with the blood-vascular system!), but never with chyme or chyle, or with crude nutritive material. *Consequently the cavities of the gastro-canal system in the Sponges and Acalephæ are not body-cavities, but an intestinal cavity.*

7. *The Origin of the Mesoderm and of the Generative Organs.*

In connexion with the preceding theory of the homology of the germ-lamellæ in the whole animal kingdom, some questions closely related to it may be briefly treated. For this purpose we assume the alleged homology as proved so far as that the primitive intestine in all animal-stocks, from the Sponges to the Vertebrata, is originally identical, and produced from the entoderm of the *Gastrula*, and in the same way the dermal lamella (neuro-corneous lamella) is produced from the exoderm of the *Gastrula**.

In the Sponges, certainly at least in the Calcispongiæ and in many other low sponges, the two germ-lamellæ persist through life in their original simplicity. In the lowest Acalephæ also we still find them so. But even in *Hydra* a third lamella,

* The opinion expressed by Kowalevsky (*l. c.* 1871, p. 6), that the intestino-glandular lamella of the insects is not homologous with that of other animals, but a perfectly distinct lamella, I regard as erroneous. It is precisely among the insects that the ontogeny is very strongly falsified by secondary adaptation. On the other hand, I regard the embryonal envelopes (and especially the amnion) as decidedly not homologous in Insects and Vertebrata. They are only analogous envelopes, and are wanting in the lower Vertebrata.

a *muscular lamella*, begins to be developed between the two lamellæ; and this constitutes, in the higher Acalephæ, a distinct mesoderm with greatly differentiated products. Now, as, according to Kleinenberg's careful exposition, this muscular lamella proceeds directly from the exoderm, and as Kölliker also with great certainty derives the mesoderm of the Acalephæ from the exoderm, the question of the origin of the middle germ-lamella ought by this means to be brought nearer to its solution. It is well known that most ontogenists derive the middle germ-lamella in the Vertebrata from the splitting of the inferior one, whilst others make it originate from the superior germ-lamella. The morphology of *Hydra*, in which the individual muscles composing the middle lamella are nothing more than internal processes of the cells of the exoderm, and remain throughout life in connexion therewith, appears to prove the origin of the mesoderm or muscular lamella from the outer germ-lamella, the exoderm (see note p. 261).

Greater difficulties are presented by the question of the origin of the *generative organs*. In the embryology of the Vertebrata, the first rudiments of the sexual glands have been derived, even in the most recent times, by some from the upper, by many from the middle, and by others from the inferior germ-lamella. Consequently all the three possible views have at present their supporters. If we endeavour to solve these contradictions on the basis of homology above affirmed by regarding the origin of the sexual cells in the Zoophytes as furnishing a rule, we find unfortunately that the same differences prevail here also. Nearly an equal number of observers represent the ova and sperm-cells of the Acalephæ as produced from the exoderm and from the entoderm. The sexual cells originate from the *entoderm*, according to my own observations in the Medusæ* (1864), according to the investigations of Kölliker† "in Medusæ and Hydroid Polypes without exception" (1865), and according to the statements of Allman‡ in the Sertulariæ and Tubulariæ (1871).

The still unpublished investigations of Dr. Gottlieb von Koch also agree with this; and he has shown me numerous preparations of Coralla (*Veretillum*, *Cereanthus*, &c.) and of Hydroids (*Coryne*, *Tubularia*, &c.) which seem to prove undoubtedly the origin of the ovicells from the epithelium of the gastro-canal spaces.

* "Die Familie der Rüsselquallen (*Medusæ Geryonidæ*)," Jenaische Zeitschr. Bd. i. 1864, p. 449.

† Icones Histologicæ, Heft ii. 1865, p. 89.

‡ Monograph of the Gymnoblastic or Tubularian Hydroids, 1871, p. 149.