Leloup, E. 1941a

Concerning the pneumatophore of *Physophora hydrostatica* (Forskål, 1775)

Bulletin de l'Institut Royal des Sciences Naturelles de Belgique **17** (31), 1-11

The siphonophores *Physophora hydrostatica* (Forsk.) possesses a relatively large float that generally has an inferior lateral orifice.

Researchers have stated, normally, that the float can empty itself of its gas content, so that the colony, becoming denser, sinks towards the depths and is maintained there.

Three hypotheses have been put forward to explain the expulsion of gas.

Firstly, E. Haeckel (1869) mentions a short pneumatic duct that is not found in the young colonies but which, in the adults, opens at the distal extremity of the pneumatosac and is directed towards the exterior through the wall of the trunk. For K.C. Schneider (1896, 1898) the funnel is followed below by a canal that opens to the exterior by a lateral duct.

On the other hand, for C. Chun (1897), the funnel, normally closed, is deprived of a pneumatic duct and the lateral orifice that opens into the gastrovascular cavity of the stem constitutes also an excretory pore for the gastrovascular liquids. However, during violent contractions of the float, the floor of the funnel is ruptured and gas, which comes to fill the apex of the gastrovascular cavity, is expelled through the excretory pore. H.B. Bigelow (1911) approved of C. Chun's opinion.

In 1925, F. Moser thought to reconcile the preceding points of view. For that author, the lateral pore opens into the gastrovascular cavity and serves as an excretory pore; and moreover, in the young physophores, the funnel possesses an inferior opening that puts its cavity in communication with the gastrovascular cavity; so that when the float contracts the funnel lengthens and forms a basal tube whose extremity, with its orifice, comes to be in apposition to the external pore and, by this means, the pneumatophore gas is expelled. After the expulsion of gas, the elongated tube of the funnel is resorbed.

Nevertheless, however ingenious it is, the hypothesis of F. Moser does not allow the concept that, without any aid and without the existence of a special morphological structure, the base of the funnel evaginates a tube that always follows the same trajectory and that the same region of the wall of the funnel, that is to say its orifice, always manages to come close to the same region of the gastrovascular wall, i.e. the lateral pore.

The lack of precision of this explanation of this mechanism necessitates some new studies.

Having had the opportunity to study some adult colonies and a young colony of *Physophora*, I report, in the present note, the results of my observations as well as the agreements and differences of these with the opinions of the preceding authors.

The structure of the pneumatophore in an adult *Physophora*.

<u>Origin and material</u>. – The three colonies examined came from the south of Iceland where this cosmopolitan species is found only fairly rarely (P.L. Kramp, 1939, p. 18). The lieutenant of the Belgian states, V. Billet, collected them onboard

the Ostend boat “O. 89” “Freddy” in a dragnet fished on 1 April, 1938, to a depth of 125-150 m, in the region between 63°20’N, 21°W and 63°17’N, 20°50’W.

The preservation, without preliminary anaesthetization, in formalin has strongly contracted these colonies, which have dropped all the appendages of the nectosome and siphosome. Their floats measured 5 mm in length and 1.5 mm in greatest diameter.

Two siphonophores have been sectioned longitudinally, the other transversely. The sections have been stained in Delafield-eosin haematoxylin.

Description. – In adult *Physophora* (fig. 1A, 2, 3; Pl. I, fig. B, C) the upper part of the trunk (*tr*.) is filled by a gaseous, ovoid vesicle, the float or pneumatophore (*pn*.) whose greatest axis describes an angle of 45° with the longitudinal axis of the trunk.

The pneumatophore consists of: a) an external sac, the pneumatocodon (*pcd*.) that is comprised of two epithelial layers, an external one with longitudinal muscles, the ectoderm (*ect*.) and an internal one with circular muscles, the endoderm (*end*.); separated by a mesogloeal layer (*mes*.), and b) an internal sac, the pneumatosaccus (*ps*.) that has two epithelial layers, the reverse of the pneumatocodon, the endoderm (*end. int*.), with longitudinal muscles, external to the ectoderm (*ect. int*.), with circular muscles, separated by a mesogloeal layer (*mes. int*.).

The internal ectoderm of the pneumatosaccus secretes a chitinous, homogeneous cuticle in the shape of an elongated bell and forming a pad at its orifice, the pneumatocyst (*pc*.), which delimits an ovoid, ventral cavity, the reservoir (*res*.) of the pneumatic cavity (*c. pt*.). Between the endoderm of the pneumatocodon and that of the pneumatosaccus, one finds the distal extremity of the gastrovascular cavity (*c. g. v*.) continuous with the stem, the pericystic cavity (*c. ppt*.). At the closed apical pole, the endoderm of the pneumatocodon is folded into that of the pneumatosaccus and delimits a rounded, discoidal area by an ectodermal pad (*b. ECT.. ap.),* which is where the communication between the ectoderm of the pneumatosaccus and pneumatocodon occurs.

Around the orifice of the pneumatocyst a massive proliferation of the basal ectoderm of the pneumatosaccus obstructs the reservoir. A mantle of secondary ectoderm (*ect. s.)* stretches up the length of the lower face of the pneumatocyst compressed thus between two endodermal layers. The pneumatosaccus elongates towards the base and encircles an extension of the pneumatic cavity where the ectoderm has proliferated, the funnel (*ent*.). This funnel continues laterally into a tube-like duct, the pneumatoduct (*pdu*.), which opens to the exterior by an orifice, the stigma (*st*) or pneumatic pore situated on the upper part of the ventral furrow (*si. v*.) of the trunk above the point where the nectophores are budded off (*b. cl.).*

Around the stigma the mesogloea thickens, and is divided into ramifying lamellae and, at this level, the longitudinal ectodermal muscles form a sphincter *(sph*.) that can close the orifice. Surrounding the stigma, a thin, internal mesogloeal lamella is detached from the mesogloea of the external wall and reunites with that of the pneumatoduct, while the ectoderm of the stem is continuous with the internal ectoderm of the pneumatoduct.

The endoderm of the pneumatocodon and that of the pneumatosaccus are united by septa or radial lamellae (*cl. r*.), made up of two endodermal layers separated by a band of mesogloea. These septa arise at the level of the funnel, but they do not reach to the apical pole: the pericystic cavity is found to be subdivided into two radial chambers (*ch. r.)* for most of its height, but the remainder is undivided and surrounds the apical ectodermal pad as a continuous annular space, the circular sinus (*s. circ.).*

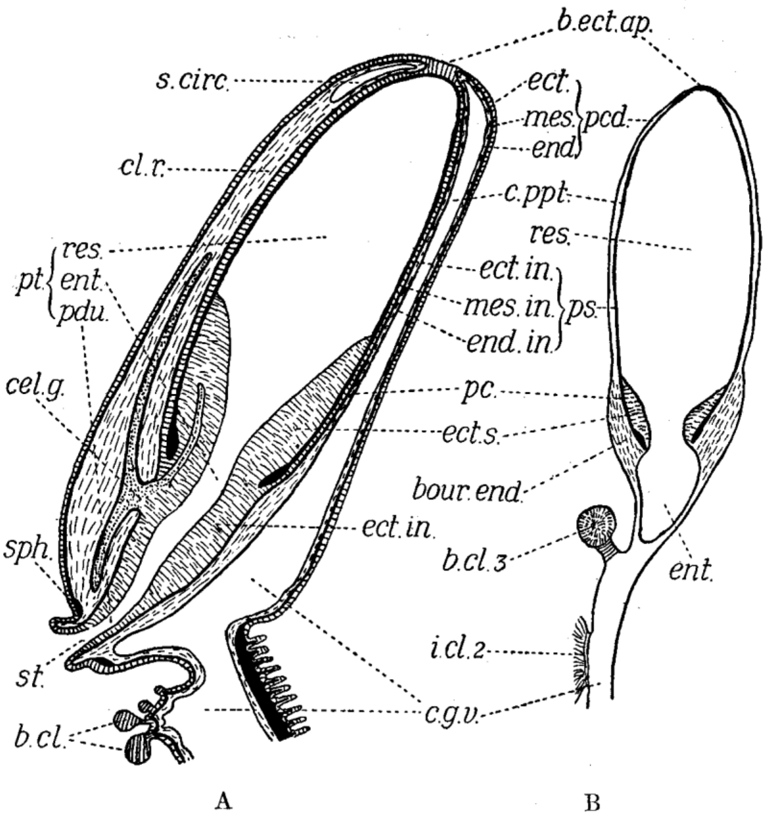


Figure 1. Semi-schematic figures representing the float of a colony.
A. adult x 13.5, B. young x 57.

Some special histological formations characterise the ectoderm of the funnel. In effect, under the base of the pneumatocyst, at the level of each radial septum, one sees a tubular cavity that is insinuated into the septum. These cavities contain some syncytia of very granulose giant cells (*cel. g.*), with an enigmatic physiological function. These syncytia, on the one hand ribbon or tube-like are inserted into the canals (*ca. mes.*) penetrating into the mesogloea of the septa and, on the other hand are undivided and anastomise into a network in the secondary ectoderm.

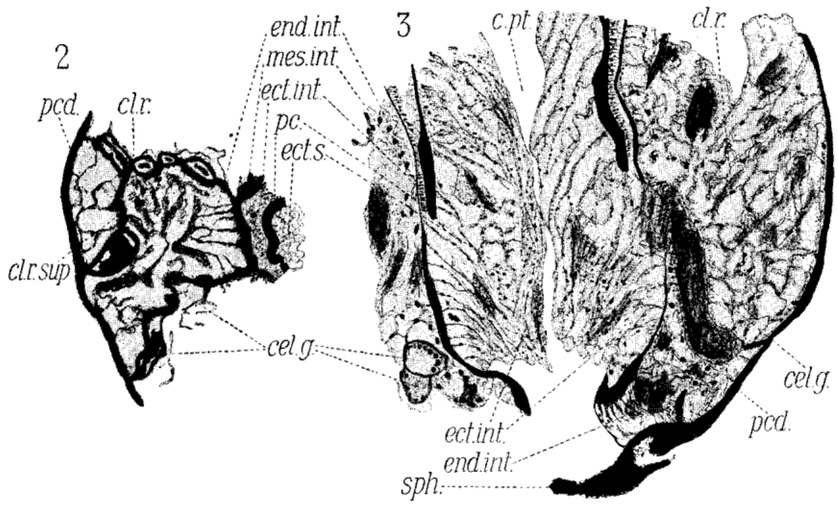
The structure of the pneumatophore in a young *Physophora*

Origin and material. – Amongst the collections of physophorids collected during the German Antarctic Expedition, on board "Meteor", one finds a young physophore. It was captured, St. 193, in the South Atlantic Ocean, to the west of Ascension Island, 12th Sept. 1926, between 100 and 50 m depth. This siphonophore (Pl. I, fig. A) possessed an elongated float (*pn.*) measuring 1 mm in height, with two developed nectophores almost superimposed (*cl. n.*), a medusoid bud (*b. cl. 3*), three palpons (*pa.*) with palpacles, and finally a gastrozooid (*ga.*) with a swollen base provided with filaments and a tentacle (t.*)* ornamented with tentilla.

The structure of the different elements of the siphosome permits us to consider this siphonophore as a young *Physophora*. It has been sectioned longitudinally.

Description. – In this young individual, the float (fig. 1, B) has the general ovoid shape of the adult float, but its greater axis is parallel with the longitudinal axis of the stem. This stem, deprived of a ventral furrow, ends at the summit by the budding of three nectophores, above which is inserted the pneumatophore. The latter is made up of a pneumatic cavity that is comprised of a) a reservoir bordered by a pneumatocyst, which has the shape of the adult, and b) of a completely closed funnel in the shape of a horn and which ends a little above the point of insertion of the nectophoral buds. The secondary ectoderm is developed already around the internal margin at the base of the pneumatocyst and a pad of large, polyhedral endodermal cells encircles the base of the pneumatocyst and the dilated apex of the funnel.

At this stage there is neither an apical pore nor an endodermal septa nor pneumatoduct nor stigma. Meanwhile the deviation of the pneumatophore from that of the morphological axis of the colony is less accentuated than in the adult.



Adult physophores, x 35
Figure 2. Transverse section passing through the base of the pneumatocyst and showing the formation of a supplementary radial septum (*cl. r. sup.*)
Figure 3. Longitudinal section passing by, to the right, a radial septum and, to the left, a radial chamber.

Remarks, agreements and differences.

a) In the epithelium of the adult funnel C. Chun (1897, pl. II, fig. 8) noted some hollows (*sp.*) that, according to him, facilitated the rupture of the tissue under the influence of gas expansion in the pneumatic cavity. But, the general orientation of the internal cells of the funnel indicates the existence of a tube whose cavity can, while leaving hollows, become virtual as a result of the joining of the tissues.

b) The number of radial endodermal septa varies. M. Sars (1877) found 9; C. Claus (1860) 8 and once 10; K. Schneider 7; C. Chun (1897) 7-9, 10.

The number of septa depends on the age of the colony and the importance of the pneumatophore. In effect, C. Chun (1897) mentions 7 in the young colonies and 9, 10 in the adults; further he shows (Pl. II, fig. 5) a septum that is doubled. Our adult colony, cut transversely, possessed 10 above the orifice of the pneumatocyst (Pl. I, fig. C^2) and 11 below (Pl. I, fig. C^3), because a septum bifurcated at its external attachment and formed an incomplete septum (fig. 2, *cl. r. sep.*) that did not reach the wall of the pneumatosaccus.

c) C. Chun mentioned and figures (1897, Pl. III, fig. 6) that the ectoderm of the pneumatocodon continued into the endoderm of the gastrovascular cavity at the level of the stigma. In 1898 K. Schneider confirmed this (p. 130); but he remarked,

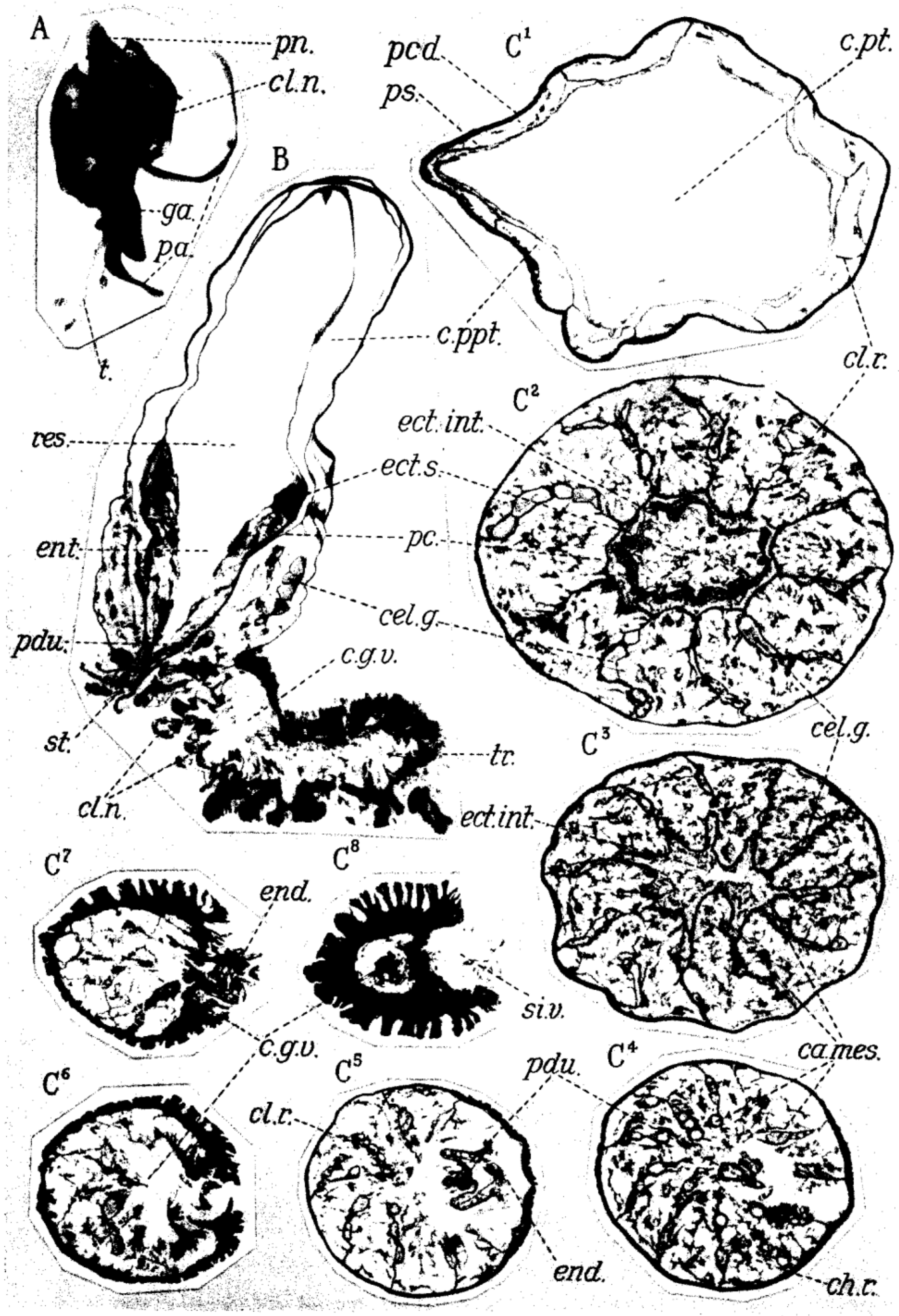


Plate I. *Physophora hydrostatica* (Forsk.)
Fig. A. young colony, float 1 mm, complete vied, x 8.
Fig. B, C.: adult colonies, float 5 mm, sections.
B. longitudinal, oblique in the upper part, x 15.
C. transverse x 24, realised C^1: in the middle of the pneumatocyst. – C^2: at the base of the pneumatocyst. – C^3: in the funnel, under the pneumatocyst – C^4: at the level of the pneumatoduct. – C^5: below the stigma. – C^6: in the stigma, under the pneumatoduct, with evagination of the gastrovascular endoderm. – C^8: at the summit of the stem, above the swimming bells.

c) C. Chun mentions and figures (1897, pl III, Fig. 6) that the ectoderm of pneumatocodon continues into the endoderm of the gastric cavity at the level of the stigma. In 1898, K. Schneider confirmed this fact (page 130); but he remarks, a few lines below, that in the stigmatic plug no longer distinguishes the ectoderm from the endoderm, and that we do not see a well-defined canal, but scattered cavities, similar to those of the funnel. Moreover, in 1896 (p. 577, Fig. A), K. Schneider shows the external ectoderm (ec) which folds continuously into the stratified internal ectoderm (dr. cc).

Our sections show, in places, that at the level of the stigma, the external ectoderm is prolonged in the internal ectoderm.

`d) C. Chun (1897) considers as belonging to a radial septum (p.46), the mesogloeal septum that he figures (Pl II, fig.8, sep, Pl. III, fig 6, lam. sept.). In fact, this partition represents the right part of the mesogloeal layer of the pneumatoduct, which (designated g. v.) seems strongly dilated, and doubts the left part stops at the indicated level (lam.).

C. Chun mentions that "die Stutzlamelle sich manchmall in den centralen Parten des Trichteirs stark verdunnt") and K. Schneider (1898, 130) adds that we particularly notice this extraordinary thinness of the mesogloea of the funnel on vesicles where the latter is very dilated, richly inflated with gas.

For Figure 8, Pl. II of C. Chun (1897), K. Schneider believes that due to the absolute lack of gas in the funnel, the wall of the latter has completely shrivelled against the reservoir. On the contrary, I consider that the figure shown by C. Chun had its funnel and pneumatoduct swollen by the gas expelled from the tank and that a sudden contraction of the funnel tissues caused the dilated pneumatoduct to be spread on the left to the extreme.

e) In my adult physophores, because of the violent contraction during fixation, the pneumatic pore is obstructed by a plug of tissue that comes from inside (Plate 1, Fig. B, C7). The authors generally mention this plug when examining fixed and preserved specimens. It must not exist in life. Indeed, W. Keferstein and E. Ehlers (1861) studying living physophores observed a live pneumatophore under the microscope and found that the compressed gas in the reservoir appears at the upper part of the trunk in the greenish glandular mass (= funnel), which is then pearled in the water above the youngest swimming bells where there is a depression of the skin (1861, Pl. IV, Fig. 18, x (= ventral groove).

Such normal and spontaneous expulsions of the gas would be incomprehensible if there was no morphological structure adapted to this function; for, or cannot conceive, like C. Chun and F. Moser, that in case of strong contraction, the homogeneous bottom of the funnel always comes to burst at the precise place where the stigma is.

W. Keferstein and E. Ehlers (18Gl) do not mention a stigmatic plug. But this plug must not be confused with what C. Chun calls "excretion bulb" (1897, Pl II, Fig. 1, 2, excr.) And represents the contracted state of the stigmatic sphincter.

At this level, the torn tissues (see note c) nevertheless make it possible to follow their contours on the microscopic sections and to see that the individuals do not always react in the same way an external excitation. Indeed, the two adult specimens studied contracted differently.

One of the physophores suddenly tightened its reservoir, the funnel and the pneumatoduct lengthened and the stigmatic sphincter contracted violently on the pneumatoduct by breaking any communication between the sphincter mesogloea and the thinned pneumatoduct. The siphonophore expelled, together with the gas, the alveolar ectoderm from its funnel: the plug is ectodermal (Plate 1, Fig. B).

In the other physophore, the funnel and the pneumatoduct have been subjected to a violent contraction towards the interior, in such a way that the stigma is partially invaginated and that the pneumatoduct has broken its relationship with the external wall, save in the upper part. At the same time, a contraction of the discoidal siphosome has driven the gastrovascular fluid towards the apex of the colony and, by the tear, existing at the level of the stigma, the endoderm of the lower part of the funnel has been expelled: the gas is endodermal (Pl. I, fig. C[7]).

f) In the young physophores, E. Haeckel (1869) mentioned the absence of a pneumatic duct. In contrast, F. Moser (1925) indicated that in the very young individuals there appears to exist an opening that puts the funnel in communication with the gastrovascular cavity. Our small well-preserved example only shows traces of a similar communication, the base of the funnel not showing any signs of the internal orifice.

g) At its base on the structure of the young float (fig. 1 B) one can easily conceive the morphological transformation that, in the following ontogenetic stages, constitute the adult float (Fig. 1 A): on the one hand, the radial septa are arranged in the endodermal pads and they push out towards the base and the apex; on the other hand, the bottom of the funnel comes to be united to the wall of the stem a little above the zone of proliferation of the medusoid bud 3, a stigma will be formed at the point of contact of the two walls; besides each process intervenes in the formation of the stigma in *Velella spirans* (Forsk.) (E. Leloup, 1929, p. 428, fig. 24)

Conclusions

My observations concerning the structure of the pneumatophore in *Physophora hydrostatica* (Forsk.), adult and young, confirm the correctness of the morphological descriptions of K. Schneider (1896, 1898); they permit me to follow that author in his theoretical vies.

In *Physophora hydrostatica* (Forsk.) there exists a morphological arrangement allowing the expulsion of gas, the pneumatoduct. This pneumatoduct can be considered as a homologue of the auroduct that characterises the Auronectid siphonophores.

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Abbreviations used in figures and Plate.

b. cl. = bud of nectophore
b. cl. 3. = bud of 3rd nectophore
b. ect. ap. = apical ectodermal pad
bour. end. = endodermal pad
c. g. v. = gastrovascular cavity
c. ppt. = peripneumatic cavity
c. pt. = pneumatic cavity
ca. mes. = mesogloeal cavity
cel. g. = giant cells
ch. r. = radial chamber
cl. n. = swimming bell
cl. r. = radial chamber
ect. = ectoderm
ect. int. = internal ectoderm
ect. s. = secondary ectoderm
end. = endoderm
end. int. = internal endoderm
*en*t. = funnel
ga. = gastrozooid
i. cl. 2 = insertion of 2nd nectophore
mes. = mesogloea
mes. int. = internal mesogloea
pa. = palpon
pc. = pneumatocyst
ped. = pneumatocodon
pdu. = pneumatoduct
pn. pneumatophore
ps. = pneumatosac
res. = reservoir
s. circ. = circular sinus
si. v. = stigma
sph. = sphincter of stigma
st. = stigma
t. = tentacle with tentilla
tr. = trunk or stem of colony.