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Dedicated to Mrs. W.S.S. van Benthem Jutting

Sense organs in *Spongiobranchaea australis* d'Orbigny, 1835 (Gastropoda, Pteropoda)

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In the Gymnosomata five types of sense organs are found: the labial tentacle, eye, rhinophore, osphradium and statocyst. A very thorough study of the anatomy of Pteropoda was made by MEISENHEIMER (1905), in which he paid particular attention to the sense organs. This study is used as the basis for this paper, as no important supplementary data appear to have been published since then. In a comparison between recently prepared histological material and the descriptions and drawings of *Spongiobranchaea australis* d'Orbigny, 1835 given by MEISENHEIMER (1905) certain differences were found. Some of these differences are discussed in this paper.

The material investigated was collected in the Atlantic sector of the Antarctic ocean at 64° 48′ S 27° 58′ E on February 9, 1960 by W. L. van Utrecht and the present author during a trip with the whale factory ship ms. "Willem Barendsz". It consisted of three specimens fixed in alcohol: serial sections, 5 μ thick, were cut and stained in haemalum eosin. It was impossible to assess the importance of artefacts, as there was no suitable material for comparison.

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LABIAL TENTACLE (fig. 1—3). — In contrast with the figures given by MEISENHEIMER (1905), the observations of the present author revealed that the labial tentacle (fig. 1a) was covered over the entire surface with ciliated epithelial cells. MEISENHEIMER only described the sensory cells with cilia (S) at the top of the tentacle. The ciliated cells on the lateral sides of the tentacle differ somewhat from the sensory cells, and in all probability receive no

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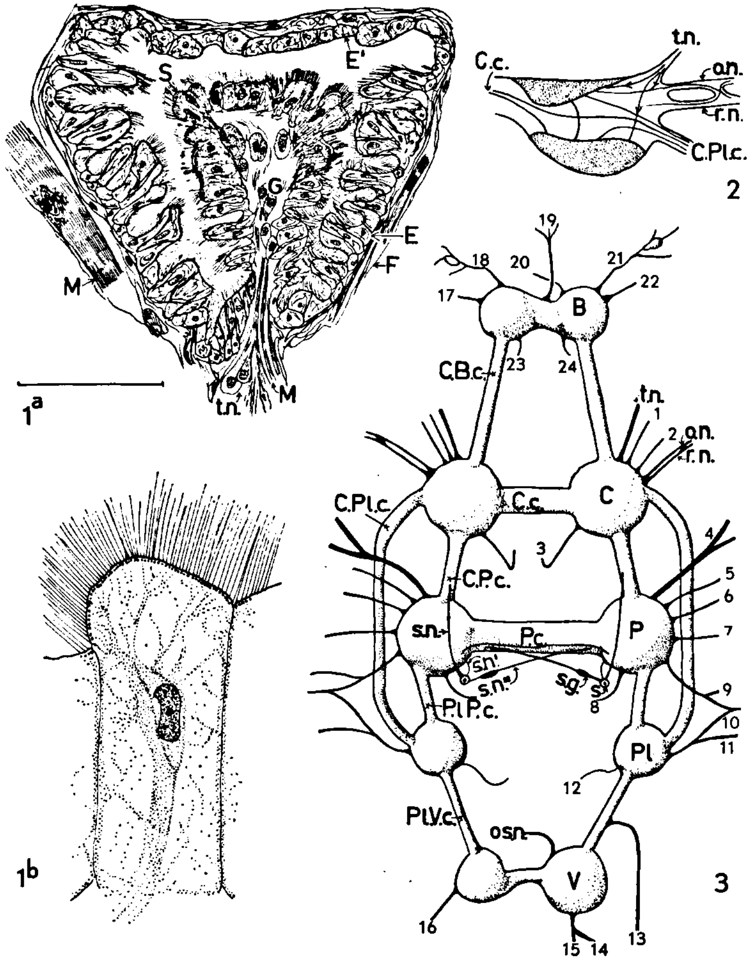

FIGS. 1—3. Labial tentacle and central nervous system in *Spongiobranchaea australis* d'Orbigny, 1835.

1a, tranversal section through a labial tentacle (scale represent 100 μ); 1b, sensory cell from the top of a tentacle, more enlarged; 2, diagram of the left cerebral ganglion with the origin of the tentacle nerve and with the nerve fibrils in this part of the ganglion, those indicated with arrows are from the tentacle nerve; 3, diagram of the central nervous system, reconstructed after serial sections.

tactile stimuli. The sensory cell (fig. 1b) can be described as follows: in the purple staining nucleus, small chromatin structures are present, nucleoli are only seldom seen; the cytoplasm, staining light purple, consists of small filaments forming a reticulum-like structure. Towards the outer edge the reticulum is more developed and stains somewhat darker, strands are connected with the basal corpuscles. Between the nucleus and cell base the reticulum changes to a bunch of reddish-purple fibres running to the nerve endings under the cell, with which they are linked. The cell walls are only delineated by protoplasm lying against them. The cell wall at the top of the cell is clearly seen with ciiia 5,5 μ in length. The basal corpuscles are found at approximately 0,5 μ beneath the cell wall and stain dark purple.

The non-sensory ciliated epithelial cells (E) differ only in a few respects from the sensory cells. The basal corpuscles are smaller, staining less dark and the cytoplasm reticulum is less developed, similar to the bunch of reddish-blue fibres under the nucleus; moreover the nucleus is more elongated than the sensory cells. With the reduction of the reticulum the cell walls are more clearly seen. No nerve fibrils were found to connect with these normal ciliated-cells. Scattered between these cells some others are present having connections with nerve endings, while the total appearance of these cells is different so that one may expect that sensory and non-sensory cells change over gradually.

The cell bodies (G) in the tentacle ganglion are rather small, provided with reddish-purple cytoplasm. This colour is exactly the same as that of the nuclei; the nuclei being even more red. Chromatin particles are numerous in the nucleus while in the cytoplasm a fine reticular structure is found. Near the tentacle ganglion the retractor muscle (M) of the tentacle is found passing through the point of attachment together with the tentacle nerve (t.n.). From figure 1a it is clear that both the tentacle and its sheath, in which the tentacle is completely retracted, are lined with ciliated epithelial cells, except for that part of the sheath directly opposite the top of the tentacle, where non-ciliated epithelial cells (E') are found.

In order to trace the pathway of the nerve which innervates the labial tentacle it was necessary to draw a reconstruction of the central nervous system. Though a reconstruction from serial sections is not reliable in all details, and figure 3 is only very diagrammatic, a description will be given of certain structures. From the cerebral ganglion (C) nerves are found innervating the labial tentacle (t.n.), the buccal mass (1), the mouth (2), the eyes (o.n.) and the rhinophores in the dorsal tentacle (r.n.) and the anterior parts of the body (3). The cerebral ganglia are connected by the cerebral commissure (C.c.). From these ganglia connectives pass to the buccal ganglia (C.B.c.), the pedal ganglia (C.P.c.) and to the pleural ganglia (C.Pl.c.). The pedal ganglia (P) give rise to six pairs of nerves (the nerves of the statocysts are left out of consideration here) viz. the nerves to the wings (4), the footlobes (5), the integument of the collar region (6), the lateral parts of the head (7), the ventral part of the body (8) and to the visceral mass and genital apparatus (9). The latter has connections with the nerves of the pleural ganglia (Pl.). Two pedal commissures (P.c.) are found, which will be discussed later, there are connectives with the pleural ganglia (Pl.P.c.). The pleural nerves (10 and 11) are both innervating the body integument. It was impossible to trace the cource of a very small nerve (12), which was not yet figured by MEISENHEIMER; the organs which were innervated by this nerve, therefore, remain obscure. The nerves of the asymetrical visceral ganglia innervate the osphradium (os.n.), the visceral mass (13), the heart and kidneys (14), the gonads and gonoduct (15) and the lateral visceral mass (16). The nerves of the buccal ganglia (B) innervate the buccal mass (17 and 22), the salivary glands (18 and 21), the hooksacs and radula (19 and 20) and the hooksacs (23 and 24). The buccal commissure (B.c.) is very short like the visceral commissure. In the explanation to the plates, the numerals used by MEISENHEIMER (1905) for the different nerves are indicated. Only nerve IV4 shown by MEISENHEIMER was not found, while he failed to identify nerve 12.

The tentacle nerve enters the cerebral ganglion near the entrance of the optic nerve. In figure 2 the course within the ganglia of some of the nerve fibrils associated with the tentacle nerve are shown. No nerve centres for the reception of stimuli from the labial tentacle are found, although such centres are present for the optic and rhinophore nerves, and for the statocyst in the pedal ganglia. Consequently one may conclude that the labial tentacle has a reduced innervation compared to the other organs mentioned. Similarly, the osphradium is, comparable with the labial tentacle, since osphradial centres are also lacking in the central nervous system.

EYE (fig. 5—7). — The eyes are described by MEISENHEIMER as rather rudimentary organs in the dorsal tentacle. It is true, that the eyes are rather small, as in all Gymnosomata, and that they are composed of only a few cells. But when light is the adeaquate stimulus, usually only sensory cells have to be present under a transparent part of the skin to build up a functional organ. In the eye of *S. australis* a transparent cornea and lens are present with an underlying basal retina innervated by the optic ganglion, so it is reasonable to suppose that we are dealing with a small but functional receptive organ.

The cornea (Co) is composed of a few thin cells about 2 μ thick, which stain very light red. A faint longitudinal striation is present in these cells. The lens (L) is a structureless body which stains light red except for the central part which is devoid of stain. The staining area of the lens is about 5 μ thick at its top and about 20 μ near the retina. The retina (Re) is composed of small nervous cells with lightly staining cytoplasm, while the nuclei are dark purple with numerous chromatin particles. The nerve cells underneath the retina, composing the optic ganglion (o.g.) have a reddish-purple reticular cytoplasm. This reticulum is continuous with the nerve fibrils of the retina cells. The nuclei of these nerve cells stain clearly red and contain numerous chromatin particles, the cells as well as the nuclei are rounded. No pigmentation was observed in the eye. Each retinal cell is connected with a single (the primary) ganglion cell, which is then directly linked with a further ganglion cell. The innervation of the optic ganglion, by the optic nerve of the cerebral ganglion will be discussed in the following section.

RHINOPHORE (fig. 4). — The other sense organ situated on the dorsal tentacle is the rhinophore, which surrounds the base of the eye. The innervation

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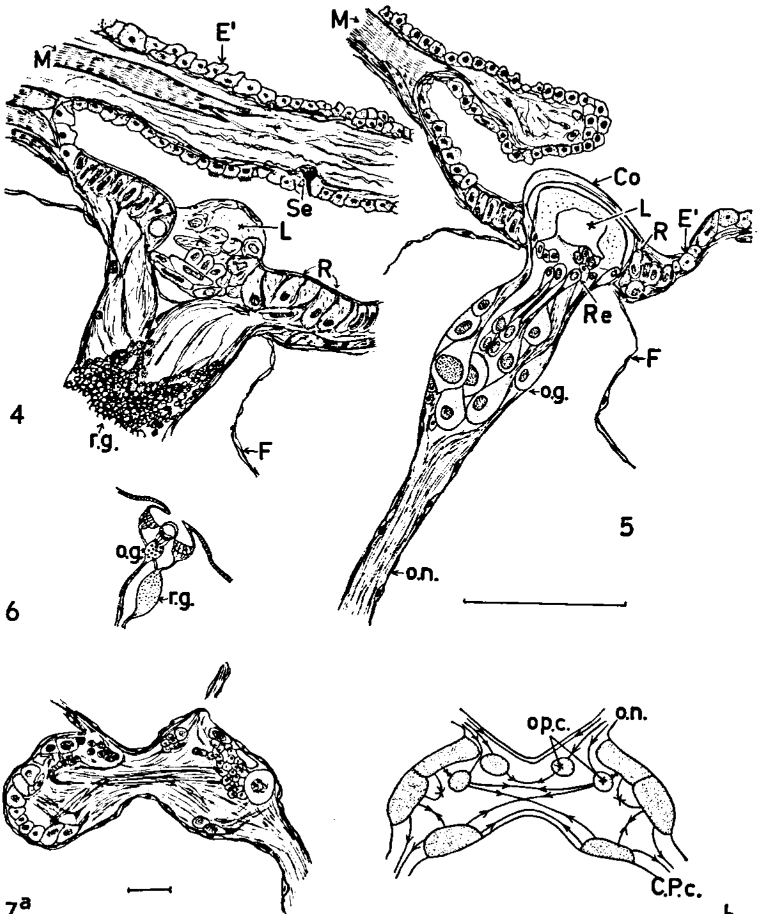


7a 7b

FIGS. 4—7. Dorsal tentacle and part of the cerebral ganglion of *Spongiobranchaea australis* d'Orbigny, 1835.
4, transversal section through the rhinophore (scale represents 100 μ); 5, transversal section through the eye (scale represents 100 μ); 6, diagram of the organisation of a dorsal tentacle, with the eye and the rhinophore and their ganglia; 7a, transversal section through the cerebral ganglion with the origin of the optic nerve and with the optic centres (scale represents 100 μ); 7b, diagram of the same part of the cerebral ganglia as in fig. 7a with the course of the nerve fibrils in the ganglia.

of the eye and rhinophore is, in *S. australis,* only completely separated near the dorsal tentacle, whereas towards the cerebral ganglion many cross connections exist. In other Gymnosomata, for example in *Clione limacina* (Phipps, 1774) the boundary between the innervation of both organs is even less distinct, as their ganglia are partly connected (MEISENHEIMER, 1905).

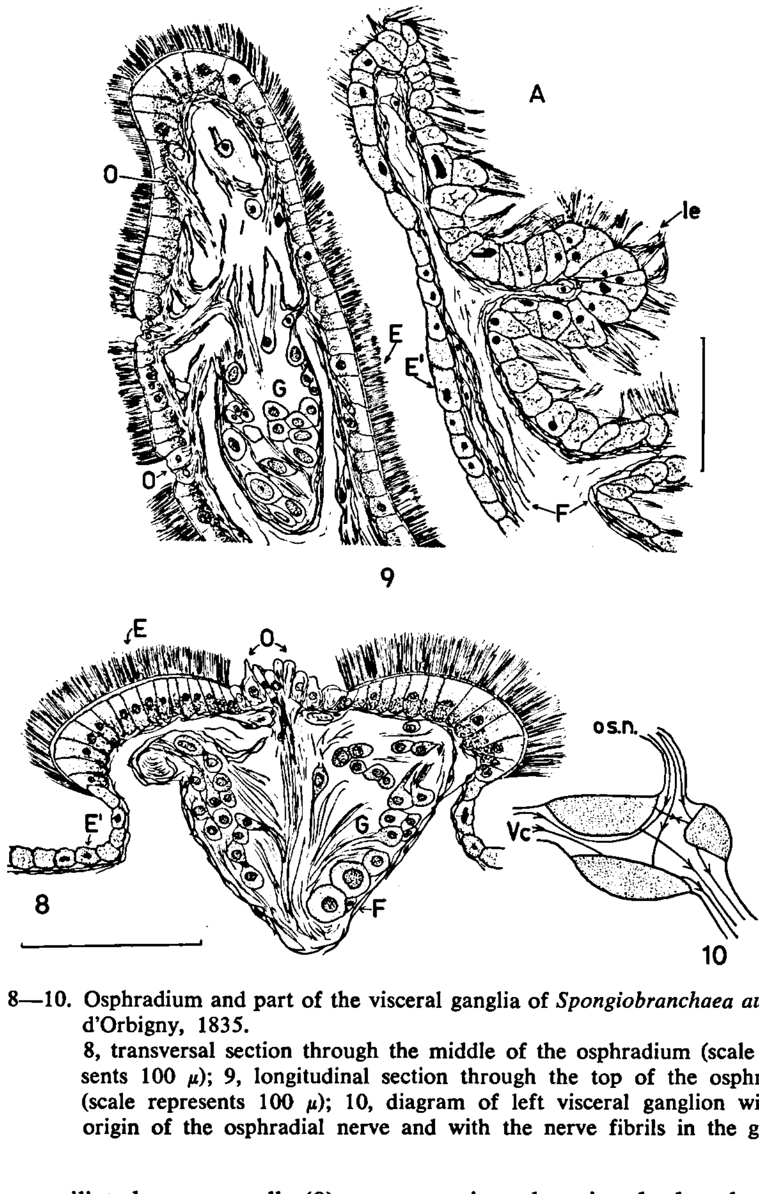
The rhinophore cells (R) are not very specialized and differ only from the surrounding epithelial cells by their more regular and elongated shape and by staining less dark. The purple nuclei show some chromatin particles. The cell wall, in contact with the outer world, is very thick and has, therefore, the appearance of the outer wall of ciliated epithelial cells, but cilia are absent. MEISENHEIMER (1905) also described these cells as common epithelial cells innervated by a special ganglion; he compared them with the rhinophore cells in other Opisthobranchia. In his opinion, the rhinophore and the eye are only effective in perception of tactile stimuli. The fact that there is no sharp boundary between retina and rhinophore cells and neither between the optic and rhinophore nerve, is in my opinion an indication that the rhinophore cells may play a role in light perception, similar to the retina cells, and may act in multiplying the optical stimulus.

As can be seen from the figures 2 and 3, connections between the optic and rhinophore nerve exist near the cerebral ganglion, and within the cerebral ganglia the optic and rhinophore nerve fibrils appear fused. As previously stated, these facts suggest that the eye and the rhinophore may receive the same stimuli with the same or comparable results. In figures 7a and 7b the course of the fibrils, here considered as optic nerve fibrils, is given. Three typically different paths are followed by these fibrils: namely one incoming fibril runs directly to the opposite eye; one runs to the optic centre (op.c.) in the centre of the cerebral ganglion and one runs to the optic centre (op.c.) near the cerebral commissure. Both centres have connections with corresponding centres in the opposite cerebral ganglion and with other cell groups in the ganglia. This may cause a very complicate coordination of the sense organs in the left and the right dorsal tentacle. In figure 2 the origin of both the optic and rhinophore nerve is given and it is clear that both are only slightly separated.

The rhinophore ganglion (r.g.) is distinctive, being composed of nerve cells with cell bodies only one third the size of those in the optic- and other ganglia, and there are more cells in this ganglion compared with the optic ganglion.

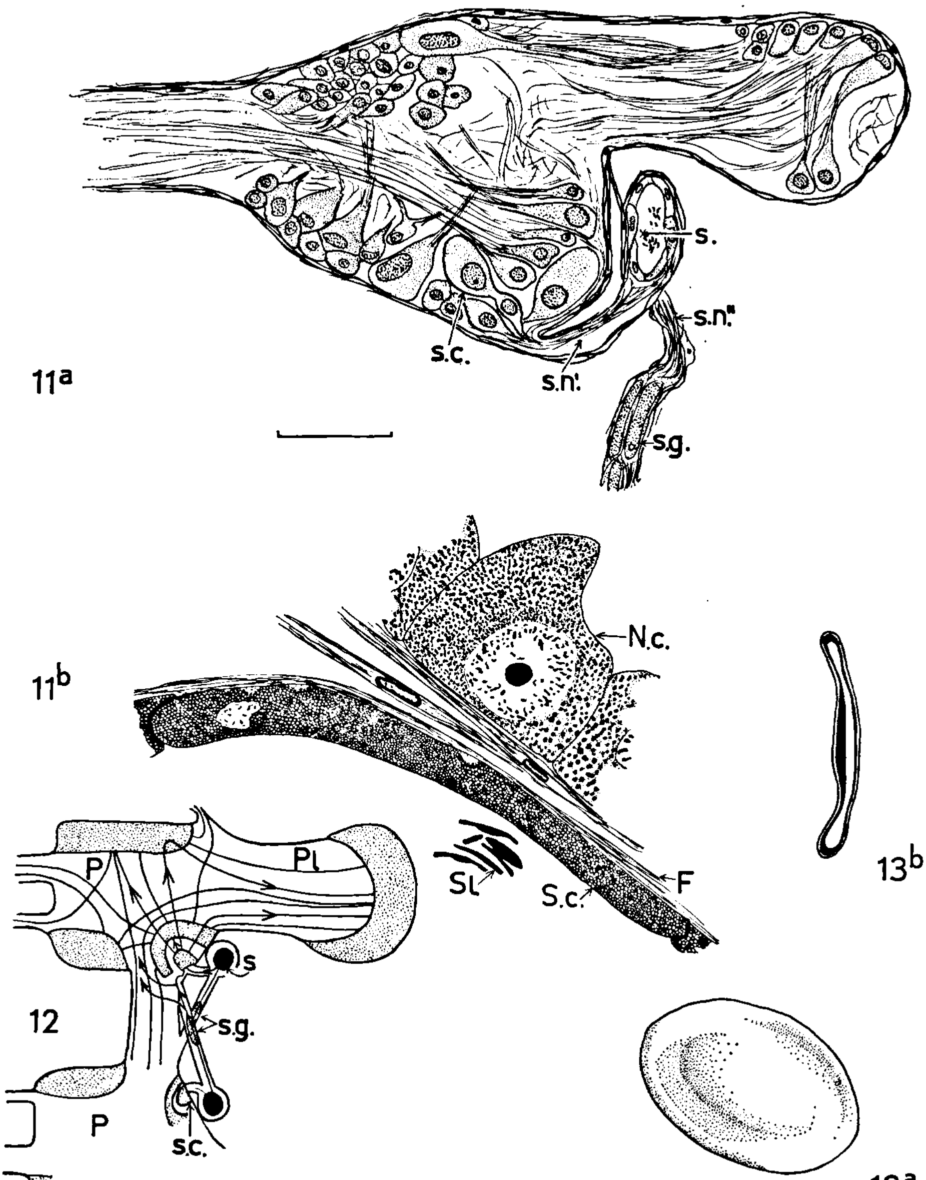
OSPHRADIUM (figs. 8—10). — The osphradium found next to the anus (A) is innervated by a nerve of the visceral ganglion. The cross section shown in figure 8 proves that the osphradium is composed of two bands of ciliated epithelium (E) with a median band of sensory cells (0), under which the osphradial ganglion is found. In figure 9 this arrangement is not so clearly visible but in this longitudinal section of the organ, nerve connections of some sensory cells, scattered between the ciliated cells, are clearly shown.

The ciliated cells (E) stain reddish-purple and the cytoplasm is reticulated, while the basal corpuscles are only faintly indicated. The nuclei are likewise reddish-purple and sometimes nucleoli are visible, accompanied by some chromatin structures. The cilia, which are 11 μ in length are regularly arranged on the cells. No sharp boundary is seen between the ciliated epithelial cells and the sensory cells as these change over gradually; in the figures this is, however, not so clearly seen.



FIGS. 8—10. Osphradium and part of the visceral ganglia of *Spongiobranchaea australis* d'Orbigny, 1835.
8, transversal section through the middle of the osphradium (scale represents 100 μ); 9, longitudinal section through the top of the osphradium (scale represents 100 μ); 10, diagram of left visceral ganglion with the origin of the osphradial nerve and with the nerve fibrils in the ganglia.

The unciliated sensory cells (0) are approximately twice the length of the ciliated cells. The exterior cell wall is very irregularly shaped, having "finger"-like protrusions, which give the cells a glandular appearance. The cytoplasm quantity, however, is poor, the cells are vacuolated, and it is evident that these cells receive nerve fibrils from the osphradial ganglion. The nuclei of the sensory cells are rather homogeneous with small chromatin particles. The ganglion cells (G) are of characteristic shape, 30 μ in diameter,



FIGS. 11—13. Statocysts, pedal and pleural ganglia of *Spongiobranchaea australis* d'Orbigny, 1835.
11a, transversal section through the left pedal and pleural ganglia with the left statocyst (scale represents 100 μ); 11b, part of the statocyst with some statoconia and the adjacent pedal ganglion cells, more enlarged; 12, diagram of the organs given in figure 11a, nerve fibrils drawn in the ganglia and nerves; 13a, aspect of one of the statoconia; 13b, optical cross section through one of the statoconia measuring 4 μ in length.

with clearly distinguishable nucleoli and chromatin particles. The cytoplasm stains lightly while the nucleoplasm stains dark purple-blue.

From figure 10 it is evident that no special osphradial centres are present in the visceral ganglia. This may be an indication that the function of the osphradium is uncomplicated. Nerve fibrils of the osphradium pass via a single nerve to the left and right visceral ganglia, which causes a bilateral innervation of the organ through a single nerve. No nerve fibrils were found going directly to other parts of the central nerve system.

STATOCYST (figs. 11—13). — The statocysts (s) are found between the pedal and pleural ganglion on both sides (fig. 11a). They are thin walled rounded sacs, enclosed in a mantle of connective tissue (F) which is a derivative from the connective tissue surrounding the central nervous system (fig. 11b). Sometimes a strip of connective tissue is found connecting the statocysts with the body wall (MEISENHEIMER, 1905), but in serial sections this band was not clearly visible. The statocyst wall is composed of elongated sensory cells of which only 3 to 4 are seen in a single cross section. The rather homogeneous cytoplasm has a dense granular structure. No cilia or other structures are found on the inner cell wall of the statocyst. The cells are about 5 μ thick and 90 μ long. The cytoplasm and nucleus stain in the same way as those of the ganglion cells. The nucleus is small and has chromatin particles; and a nucleolus was never observed. The lumen of the statocysts is empty except for the small statoconia (S1), measuring about 4 μ in diameter, which are present in large numbers (fig. 13a and 13b). These statoconia are hollow disc shaped with a somewhat thicker border and centre. The cells in the pedal ganglion that connect with nerve fibrils of the nerve s.n.′ and s.n.″ are similar to the other pedal ganglion cells, and only recognizable by tracing the incoming fibrils. Their protoplasm is reddish-purple and the nucleus is full of chromatin particles and has a bright nucleolus. These groups of cells in the pedal ganglion compose the pedal-static centres (s.c.). On either side they are connected with the nerve cells of the pleural ganglia by at least two groups of nerve fibrils and with the pedal nerve cells at the opposite side of the ganglia by further nerve fibrils. Indirect connections are found with the cerebral ganglia.

It has been stated that the innervation of the statocysts (s) is effected by a pair of nerves of the cerebral ganglia (C) (MEISENHEIMER, 1905); it was, however, very difficult to recognize these nerves in serial cross sections. Careful reconstruction showed that three nerves were found connected with each statocyst wall (figs. 3 and 12). One of these was easy to follow, as it immediately penetrates the pedal ganglion; it measured only 15—20 μ in diameter. A second small nerve (s.n.″) was found linked with the pedal commissure (P.c.), this nerve was 50 μ in diameter. In contrast to the first nerve (s.n.′) which was only marked by some nerve fibrils, the second one showed in addition some nerve cell bodies, grouped in the middle of the nerve in a ganglion-like structure (s.g.). Most of the nerve fibrils of nerve s.n.″ enter the pedal commissure near the opposite pedal ganglion with which they finally connect. The majority of these fibrils merge directly into the cerebro-pedal connective (C.P.c.); one group of fibrils, however, link with the nerve cells forming the pedal-static centre which also receives nerve fibrils from nerve s.n.′. Therefore, these static centres receive stimuli from the right and the left statocyst.

The innervation of the statocysts by the nerves s.n. derived from the cerebral ganglia, which innervation is the usually mentioned one, could only be traced by longitudinal serial sections. This nerve s.n. is indeed much larger than the two other ones, being 70 μ thick, and is provided with nerve cell bodies over its entire length. It was impossible to make a clear reconstruction of the nerves s.n. and s.n.″ to determine whether both nerves were fused near the statocysts, as two animals had to be used for this part of the work. When the exact course of the three nerves is as described, which may be possible, there is still one problem to be dealt with in regard to the work of MEISENHEIMER (1905). From serial sections and a macroscopic examination it is evident that the pedal commissure is not one simple connective between the two pedal ganglia. In figure 3 the pedal commissure is divided into two parts by a line running immediately under the letters P.c. The small band under the line is the anterior pedal commissure while the remainder above the line must be considered as the posterior pedal commissure. The anterior part is for its greater portion composed of nerve fibrils of the nerves s.n.″. The problem is that MEISENHEIMER figured this double commissure like he did for a number of other Gymnosomata, but he failed to note the connection of the "vordere Pedalkommissur" (anterior pedal commissure) with the statocysts. The nerve s.n.′ is very small and it is not strange that it has so often been overlooked.

SUMMARY

The sense organs: the labial tentacles, eyes, rhinophores, osphradium and statocysts of *Spongiobranchaea australis* d'Orbigny, 1835 are described together with their innervation. The descriptions are based on serial sections of three animals.

RÉSUMÉ

Les organes de sens: les tentacules labiaux, les yeux, les rhinophores, l'osphradium et les statocystes, de *Spongiobranchaea australis* d'Orbigny, 1835 ont été décrits ainsi que leur innervation. Les descriptions ont été faites avec l'aide de trois animaux sectionnés en séries.

LITERATURE

MEISENHEIMER, J.
1905 Pteropoda. — Wiss. Ergebn. Deutschen Tiefsee-Exp. "Valdivia", **9**: I—IV, 1—314, figs. 1—32, pls. I—XXVII, maps I—IX.

EXPLANATION OF NUMERALS AND LETTERS USED IN THE ILLUSTRATIONS

1	nerve	(I1)	innervating	anterior buccal mass
2	„	(I3)	„	mouth organs
3	„	(I4)	„	cranial body parts

4	„	(II1) „	wings
5	„	(II2) „	footlobes
6	„	(II3) „	integument of collar region
7	„	(II4) „	lateral parts of the head
8	„	(II6) „	ventral body parts
9	„	(II5) „	lateral body integument and genital apparatus
10	„	(III1a) „	body integument
11	„	(III1b) „	body integument
12	„	(not given by MEISENHEIMER, 1905)	
13	„	(IV5) innervating	visceral mass
14	„	(IV3) „	heart and kidneys
15	„	(IV3) „	gonad and gonoduct
16	„	(IV2) „	lateral parts of the body and visceral mass
17	„	(V3) „	buccal mass
18	„	(V2) „	oesophagus and salivary glands
19	„	(V1) „	hooksacs and radula
20	„	(V1) „	hooksacs and radula
21	„	(V2) „	oesophagus and salivary glands
22	„	(V3) „	buccal mass
23	„	(V4) „	hooksacs
24	„	(V4) „	hooksacs

Numerals in brackets are those given by MEISENHEIMER (1905) in Pl. XIX fig. 4; nerve IV4 was not found. The nerves indicated below with t.n., o.n., r.n. and os.n. are given by MEISENHEIMER with resp. the figures I2, I6, I5 and IV1.

A	anus	P.c.	pedal commissure
B	buccal ganglion	Pl	pleural ganglion
C	cerebral ganglion	Pl.P.c.	pleuro-pedal connective
C.B.c.	cerebro-buccal connective	Pl.V.c.	pleuro-visceral connective
C.c.	cerebral commissure	R	rhinophore cells
Co.	cornea	Re	retina
C.P.c.	cerebro-pedal connective	r.g.	rhinophore ganglion
C.Pl.c.	cerebro-pleural connective	r.n.	rhinophore nerve
E	ciliated epithelial cells	S	sensory cells in labial tentacle
E′	non-ciliated epithelial cells	s	statocyst
F	connective tissue fibres	S.c.	statocyst cells
G	ganglion cells	s.c.	static centre
Ie	intestine epithelium	Se	secretory cells
L	lens	s.g.	static ganglion
M	muscle cells	Sl	statoconia
N.c.	nerve cells in pedal ganglion	s.n.	static nerve (first)
O	osphradial sensory cells	s.n.′	static nerve (second)
o.g.	optic ganglion	s.n.″	static nerve (third)
o.n.	optic nerve	t.g.	labial tentacle ganglion
op.c.	optic centre	t.n.	labial tentacle nerve
os.n.	osphradial nerve	V	visceral ganglion
P	pedal ganglion	V.c.	visceral commissure

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