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XXIX.—*The Affinities and Origin of the Tardigrada.*  
By Prof. J. von KENNEL\*.

LIKE the majority of the so-called aberrant groups in the Animal Kingdom the Tardigrada have met with the most diversified experiences in systems of classification. At one time they were ranked among the "Worms," at another among the Arthropods, and they have been assigned at different periods both to Crustacea and Tracheata. They were treated as an "appendage" to these groups or else as "ancestors" of them, and were regarded as degenerate or greatly reduced or as highly primitive forms. A comparison of the various views upon this question has been furnished by Plate †, who also discusses in a subsequent paper ‡ a theory by Bütschli § which had previously escaped his notice.

Now I am in entire agreement with Plate's view that the Tardigrada can be brought into relationship only with the tracheate Arthropods, and do not consider it necessary to support or amplify the arguments which he advances against

\* Translated from the 'Sitzungsberichte der Naturforscher-Gesellschaft bei der Universität Dorpat,' ix. Bd. Heft iii. (Dorpat, 1892), pp. 504–512.

† Plate, "Zur Naturgeschichte der Tardigraden," Zool. Jahrb. Bd. iii.

‡ Plate, "Die Rotatorienfauna des bottnischen Meerbusens &c.," Zeitschr. f. wiss. Zool. Bd. xlix.

§ O. Bütschli, "Untersuchungen über freilebende Nematoden und die Gattung *Chaetonotus*," Zeitschr. f. wiss. Zool. Bd. xxvi.



their being allied to the Crustacea. Notwithstanding this, however, with regard to the systematic position of these animals I have arrived at quite a different conclusion, which more nearly resembles the older ideas, and regards the Tardigrada as degenerate forms of higher Tracheates. Plate declares that "the Bear-animalcules are the lowest of all the air-breathing Arthropods with which we are at present acquainted, and must be placed at the bottom of the Tracheata, even below the Onychophora." Nevertheless, as may well be imagined, he does not derive *Peripatus* from them, but states that "they form an offshoot of the great Tracheate stem, which, however, lies much nearer the root of the latter than any other branch of that stock. They are the group in which the transition from the Annelids to the air-breathing Arthropods is most clearly expressed and most distinctly recognizable."

To this opinion I am unable to assent. In the species of *Peripatus* we have animals which furnish the best transition between Annelids and Tracheates, and I have elsewhere \* explained at length the reasons why it is probable that forms resembling *Peripatus* were the ancestors of the Myriapod-like Tracheata, from which again the rest of the Tracheata are descended. The bodily form, the organs of locomotion, the commencing formation of head and jaws, the nervous system, the eyes, the sexual organs, and the tracheæ of this group of animals may without difficulty be brought into agreement both with the conditions of the Annelids as also with those of the Tracheates, and, in addition, we have the segmental organs, which have been transmitted from the Annelids.

Conditions are different among the Tardigrada, which present far less resemblance to the Annelids. In the first place we are acquainted with no Annelids whose bodies consist of so few segments as is the case among the Bear-animalcules. It is true that such might have existed, or the number of the segments might have been subsequently reduced. But the Tardigrada do not possess even a trace of true segmental organs, but are provided with Malpighian vessels in their stead, and consequently in this respect they must have receded far more from the Annelidan ancestors than even the existing species of *Peripatus*; they are in this point much more Arthropods than the latter. The muscu-

\* Kennel, "Die Verwandtschaftsverhältnisse der Arthropoden," Schriften herausg. von der Naturforscher-Gesellschaft bei der Universität Dorpat, vi.



lature of the Bear-animalcules, too, diverges from the dermal muscle-sheath of the Annelids much further than does the musculature of *Peripatus*; they have isolated muscle-strands, which run freely through the body-cavity, decussate, and are inserted at different points of the integument; in accordance with their small size these are of very simple structure and consist of few fibres. This arrangement reminds us forcibly of the distribution of the muscles in many highly developed Tracheates, which will be discussed later on. The nervous system of the Tardigrada can, it is true, be easily compared with that of the Annelids, but it also differs in no way from that of higher Tracheates, in which the sense-organs of the head are slightly or not at all developed. At any rate in its configuration as a chain of ganglia it surpasses that of *Peripatus*, which has a very irregular rope-ladder-like nervous system. On the other hand, however, the eyes of the Tardigrada are such insignificant dots of pigment that we can scarcely find more simple ones among the Annelids; they can only be regarded as rudimentary structures, but not as engaged in progressive development.

While the sexual organs of *Peripatus* can at once and by means of embryological proofs be traced back to those of the Annelids, and their ducts to segmental organs, this is not possible in the case of those of the Tardigrada, since in the first place they are unpaired, and, secondly, open dorsally into the posterior portion of the intestine. This condition also is more readily intelligible on the theory of reduction and degeneration, as I shall subsequently show.

If we regard the Tardigrada as an offshoot from the root of the Tracheata, we certainly need make no attempt to think out the conditions of their organization in their further development into Arthropods. If, however, they "most clearly express the transition from the Annelids to the air-breathing Arthropods," the ancestors which were common to them and the Tracheata would yet have to be supposed to have resembled them fairly closely. But here great difficulties crop up in relation to the appendages. The four pairs of appendages of the Tardigrada are post-oral, and are innervated from the ventral chain of ganglia, while the Tracheata nevertheless possess a pre-oral pair of appendages in the shape of the antennæ.

Now this pair of appendages must either have disappeared in the Tardigrada or it must be regarded as a new development in the rest of the Tracheata; for the first pair of leg-stumps of the Bear-animalcules is innervated from the first ventral ganglion. Should we wish to interpret the absence



of the antennæ as due to reduction, which may well be the only possible explanation, it would follow that the first three pairs of appendages of the Tardigrada are homologous with the mouth-parts of the Tracheata, and only a single segment would be left for the body. This would entail the conclusion that the rest of the trunk-segments of the Tracheates have arisen in consequence of continued segmentation on the part of the common ancestors of Tardigrada and Tracheata. Although this would be an absolutely permissible supposition, we must nevertheless consider that in the *Peripatus*-like Protracheata we have animals which, with a larger number of segments, combine Annelidan characters even in a far greater degree, and consequently fulfil all demands that can be made upon transitional forms. Moreover all Myriapods, from which the rest of the Tracheata can be derived by the process of concentration of segments &c., possess altogether a larger number of segments and a fully developed head, the rudiments of which are already in process of formation in *Peripatus* in the shape of antennæ, jaws, and slime papillæ.

Let us now consider whether the peculiar conditions of the Tardigrada cannot after all be derived more easily and simply from higher Tracheates by the method of reduction and simplification. Let us just take the Tardigrade body as we see it—a segmented animal which, according to its nervous system, consists of five segments. It must certainly be admitted that we are acquainted with no Tracheate Arthropod which is composed of so few segments. But we nevertheless find in the entire Tracheate stem a reduction of the number of segments from the Myriapods upwards, which is brought about in part by the actual absence of posterior abdominal segments, and in part by fusions and intimate union of several segments. As a general rule among the higher Tracheata four cephalic, three thoracic, and a somewhat fluctuating number of abdominal segments are present; the latter, however, in the Mites and the true Spiders are fused into one piece, which is greatly reduced in the case of the former. A reduction such as this may have occurred in other Tracheata also. Moreover, we are acquainted with stages of Tracheates, namely their larvæ, in which the divisions of head, thorax, and abdomen are not differentiated; larvæ in which the appendages have disappeared in adaptation to certain conditions of existence (maggots); and, finally, larvæ in which new stumps of appendages, in the form of simple dermal protuberances provided with claws of different shapes, have appeared secondarily upon all the segments of the body or upon a portion of them. I merely recall the caterpillars with



their "pro-legs" and many dipterous larvæ with leg-stumps. Most important of all is the fact that in dipterous larvæ of this kind the entire head is wanting, since the four foremost segments of the body are invaginated and constitute the œsophagus of the larva.

In the metamorphosis of the larva all portions of the head of the imago are formed in a reversed position out of rudiments in the wall of the larval œsophagus, and are everted in the pupa. That which is known to us as a maggot is merely the trunk, externally wholly unsegmented, enveloped in a resisting cuticle, and apodous or with a very variable number of secondary leg-stumps. If we imagine the trunk of such a dipterous larva reduced to four segments we have in essentials precisely the body of a Tardigrade.

In the secondary œsophageal tube formed by invagination of the four cephalic segments there lie in the case of the maggots of *Diptera* the two stylets of chitin as masticatory organs of local origin, not homologous with any appendages, precisely like the chitinous rods in the œsophagus of the Tardigrada. The musculature of a dipterous maggot is certainly more complicated than that of a Tardigrade, but exhibits so surprising a similarity in arrangement and distribution that we are involuntarily impelled to institute a comparison. It is true that the muscles of the Tardigrada are not transversely striated, but this, in the light of present views, will surely not carry much weight. In the larvæ of many *Diptera* (*Stratiomys*, *Mycetophilidæ*, &c.) leg-stumps occur in different numbers as independent new formations. I myself when a student, some seventeen years ago, found beneath a stone in the Black Forest a number of very peculiar dipterous larvæ, which I have never yet been able to determine and which bore upon the flat ventral surface four pairs of such leg-stumps provided with claws. Salivary glands and Malpighian vessels are present in the larvæ of *Diptera*. How greatly the condition of the alimentary canal can alter according to the mode of life is shown with the greatest distinctness precisely by Insect larvæ. Thus we next come to the tracheæ. These are, indeed, present in larvæ of *Diptera*, but the number of the stigmata is considerably reduced; that tracheæ, however, may disappear, especially in very small Arthropods which live in damp surroundings, is shown among others by the *Acarina*.

We have now only to deal with the nervous system and sexual organs.

The nervous system varies exceedingly in dipterous larvæ, even in those which we may designate as maggots. The



supra-oesophageal ganglion is, in accordance with the invagination of the first segments, placed far back, while the ganglion-chain is sometimes exceedingly concentrated, forming a short band-shaped mass, from the lateral margins and hinder end of which the nerves radiate into the segments after the manner of a *cauda equina*—and sometimes also a well-developed chain. If we retain the last case and assume a great reduction in the number of body-segments, the conditions in the Tardigrades present no further difficulty.

Now, however, it is precisely among dipterous larvæ that we observe in a series of forms that they are **capable of reproduction as larvæ** (*Cecidomyia*). In these larvæ a head is never developed: it remains after a fashion latent for generations. The larval sexual organs, which are in this case only female ones, are situated, in the shape of small paired sacs, upon the dorsal side of the intestine and have no ducts; the differentiation of the germ-cells into egg- and nutritive cells appears to be abolished or at any rate not sharply expressed. Now if we were to suppose that larvæ of this kind had ceased to undergo their metamorphosis, that they always reproduced their species as larvæ, and that, in consequence of adaptation to the very peculiar conditions of existence in damp moss and water, they had become modified in one direction and had then undergone further development, we might regard them as constituting a transition to forms which we now know as Tardigrades—**Arthropods in the larval stage, without a head, and with a body consisting of a reduced number of segments, and bearing a few (secondary) leg-stumps.** In the course of this process a few peculiarities must naturally have received especial emphasis. In the first place, not only female but also male larvæ must have remained in this stage. Now we actually find, as, for instance, in the case of *Cecidomyia*, that after a series of pædogenetic and parthenogenetic larval generations the spontaneous production of male larvæ occurs, since finally both males and females appear as imagines. The idea that under certain circumstances male larvæ of this kind also failed to undergo metamorphosis must not be rejected offhand. We need simply and solely suppose that the sexual organs gradually redeveloped a duct—in the present case a short canal in communication with the rectum. And this supposition is certainly not outside the limits of what we otherwise concede to the capacity for modification shown by the animal body. It is likewise conceivable that independent efferent ducts, which were previously present, came into communication with the rectum through invagination of the posterior body-segments, while in this way the



reduction in the number of the segments would also become more intelligible. The enigmatical "gland," which occurs in both sexes of Tardigrades (*cf.* Plate, *loc. cit.*), is perhaps nothing else than the degenerate second ovary or testis, just as in the case of birds also, at least in the female sex, only one half of the genital apparatus arrives at maturity.

Now it is by no means my intention to put forward dipterous larvæ as actually the ancestors of the Tardigrada; on the contrary, I merely selected these larvæ in particular because they combine in themselves a series of peculiarities which show how great the capacity for modification may be in such animals, and because these peculiarities occur in a precisely similar manner in the Tardigrada. Just as in the case of Diptera such very far-reaching secondary changes were possible in the larval stage in adaptation to certain conditions of existence, so this might equally well have happened in the case of the larvæ of other insects also of which we have lost all knowledge. I merely mean that, of all tracheate Arthropods with which we are at present acquainted, no single form so simply and so readily enables us to interpret the Tardigrade body as these very dipterous larvæ. I do not believe that the Tardigrades can be placed at the root of the tracheate stem or in the neighbourhood of it; for the conditions of their organization diverge more from those of the Annelids than do those of indisputable Tracheates of much higher rank. If my memory serves me it was once declared by Ray Lankester that in the case of animals of very small size but of relatively complicated structure we must first direct our thoughts towards degeneration and reduction from higher forms. If we derive the Tardigrada in the manner indicated above from pædogenetic and greatly modified Tracheate larvæ we can regard the entire body of these animals as an Arthropod trunk of four segments, of which the head ceased to be developed, and of the cephalic organs of which the supra-oesophageal ganglion is the sole remnant. The first three ganglia of the ventral cord, which in higher Arthropods are fused together to form the suboesophageal ganglion and innervate the mouth-parts, may very well in the course of time have degenerated and disappeared, since the organs which they had to supply were no longer developed. The four ganglionic centres of the Tardigrades may then correspond to three thoracic and one abdominal ganglion. If we consider that the young of many Myriapods leave the egg at a very early stage with quite a small number of segments, and only develop the remainder during free existence, we can also conceive that this may have been possible several times, and that such immature larvæ



having ceased to develop at an early stage, and being remodelled after the fashion of the dipterous larvæ which we have been discussing, might have acquired the power of pædogenetic reproduction. I readily admit that our hypotheses are somewhat many in number; but there is not a single one among them which has not been actually observed in the Arthropod phylum itself, and more frequently in combinations. Whether the leg-stumps of the Tardigrades have arisen by degeneration from Arthropod appendages of their ancestors, or whether they may be new formations like the pro-legs and claspers of the caterpillars, is a question which is difficult to decide. Its solution, however, be it as it may, needs to alter nothing in the whole conception.

If we once more briefly sum up the points of agreement between the Tardigrades and greatly modified Tracheate larvæ, somewhat of the type of the maggots of *Cecidomyia*, we find:—absence of a head, chitinous stylets in the œsophageal tube, absence of any ciliated epithelium and of a dermal muscle-sheath, musculature broken up into isolated cords, supra-œsophageal ganglion and ventral ganglion-chain, simple structure of the sexual organs, and, lastly, Malpighian vessels. The differences depend upon further advanced degeneration of the Tardigrades, and include:—small number of the ganglia (disappearance of the parts of the subœsophageal ganglion), smooth musculature, absence of tracheæ and circulatory organs, and the probable reduction of the one germ-gland. As new formations we may perhaps regard the efferent duct of the sexual organs and, at any rate, the leg-stumps, if these are not an ancestral character.

Embryology as yet affords us no explanation; besides the development need no longer be of the typical Arthropod type, but may have secondarily undergone great modifications.

XXX.—On some newly-described Jurassic and Cretaceous Lizards and Rhynchocephalians. By G. A. BOULENGER.

IN a paper published two years ago (2), whilst dealing with a few points in the osteology of *Heloderma* and the systematic position of that genus of lizards, I ventured to express some views on the probable phylogeny of the order Squamata, which comprises the existing group of true lizards, chameleons, and snakes. I pointed out that the Cretaceous lizard *Hydrosaurus lesinensis*, regarded by some authors as a member





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