Metamerism in Enteropneusta.

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With 3 Text-figures.

THE Chordate affinities of the Enteropneusta were advocated first by Bateson, who even included this group of animals amongst the Chordata. Most subsequent investigators of the Enteropneusta (MacBride, Willey, Ritter, and Heider in particular) supported Bateson's conception and even tried to give it more evidence. On the other hand, Spengel, the accepted imperator in the knowledge of the group, as Ritter rightly observes, denies all relationship between the Enteropneusta and the Chordata; he believes that Balanoglossus is distantly allied to the Annelida, and that the Tornaria is a modified Trochosphere. If the relations of the Enteropneusta with the Pterobranchia, Phoronis, and Echinoderms be left out of the question, as these can be considered to be mere side-lines in the course of evolution, it becomes apparent that the Enteropneusta, either through their relation to the Annelida or to the Chordata, are allied to segmented animals.

Spengel found no support for his view that the Enteropneusta are related to the Annelida, and MacBride in his review of Spengel's monograph has given good evidence that Spengel's conception rested on no solid foundation and is therefore of no value. The Chordate affinities of the Enteropneusta, on the other hand, are well established and generally accepted nowadays. In his last publication on the Enteropneusta in 'Handwörterbuch der Naturwissenschaften', Spengel himself seems to be inclined to leave at least room for the relationship between Enteropneusta and Chordata.

If the Enteropneusta are related to segmented animals, as

the Chordata are, the question arises whether there is any evidence of metamerism in Balanoglossus. The body consists of three parts: proboscis, collar, and trunk, each with its own coelomic cavity; the same arrangement is found in Pterobranchia, Sagitta, the Actinotrocha, and Echinoderm larvae. An indication of this trimerism is found, according to van Wijhe, also in the early development of Amphioxus. In Balanoglossus this metamerism is to some extent obscured by the great length of the trunk. If the posterior region of the animal had the same length as the collar, as Morgan suggests—and in early post-larval life they are equal in length—no one would doubt that we were dealing with a metameric animal consisting of three segments. The question naturally arises whether the long trunk of Balanoglossus really represents a single segment. If we accept that segmentation is largely due to the mode of locomotion, it becomes clear why a further segmentation of the trunk has either not been developed or has been lost in the Enteropneusta. Here locomotion is effected for the greater part by the action of the proboscis and the collar. According to Ritter the whole body is drawn forward, especially in Dolichoglossus with its long proboscis, by means of the contraction of the longitudinal muscles of the proboscis and the collar. Thus, if traces of metamerism are to be found in the trunk, one should not expect to find them in the coelom nor in the muscles, though these structures are most important in the segmentation of the Annelida and the Chordata. Thus real segmentation is excluded in Enteropneusta and only pseudometamerism in some form or other can be expected to be seen.

The gills, numbering usually from 50 to 100 pairs, form a regular row at both sides in the anterior part of the trunk. These show a metameric arrangement, but this alone is not sufficient proof for metamerism. If this branchiomerism has anything to do with metamerism in the trunk, other organs, coinciding in their arrangement with the gills, will have to be looked for. Of course, these organs must be in themselves independent of the gills. This excludes the vascular system at once. The branchial veins and arteries, of course, show the same

arrangement as the gills, and when the cutaneous vessels open into the branchial veins, as is the case for example in Glandiceps talaboti, their more or less metameric arrangement is also of no further interest. The nervous system shows no trace of metamerism at all, as could hardly be expected. Thus there are left only the intestine, the skin, and the gonads.

There is, connected with the intestine, besides the gills, another structure that shows a metameric arrangement to some degree. A number of sacculations, protruding at the dorso-lateral sides of the trunk, are present in a certain region of the gut. These are noticed in the Ptychoderidae, but are absent in the Harrimanidae, and in the Spengelidae they may be present or not. These hepatic caeca are placed in two regular rows and give the impression of a metameric arrangement. As the liver region is always situated far behind the branchial region, the arrangement of the saccules cannot be compared with that of the gills, and taken alone these caeca give as little proof of metamerism as the gills.

The epidermis shows a certain zonulation, having the glandular cells arranged in zones separated by interannular depressions with or without a small number of glandular cells. Kowalewsky found that the number of these epidermal rings practically corresponds to the number of gills in Glossobalanus minutus, but in Balanoglossus clavigerus he found far more rings than gills. These rings are not limited to the branchial region; they extend over the whole length of the trunk, and in the abdomen they may be even more pronounced than in the branchial region. Willey expressed the opinion that this epidermal zonulation has not been well considered, and has been unjustly treated as having no deep-lying significance at all. His view, that the gill-slits originally arose as perforations in the interannular grooves, was opposed by Spengel, though a segmentation of the epidermis would fit in very well in his supposed relationship between Enteropneusta and Annelida. Spengel's objection, that the zonulation is produced only by a certain arrangement of glandular cells, is of no value, as glandular cells may show a metameric arrangement as well as

any other organ, and in some animals they actually show this. Spengel has pointed out that the zonulations, even in such an animal as Ptychodera flava, where they seem to have a fairly regular arrangement, show too many irregularities at closer examination, in order to give sufficient proof of a metamerism. It is probably better to leave these epidermal zonulations out of the question until an Enteropneust is found in which they are really metamerically arranged, than to build up theories around supposed structures.

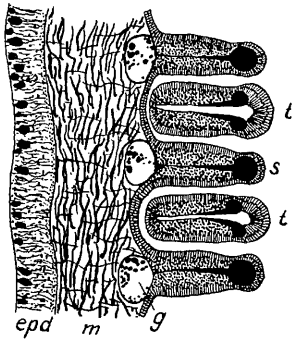
Lastly come the gonads. Gills and gonads are relatively independent structures, and the genital and branchial regions coincide to a large extent in the greater number of Enteropneusta. This makes the arrangement of the gonads a matter of great importance for the present question. Spengel could not find any relation at all between the arrangement of the gonads and the gills in the very extensive material that he studied, and thus expresses the opinion that the gonads cannot be looked upon as segmental organs, and, if they are, that the gonadomeres nevertheless do not correspond in any way to the branchiomeres. It is somewhat surprising that MacBride in his review of Spengel's monograph figures, apparently without any other excuse than the possession of a foreseeing mind, a schematic horizontal section of Balanoglossus in which the gonads regularly alternate with the branchial sacs. Willey, also, without giving any further evidence, accepted a regular alternation of gonads and gills, the gonads having a zonary disposition and the gill-slits occupying the interzonal depressions. On this supposition he based his theory that the primary function of the gill-slits is the oxygenation of the gonads, and their secondary function being the respiration of the individual. This is one of Willey's rather wild theories of which Spengel says: 'Es wird einem ja schwindlich, wenn man an diesen babylonischen Turmbau nur denkt.'

Yet there is a relation between the arrangement of the gill-slits and the gonads. Branchiomerism and gonadomerism coincide. Meek found this realized in Glossobalanus marginatus, where a certain region bears the same number of gonads as

gills. The same holds true for young specimens of Glossobalanus crozieri; gonads and gills are present in the same number, and to each branchial pore a genital opening is present, of course, only as far as the genital and branchial regions overlap.

The most indubitable evidence is given by Dolichoglossus caraibicus. This species has over fifty pairs of gill-slits. The first gonads are found between the fourth and fifth gill-slits at both sides of the body, and then a regular alternation

TEXT-FIG. 1.



Dolichoglossus caraibicus. Part of an horizontal section of the branchial region. × 66.

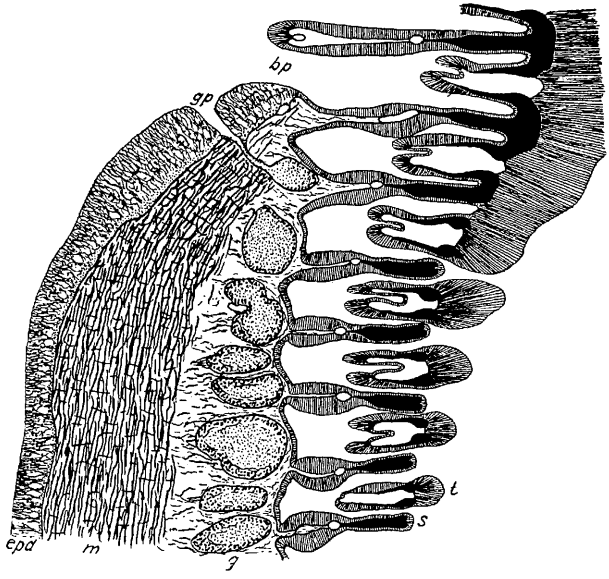
bp, branchial pore; *epd*, epidermis; *g*, gonad; *gp*, genital pore; *m*, musculature in body cavity; *s*, branchial septum; *t*, branchial tongue.

of gonads and gills is found till the end of the branchial region, so that at the peripheral side of each septum a gonad is situated (Text-fig. 1). The genital pores are found exactly between the succeeding branchial apertures. This relation between these two organs is very clear in Dolichoglossus caraibicus, as the gonads are very small and simple in the only available specimen.

The same phenomenon is found in Glandiceps talaboti, though a closer examination is necessary here, because the gonads

are large and branched. Near the external orifice the gonad is situated at the outer side of a gill-septum, but soon it becomes broader, extending to the back of the branchial sac (Text-fig. 2).

TEXT-FIG. 2.

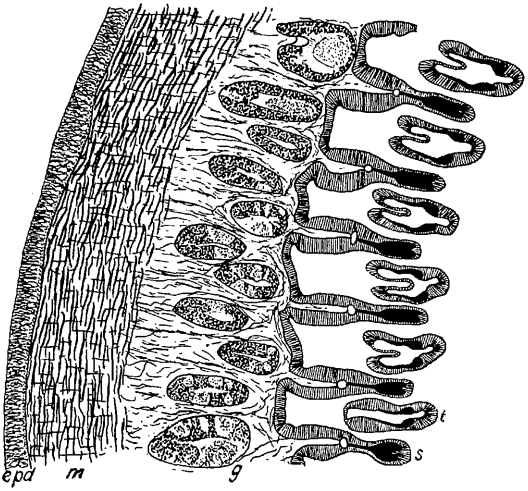


Glandiceps talaboti. Part of an almost horizontal section of the branchial region at the level of the pores. × 40.

A little more ventrally the gonad branches into two, and these branches occupy a very definite position with regard to the gills ; one is situated outside a septum, the other at the back of the branchial sac (Text-fig. 3). In the ventral part of the body, where the gonads may branch repeatedly, this relation between gills and gonads is quite disturbed.

Thus there are four species, representatives of the three families of Enteropneusta, in which the gonads alternate with the gills, that is in which gonadomerism corresponds to branchiomerism. Though no trace of this relation has been found in the

TEXT-FIG. 3.



Glandiceps talaboti. Part of an almost horizontal section of the branchial region, ventral to that figured in Text-fig. 2. × 40.

majority of Enteropneusta, it does not appear to be too hazardous to accept this relation as an original character of the Enteropneusta, a character that has, however, been lost in some way or other in most of them.

There is a species that gives an indication of one way in which this arrangement has been lost. This species is Dolichoglossus otagoensis. The small number of gill-slits, about ten, does not make it very suitable for the purpose, nevertheless it

shows that there is some relation between the gills and the gonads. The small gonopores are in the same, or nearly the same, section in which the front end of the branchial pore is found. As the branchial pores are very wide and the space between them is correspondingly narrow, it follows that the gonopores are situated at the same level as the septa. Thus to every septum, except the first two, there is a corresponding gonad. In a young specimen with only six gill-slits this was found without exception. In older specimens more gonads may be present; thus in a specimen with ten gill-slits there were found two extra gonads, not situated at the level of a septum, in addition to those at the sides of the third to the tenth septa (the caudal wall of the last slit being considered as a septum). These gonads, however, were very small and apparently secondarily formed. Spengel described a new formation of gonads intercalated between the older ones in Harrimania kupfferi, and the same is found here in Dolichoglossus otagoensis. When these gonads mature, they push away the primary ones, in this way disturbing the original relation between gonads and gills.

Another manner in which the original relation may have been lost is that the gills lost their metameric arrangement in the same way as this occurs in Amphioxus. On comparing, e.g., the genera Balanoglossus or Ptychodera with Dolichoglossus or Harrimania, it is striking to notice that in the former the gills are far more crowded. As it is impossible to give any proof of this supposed compression of the gills by comparison with other organs, this is only a supposition.

In Vertebrates branchiomerism does not correspond to the general segmentation of the body, but in Amphioxus it does. Furthermore, Amphioxus shows, at least during the earlier stages of its development, exactly the same relation between gills and gonads as mentioned above for some Enteropneusta. Also in the young Amphioxus the gonads are situated between the gill-slits, i.e. opposite the branchial septa. This may be considered to be another proof of Chordate relationship of Balanoglossus, as this was accepted first by Bateson.

As the coelomic cavity of Enteropneusta, besides the trimerism in prostomium, collar, and trunk, does not show any further tendency to segmentation, this arrangement of the gills and gonads can be considered only to be a case of pseudometamerism. Compared with their distant allies, the Chordata, the Enteropneusta are, undoubtedly, very primitive animals; even Amphioxus shows a far higher organization. If the Enteropneusta are related to completely segmented animals, as the Chordata, it is possible that their pseudometamerism, which can be considered to be an original character of the group that has been lost in the majority of them, is only a relic of a former stage in which segmentation was more complete. It might have been lost in relation to their mode of life and locomotion in the same way as this can be accepted for Echiuroids. Another possibility, put forward by Heider, is that the metamerism of the vertebrate-body has as its distant predecessor the pseudometamerism of the Enteropneusta, and taking into consideration that the other relations of the Enteropneusta do not prove anything beyond the original trimerism, I am inclined to share this opinion of Heider.

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