between the membrane of the test and the madreporic plate. Other tubular glands, situated on the opposite side of the œsophagus, in the thickness of the mesentery itself, open in part with this excretory duct, and in part directly beneath the madreporic plate, the pores of which probably give issue to the secreted liquid. It is to be observed that, by the intermediation of the infundibuliform space situated below the madreporic plate, the circulatory apparatus and this glandular apparatus communicate with each other, so that an injection driven through the supposed heart may descend again through the sand-canal.

In the Spatangidæ (*Amphidetus*), which have been said to have no trace of a heart, I have found a gland exactly similar to that which hitherto has been regarded as the heart in the Echinida.

Lastly, I have ascertained, by varied experiments, that the water which fills the cavity of the test of the sea-urchins can only penetrate them slowly and by endosmose, either through the buccal membrane or through the ambulacral tubes. When sea-urchins have lived for some time in sea-water coloured with aniline, we very regularly find the entire œsophagus and the siphon by which it communicates with the point of reflexion of the intestine coloured red. There has consequently been an introduction of water into the intestine by this course, and a possible passage of a part of this water into the general cavity through the walls of the digestive tube. —*Comptes Rendus*, November 16, 1874, tome lxxix. pp. 1128–1132.

Embryology of the Ctenophora. By Alexander Agassiz.

The question of the systematic position of the Ctenophora can now, thanks to the greater knowledge we have of their embryology, be treated more intelligently. The position taken by Vogt, who follows Quoy in removing them from the Acalephs altogether, and associating them with the Mollusks on account of the apparent bilaterality so strongly developed in some families (*Cestum*, *Bolina*, and *Mertensia*), seems not untenable. The nature of their relations to Echinoderms, Polyps, and Acalephs, as well as the general relations of the Cœlenterata to Echinoderms, may be discussed again, especially as having an important bearing not only on the value of the Cœlenterata as a primary division of the animal kingdom, but also on the limits of the Radiata, and the possible affinities of the Sponges and Cœlenterata suggested by Häckel*. A still more important point developed from this embryology is its connexion with the *Gastræa* theory of Häckel†, for which he claims that it will supplant the type theory, and give us in its place a new system based upon the homology of the embryonic layers and of the primitive digestive cavity. Häckel attempts, in his *Gastræa* theory, to find an explanation for the natural development of species from a purely mechanical cause, and has been bold enough not only to

* E. Häckel, 'Die Kalkschwämme,' Berlin, 1872.

† E. Häckel, "Die *Gastræa*-Theorie," Jenaische Zeitschrift, ix. 1874.

name, but also figure, the primitive ancestor from which all types of the animal kingdom have been developed! This unknown ancestor, he says, must have been built much like his *Gastrula* (only another name for what has long been known to all students of Invertebrates as the *Planula* of Dalyell). Häckel would lead us to believe that this *Gastrula* is a newly discovered embryonic stage; all he has done in reference to it is to recall the existence of *Planulæ* among Sponges, which had previously been discovered by N. Miklucho-Maclay*. Since the publication of Häckel's article, his special interpretation of fanciful affinities and homologies existing only in forms conjured up by Häckel's vivid imagination, have been sufficiently criticised by Metschnikoff†; so that until we know something more of the development of Sponges we may leave the discussion of their affinities with Cœlenterates out of the question, in spite of the ingenious arguments advanced to support Leuckart's views on the subject.

The existence of *Planulæ*, the walls of which consist of an ectoderm and entoderm, has been distinctly proved for Acalephs, Echinoderms, Polyps, Worms, Arthropods, Tunicates, Mollusks‡, and finally for *Amphioxus*; the papers of Johannes Müller, Krohn, Agassiz, Kowalevsky, Sars, Allman, Claparède, Kupfer, Metschnikoff, and others are too well known to need citation in this connexion. So far we are in perfect accordance with Häckel and cordially agree with him in his estimate of the systematic value of this early embryonic stage, whether we call it *Planula* or adopt his latter name of *Gastrula*. But let us follow his subsequent steps and separate what is known from what is stated as known by Häckel. It is known that the *Planula* consists of an entoderm and of an ectoderm. It is known that the primitive digestive cavity is, in the case of Echinoderms, of Ctenophora, and of some Discophora, formed by the turning-in of the ectoderm, so that the wall of this primitive cavity is, in their case at least, invariably formed by the ectoderm. It is known, on the other hand, that in Actiniæ, in Worms, in Hydroids§ this primitive digestive cavity is hollowed out of the inner yolk mass of the embryo, and has its walls formed by the entoderm. We must lay great stress on this point, which is alluded to by Häckel as of no consequence‖; for this seems to us to destroy the very base of his argument. If the *Gastrula* can in one case, and in such closely allied classes as Actiniæ and Hydroids on one side, and Echinoderms and Ctenophora on the other, be built so differently that in the first case the walls of the primitive cavity are formed by the entoderm, and in the other of the ectoderm, what becomes of all

* N. Miklucho-Maclay, Jen. Zeitschrift, iv. 1868.

† E. Metschnikoff, "Zur Entwickelungsgeschichte d. Kalkschwämme," Zeits. f. wiss. Zool. xxiv. 1874.

‡ E. R. Lankester, "On the Primitive Cell-layers of the Embryo," Ann. Mag. N. H. May 1873.

§ H. Fol, "Die erste Entwickelung d. Geryonideneies," Jen. Zeitsch. vii. p. 471.

‖ Häckel and Lankester both seem to think that because the result is a similar form it must be homologous.

his subsequent generalizations of the value for systematic purposes of these two layers? The distinction of entoderm and ectoderm is, as Häckel himself acknowledges, and as is sufficiently shown by Kowalevsky, of the greatest anatomical value; yet how is it possible that these differently constructed *Planulæ* should have the genetic connexion claimed for them by Häckel, if in their very embryonic stages the differences are of so radical a nature that, according to the very theory of embryonic layers so strongly insisted upon by Häckel, they could have no possible relation, the one being a product of the entoderm, the other of the ectoderm, the two primitive embryonic layers?

It is not known, as is stated by Häckel, that the walls of the primitive digestive cavity are invariably formed of the entoderm; and when Häckel states the result (the *Gastrula*) to be the same whether formed by the ectoderm or entoderm, he states what is known to be exactly the contrary. It is not known, as is stated by Häckel, that the mere fact of a *Planula* fixing itself by one extremity or not, will in one case lead to a radical type, in another to a bilateral type. What becomes of all the free-swimming embryos of Echinoderms, of Acalephs, of Polyps? Are they bilateral? It is true Häckel is obliged, to suit his theory, to consider the Echinoderms as an aggregation of individuals; but he has not the countenance of a single zoologist whose opinion on Echinoderms is of any value. When he says that Sars, whose knowledge of the development of Echinoderms was so accurate, agreed with his peculiar views, we can only reply that his agreement must be based upon a misunderstanding. We have equally as many radial and bilateral types developed either from fixed or from pelagic *Gastrulæ*; and to cite this as a *causa efficiens*, the mechanical reason of the genetic descent of all radiates from a fixed *Gastrula*, and of all bilateral types from a free-swimming one, is simply fantastic. How is it that so many Actiniæ and Acalephs have their radiate structure developed long before they become fixed? It is not known that the embryonic layers of Acalephs are truly homologous to those of the higher Vertebrates. Huxley simply speaks of their bearing the same physiological relation to one another; but until we know the *Gastrula* of other Vertebrates than *Amphioxus* it is idle to talk of the continuity existing between the ontogeny of *Amphioxus* and the remaining members of the Vertebrate branch, and to say that hence there is *no doubt left* that the ancestors of the Vertebrates must, in the beginning of their development, have passed through the *Gastrula* form! Neither Häckel nor any one else has seen this; it is a pretty hint which may or may not be proved.

Considerable confusion arises in Häckel's classification from his adopting at one time as of primary importance the development of the cavity of the body and making it the main point in his phylogenetic classification, while previously the relations of the phylum to *Protascus* and *Prothelmis* (names he gives to the unknown ancestors of the radial and bilateral types) formed the basis of his classification. This places him in the awkward predicament of having a phylum of the animal kingdom (the radial) which has lost the

capacity of forming a body-cavity, and yet its descendants have in some unaccountable manner (entirely against the rules of Häckel's theory) managed to get one by some unexplained method. We do not see how it can be so confidently stated by Häckel that Echinoderms have lost their original central nervous organ; there is no proof whatever of its once having existed. There is as yet no proof whatever that the organs of sense (which, as had already been so often insisted upon by Agassiz, are not homologous in the different branches of the animal kingdom) have the same phylogenetic origin. When Häckel says that the mouth of Echinoderms is not homologous to the primitive mouth, we can only refer him to the memoirs of Müller, Metschnikoff, and myself on Echinoderm embryos for proof to the contrary.

There seems no doubt, as Häckel insists, that to the majority of zoologists of the present day the idea of type is a very different one from that of type as understood by Baer and Cuvier. The probability of their original community of origin is hinted at from the many so-called intermediate forms, both living and fossil, which, though we may enroll them either in one great branch of the animal kingdom or another, yet show that we can no longer consider the great types of the animal kingdom as closed cycles, but must hereafter regard them as holding to one another relations similar to those which the remaining categories of our systems have to one another. This change has principally been brought about by a better knowledge of the embryology of a few well-known types.

But what becomes of all the assumptions of Häckel which form the basis of his *Gastræa* theory? They are totally unsupported; and with their refutation must fall his theory; it can only take its place by the side of other physiophilosophical systems; they are ingenious arrangements laboriously built up in the interests of special theories, which fall to the ground the moment we test them by our actual knowledge. That the time has not yet come for embryological classifications, the attempts of Häckel plainly show; for they are in no wise in advance of the other embryological classifications which have preceded them: we get new names for somewhat different combinations; but a truly scientific basis for a classification based upon the value of embryonic layers is at present impossible; such attempts can be only speculations, to be proved or disproved on the morrow.

What Häckel substitutes in the place of the accepted types of the animal kingdom is simply another view of these same types; and his *Gastræa* theory is in no danger of upsetting, at present at least, zoological classification as now understood. Indeed, if we need an ancestor for our phylum, why not at once go back to the cell? There we have a definite starting-point, a typical element which underlies the whole of the animal kingdom, and which forms the walls of Häckel's *Gastrula*. Then we shall all be agreed; and when we frankly state that all organisms are derived from a primitive cell and from its subsequent increase, we come within the range of positive knowledge, but we are unfortunately as far as ever from having for that reason been able to trace a mechanical

cause for the genetic connexion of the various branches of the animal kingdom. We must meet the direct issue raised by Häckel (that such a genetic connexion either does or does not exist) by repeating what has so often been said by others:—This genetic connexion may exist; but we have at present no proof that it does exist. And, at any rate, his *Gastræa* theory does not bring us any nearer to a mechanical explanation of such a genetic connexion, however probable it may be. . . . .

Here we must call attention to a marked difference between Acalephs and Polyps on one side, and Echinoderms on the other—that while in the former the connexion between the digestive cavity and the water-system always remains open, it is at one time disconnected in the Echinoderms, though it is eventually reopened through anastomoses of the water-tubes. The anal opening holds in Ctenophora very much the same relation which it holds in Echinoderm larvæ, in which the water-tubes are still connected with the primitive digestive cavity. When we find, as we do, that in Ctenophora, as well as in Echinoderms, the primitive digestive cavity is formed by the inturning of the ectoderm, that in both classes the water-system is developed as diverticula from this digestive cavity, we fail to see how we can separate the Ctenophora from Echinoderms and place them with Polyps in a separate subkingdom of the animal kingdom. No one questions the relationship of Ctenophora to Acalephs; yet from embryological data it would be more natural to associate Echinoderms and Ctenophora into one subkingdom, characterized by the mode of formation of the water-system as diverticula forming eventually chymiferous tubes in both classes, and to associate the other Acalephs with the Polyps*, where the chymiferous tubes and cavities are formed by the liquefaction of the interior of the *Planula*. Any one who will compare the figures of the embryos of starfishes (A. Agassiz, Embryol. Starfish, pl. ii. fig. 8) and Ctenophora (pl. iii. figs. 6–10, pl. v. figs. 5, 11) at the time when the chymiferous tubes are reduced to mere diverticula, cannot fail to feel satisfied of their complete identity of plan. Metschnikoff has made, in addition to the homologies I have just recalled, a most interesting comparison between an Echinoderm larva and a Ctenophore; he shows that, even in the adult Ctenophore, the identity of plan is not destroyed, and is carried out to the smallest details. The only point in which I would differ from him is in his comparison of the abactinal cœliac openings to the actinostome: he seems to forget that in Echinoderm larvæ what at first performed the part of anus and mouth eventually becomes the mouth alone; so that his figures should be reversed, and then the identity will be found complete between an Echinoderm larva (see A. Agassiz, Embryol. Starfish, pl. iii. fig. 6, and pl. vii. fig. 8) with its œsophagus, digestive cavity, alimentary canal and its chymiferous pouch (water-system), from which run the diverticula eventually to become the water-tubes,

* See Allman's views on the position of the Ctenophora as contrasted with the Actinozoa, Trans. R. S. Edinb. xxvi. pt. ii. p. 466, 1871.

and a Ctenophore (pl. iii. fig. 25) with its lateral tubes on the sides of the digestive cavity (*g*), leading into the chymiferous pouches (*w*), branching into the chymiferous tube. The cœliac openings (pl. iii. fig. 45, *ca*) of the funnel he looks upon as representing the madreporic body, while I look upon them as the anal openings. In this view of the case, the Ctenophore is rather more in the embryonic condition of the Echinoderm larva, when the actinostome leading into the digestive cavity should perform at the same time the function of mouth and anus, which it occasionally does, although at other times the cœliac opening of the funnel seems to be the true anal opening, while, according to Metschnikoff, it is the madreporic body which performs the part of an anal opening. He says it only acts to introduce water into the system, which is contrary to my observations.

I may here recall former statements* concerning the affinities of the Ctenophora, when describing some of the younger stages. It could only be after a careful comparison of Ctenophorous and Echinoderm embryos that undoubted evidence of their identity of plan might be obtained. The Ctenophora retain the permanently embryonic features of Echinoderm embryos, in which the water-system is still connected with the digestive cavity. The formation of a funnel as a sort of alimentary canal, opening externally through the cœliac apertures at the abactinal pole, corresponds to the existence of a short alimentary canal in Echinoderm larvæ. The Ctenophora are, from their embryology, more closely related to the Echinoderms than to the other Acalephs; and it seems natural to separate the Acalephs into two orders—the Ctenophora, characterized by the presence of locomotive flappers, and the Medusidæ, including the Discophora and Hydroids.—*From the Memoirs of the American Academy of Arts and Sciences*, vol. x. no. iii., August 1874.

Notice of Papers on Embryology by A. Kowalevsky. By A. Agassiz.

A. Kowalevsky has published, unfortunately in Russian, two capital papers on embryology. The one continues the investigations he had been carrying on regarding the existence of an ectoderm and entoderm layer in the early embryonic stages of Invertebrates. In the present paper he has given a summary of the early stages of a *Campanularia*, confirming the observations of Wright and A. Agassiz. For *Rhizostoma* and *Cassiopea* he shows that the digestive cavity is formed by the invagination of the ectoderm. This is contrary to the results of previous observers, except Schneider. For *Pelagia* he shows a direct development from the egg remarkably similar to that of the Geryonidæ as we know it from Häckel, Fol, and Metschnikoff. He adds nothing to the embryology of Actinia not already known from the magnificent monograph of Lacaze-Duthiers. He then passes on to the development of *Alcyonium*, of which he gives an extremely interesting sketch supplemented by fragments on the embryology of *Astræa*, *Gorgonia*, and *Cerianthus*: the development of the latter is strikingly similar to that of *Edwardsia*, as we know it during its passage from *Arachnactis* to *Edwardsia*. He

* Alexander Agassiz, Ill. Cat. M. C. Z. no. 2, p. 12, 1865.