Planctosphaera and Tornaria.

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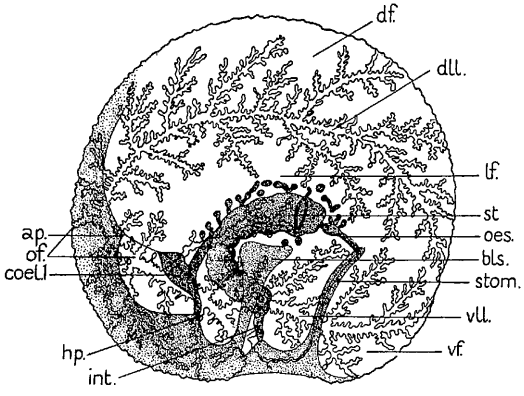
With 3 Text-figures.

THE Norwegian 'Michael Sars' North Atlantic Expedition, 1910, collected in the Bay of Biscay two transparent, spherical animals, one of which was badly damaged. Mortensen recognized these animals as nearly related to the Tornaria, the larval form of the Enteropneusta, and they were therefore sent to Spengel, the well-known authority on Enteropneusta, for further examination. Spengel wrote a report on these animals, naming them Planctosphaera pelagica. This report, however, was published only in 1932, long after his death (1).

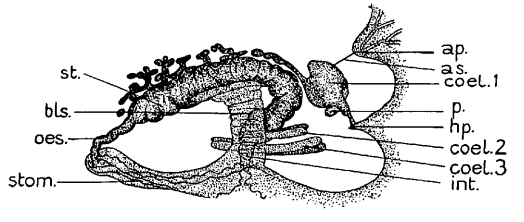
In his report Spengel described this animal as accurately as the material allowed and he gave some excellent drawings, illustrating the animal from all possible sides, as well as its internal organs. It appears that the larva, notwithstanding its spherical form, is bilaterally symmetrical. All its internal organs are situated in one quadrant, mouth and anus lie close together, and this side of the animal's body can best be designated as its ventral side. A narrow deep median groove extends over the ventral side, ending slightly beyond the posterior pole (Text-fig. 1).

The internal organs are similar to and even show a great similarity in form to those of Tornaria (Text-fig. 2). The alimentary canal consists of oesophagus, stomach, and intestine; the mouth is situated at the end of a long stomodaeal canal such as is also found in the large tentaculated Tornaria. The unpaired anterior coelom or hydrocoel with its hydropore opening to the exterior and connected by an apical string to the apical plate, the paired collar and trunk coelomic cavities,



TEXT-FIG. 1.

Planctosphaera pelagica. Lateral view. After Spengel. *ap.*, apical plate; *bls.*, blind-sac; *coel.*1, anterior coelomic cavity; *df.*, dorsal field; *dll.*, dorso-lateral lobe; *hp.*, hydropore; *int.*, intestine; *lf.*, lateral field; *oes.*, oesophagus; *of.*, oral field; *st.*, stomach; *stom.*, stomodaeal canal; *vf.*, ventral field; *vll.*, ventro-lateral lobe.



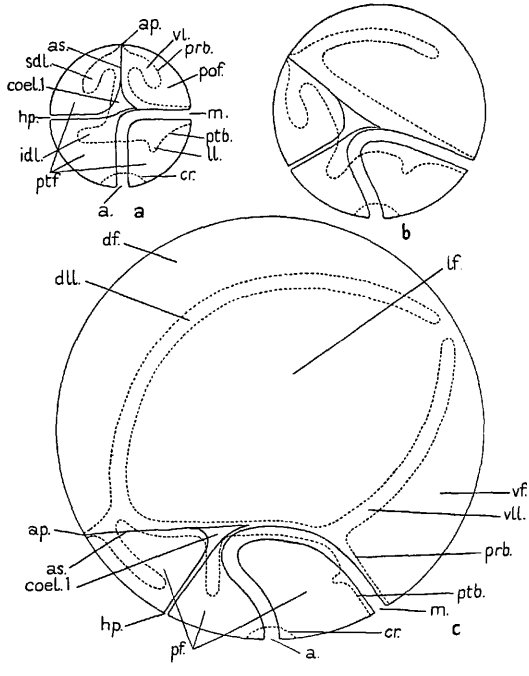
TEXT-FIG. 2.

Planctosphaera pelagica. Internal organs. After Spengel. *ap.*, apical plate; *as.*, apical string; *bls.*, blind-sac; *coel.*1., anterior coelomic cavity; *coel.*2, collar coelom; *coel.*3, trunk coelom; *hp.*, hydropore; *int.*, intestine; *oes.*, oesophagus; *p.*, pericardium; *st.*, stomach; *stom.*, stomodaeal canal.

lying in the form of narrow tubes at both sides of the intestine, and the pericardium are all similar to those of Tornaria. Externally there are also pre- and post-oral ciliated bands, as well as an apical plate; the latter, however, lacks the eye-spots of the Tornaria.

There is, nevertheless, a striking difference between Planctosphaera and Tornaria. In a median section of the Tornaria the pre-oral field, surrounded by the pre-oral ciliary band, occupies about one-quarter of the circumference. The other three-quarters is formed by the post-oral field, at least if the anal field, which only later during development becomes separated from the post-oral field by the ciliary ring, is regarded as part of the post-oral field. In Planctosphaera these relations are just the reverse. As Planctosphaera is much larger than most Tornaria, being about 10 mm. in diameter, one can imagine that the pre-oral field has greatly extended, while the rest of the body has retained the size it had in the Tornaria. I have tried to illustrate this relation between Planctosphaera and Tornaria in the diagrams of fig. 3.

The ciliary bands of Planctosphaera are much more intricate than those of Tornaria, and at first sight a comparison between the two animals seems hardly possible. In Tornaria the ciliary bands form primary and secondary lobes; in Planctosphaera tertiary and even lobes of higher orders are added to these. In the Tornaria the oral field, extending itself between the two bands, has about the same dimensions as the pre- and post-oral fields. Only in the large tentaculated Tornaria is the oral field much narrower, so that the pre- and post-oral ciliary bands are parallel to each other, and in the lobes the ascending and descending loops of one band are also parallel. In Planctosphaera this is even more marked; the oral field is reduced to a narrow strip with a ciliary band on each side. The lobes of the oral field, formed by the loops of the ciliary band branch over the whole surface of the animal, dividing the pre- and post-oral fields into different parts. It is quite easy to recognize the main part of the oral field, delimited on the one side by the pre-, on the other by the post-oral ciliary band. Starting at the mouth, in the depth of



TEXT-FIG. 3.

Diagram illustrating the relation between Tornaria and Planctosphaera. (*a*) Spherical Tornaria; (*b*) hypothetical intermediate form; (*c*) simplified Planctosphaera. *a.*, anus; *ap.*, apical plate; *as.*, apical string; *coel.* 1, anterior cloeomic cavity; *cr.*, ciliary ring; *df.*, dorsal field; *dll.*, dorso-lateral lobe; *hp.*, hydropore; *idl.*, inferior dorsal lobe; *lf.*, lateral field; *ll.*, lateral lobe; *m.*, mouth; *pf.*, posterior field; *pof.*, pre-oral field; *prb.*, pre-oral ciliary band; *ptb.*, post-oral ciliary band; *ptf.*, post-oral field; *sdl.*, superior dorsal lobe; *vf.*, ventral field; *vl.*, ventral lobe; *vll.*, ventro-lateral lobe.

the stomodaeal canal, we see that the oral field, which in this region is very narrow, turns at first in a lateral direction and then proceeds in a curve in the direction of the posterior end of the body. Not far from the posterior end it turns again at right angles, and then the oral field of the one side of the body meets its fellow of the other side at the posterior pole. This place thus corresponds to the apical plate of the Tornaria.

Near the posterior side of the body, where the oral field turns at right angles towards the posterior pole, the main part of the oral field seems to be continued into a large branch or lobe, formed by the pre-oral ciliary band only. This lobe runs along the dorso-lateral side of the body and ends very near its anterior pole. A similar large lobe, running along the ventro-lateral side, branches off from the oral field not far from the entrance of the stomodaeal canal. The course of these branches and all the ramifications of the oral field have been adequately described by Spengel.

The lobes made by the pre- and post-oral ciliary bands of the Tornaria are arranged in such a way around the apical plate that the animal is nearly radially symmetrical in external appearance. A similar radial symmetry is exhibited by Planctosphaera in the arrangement of the two dorso-lateral and the two ventro-lateral lobes of the oral field, but in Planctosphaera the centre of symmetry is found at the anterior pole of the body, just opposite the apical plate. No doubt this radial arrangement of the ciliary bands is of great importance for the locomotion of the animal. Presumably it swims with the anterior pole of the body forwards.

By the ciliary bands the body is divided into several fields. The designations given by Spengel to these fields do not seem to me to be very adequate. Spengel calls the large field between the two dorso-lateral lobes 'Hinterfeld', but as it extends over the whole dorsal area of the body from the posterior to the anterior pole, dorsal field would be a better name for it. In the same way the field between the two ventro-lateral lobes is best called ventral field and not 'Vorderfeld', even though it does not extend over the whole ventral surface of the animal but only over the anterior half of it. Between the dorso- and

ventrolateral lobes are found the lateral fields or 'Seitenfelder' of Spengel. Finally there is the area between the mouth and the apical plate, surrounded by the post-oral ciliary band. Spengel calls this area 'untere Hinterfelder'. These two 'Felder' are separated from each other by the median groove, not by a ciliary band, so that in reality they form only one field, which is best described as the posterior field. This posterior field corresponds to the whole post-oral field, including the anal field, of the *Tornaria*, whereas the dorsal, ventral, and two lateral fields, which merge into each other at the anterior pole, correspond to the small pre-oral field of the Tornaria.

It is possible that Planctosphaera has also a ciliary ring separating the anal from the post-oral field. At least Spengel was able to discern a dark ring surrounding the anus. This ring, however, is incomplete; it is open at the side of the mouth, and no cilia could be detected on it.

Text-fig. 3 also shows very clearly in what way the lobes of Planctosphaera may be related to those of Tornaria. The large dorso-lateral lobes correspond without doubt to the ventral lobes of Tornaria, whereas the ventro-lateral lobes of Planctosphaera are not represented in Tornaria. The post-oral ciliary band of Tornaria forms three primary lobes, viz. the superior and inferior dorsal lobes and the lateral lobe. The determination of these lobes in Planctosphaera cannot be done with the same degree of certainty. However, in this animal two pairs of large lobes penetrate into the posterior field, one near the apical plate and running parallel to the median groove and the other from the sides. If they correspond to any of the tornarian lobes, it is probable that they represent the superior and inferior dorsal lobes. A small lobe near the entrance to the stomodaeal canal might be the lateral lobe of Tornaria.

Of the internal organs the position of the unpaired anterior coelomic cavity is peculiar. In Tornaria this cavity is found at the anterior end of the stomach near its junction with the oesophagus; in Planctosphaera it is situated near the posterior end of the stomach. According to Spengel this position can be explained in two ways. It may be supposed that the

coelomic cavity was separated from the top end of the archenteron as in Tornaria and has shifted from there along the dorsal side of the stomach to its more posterior position. In this case, this shifting should have taken place directly after the separation and before the hydropore and the apical string, connecting this cavity with the epidermis, are formed. Another possibility, and one which is more favoured by Spengel, is that the whole wall of the archenteron might form the coelomic vesicle, and that under the influence of the apical plate the anterior part is activated to do so in the Tornaria and the more posterior part in Planctosphaera. To me the following explanation seems much more likely. The coelomic cavity is separated off from the top end of the still small archenteron in the same way as in the Tornaria. After this separation, and as a direct result of the enormous extension of the pre-oral side of the body, the archenteron grows out to form the long stomach of Planctosphaera and to connect with the stomodaeal canal for the formation of the mouth. The position of the anterior coelom in relation to the other coelomic cavities is the same in both larvae.

The occurrence of one organ in Planctosphaera is remarkable, were it only for the fact that it is not found in Tornaria. From the ventral side a pair of blind-sacs penetrate into the body from the surface. They converge towards the interior, their external openings being farther separated from each other than their tops. These tops lie at the sides of the stomach though not actually touching its wall, and at their tops the sacs are widened out in an anterior direction.

Though in several respects Planctosphaera is very similar to the Tornaria, yet it differs too much from the Tornaria in the general form of its body and also in the presence of these blind-sacs to be a larval Enteropneust. Moreover, by the work of Stiasny we know rather accurately to which genera of adult Enteropneusta the different types of Tornaria belong. With only one exception the tornarian type is known of all genera undergoing an indirect development. As all genera of Enteropneusta as well as all types of Tornaria exhibit similar characters, there seems no

justification for regarding Planctosphaera as the hitherto unknown larva of Schizocardium.

The difference between Planctosphaera and the larva of Cephalodiscus is even greater, and this makes it very unlikely that Planctosphaera is the unknown larva of Rhabdopleura. Planctosphaera is also comparatively much larger than Rhabdopleura, so that for this reason alone it can hardly be its larva.

Spengel, therefore, is quite right when he puts Planctosphaera in an order by itself. The class of the Hemichordata should then be divided into three orders, viz. Enteropneusta, Pterobranchia, and a third, which could provisionally be called Planctosphaeroidea, until the adult animal is found.

Little can be said about the form of this adult animal. It would also be impossible to visualize an adult Enteropneust, if only a Tornaria was known. In its general form I suppose it will bear more resemblance to an Enteropneust than to any other animal. Most likely the great extension of the pre-oral part of the body is only a larval character. As in Enteropneusta, the ciliary band will disappear during metamorphosis and the body of the adult animal will be formed from the ventral part of the larval body, where the different organs are situated.

The two blind-sacs penetrating into the larval body seem to be of great importance. Apparently they are not larval organs and have no functions at all during larval life. These sacs can only be the rudiments of some organ of the adult animal. It is only the question what organ that can be. Spengel tried to solve this problem, and in accordance with his firm conviction that the Enteropneusta are not related at all to the Chordata, he compared this organ with the ectodermal invagination of Actinotrocha, which becomes everted to form the body of Phoronis. This invagination, however, is from the beginning a median organ, attached by the mesentery to the intestine. The blind-sacs of Planctosphaera, on the other hand, are paired; they are not attached to the intestine by a mesentery, which is only formed later. If they were

capable of eversion as in Phoronis, they would have to fuse with each other first and a mesentery would have to be formed between these fused sacs and the intestine. Spengel accepted this and imagined that by the eversion and further outgrowth of the sac the anus would come to be on the other side of the mouth, in which case the animal would acquire a form more or less similar to that of Cephalodiscus.

Most students of Enteropneusta, following Bateson, accept the chordate affinities of this group of animals, and I think in this direction lies the solution of these remarkable organs. The only other structures with which they show a great similarity and with which I can identify them are the rudiments of the peribranchial cavity of Ascidians. This cavity also arises as two separate blind-sacs penetrating from the outside into the body and lying with their blind ends at the side of the intestine. Only later their openings fuse to form the egestion aperture of the adult animal. I can only come to the conclusion that these blind-sacs are the homologues of the peribranchial cavity of Tunicates and therefore of the atrium of Amphioxus. Thus Planctosphaera would be the larva of an animal, either sessile or free living but more probably the latter, nearly allied to the Enteropneusta and exhibiting most of the characters of Enteropneusta, but by the presence of an atrial cavity intermediate between this group of animals, the Tunicates and Amphioxus. I wonder when this animal will be found, and what it will look like!

Literature

1. J. W. Spengel, Planctosphaera pelagica. Report on the scientific results of the 'Michael Sars' North Atlantic Deep-Sea Exped., 1910, vol. 5. Bergen, 1932.