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LI.—*On the Morphology and Phylogeny of the Organization of the Cestoda.* By C. Claus *.

For a number of years past I have represented in my lectures a view of the nature of the Cestode body which differs materially from that propounded by Steenstrup and strengthened by the researches of von Siebold, van Beneden, and Rudolph Leuckart: nevertheless the *ensemble* of the facts and the results of numerous later investigations prove it to be the only true and satisfactory one. The main features of this altered view of the case, which, moreover, in many respects does not differ so very widely from Rud. Leuckart's latest treatise on the Helminthes†, are to be found briefly indicated in the latest editions of my text-books ‡; but, so far as I am aware, a more precise explanation of my theory on a directly comparative basis has not yet been attempted. The following brief account is intended to supply this deficiency.

* Translated from the 'Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station in Triest,' Bd. viii. Heft iii.: Alfred Hölder, Vienna, 1889.

† Rud. Leuckart, 'Die Parasiten des Menschen und die von ihnen herrührenden Krankheiten, Ein Hand- und Lehrbuch für Naturforscher und Aerzte,' Leipzig, 1879–1886, Bd. i.

‡ C. Claus, 'Grundzüge der Zoologie,' Marburg, 1879, IV. Aufl. Bd. i. ii. Lieferung, p. 388 &c.; 'Lehrbuch der Zoologie,' Illustrirte Ausgaben, ii., iii., and iv. Aufl.

As is well known, it was the "proglottis," the segment full of ova and embryos and liberated from the body of the Cestode, which, in accordance with the doctrine of Alternation of Generations, was held to be the sexual individual and furnished the starting-point for a comparison with the closely allied but higher organized Trematodes. The proglottis was regarded as the equivalent of the Trematode, which, arising by means of terminal gemmation at the posterior end of an individual belonging to another generation and functioning as "nurse-form"—the Cestode-head or "scolex," with the loss of mouth, alimentary canal, and organs of adhesion, did actually possess the latter, in common with all the other joints of the chain, while it formed part of the chain of segments, in the shape of the circlet of hooks and the suckers of the scolex. The fact that there are Cestodes which are devoid of any trace of segmentation (e. g. *Caryophyllæus*), and in whose simple Trematode-like body scolex and proglottis are not differentiated, appeared to agree very well with this view, and was explained as a secondary condition, inasmuch as it was supposed that the forms which are spread over two generations in the case of the ordinary Cestode were, just as in other cases of alternation of generations, as a result of simplified and abbreviated development united together again in one individual (Rud. Leuckart). But the *ensemble* of the phenomena proves that in point of fact exactly the opposite condition obtains, and that alternation of generations in the Cestodes must be regarded not as a primary but as a secondary developmental process.

The starting-point of a comparison with the organization of the Trematodes, from which all authors agree that the Cestodes have been derived, is to be furnished not by the proglottis but by the entire Cestode, and, moreover, not as a chain of segments, but in its simplest form, as represented by the genus *Caryophyllæus*, as an unsegmented worm resembling the genera *Amphilina* and *Amphiptyches*, which are to be regarded as connecting-links between the Trematodes and Cestodes. The unisegmental Cestode with a single set of genital organs was the primeval form, from which, by means of further and fuller adaptation to the favourable conditions of nourishment and growth in the interior of the alimentary canal, the segmental Cestodes, with progressive individualization of the joints repeating themselves by growth in the longitudinal axis, have only secondarily been developed. Next to the Caryophyllidæ come the Ligulidæ, in whose ribbon-like body the generative organs indeed are metamerically repeated, though there is no corresponding outward segmen-

tation; following these we have the Bothriocephalidæ, with short but sharply defined joints, which, however, are not yet set free as separate units, but are liberated from the body of the Cestode in larger sections after the sexual organs have arrived at maturity. A higher stage of individualization is reached in the Tæniadæ, where the proglottids are set free singly; and, lastly, the highest stage of all is attained in the case of many Phyllobothridæ, the joints of which undergo a further development after separation, with considerable increase in size, and are capable of independent existence for some time (*Echinobothrium*).

In spite of the similarity which exists between the alternation of generations in the Cestodes and that in the Acalephæ (Scyphomedusæ), a similarity so complete that the same term "strobila" is applied to the segmented stage in both cases, the origin of it in each case requires a very different explanation. The alternation of generations in the Scyphomedusæ, which are asexually produced as sections of a polype which segments and forms the strobila, appears, as compared with the simple direct development of certain Medusæ (*Pelagia noctiluca*), to be a primeval developmental process of palingenetic importance. Accordingly the *ephyra*, which is set free by fission at the distal end of the strobila, represents when contrasted with the young polype the morphologically higher and more perfectly organized form. The exceptional case of direct development, which is found in *Pelagia noctiluca* owing to omission of the strobila-stage, is to be regarded, on the other hand, as an entirely secondary condition, derived from the alternation of generations by a shortening of the developmental process.

In contradistinction to the Medusa set free at the distal end of the Acalephæ-strobila, the proglottis liberated from the Cestode-strobila represents, when compared with the ancestral Trematode, a lower form, simplified and to a certain extent retrograded by the disappearance of the organs of adhesion and of the alimentary canal, though in point of fact the reduction of the organs was a condition of its individualization. While in the former instance the alternation of generations is the original and primary process, and the completion of the metamorphosis in the same individual the later one, secondarily produced by shortening and simplifying the development, in the Cestodes exactly the opposite is the case, and the alternation of generations is the later form of development, secondarily derived from the metamorphosis which was formerly undergone by one and the same individual, in connexion with the simplification of the organization and the

more favourable conditions of nourishment and growth owing to intestinal parasitism. It follows that we have to define the development of the Acalephæ as alternation of generations *, which in certain cases can be simplified by shortening into metamorphosis, while we must interpret the development of the Cestodes, on the other hand, as *metamorphosis, which, owing to individualization of certain products of growth, can give rise to variously complicated forms of alternation of generations.*

However, we have not yet taken into account the first most variable series of manifold and complicated developmental stages, by which the embryo produced from the fertilized ovum is transformed into the scolex. But it is precisely this portion of the ontogeny which is of peculiar importance for our problem, not only because by the appearance of a stage capable of asexual reproduction, and therefore distinguished as the primary nurse-form, the complication of the developmental processes interpreted as an alternation of generations is increased and the justice of such an interpretation thereby strengthened, but also because it is just this section of the development which is to be brought into direct comparison with that of the Trematodes. And if we are right in tracing the phylogeny of the Cestodes from the Trematodes, the development of the latter, which for a long time was itself considered as alternation of generations, must be repeated, though in a modified form, in their descendants.

Every one is aware that the digenetic Trematodes—and these alone, and not the monogenetic forms, can be considered in the comparison—as well as the Cestodes pass their immature stages in other hosts than those of the sexual animals, whereby a change of hosts becomes a necessity. In the case of the former it is usually a mollusk or other Invertebrate in whose body the intermediate generations develop themselves as the so-called "sporocysts" or "rediæ," according as they do or do not possess a mouth and alimentary canal, together with their progeny, the "Cercariæ" or Distoma-larvæ. In the case of the Cestoda, too, the part of first host is sometimes played by an Invertebrate, but generally it is a Vertebrate in which the young forms are to be found as "Cysticercoids" or

* It is owing to the astonishing similarity existing between the phenomena of growth and fission in the Acalephæ- and Cestode-strobilas, and between the formation of ephyræ and proglottids, that the phylogenetic contrast has been overlooked and the morphological value of the sexual generations in both cases identified, and that the mistake has then been made (Götte) of not admitting the development of the Acalephæ to be an instance of alternation of generations, but interpreting it as a metamorphosis.

"Cysticerci"—the latter usually encysting in parenchymatous organs. There can therefore be no question but that we must trace back Cysticercus as well as Cysticercoid either to the Cercaria-producing redia or sporocyst, or else to the Cercariæ themselves, provided that we admit the origin of the Cestodes from the Trematodes.

The choice between the two alternatives appears at first sight to be by no means an easy one; but, taking into consideration the analogy of the proliferation of the Cysticercus, it would seem to rest with the redia or sporocyst as the equivalent of the latter. However, a closer comparison shows us that in this proliferation we have to deal merely with analogous and not with homologous processes, since the germs produced by the sporocysts and rediæ, which were formerly regarded as spores, or even as internal buds, cannot be placed on the same level as the buds on the wall of the Cysticercus-vesicle, but must be considered as formations of quite a different kind. It is true that for a long time (that is to say as long as the theory that the Distoma-development was a case of alternation of generations remained undisputed) these formations were regarded as products of an asexual reproduction, that is as spores or buds, until the discovery of pædogenesis in Diptera-larvæ, and the precocious separation of the first sexual cells, which sometimes even takes place during the segmentation of the oosperm *, led to an entirely different view—a view which, supported by the consideration that spore-formation in Metazoa is *à priori* highly improbable, has now come to be the one which is generally accepted. In accordance with this view the so-called germ-cells in the sporocysts and rediæ are considered to be ovarian cells separated early and developing in the body of the larva; that is to say, they are held to be ova developing parthenogenetically †, and the development of a Distoma is no longer explained as a case of alternation of generations, but as a form of *heterogamy*. The sporocysts and rediæ would then be explained simply as larval forms which have undergone a retrogressive metamorphosis or else have been checked in their development for the purpose of aiding the rapid and extensive reproduction of individuals; they would correspond to larval

* Compare C. Grobben, "Die Entwicklungsgeschichte der *Moina rectirostris*," Arbeiten aus dem Zoologischen Institute in Wien und der Zoologischen Station in Triest: Vienna, 1879, Bd. ii.

† This interpretation, first given by Grobben (*loc. cit.*), has since been repeated by other investigators also in a precisely similar way, and may be said to have met with pretty general acceptance at the present day. *Cf.* also H. Schauinsland's 'Beitrag zur Kenntniss der Embryonalentwickelung der Trematoden,' Jena, 1883.

forms left behind at various stages of development, and from a morphological standpoint would have to be regarded as simplified progeny-bearing Cercariæ. It follows that the Cercaria alone would figure as the equivalent of Cysticercoid or Cysticercus. Now, as a matter of fact, this larval form does afford an immediate and natural comparison with those developmental forms of the scolex which on a number of other grounds we are compelled to regard as the primary and original ones. These are the little Cysticercoids which inhabit the bodies of Invertebrates, and which have only become known comparatively lately. While authors were formerly inclined to derive the Cysticercoid from a Cysticercus, simplified and diminished in size, and so to regard it as a Cysticercus whose vesicle, owing to unfavourable soil, had shrunk up and degenerated into a little appendage scarcely capable of containing the body of the scolex, they will now, on the contrary, have to derive the Cysticercus-vesicle from the enlarged caudal appendage of the Cysticercoid, which has become inflated owing to the collection of an aqueous fluid, and to consider it as a secondary modification which has arisen from this and adapted itself to a parasitic existence in the body of a Vertebrate. That this view is actually the correct one, and that the Cysticercoid and not the Cysticercus represents the primary form, from which the other must be derived, is not only rendered probable at the outset by the simpler structure and smaller size of the former, as well as by its sojourn in the bodies of the phyletically older Invertebrates, but also by the surprising similarity of form existing between certain Cysticercoids and Cercariæ, which renders possible, strengthens, and confirms a direct homology between the two.

The Cysticercoid of *Arion empiricorum*, which was first described by Stein, being divided by a constriction into a body and a caudal appendage, at once reminds us of the Trematode-Cercaria. To a much greater extent is this agreement seen in *Archigetes Sieboldii*; this is a Caryophyllid allied to *Caryophyllæus* and occurring in Naidæ in a sexual scolex-stage. Leuckart* states that the creature consists "like the Cercaria, of a flattened oval body and a cylindrical tail, which is inserted in a pit-shaped depression at the posterior end," so that without closely examining it one would suppose it to be a Cercaria. Not less striking is the resemblance of the Cysticercoid inhabiting the dog-louse and the

* Rud. Leuckart, "*Archigetes Sieboldii*, eine geschlechtsreife Cestodenamme, Zeitschrift für w. Zoologie, Supplementband, 1878, Bd. xxx.

flea, from which *Tænia elliptica* (=*cucumerina*) of the human intestine is derived.

It is only recently that we have received full details concerning this larval form and its caudal appendage, through the observations of Grassi and Rovelli *. Both of these authors recognized the soundness of the homology of body and tail-portion with the corresponding parts of the Cercaria, though they perhaps went too far in interpreting the anterior invagination of the Cysticercoid as the equivalent of the buccal cavity, the rostellum as the everted pharyngeal bulb, and the body-cavity without sufficient basis as the commencement of the mid-gut.

In correspondence with this comparison we also have the apparent agreement between the development of the Cercaria-tail and that of the caudal portion of the Cysticercoid, which, moreover, with reference to the position of the embryonic hooks, had been regarded as the enlarged body of the hexacanth embryo, and accordingly styled "head-maker" (*Kopfbildner*), and explained as nurse of the presumably subsequently formed scolex. As a matter of fact, however, it by no means represents the whole of the body of the embryo, but only the smaller portion thereof, from which, just as in the case of the cells budded off from the inner surface of the Redia to form the Cercaria, a broader section is differentiated as body and a narrower one as caudal appendage †. But this establishes beyond a doubt the value as individuals of the Cysticercoid and of the Cysticercus which is to be derived from it, in opposition to that view which would see in the Cysticercus a colony composed of at least two individuals, namely of the embryo, metamorphosed into the caudal appendage, or, rather, vesicle-wall, of the Cysticercus, and of the Cestode-head or scolex subsequently produced from this by budding.

The changes experienced by the Trematode-larva in its transition to the Cestode-larva also affect, in correlation to the atrophy of the alimentary canal and the consequent

* "Embryologische Forschungen von Prof. Battista Grassi und Dr. Giuseppe Rovelli," Centralblatt für Bacteriologie u. Parasitenkunde, Cassel, 1889, v. Band, no. 11.

† Grassi's observations on the development of the Cysticercoids of *Tænia elliptica* and *murina* have proved this deduction to be well founded; but in direct contrast thereto Villot regards the caudal appendage of the Cysticercoids as a new formation which has arisen from the embryo by budding. He does not, however, establish his contention, which is also directly opposed to the older view of the caudal appendage as the body of the embryo. Villot, "Mémoire sur les Cysticerques des Ténias," Annales de Sc. Nat. 1883, Tom. xv.

simplification of the organization, the anterior section of the body armed with its suckers and chitinous hooks, which was at an early period invaginated into the posterior portion and surrounded by this as by a protecting envelope. The evident necessity for protection, which was to a certain extent satisfied by this process, may also have determined the change of function of the tail, which from an organ for effecting the change of locality was transformed into a larger or smaller vesicle, accommodating the whole of the scolex inside itself; or again—and in all those cases in which the simple invagination of the scolex-head into the scolex-body gave a sufficient protection—degenerated into an apparently functionless rudiment, in order in the end to drop off entirely (*Bothriocephalus*). In the first case, however, in which the tail became a large vesicle filled with watery fluid, its great increase in size enabled it to acquire yet another important function—*proliferation* — and to produce by budding numerous scolices (*Cœnurus*), in some cases brood-capsules with scolices, either directly or by means of a second and third generation of vesicles (*Echinococcus*). While the metamorphosis was simplified in one direction, in the case of degeneration and shedding of the caudal appendage, into a more direct development, in the other it grew more complicated and assumed various forms of alternation of generations. In the latter, to a certain extent by way of compensation for diminished productiveness, owing to the loss of pædogenesis, the necessity for increasing the race was satisfied in a *newly acquired* way, namely by means of budding on the enlarged surface of the vesicle.

The power of proliferation, which has been only secondarily acquired by certain Cysticerci (*Cœnuri* and *Echinococci*), was, like the process of proglottid-forming by the strobila, wrongly used as a standpoint from which to interpret the whole Cestode development. From this point of view the scolex was regarded as the gemmation-product of the embryo, the proglottis as that of the scolex, and, in accordance with the interpretation of the individualized joints of the Cestode as sexual animals, the complicated five-jointed scheme of the *Cestode-metagenesis* was set up. In this arrangement the embryo figured as primary nurse-form, the scolex as nurse, and the proglottis as sexual individual, while the Cysticercus- and Strobila-stages, which furnish the connexion between primary nurse-form and nurse, and between nurse and sexual individual, were regarded as polymorphic colonies.

Thus then the metamorphosis of the parasitic Platyhelminthes led in the case of the Trematodes, owing to the pædo-

genesis of the larval forms known as Sporocysts and Rediæ, to a heterogamy which was for a long time believed to be alternation of generations; in the case of the Cestodes, on the other hand, it produced, owing to individualization of gemmation and fission-products of certain developmental stages, various more or less complicated forms of alternation of generations, the modifications of which receive their natural explanation and interpretation in the present *résumé*.

Both the budding on the wall of the Cysticercus-vesicle and the constriction and liberation of segments of the strobila are already foreshadowed in the development of the Distomæ—the former in the budding-power possessed by certain sporocysts (*Leucochloridium*), and the latter in the regular separation between the body and tail of the Cercaria and in the fission-phenomena presented by certain sporocysts (*e. g.* those of *Cercaria minuta*) and rediæ (those of *Cercaria echinata* and *fulvopunctata*). The caudal appendage also, the primary function of which is that of a motile organ, is to be regarded as a portion of the body which is capable of individualization. This results from the surprising discovery made many years ago by Alex. Pagenstecher * in the case of *Bucephalus*, and only recently confirmed and also established in many other cases by Ercolani †, that the tail is capable of transforming itself into a brood-producing fragment—that is, as it were, into a sporocyst. This process also elucidates the contrast between the caudal appendage of the Cysticercoid and the Cysticercus-vesicle and the invaginated neck or body of the scolex, exhibiting the latter in the light of a further section of the body of the worm, which, before the formation of proglottids sets in, perhaps regularly separates itself from the foremost portion representing the true head, and morphologically is by no means so very different from the tail.

Presuming it to be a legitimate and well-grounded assumption, owing to the *ensemble* of the facts, that just as the innumerable parasitic Copepoda, which present such manifold variations and often such grotesque shapes, have been developed from free-swimming Crustacea, so also the intestinal worms, through adaptation to a parasitic mode of life and the conditions of existence modified thereby, have arisen from free-living worm-forms; then, with regard to the Platyhelminthes, no doubt can exist that it was the Planarians—so closely allied to the Trematodes—to which they owe their

* Alex. Pagenstecher, "Trematodenlarven und Trematoden" (with six plates), Helminthologischer Beitrag: Heidelberg, 1857.

† G. B. Ercolani, 'Nuove ricerche sulla storia genetica dei Trematodi,' Tom. i. 1881, and Tom. ii. 1882.

origin. As the Dendrocœle Turbellaria of fresh and salt water exchanged a free existence for a parasitic one and adapted bodily form and structure to the new conditions of life—losing the outer covering of cilia (with the exception of the vestige still remaining during larval existence), while they acquired suckers and organs of adhesion of various kinds —they became Trematodes, which, in connexion with the easier and more favourable nourishment in the body of a host, acquired the power of producing a far more numerous progeny.

The closer representation of these processes becomes more complicated and difficult owing to the fact that in the case of so large a number of Trematodes, and practically universally among the Distomæ, with which we are especially concerned, we have *two different hosts* between which the life-history of the species is distributed. The one functions to a certain extent as intermediate host, and brings the intruding parasite only up to a certain stage of development; it conceals in its body the larval form, though even at this stage it may be capable of reproduction. The second host receives the parasite, which has reached it either actively or passively, and brings it to full development and sexual maturity; it harbours the sexual form. Now are the intermediate hosts —and this is a question which has already been sagaciously propounded by Rud. Leuckart*—" merely later intruders into the life-history of the Helminthes," or are they " the original genuine hosts, which primitively brought their intestinal worms to sexual maturity, but were subsequently degraded to the position of intermediate hosts, owing to the fact that the life-history of their parasites, through further development and differentiation, has been spread over a larger number of stages?" The first case would, to make use of E. Hæckel's noteworthy expression, represent a *cœnogenetic*, the latter a *palingenetic* condition. In the former rediæ and sporocysts would be later developed forms (*i. e.* than the sexual stages), secondarily and cœnogenetically modified through adaptation; in the latter, on the other hand, they would represent earlier-existing, philetically older, and once sexual forms. Now when Rudolph Leuckart very emphatically selects the second alternative, pointing by way of justification to the fact that at the present time nearly all Entozoa live during the sexual stage in the bodies of Vertebrates, which are undoubtedly of later origin, it seems to me that he has not hit the right nail on the head. Apart from the fact that fish and other aquatic

* Rud. Leuckart, 'Die Parasiten des Menschen,' part 2, Bd. i. p. 148.

Vertebrata were already in existence in Palæozoic times, and that for this reason alone the argument adduced loses its cogency, another circumstance seems to me sufficient to refute his view, at any rate as far as the Platyhelminthes are concerned. I refer to the remarkable agreement existing between Trematodes and Dendrocœle Turbellaria in the organization of the fully developed sexual forms, an agreement which, if the view in question were correct, could only be explained by means of a convergence of development, which is highly improbable, especially in view of the contrast between the conditions of life in the two cases.

At the same time, however, it by no means follows that we are bound to regard the intermediate hosts of the larval stages as only later intruders into the life-history of the Helminthes; far rather may we well maintain the notion that the young worms found their way into the bodies of Invertebrates at the very beginning of the phylogenetic process, but were there unable to arrive at full development and sexual maturity. On the other hand, owing to the altered conditions of subsistence, they underwent a necessary change of form, by virtue of which they, either themselves or in the persons of their pædogenetically-produced offspring, were enabled to leave their intermediate host once more by means of active or passive migration, and, being now transferred into the body of a Vertebrate under more favourable conditions of nourishment, they underwent in their new host, as the definite carrier of the sexual animal, their full morphological and digenetic-sexual development. In this manner the regular occurrence of an intermediate host in the life-history of the Helminthes and the distribution of the developmental phases between two (or more) hosts may find an unstrained explanation. It will also appear quite comprehensible that in the case of numerous intestinal worms not one single, but many *, generally

* Many of the intestinal worms appear to possess an especially great adaptability to the conditions of nourishment in the bodies of their hosts, which renders intelligible the occurrence of one and the same species of Entozoon in different and even widely distant hosts. For instance, *Distomum echinatum*, which is developed from the *Cercaria echinata* of various species of mollusks, is found sexually mature not only in the intestine of the duck and other waterfowl, but also in that of the dog, the rat, and the mouse. The *Cysticercus cellulosæ* of *Tænia solium* lives not only in the body of the pig, but also in the most dissimilar organs of the human subject, and has also been found in the muscles of the roe, the dog, and the cat. *Tænia elliptica* occurs not only in the intestine of the cat, but also (*cucumerina*) in that of the domestic dog and of man. We may further instance the distribution of *Echinococcus* and of numerous Nematodes, especially of *Trichina spiralis*, in the bodies of the most widely different mammals.

closely-allied species of animals are found as the intermediate hosts of the same species of worm, and that the same thing also recurs in the case of the hosts of the sexually mature Helminthes.

Now if as early as in the case of the Trematodes, which are phylogenetically to be derived from Dendrocœle Turbellaria, the intermediate hosts were not the original hosts of the sexual worms, much less can this have been the fact with regard to the Cestodes which have been developed from them; neither Cysticerci nor Cysticercoids in the bodies of their victims will ever have represented the terminal stages with digenetic reproduction in the life-history of these Helminthes. Like the larvæ of the Trematodes the young stages also of the oldest Cestodes, living in the intestines of fish and other aquatic Vertebrata, penetrated the bodies of Invertebrates, and there transformed themselves, instead of Rediæ and Cercariæ, into Cysticercoids.

It was only later on, with the appearance of birds and mammals, that the Tæniadæ came into existence, the larval stages of which remained only to a limited extent in Invertebrates, but in the majority of cases migrated into the bodies of Vertebrata, in which from Cysticercoids they developed into Cysticerci. The reader will be reminded by these observations of the doctrine of von Siebold, who regarded the Cysticerci as tapeworms gone astray into the wrong animals, becoming in a strange abode dropsical and degenerate, whereby he for a long time denied the value of the Cysticerci as normal larval stages of Cestodes. As a matter of fact we might just as well speak of going astray in the case of phylogenetic development as in that of free-living animals, certain individuals of which are cast away beyond the limits of distribution of the species into domains far distant and separated by mighty barriers, and there, as a result of the entirely altered conditions of subsistence, give rise to the development of new species and groups. And since in physiology no hard-and-fast line is to be drawn between the normal and the pathological, and only so far in theory, as the latter processes bring with them disturbing results *detrimental to the life of the individual*, we should even hold the conception of the dropsical degeneration to be justified *, though certainly in a sense very different from that of Siebold's doctrine, which was entirely opposed to the idea of transmutation, and, as compared with the results of Kuchenmeister and R. Leuckart's investigations, merely defended an *error*. It is therefore a serious and

* C. Claus, 'Grundzüge der Zoologie,' 4th edition, part ii. 1879, p. 389.

scarcely intelligible exaggeration when E. Hæckel *, who criticises the phylogenetic relations of the Cestodes in a similar manner, vindicates the merits of von Siebold in having been the first to discover the true explanation and point out the way by which we may be enabled to understand the causes of the ontogenetic phenomena.

Up to the present only a single exceptional case has become known of a Cestode already sexually mature in the Cysticercoid state. I allude to the parasite from the body-cavity of the Naidæ, described by its discoverer, Ratzel, as *Caryophyllæus appendiculatus*, but which was first shown by Rud. Leuckart to be fully sexual and capable of reproduction, and constituted by him the representative of a special genus *Archigetes*. Although this exceptional case appeared to afford a yet firmer basis to the hypothesis of the renowned helminthologist, that the larval stages living in the intermediate hosts were originally the sexual forms, it should nevertheless be far more natural, in view of the relations which we have discussed, to recognize in this case no exceptional survival of a primitive condition, but to interpret it in the light of a secondary transference of sexual maturity to the larval state, just as encysted larval stages of Trematodes (*Gasterostomum gracilescens* in cysts of *Gadus* and *Distomum agamos* of the Gammarinæ) may also become sexually mature.

The designation *Archigetes* ("ancestor") bestowed by Rud. Leuckart on the parasite of *Sœnuris* as the result of his interpretation of it, would apply to our divergent interpretation also, in so far as we have in *Archigetes* a Caryophyllid devoid of the power of proglottid-formation and with simple sexual organs. In this sense, however, it would meet with our approval the more unreservedly, as with it not only may the view of the unsegmented Cestode—in contradistinction to the proglottis—as the equivalent of the Trematode be confirmed, but also, as a further result, the attempted derivation of the Cestode-body in the foregoing exposition may be completely justified. Moreover, in our at present imperfect knowledge of the development of *Archigetes* the possibility appears by no means excluded that this interesting parasite also possesses its *Caryophyllæus*-stage in the intestine of fish, and only under certain conditions attains to degenetic maturity in the body of Naidæ. We may have here a similar dimorphism to that with which Zeller's excellent work has made us acquainted in the case of *Polystomum integerrimum*, with its two sexually mature forms—the one on the gills of the tadpole, the other in the urinary bladder of the frog.

* E. Hæckel, 'Metagenesis und Hypogenesis von *Aurelia aurita*,' Jena, 1881, p. 33.

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