Zoology. — *"On the relationship of various invertebrate phyla."* By Prof. A. A. W. HUBRECHT.

In an elaborate paper entitled "Beitrage zu einer Trophocoltheorie," published in 1903 in the 38th volume of the "Jenaische Zeitschrift fur Naturwissenschaft," Prof. ARNOLD LANG of Zurich (p. 68—77) gives a clear exposition of what has been, in his opinion, the phylogenesis of the Annelids.

In this pedigree he places, beginning with a protocoelenterate, a ctenophore-like being, a plathelminth, an intermediate form resembling a triclade, an animal in the shape of a leech which already possesses metameric segmentation and finally a proto-annelid.

The grounds on which he bases this phylogenesis, compel us to acknowledge important relations between these animal groups. But whether this kinship testifies to a descent in the order given by Lang, or whether the order has for the greater part been a reversed one, deserves to be examined more closely.

In my opinion there Ctenophores should not be placed at the beginning of the series, nor are they to be considered as links between Coelenterates and worms, but they have to be looked upon as animals, which form the last offshoots of an evolutionary series, leading from the Annelids via the Hirudinia and the Plathelminthes. Of these latter there have been some which gradually assumed a pelagic mode of life and have become Ctenophora, the external resemblance of which with transparent jelly-fish seemed to justify their being placed by the side of the Coelenterates.

Let us first test the grounds on which that combination has until now been defended (see e. g. G. C. BOURNE in RAY LANKESTER'S Treatise on Zoology, 1900).

The presence of a gastro-vascular system and the absence of an independent coelom, as well as the presence of a subepithelial nerveplexus are characteristics which can be found not only with the Coelenterates, but also to a great extent with the Plathelminths.

The tentacles of the Ctenophores have quite wrongly been compared to those of the medusae, while the analogy of the adhesive cells of the Ctenophora with the nematocysts of the Cnidaria is also defective. And if nematocysts should be found in some Ctenophora, no conclusions should be based on this, because they also occur in Molluscs, Plathelminths and Nemertines.

The absence of nephridia, the general structural proportions and the gelatinous composition of part of the organism are details which

by no means interfere with a view which would see in the Ctenophora Plathelminths that have become pelagic.

That the connection which HAECKEL intended to establish between Coelenterates and Ctenophora, when describing Ctenaria ctenophora, is an imaginary one, has already repeatedly been shown, so e. g. by R. HERTWIG ("Jen. Zeitschr". Bd. 14, p. 444), G. C. BOURNE (l. c. p. 445) and others. The first-mentioned author says emphatically (l. c. p. 445): "Die Ctenophoren sind Organismen welche sich von den übrigen Coelenteraten sehr weit entfernen." Also KORSCHELT and HEIDER in their excellent handbook on the embryology of the invertebrates are inclined (p. 100) to look upon the Ctenophora rather as an independent branch of the animal kingdom, the connection of which with that of the Coelenterates lies far backward. On the other hand they point out unmistakable relations between the phylogenesis of the Ctenophora and that of the Bilateria (Annelids, Arthropoda, Molluscs etc.). They expressly add that the side-branch of the animal kingdom on which the Ctenophora are placed *cannot be considered as having furnished a starting-point for higher animal forms.*

Ctenoplana and Coeloplana are consequently not considered by them as advancing steps of development in the direction of the Plathelminths, but as aberrant, creeping Ctenophora. LANG himself has acknowledged on page 72 of his great handbook that the place of the Ctenophora among the other Cnidaria is a very problematical one and that their embryology distinguishes them from all Cnidaria.

So there can be no doubt, considering all this, that the tie which nowadays keeps together the Ctenophora with the Coelenterates has of late years been considerably slackened. One effort and it may be entirely removed [1]).

What on the other hand have we to think about possible relations between Ctenophora and Plathelminths? These relations appear especially striking to those who have occupied themselves with the embryological development of both classes.

Thus SELENKA has already in 1881 summarized this analogy under twelve heads (zur Entwickelungsgeschichte der Seeplanarien, S. 283). Also LANG in his monograph on Polyclads (1884) has emphatically pleaded for that relationship, although in a separate paragraph he acknowledges the existence of real difficulties. Also in his most recent paper he adheres to the same opinion.

The discovery of two very peculiar genera of animals has still more

[1]) A paper, published very recently in the Zoologische Anzeiger (Bd. 27, p. 22 3) on a new, much simplified Ctenophore, does not, as its author DAWYDOFF suggests, strengthen the bond between Coelenterates and Ctenophora.

emphasized the problem of the relationship between Ctenophora and Plathelminths, I mean Ctenoplana and Coeloplana. In different degree they unite properties of both classes as has already been clearly elucidated by their discoverers: KOROTNEFF and KOWALEWSKY. Yet neither BOURNE who prepared the Ctenophora for RAY LANKESTER's large Textbook of Zoology, nor KORSCHELT and HEIDER in their handbook mentioned above, nor WILLEY, who lately studied Ctenoplana in a living condition, are really convinced of the possibility of a derivation of Plathelminths from Ctenophores, in which case these two genera should have to be considered as intermediate forms in that direction.

So WILLEY e.g. points out that it is not very probable that littoral forms would have sprung from pelagic ones, whereas generally the contrary is observed. This would according to him have been a reversion of the natural sequence. The future will show, in my opinion, that the difficulties mentioned, and raised by such able experts, will for the greater part vanish as soon as relationships "against the grain", i. e. in the unnatural order, are no longer accepted, but when both genera are considered as gradually mutating Plathelminths which are already fairly on the way of assuming ctenophoran habitus.

From what precedes we may at any rate infer that whereas the Coelenterate relationship of the Ctenophora has faded, their comparability with the Plathelminths has come to the fore.

The data for judging in how far a derivation of the Annelids from Plathelminths might be possible are given in extenso especially in LANG's earlier and later publications, more particularly in his well known Gundapaper (1881) of which he has given an improved and partly modified edition in his most recent essay, quoted in the beginning. So I need only refer to this latest paper here.

I for my part must now try to show that a derivation *in the opposite direction* presents no difficulties. We then should look upon Plathelminths and Ctenophores no longer as ancestral forms but as modified and in many respects unilaterally modified descendants of a more primitive, Annelid-like type.

LANG has already in his Polyclad-monograph (p. 674) openly declared himself against such a view. Yet in the twenty years which have since elapsed, various considerations have changed and it seems that CALDWELL's view (Proc. R. Soc. 1882 no. 222) has become more probable again, according to which "there is a presumption ... that in fact Platyelminths are degenerate Enterocoeles."

I should be willing like to undertake the defence of this thesis and to see in the Plathelminths degenerate forms in which the

coelom has almost entirely disappeared, while the genital apparatus has obtained a maximum degree of complication.

At the outset it seems to me to be less probable that at the base of the pedigree of the Annelids such animals should stand like the hermaphrodite Plathelminths with their ovaries, testes, vitellaria, so greatly varying in size and shape; with their shell-glands, ootype, cirrus, penes, uterus, spermatheca, etc., not even to mention the vitello-intestinal, the Laurer- and other canals. Does not this very complication force us to place such animal forms rather in the peripheral branches than near the root of any pedigree?

On the other hand we can state that in those Polychaeta which have retained archaic characters, such as Polygordius, Protodrilus and Saccocirrus, various peculiarities draw our attention which in Plathelminths are further developed. So the phylogenesis of the Plathelminths would not necessarily have to be so long, via Polychaeta, Oligochaeta, Hirudinea, but the type of Plathelminths might already at an early period have been a deviation of the original coelomatous ancestral forms, while in the course of this evolutionary process also the present Oligochaeta and Hirudinea might have sprung off laterally.

Meanwhile the stronges argument for the degeneration of the Plathelminths seems to me to be found in their early ontogenesis.

When we consider this in the light which not long ago especially American workers have procured to us, we ought to pay attention to the phenomena of *cell-lineage:* the descent of special groups of tissue from certain mothercells. WILSON, CONKLIN, MEAD and others have shown us the way here.

Of paramount importance is the fact that Annelids (Polychaeta Oligochaeta, Hirudinea) and Molluscs in those earliest phases of development show a striking uniformity and that e.g. in all of them the couple of mothercells of the so-called mesoblast-bands, within which the coelom and metamerism appear first, originate in a similar manner from one cell, the oldest, unpaired, mesodermic mother-cell, belonging to the 64-cellular cleavage phase.

This cell lies in the second quartet of cells reckoned from the vegetative pole and is produced by a plane of division slanting to the left. The next cleavage always divides this cell into a right and left mesodermic cell; these two develop into the paired mesodermic bands.

All this is always observed in the animal phyla above-mentioned. Concerning the Plathelminths LANG provided us already twenty years ago with extensive data, which however do not constitute an unbroken series such as is necessary for establishing the cell-lineage. Such a series was given us a few years ago (1898) for Leptoplana

by E. B. WILSON (Annals of the New-York Academy of Sciences, vol. XI p. 13). From his publication we may conclude as follows:

1. That a cell-couple as represented by LANG for Discocoelis, is also present in Leptoplana, which MEAD has compared to the mother-cells of the mesoblastbands of Annelids and Molluscs, *although from this cell-couple no mesoblast develops in either genus of Plathelminths.*

2. That, moreover, with Leptoplana, four cells of the second cell-quartet (counted from above) become the mother-cells of "larval mesenchym", that they remove to the interior and that by further subdivision they gradually furnish the whole mesoblast of Leptoplana. This origin of the mesoblast in Plathelminths was also already known to LANG.

3. That also with Molluscs (Unio, Crepidula) and probably also with certain Annelids (Aricia), beside the two symmetrical mesoblast bands still another source of mesoblastic tissue occurs, which is directly comparable to the source of larval mesenchym mentioned in 2, and that also these mesenchym mother-cells originate from cells belonging to the ectoblast quartet, as with the Plathelminths.

4. That consequently it may be considered a settled fact that with Annelids and Molluscs the mesoblast has a twofold origin [1]).

CONKLIN (Vol. XIII, Journal of Morphology, p. 151) has emphasized that thus mesoblast is furnished by each of the four quadrants, viz. the mesenchym by the micromeres of the second quartet of *A*, *B*, and *C*, the mesoderm-bands by *D*.

This latter phenomenon is always connected with lengthening of the body and with teloblastic growth, even with animals like Lamellibranchia and Gastropoda, although the latter are not generally looked upon as longitudinally developed forms. From this CONKLIN justly inferred that the radial mesoblast has a still more primitive character than the bilateral.

Whoever considers more closely the correspondence here noticed in the development of the Polyclada with that of the Annelids and Molluscs, will have to acknowledge that only that solution can be satisfactory which considers the two cells, mentioned in 1, as the last remnant of the no longer fully developing mesoblast-bands with the degeneration of which the disappearance of the coelom and of a distinct metamerism has gone hand in hand.

---

[1]) I may briefly call attention to the fact that I also pleaded for a manyfold origin of the mesoblast with mammals, on account of what had been found in Tarsius (Verh. Kon. Ak. v. Wet. Amsterdam, vol. VIII n⁰. 6 1902, p. 69) and that I concluded from it that the mesoderm is not equivalent to the two primary germ-layers, but that KLEINENBERG was right when he qualified it as a complex of originally independently developing organs.

To look upon them as potential mother-cells of those mesoblast-bands would be against all known laws of heredity, where in all other points there is so great a resemblance, also with regard to the mesenchym, between this 64-cellular stage and that of Annelids and Molluscs and where it would be entirely impossible — supposing evolution to have followed the line: Coelenterates, Ctenophora, Plathelminths — to derive the mesoblast-bands, which must anyhow lie accumulated in the cells mentioned, from these preceding ancestral forms. On the other hand it can easily be understood that these bands have gradually assumed their present form and peculiar characteristics in the long (and to us unknown) series of the ancestral forms of Annelids, Molluscs and Polyclada, and that with these latter and still more with the Ctenophora (which have an ontogenesis so much resembling that of the Polyclada,) the part played by these mesoblastic mother-cells has again receded to the back-ground.

We must then, especially on account of what ontogenesis has taught us, consider the Plathelminths as degenerate descendants of Coelomata and so the strobilation of the Cestoda, which are still further degenerated by parasitism, again falls within the reach of an explanation which would homologize it with the metameric structure of the Annelids.

How the gradual reduction leading from Polychaeta via Oligochaeta and Hirudinea to Plathelminths, has left its traces in all the different organs and tissues I will not develop more extensively here; I may suppose these points to be generally known.

It is obvious, after what has preceded, that we ought not to attempt to derive the metamerism of the Annelids from the pseudo-metamerism of the Turbellaria as LANG does. I prefer to accept the hypothesis formulated already in 1881 by SEDGWICK, according to which a longitudinally extended, actinia-like being, possessing wormlike free motility, formed the starting-point. Gradually cyclomerism was converted into bilateral symmetry and linear metamerism, in the same way as now already certain Actinia show a tendency to bilateral symmetry.

ED. VAN BENEDEN afterwards indicated (1894), though only in an oral adress which has never been published, how SEDGWICK's view might be extended to the Chordates. In 1902 in the "Verhandelingen" of this Academy, I have tested the possibility of applying SEDGWICK's theory to the facts that are revealed to us by the development of mammals. And the facility with which the explanation of SEDGWICK can be extended both to Vertebrates and Invertebrates, is undoubtedly an argument in its favour.

LANG and HATSCHEK object that a prolonged actinialike being would

also have possessed unpaired tentacles and an unpaired gastral division in the median line. They forget that such an unpaired medial coelomic cavity is already present in Balanoglossus and that LANGERHANS ("Zeitschr. für wiss. Zool." Vol. 34. 1880) and GOODRICH (Q. J. Microsc. Sc. Vol. 44, 1901) have also shown the existence of an unpaired coelomic cavity in Saccocirrus, while cases of unpaired median sensory spots could be enumerated in Coelomata. The well-known antithesis of headsegment and pygidium as compared with the trunk in the bilaterally metameric Coelomata is an argument that goes far to meet LANG's and HATSCHEK's contention.

Neoformation of segments, still pretty equally distributed with the cyclomeric Coelenterates, but there also already variable, occurs with the Coelomata exclusively at the posterior end and with many of them only during embryonic life.

If we assume in accordance with E. VAN BENEDEN (see Verh. Kon. Akad. v. Wet. Amsterdam. Vol. VIII p. 69) that the stomodaeum of an actinia-like ancestral form has been the precursor of the chorda dorsalis, beside and above which the nerve-ring unites to a spinal chord, while under it a connection between the stomodaeal fissure (the chordal cavity) and the gastral diverticula (coelomic cavities) can be observed, then it follows from this that the ancestral forms of the aquatic Chordata are moved about in the water in a position different from that of the ancestral Articulates by 180°. The mouth of the Chordates would then have arisen later as a new formation, as has already repeatedly been asserted. It is an undoubted simplification of our phylogenetic speculations if we are entitled to look for this difference in orientation already in very early ancestral forms and can so avoid GEOFFROY ST. HILAIRE's error who shifted the process of reversion to a much later stage of development.

If thus the phylogenesis is very considerably shortened, I may call attention to the fact that even with respect to the mammalian foetal envelopes, I showed in the above-mentioned publication the possibility of a similar shortening of their phylogenesis, by not admitting that these embryonic coverings have originated from those of reptiles and birds, as was done until now, but by considering them in direct connection with larval envelopes of invertebrate ancestral forms.

In the grouping of bilaterally symmetrical, coelomatic animals (resp. of such as have lost their coelom again) which has here been attempted, important phyla (Nemertea, Nematoids' Prosopygii, Chaetognatha, etc.) have been left out of consideration.

There are still too many gaps in our knowledge of their anatomy

and their development, to enable us to form a correct judgment about their exact position.

With regard to the Nematoda I want to add that to me it seems to be an error to look upon the parasitical Nematoda as descended from those which are nowadays found living freely in the sea or in fresh water or in moist soil. All these latter are far too uniform to allow us to look upon them as ancestral forms. This phylum can be better understood, when we consider the parasitical forms as the older primitive ones and on the other hand derive the free-living forms from them, as parasites which have adapted themselves secondarily to a free existence. What the origin of the parasitical Nematoda in their turn may have been remains an open question for the present.

Of what has been briefly summarised above, I hope to give a more elaborate exposition in the current number of the "Jenaische Zeitschrift fur Naturwissenschaft" which is now going through the press, in which periodical also LANG's paper, which induced me to write this article, appeared. To that number I refer for further particulars.

Zoology. — Prof. MAX WEBER reads a paper: "*On some of the results of the Siboga-Expedition.*"

(This paper will not be published in these Proceedings).

Anthropology. — Prof. L. BOLK reads a paper on: "*The dispersion of the blondine and brunette type in our country.*"

(This paper will not be published in these Proceedings).

Chemistry. — Prof. C. A. LOBRY DE BRUYN also in the name of Dr. R. P. VAN CALCAR presents a paper on: "*Changes of concentration in and crystallisation from solutions by centrifugal power.*"

(This paper will not be published in these Proceedings).

Chemistry. — Prof. C. A. LOBRY DE BRUYN presents a paper of Mr. C. L. JUNGIUS: "*Theoretical consideration concerning boundary reactions which decline in two or more successive phases.*"

(This paper will not be published in these Proceedings).

(May 27, 1904).