THE

VOYAGE OF H.M.S. CHALLENGER.

ZOOLOGY.

REPORT on the PTEROPODA collected by H.M.S. Challenger during the Years 1873–76. By PAUL PELSENEER, D.Sc. (Brussels).

PART III.—ANATOMY.

INTRODUCTION.

THE collection of Pteropoda, preserved in alcohol, brought home by the Challenger, includes specimens of all the known genera except *Cymbuliopsis* and *Clione*.

This collection having been placed in my hands for purposes of systematic study, I was, when this part of the work was concluded, in an exceptionally favourable position for undertaking a monographic examination of the organisation of this group of animals. Since the publication of Souleyet's memorable work, the anatomy of the Pteropoda has been studied almost exclusively by means of European species, and this is the first time since that epoch that such an important collection as the present one has been made, including, as it does, forty-four species out of the sixty-three actually known, and specimens of nearly all the genera.

Hence although the time at my disposal was very limited, I could not allow an opportunity to escape which would probably not soon occur again.

By adding to the Challenger collection some specimens of *Clione limacina* which Mr. John Murray placed at my disposal, and a specimen of *Cymbuliopsis* of my own, I was able to investigate all the known genera of Pteropods, so that the conclusions at which I have arrived have not been drawn from the organisation of a few species only, but from that of the entire group, each genus, and usually several species of each genus, having been studied.

As the conclusion of these researches an analytical exposition of the whole organisation of each genus might be expected, but this would have extended the present Report beyond reasonable dimensions, and would have occasioned much repetition, since several of the genera of Pteropods are very closely related, and the number of distinct types is far from large. Besides, as I have already remarked, the limited time at my disposal did not permit me to enter upon an anatomical monograph, and indeed, even if a longer period had been available, the following considerations would have deterred me from such a course :—

1. We already possess a very considerable acquaintance with numerous points in the organisation of the Pteropoda, thanks to the general works, based upon several different genera, of van Beneden,[1] Souleyet,[2] and Gegenbaur,[3] and to the special memoirs, treating only of a single form, of Eschricht[4] and Wagner.[5] In many respects an anatomical monograph would simply be a reprint of what has been published by these authors.

2. The systematic position of the Pteropods is the subject of much discussion, and their phylogenetic relationships have been very variously interpreted.

For several years[6] I have followed Spengel,[7] along with Grobben[8] and Boas,[9] in the opinion, not shared by most zoologists, that the Pteropoda do not constitute a distinct class among the Mollusca, comparable with the Cephalopoda, Gastropoda, Scaphopoda, and Pelecypoda. Further, I am, like Boas, of opinion that even within the Gastropoda they do not constitute a primary division, but only a group of much lower rank among the Opisthobranchiate division of the Tectibranchiate Euthyneura.

This opinion, it must be added, is not new; it was expressed during the first half of this century by de Blainville.[10] Souleyet[11] was the first, and indeed the only, investigator who has attempted to give any proof of it, and he was not very successful,

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[1] Exercices Zootomiques, *Mém. Acad. Sci. Bruxelles*, t. xii., 1839; Mémoire sur la Limacina arctica, *op. cit.*, t. xiv., 1841.

[2] Voyage de la Bonite, Zoologie, t. ii. pp. 37–288, 1852.

[3] Untersuchungen über Pteropoden und Heteropoden, 1855.

[4] Anatomische untersuchungen über die Clione borealis, 1838; in Danish, Anatomiske Undersøgelser over Clione borealis, *K. dansk. Vidensk. Selsk. Afhandl.*, 7 Deel, p. 327.

[5] Die Wirbellosen des weissen Meeres, Bd. i. pp. 89–120, 1885.

[6] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. p. 373, 1880.

[7] The cephalic appendages of the Gymnosomatous Pteropoda, *Quart. Journ. Micr. Sci.*, N.S., vol. xxv. p. 505, 1885. Description d'un Nouveau genre de Ptéropode Gymnosome, *Bull. Sci. Dép. Nord*, p. 222, 1886. Recherches sur le Système Nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 127, 1886.

[8] Morphologische Studien über den Harn- und Geschlechtsapparat sowie die Leibeshöhle der Cephalopoden, *Arb. Zool. Inst. Wien*, Bd. v. p. 245, 1884.

[9] Spolia atlantica, Bidrag til Pteropodernes Morfologi og Systematik, &c., *K. dansk. Vidensk. Selsk. Skrift.*, Raekke 6, Bd. iv. p. 12.

[10] Manuel de Malacologie, p. 460.

[11] Voyage de la Bonite, Zoologie, t. ii.

because he had opposed to him the dogmatic views of Cuvier, which were then all-powerful. Recently, however, the authors above mentioned have returned to an opinion closely resembling that of de Blainville; but in order to place this upon a firm basis, further demonstration is still necessary.

On these grounds I have proposed to make the present Report a comparative anatomical study of these animals rather than a descriptive anatomical monograph, and shall attempt mainly to throw light upon their systematic position; and by the permission of Mr. John Murray to conclude this third part of my Report upon the Pteropoda by an exposition of my views regarding their relations to the other groups of Mollusca.

Having thus defined the object of the present work and the spirit in which it is conceived, I may say a few words regarding the method which has been followed in its elaboration and the manner in which I have divided it.

The first portion of this Report bears upon the descriptive anatomy of the Pteropoda, taken genus by genus, treating first of the Thecosomata, then of the Gymnosomata. As I have indicated above, no attempt will here be made to discuss the whole organisation of each genus, but I shall study especially—

1. The points neglected or misinterpreted by previous authors, in order, if possible, to elucidate them.

2. The points which seem to me to have an important bearing upon the relations and systematic position of the Pteropoda.

In this portion I shall not attack the question of the embryonic development of the Pteropoda. Too few embryos were collected by the Challenger to furnish any new facts which might serve as a basis for a discussion of this special subject. The histology of the Pteropoda, too, will only occupy an unimportant place in our discussion, for the specimens collected by the Challenger were not preserved with a view to histological examination. Hence, in order to fill up the numerous lacunæ which will occur in the present work, I hope to publish hereafter the results of my examination of fresh specimens at the Naples Zoological Station.

In the second part it is proposed to study the relations and affinities of the group of Mollusca called Pteropoda by a comparison of their organisation (as ascertained by the investigation described in the first part) with that of other Mollusca.

CONTENTS.

I. ORGANISATION OF THE PTEROPODA.

I propose to study the Thecosomata and the Gymnosomata separately, and as I have enumerated the differential characters of these two divisions in the Systematic Report on Gymnosomata,[1] there is no need to repeat them here. The phylogenetic origin of the two groups will be examined in the sequel.

I. THECOSOMATA.

We shall now proceed to examine in succession each of the genera recognised in the Systematic Report on the Thecosomata.[2]

Family I. LIMACINIDÆ.

The knowledge of the organisation of the Limacinidæ is of the utmost consequence in the morphological study of the Pteropoda, because the true phylogenetic relations of the typical Thecosomata (Cavoliniidæ) are entirely concealed by an adventitious modification upon which we shall enlarge hereafter. This masks their true relationship, and if the Limacinidæ did not exist at the present time it would probably be impossible to explain this modification, and consequently very difficult to establish the real affinities of the Thecosomata.

The only information we possess regarding the organisation of the Limacinidæ is to be found in the memoir of van Beneden on *Limacina arctica* (=*helicina*),[3] and in the rather brief anatomical study of the "genus" *Spirialis*, published by Souleyet in the Voyage of the "Bonite."[4] These two works, however, in addition to being brief, include numerous gaps and several inaccuracies, which defects I shall endeavour to remedy.

Limacina helicina (*Limacina arctica*), the species studied by van Beneden, is of large

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[1] Zool. Chall. Exp., part lviii. pp. 4–6.

[2] Zool. Chall. Exp., part lxv.

[3] *Mém. Acad. Sci. Bruxelles*, t. xiv.

[4] Voyage de la Bonite, Zoologie, t. ii. pp. 208–216.

dimensions, whilst *Limacina australis*, which was the subject of Souleyet's investigations, is one of those small forms classed by him under the generic name *Spirialis*. He recognised, however, their close relationship to the larger *Limacinæ*, the only difference which he stated to exist between them—the absence of the operculum in *Limacina*—has been found to have no foundation, for it is only that the adults in the large forms have lost the operculum. In consequence of the small size of his specimens a number of points in their organisation have escaped him.

In the Challenger collection there was only one specimen of a large *Limacina* (*Limacina antarctica*) which I have therefore been compelled to preserve intact; but since Mr. John Murray has placed in my hands a number of specimens of *Limacina helicina* from Hudson's Strait, I have been able to study a great part of the organisation of the genus, upon a large species and upon small forms (*Limacina lesueuri* and *Limacina australis*), which latter have served more especially for special points and for purposes of comparison.

Lastly, as regards the genus *Peraclis*, the form studied is *Peraclis reticulata*: but as specimens of this genus are very rare, I have only been able to make use of two, and hence have not been able to push my researches so far as I could have wished.

In all the Limacinidæ the shell is sinistral, and hence the animal is coiled in a left-handed direction; but although twisted in this manner, in all its organisation the animal is dextrorsal, that is to say, that in the asymmetrical disposition the right side predominates; it is here that are found the anus, the genital aperture, and the copulatory organ.

This is a fact opposed to the usual condition in the sinistrorsal Gastropods. In *Physa*, for example, the spiral (and hence the shell) is sinistral; the anus, the genital aperture, and the copulatory organ are all placed on the left side, and hence it is this side which predominates in the asymmetry of the animal. Thus the direction of the spiral corresponds with the kind of asymmetry observed in this Mollusc.

The difference between these two cases shows, however, that the mode of asymmetry in a Mollusc is in no way dependent upon the direction of its coil. In *Physa* there is a complete *situs inversus*; and it is this which has brought about the left-handed twisting of the animal and the sinistral character of its shell, for we are acquainted with no Gastropod which has acquired a left-handed asymmetry of organisation, and had at the same time preserved a dextral shell. In this case, then, the sinistral coiling appears to be only one of the consequences of the *situs inversus*.

On the contrary, as we see in the Limacinidæ, an animal with dextral organisation may be coiled sinistrally. The case of the Limacinidæ, too, does not seem to be unique, since, according to Bouvier,[1] the genus *Lanistes* (*Ampullaria* with left-handed spiral) also has a dextral organisation.

The direction of the spiral, then, does not permit us to determine the mode of the

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[1] Sur le système nerveux typique des Prosobranches dextres ou sénestres, *Comptes rendus*, t. ciii. p. 1276, 1886.

asymmetry of the Mollusc, any more than this latter enables us to determine the direction of the spiral (in contradistinction to the opinion of Lacaze Duthiers[1]); hence an animal with dextral asymmetry may be twisted directly or inversely, or may not be twisted at all (Patelloid Gastropoda).

Besides, the direction of the spiral must be of very slight morphological importance, since in the same genus (*Neptunea*, *Pyrula*, *Vertigo*, &c.) there are some species which are dextral, and others which are normally sinistral.

1. *Limacina.*

The Head is distinct, surrounded on each side by the fins, which reach to the dorsal aspect, where is found a pair of tentacles.

These latter are asymmetrical, the left being much less developed than the right; in *Limacina helicina* and *Limacina antarctica* it is almost completely atrophied, and is situated rather posteriorly to the right. In *Limacina inflata* and *Limacina lesueuri* it is somewhat larger. In all the Limacinæ the right tentacle is very long when fully developed (Pl. I. fig. 1, *a*), and is surrounded at the base by a short everted sheath, such as is found in certain Nudibranchs. This sheath also occurs in the smaller forms ("*Spirialis*"), where Souleyet[2] did not succeed in finding it.

The Foot.—The fins form at the anterior extremity of the body a natatory surface, oblique with respect to the transverse plane of the body, the ventral margin being lower than the dorsal. On this surface the mouth opens, and at the right, near the dorsal margin outside the lip, is the orifice of the copulatory organ, to which the seminal groove leads, passing from the right side of the cervical region over the dorsal border of the fin.

On the dorsal margin of the fin, near the middle, is a little tentaculiform lobe, which differs in structure from the remainder of the fin, and contains the termination of a slender nerve; probably it is a tactile organ. This lobe or papilla does not exist in all species. I have only demonstrated its presence in *Limacina helicina*, *Limacina antarctica*, and *Limacina australis*; it is wanting on the other hand in *Limacina bulimoides*, *Limacina trochiformis*, *Limacina lesueuri*, and *Limacina inflata*.

This little lobe corresponds to an analogous organ found in the subgenus *Creseis*, of the genus *Clio*. Van Beneden[3] regarded it as a tentacle, and Huxley[4] identified it with the long cephalic appendage of *Halopsyche*. These two opinions are both erroneous.

The fins are continuous and united ventrally by the posterior lobe of the foot, which is slightly notched in the middle of its ventral border, and carries the operculum. I have

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[1] Du système nerveux des Gastéropodes pulmonés aquatiques, *Arch. de Zool. Expér.*, sér. 1, t. i. p. 402.

[2] Voyage de la Bonite, Zoologie, t. ii. p. 209.

[3] Mémoire sur la Limacina arctica, p. 3, *Mém. Acad. Sci. Bruxelles*, t. xiv.

[4] On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 41.

already said that in *Limacina helicina* and *Limacina antarctica* the operculum is caducous in fully-grown specimens, a fact which explains how it is that these species have often been regarded as lacking this organ.

The Mantle is open dorsally, and united to the body behind the foot (on the ventral surface of a spread out *Limacina*). Its margin is simple; it presents, on the right side, a little ventrally, a rather narrow lobe, terminating in a point, and called the "balancer," the considerable development of which perhaps enables it to play the part of a counterpoise during swimming, the coiled Pteropods not being symmetrical like the straight forms. Possibly this lobe is also sensory, as its whole surface is ciliated.

The dorsal portion of the mantle which covers the pallial cavity presents a rather thick glandular area, corresponding to the "shield" of the Cavoliniidæ. The structure of this organ is already known and is practically the same in *Limacina* as in the Cavoliniidæ; but in the present case it is asymmetrical (Pl. I. fig. 5, *a*) and uniform in structure throughout its extent.

The Digestive Tract.—The mouth opens in the natatory plane formed by the two fins enveloping the cephalic region; it is situated towards the dorsal border of this plane and bounded by two lips, united dorsally and separating towards the other side.

The mouth is succeeded by a buccal mass, the cavity of which encloses two lateral jaws, such as have already been described by Sars.[1] The number of folds presented by these jaws varies in different species. The disposition of the radula agrees with that of all the odontophorous Mollusca, but the ribbon is very short, the number of transverse rows being but small. The number of longitudinal series is three, as in all the Thecosomata.

On either side of the radula opens a salivary gland. These organs have escaped the attention of the different naturalists who have studied *Limacina* (van Beneden,[2] Souleyet[3]). According to Gegenbaur[4] they are wanting in all Thecosomata, nevertheless all these are provided with them. In *Limacina* these glands are small, short, oval, and without a differentiated duct.

The œsophagus, rather long and longitudinally plicated within, leads into an enlargement of the digestive tube called the stomach, which here, as in all Thecosomata, is in reality a masticatory gizzard. Its walls have about the centre a large muscular transverse band, which actuates a number of horny plates situated within it.

These masticatory plates are four in number and are placed symmetrically (two ventral and two dorsal); a fifth has not been observed by the anatomists, although the embryologists have recorded its existence (Krohn,[5] Fol[6]). The four symmetrical plates

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[1] Mollusca regionis arcticæ Norvegiæ, pl. xvi. fig. 17.

[2] Mémoire sur la Limacina arctica, *loc. cit.*

[3] Voyage de la Bonite, Zoologie, t. ii. p. 210.

[4] Untersuchungen über Pteropoden und Heteropoden, p. 10.

[5] Beiträge zur Entwickelungsgeschichte der Pteropoden und Heteropoden, p. 42.

[6] Sur le développement des Ptéropodes, *Arch. de Zool. Expér.*, sér. 1, t. iv. p. 162.

are of a rectangular outline, elongated in the direction of the axis of the digestive tube, the dorsal pair being a little shorter than the ventral. Their free surface bears a rather sharp prominent crest. The fifth plate is situated behind the other four, between the two dorsal ones; its form is almost triangular, one of the angles being directed forwards. These masticatory plates have a structure resembling that of the "shell" of the Cymbuliidæ, but are rather more dense; striæ of growth may be observed in them, and they are covered by the gastric epithelium.

Behind the muscular band the stomach gradually narrows to pass into the intestine, and into this hinder portion of the organ on the left side opens the bile-duct.

Huxley[1] asks with respect to the Limacinidæ "whether the first flexure of the intestine is also dorsal" (like the pallial cavity) "or whether, as in all other Pteropods, it is ventral." In *Limacina* from its origin the intestine bends towards the right and dorsally, and eventually opens at the right side of the pallial cavity. Its flexure is thus the same as that called "dorsal" or "hæmal" among the Gastropods (Pl. I. fig. 3).

The Circulatory and Excretory Organs.—The heart is situated at the posterior end of the pallial cavity, and is even visible, owing to the transparency of the mantle, behind the shield. It presents an auricle directed towards the left and a ventricle lying posteriorly, both contained in a pericardium, which is quite excluded from the circulation. In front of the heart is the elongated, thin-walled kidney, arising from the pericardium, with the cavity of which it communicates. It enlarges anteriorly in such a way as to form an elongated triangle whose base is forwards, and opens into the pallial cavity by a small narrow aperture.

The Generative Organs.—The gonad, which in this case is a hermaphrodite gland, occupies all the initial portion of the visceral mass. The efferent duct arises anteriorly at the ventral aspect of the gland, and then passes forwards across the intestine and to the right of the œsophagus. This duct (Pl. I. fig. 3, *j*) is very thin at its origin but expands about its middle, where its walls become glandular; it then contracts again and reaches the accessory glands (albuminiparous and muciparous glands) and the receptaculum seminis.

The genital aperture is situated at the right side of the cephalic region, and is protected by a kind of little operculum. At this opening commences the spermatic groove (Pl. I. fig. 3, *l*), formed by a fold of skin, which is directed towards the dorsal surface of the head, passes to the right side of the right tentacle, and reaches the anterior surface of the fins, where it terminates at the opening of the copulatory organ. This is the same disposition as that already known to exist in the Cavoliniidæ. When protruded the copulatory organ divides into two branches, for instance in *Limacina lesueuri* (Pl. I. fig. 2, *c*).

Nervous System.—The nervous centres are united around the œsophagus behind the buccal mass. The cerebral ganglia (Pl. I. fig. 7, *c*) are situated at the sides of the œsophagus, and connected by a long supra-œsophageal or dorsal commissure.

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[1] On the Morphology of the Cephalous Mollusca, *loc. cit.*, p. 43.

The infraœsophageal portion of the nervous centres (Pl. I. fig. 8) consists of two portions: an anterior, pedal, and a posterior, visceral. The pedal group (*b*) is composed of two large symmetrical ganglia, pressed one against the other and in juxtaposition with the corresponding cerebral ganglia. On the posterior margin of each is an otocyst (*e*).

The visceral group consists of two ganglia, each of which is also approximated to the cerebral ganglion of its own side; they are, however, asymmetrical, inasmuch as the right ganglion (*c*) is much larger than the left (*d*), and the groove which separates them does not lie in the middle line of the body, but is displaced towards the left. The rule of Lacaze Duthiers,[1] according to which, in sinistrorsal Gastropods, the left half of the visceral commissure is the more developed, does not therefore hold good in the present case.

This asymmetry was unobserved by van Beneden and Souleyet, and has not since been recorded, although it is very striking; van Beneden[2] figures two symmetrical ganglia, and Souleyet[3] a single symmetrical ganglionic mass as in *Cavolinia*.

(1) *Cerebral Ganglia.*—From the anterior portion of these ganglia proceed the nerves which supply the head and tentacles (Pl. I. fig. 7, *i*). They probably also give origin to the auditory nerves which proceed to the octocysts, as is observed in all other Mollusca, and as I have also seen in certain Thecosomatous and Gymnosomatous Pteropods, as I shall show further on; I have not, however, been able to make out this nerve in *Limacina*.

(2) *Pedal Ganglia.*—These give origin at their anterior aspect to large nerves passing to the foot and the fins (Pl. I. fig. 8, *f*); a branch of the nerve to each fin goes to the little lobe which is found on its anterior border in certain *Limacinæ*.

(3) *Visceral Ganglia.*—These ganglia are asymmetrical not only in point of size but also in the nerves which proceed from them; from the large ganglion on the right proceed three nerves, only one from that on the left.

(i.) *Right Ganglion.*—The outer nerve (*1*) passes to the right side of the mantle and to the osphradium, and is probably homologous with the branchial nerve of Gastropods; the two median nerves (*2*, *3*) supply the viscera (heart, kidney, and generative organs).

(ii.) *Left Ganglion.*—The single nerve (*4*) goes to the left side of the mantle.

The preceding description relates to *Limacina helicina*. In the small forms ("*Spirialis*" of Souleyet) the disposition of the nerve centres is the same. Souleyet[4]

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[1] Du système nerveux des Gastéropodes pulmonés aquatiques, *Arch. de Zool. Expér.*, sér. 1, t. i. p. 494, No. 13.

[2] Mémoire sur la Limacina arctica, *Mém. Acad. Sci. Bruxelles*, t. xiv. pl. v. figs. 7, 13.

[3] Voyage de la Bonite, Zoologie, Mollusques, pl. xi. fig. 21.

[4] *Ibid.*, t. ii. p. 213.

describes the visceral ganglia in "*Spirialis*" *australis* as like those of *Cavolinia*, that is as forming a single mass. I have had the opportunity of studying this form as well as *Limacina helicina*, and can state that in it, as well as in *Limacina lesueuri*, *Limacina trochiformis*, and *Limacina inflata*, the ganglia of the visceral commissure are disposed in the same asymmetrical fashion. The distribution of the nerves is also certainly identical, but it is difficult to distinguish this in the case of such small animals.

The enteric or stomato-gastric nervous system includes a pair of buccal ganglia, united by a thick and rather long commissure. These ganglia are placed in contact with the œsophagus below the pedal ganglia; each of them is joined to the corresponding cerebral ganglion by a thin connective. They give off anteriorly the nerves to the buccal mass, and posteriorly two filaments which pass along the œsophagus to the stomach, where they ramify and anastomose, so as to form a plexus whose appearance varies a little in different individuals. Some ganglionic thickenings are observed in the plexus.

2. *Peraclis.*

The Head is quite differently shaped from that of *Limacina*: it is quite distinct, as I have already had occasion to point out in the systematic part of this Report; it has the form of a short proboscis issuing from the dorsal margin of the fin (Pl. I. fig. 9, *a*), the two lips uniting dorsally and ventrally; the two tentacles are symmetrical, and have no sheath. It is this proboscis which in Costa's figure[1] might easily be taken for the ventral lobe of the foot, which would be notched in the middle of its free margin.

The Foot.—The fins have no tentaculiform lobe; the ventral lobe of the foot is not notched in the middle of its free margin, but is broader at the base than at this margin.

The Mantle has on its right margin, a little ventrally, an appendage in the form of a triangular lobe, analogous to the balancer of *Limacina*. The dorsal pallial gland (shield) is shorter than in *Limacina*. It is not homogeneous, as in the case of this latter, which resembles that of *Clio* (subgenus *Creseis*), but presents alternating transverse bands (Pl. I. fig. 10). It is asymmetrical like that of *Limacina*.

The Digestive Tract agrees with that of *Limacina*, both in the relative position of its constituent parts and in their shape. As in *Limacina* there are two lateral jaws, two little salivary glands, and five large masticatory gastric plates, of which four are symmetrical, and the fifth triangular, posterior, and dorsal. Furthermore, as in *Limacina*, the bile-duct opens into the left of the digestive tract, and the flexure of the intestine is dorsal and to the right.

The visceral anatomy of *Peraclis* is otherwise very similar to that of *Limacina*, and

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[1] Illustrazione della Spirialis recurvirostra, *Ann. Mus. Zool. R. Univ. di Napoli*, anno iv. pl. iv. fig. 12.

I have scarcely been able to establish any noteworthy differences either in the principal parts of the circulatory and excretory apparatus, or in the organs of generation. As in *Limacina*, there are at the end of the hermaphrodite duct a large muciparous gland, an albuminiparous gland, and a receptaculum seminis (Pl. I. fig. 11).

Nervous System.—The cerebral and pedal ganglia are disposed as in the case of *Limacina* and all Thecosomata; that is to say, the former, united by a long cerebral commissure, give origin to the nerves of the head and tentacles, and the latter to the nerves of the fins and posterior lobe of the foot.

But that which distinguishes the central nervous system of *Peraclis* from that of *Limacina* is the arrangement of the visceral commissure. Instead of the two asymmetrical ganglia we have here three ganglia, the two lateral of which are symmetrical, and a little smaller than the central one (Pl. I. fig. 12, *c*, *d*, *e*).

This disposition is identical with that which I have already indicated as occurring in *Cymbulia*,[1] and which, as will appear in the sequel, is characteristic of the whole family Cymbuliidæ.

In an animal so small as *Peraclis* it is very difficult to distinguish clearly the nerves issuing from the ganglia. I have seen, nevertheless, the nerve (*1*) proceeding from the right visceral ganglion, and a larger (genital) nerve (*3*) proceeding from the median ganglion, comparable with the corresponding nerves in *Cymbulia*. Further, I cannot doubt that the visceral nerves in *Peraclis* have a disposition identical with that found in all the Cymbuliidæ; that is to say, each lateral ganglion gives off a pallial nerve, of which I have made out that on the right, and the large median ganglion gives off from its right side a slender visceral nerve in addition to the large genital one.

The buccal or stomato-gastric ganglia are similar in form and arrangement to the corresponding parts in *Limacina*.

Family II. CAVOLINIIDÆ.

These are the typical Thecosomata, the forms which have been most frequently studied, and which are consequently the best known. Their visceral anatomy being tolerably well known, there are certain points over which I may pass rapidly.

It has already been shown[2] that this family contains three genera, namely, *Clio*, *Cuvierina*, and *Cavolinia*, and furthermore, that the first of these includes divisions of subgeneric value, *Creseis*, *Hyalocylix*, and *Styliola*, which differ from each other in certain points of their organisation. We shall examine the three genera of this family in succession, and during the discussion of the genus *Clio* we shall have occasion to demonstrate some characters which distinguish its different sections.

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[1] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 117, pl. iv. fig. 12.

[2] Zool. Chall. Exp., part lxv. p. 41.

1. *Clio.*

The Head in *Clio* resembles that of *Limacina*, but *Creseis* has the left tentacle very little developed, as in *Limacina*, whilst in the others (*Hyalocylix*, *Styliola*, and *Clio*, *s. str.*) it is almost as large as the right.

It has also been shown above, as a distinctive character, that in *Creseis* the fins are provided with a little tentacular lobe on the dorsal margin, as in *Limacina*. In *Hyalocylix* the area on the margin of the fin devoid of muscular fibres is situated towards the dorso-lateral angle. In *Styliola* and *Clio* (*s. str.*) this area is found towards the middle of the lateral margin.

The Foot has the posterior lobe rather short in *Creseis*, short in *Hyalocylix*, and long in *Styliola* and *Clio* (*s. str.*).

The Mantle is quite open in front in *Creseis*, *Hyalocylix*, and *Styliola*, whilst in *Clio* (*s. str.*) its margins are slightly united at the sides, so that the aperture of the mantle is narrower than that of the shell. In all four subgenera the lateral lobe of the mantle (balancer) is less developed than in the Limacinidæ, and is situated on the left side.

The pallial gland (shield) is bilaterally symmetrical in all cases, but presents a different appearance in the different subgenera. In *Creseis* it is homogeneous, like that of *Limacina*. In *Hyalocylix* (Pl. II. fig. 4) a transparent transverse band divides it into an anterior and a posterior portion, the former of which further exhibits on each side a small distinct triangular patch. In *Clio* (*s. str.*) (*e.g.*, *Clio pyramidata*, Pl. II. fig. 2), in the anterior portion, in the centre of a more transparent space, is a median rhomboidal tract, on each side of which are two rather narrow bands.

The pallial cavity, which is ventral in contradistinction to the Limacinidæ, extends rather far backwards, owing to the generally elongated form of the genus *Clio*.

The Digestive Tract.—The mouth, lips, and the whole buccal mass are disposed as in *Limacina*. The jaws are firmer; they and the radula have been described and figured so often that it is not necessary to dwell upon them further.

All forms of the genus *Clio* possess very appreciable salivary glands, which are rather short, ovoid, and without any differentiated duct.

The œsophagus varies in length, being rather short in *Clio* (*s. str.*) and *Styliola*, long in *Hyalocylix* and *Creseis*, and of inordinate length in *Clio* (*Creseis*) *virgula*; it is strongly folded in the direction of its length.

The stomach possesses, as in the Limacinidæ, five large masticatory plates, four quadrangular and symmetrical (Pl. II. fig. 1, *g*), like the corresponding plates of *Limacina*, and a fifth triangular, situated on the ventral aspect, posterior to the preceding (Pl. II. fig. 1, *h*). The two ventral quadrangular plates are shorter than the two dorsal (Pl. II. fig. 5).

But, in addition to the five large plates, several species have in front of them double the number of small plates (Pl. II. fig. 5, *b*); these latter[1] are triangular, and are situated in front of the four large symmetrical plates and of the intervals between them. They alternate in size, the four which are situated in front of the large plates being smaller than the others.

In most species of *Clio* a narrow cæcum of varying length opens into the posterior portion of the stomach.

The liver agrees in form and situation with that of *Limacina*, but its duct opens into the posterior part of the stomach on the *right* side (Pl. II. fig. 1). *Clio* (*Creseis*) *acicula* retains in this respect a primitive disposition, the part corresponding to the liver in the adults of other species being but slightly developed.

The intestine is bent to the left and ventrally;[2] its termination is at a greater or less distance forward, according to the subgenus in question; in *Creseis* and *Hyalocylix* (Pl. II. fig. 1) the anus is placed very far back in consequence of the great length of the œsophagus; in *Styliola* the œsophagus is not so long, and the intestine terminates further forwards; lastly, in *Clio* (*s. str.*) the anus is situated far forwards, not far from the aperture of the mantle (Pl. II. fig. 7, *e*).

In the pallial cavity, close to the anus, between the mantle and the intestine, is a flattened gland, somewhat triangular in form and somewhat similar in structure to the shield (pallial gland). This organ (Pl. II. fig. 7, *f*), which I propose to call the "anal gland," does not appear to have been mentioned by any previous author.

The Circulatory and Excretory Organs.—The disposition of the central circulatory organ is well known (Pl. II. fig. 8); it is situated on the ventral surface in front of the genital gland; the auricle (*b*) is behind and the ventricle (*a*) in front. Both are rather elongated, and situated in a very long pericardium (*c*).

The kidney is placed close to the latter (Pl. II. fig. 8, *d*); it is flattened, with thin almost transparent walls, and has the form of an elongated more or less recurved triangle, the apex being directed backwards. It communicates (through *f*) with the pericardium and opens into the pallial cavity by a narrow orifice (*e*), situated towards the left angle at the base of the triangle. This orifice escaped the notice of Souleyet,[3] so that he was unable to interpret the kidney correctly.

As to the gills, they are entirely absent in *Clio* as well as in *Limacina*. The organs which have been regarded by previous writers (van Beneden,[4] Souleyet,[5] &c.) as gills are merely folds of the mantle in specimens preserved in spirit.

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[1] They are visible even in the larvæ; compare Fol, Sur le développement des Ptéropodes, *Arch. d. Zool. Expér.*, sér. 1, t. iv. pl. vi. fig. 8, *sp.*

[2] Gegenbaur is mistaken when he depicts (Untersuchungen über Pteropoden und Heteropoden, pl. ii. fig. 1, *g*) the intestine as curved *dorsally* in *Clio* (*Creseis*) *acicula*.

[3] Voyage de la Bonite, Zoologie, t. ii. pp. 168, 169.

[4] Exercices zootomiques, part ii. p. 42.

[5] Voyage de la Bonite, Zoologie, t. ii. p. 170.

The Generative Organs.—The genital gland (Pl. II. fig. 1, k) occupies the posterior part of the visceral mass. The duct (l) issues from it dorsally, passes to the left side of the alimentary canal and then to its ventral surface, and terminates by opening at the right side of the cephalic mass (o).

At the distal extremity of the genital duct are situated the accessory genital glands (Pl. II. fig. 1, m). In *Clio* (*Creseis*) *acicula* I have sought in vain for the receptaculum seminis with a long duct, figured by Gegenbaur.[1] In *Styliola* only the receptaculum seminis is a little elongated. Generally (*Creseis*, *Hyalocylix*) there is a swelling (probably glandular) near the origin of the genital duct.

The genital aperture is connected by a ciliated spermatic groove with the orifice of the penis (Pl. II. fig. 1, q), which is placed as in *Limacina*.

The Nervous System.—In all species of *Clio* the cerebral and pedal ganglia agree in structure and position with those of *Limacina*.

If the nervous system of *Clio* be examined by a series of transverse sections, it is found (Pl. II. fig. 9) that though each cerebral ganglion is outwardly single, yet it contains two distinct centres; the pleural ganglion (b) is fused with the cerebral ganglion proper (a), and is not recognisable on superficial examination. The same is the case in all Thecosomata, except as we shall see in *Cuvierina*, in which the pleural ganglion is just noticeable externally.

In *Clio*, as in all the other Cavoliniidæ, the ganglionic elements of the visceral commissure do not form a bilaterally symmetrical mass as has been usually represented, and as indeed I myself have previously figured in a somewhat diagrammatic sketch of the central nervous system of *Cavolinia*.[2]

The left half of the visceral ganglionic mass is always larger than the right; and in the case of *Clio* this is particularly prominent in the subgenus *Creseis*. This shows clearly that, as in *Limacina*, the ganglion called "abdominal" is fused with one of the anterior visceral ganglia (in all the Cavoliniidæ this is the subintestinal), for the visceral nerves (that is to say, those of the abdominal ganglion, viz., the visceral nerve supplying the heart and the kidney, and the genital nerve) and the left pallial nerve issue from the left portion of the visceral ganglionic mass, whilst from the right half of this mass there issues only the right pallial nerve, which supplies the right half of the mantle and the osphradium.

The description given by Stuart[3] of the nervous system of *Clio* (*Creseis*) *acicula* is so strange and inaccurate that it would require too long to attempt to correct it here.

The enteric or stomato-gastric nervous system is composed of the same elements as that of *Limacina*, and only differs from it in the fact that the two buccal ganglia are approximated to each other instead of being separated and joined by a commissure.

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[1] Untersuchungen über Pteropoden und Heteropoden, pl. ii. fig. 3, c, d.

[2] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. pl. iv. fig. 11.

[3] Ueber das Nervensystem von Creseis acicula, *Zeitschr. f. wiss. Zool.*, Bd. xxi. pl. xxiv. A.

The otocysts are situated on the ventral face of the central nervous system, between the pedal and visceral ganglia; each of them encloses a number of otoliths (Pl. II. fig. 9, *d*).

Osphradium.—The right pallial nerve (*i*, in the figures of the central nervous system) bifurcates shortly after its origin. Its posterior branch leads to a ciliated pad, situated on the inner face of the mantle. This pad, nervous in its nature, is the osphradium, which has the same position and structure in *Clio* as has been represented by Gegenbaur in *Cavolinia*. Its deeper portion is a ganglionic band with numerous cells, whilst the superficial portion consists of an epithelium with ciliated columnar cells.

2. *Cuvierina.*

The Head and Foot.—In this genus the head and tentacles agree with those of *Styliola* and *Hyalocylix*, and the fins with those of *Styliola* and *Clio* (*s. str.*). The posterior lobe of the foot resembles that in the two latter subgenera, but is somewhat notched in the centre of its free border (Pl. II. fig. 6, *b*).

The Mantle.—The mantle-opening, like that of *Clio* (subgenus *Clio*, *s. str.*) is as large as the opening of the shell, the margins of the mantle being entirely separated.

The shield (pallial gland) is long, and is divided into two halves by a transparent transverse band, like that of *Hyalocylix*, but it does not exhibit the two small latero-anterior portions of this latter. As for the lateral lobe of the mantle (balancer), situated here, as in all Cavoliniidæ, on the right side, it is somewhat reduced, and does not arise from the very border of the mantle but a little within it; on the other side, in an almost symmetrical position, is another appendage somewhat similar to it and of almost the same size. The columellar muscle is very large.

The Digestive Tract.—An examination of this part of the body shows that the jaws, closely resembling those of other Cavoliniidæ, are well developed, and that the radula is proportionally longer than in other Thecosomata. The salivary glands resemble in shape those of other Cavoliniidæ, but are much larger.

The œsophagus, at a little distance from the buccal mass, traverses a partition (Pl. II. fig. 6, *f*) which exists indeed in all Pteropoda. The stomach and liver are like those of *Styliola* and *Clio* (*s. str.*), but I have seen no gastric cæcum.

The flexure of the intestine is lateral in *Cuvierina*, as in all Thecosomata, and to such an extent that the œsophagus and intestine are here almost in the same longitudinal plane, and not at all in the same sagittal plane.

The anus is situated far forward, near the mantle-opening, as in *Clio* (*s. str.*). It presents an anal gland as in other Cavoliniidæ.

The Circulatory and Excretory Organs.—*Cuvierina* has no gill any more than *Clio*, and further, there do not exist between *Clio* and *Cuvierina* any differences in the form and disposition of the heart and kidney.

The Generative Organs.—The genital duct has no vesicula seminalis in its course. The accessory genital glands resemble those of *Clio*, but the genital aperture is characterised by the frequent presence of a long flattened appendage, situated on its ventral aspect. This organ is narrow at its base, and divides further on into two branches, of which the right terminates in a point, whilst the left enlarges as it proceeds, expands into the form of a fan, and is truncated at its extremity where it ends in a pad. This appendage, like the whole cervical region, is innervated by the pedal ganglion. Its function is not hitherto known with certainty. Several naturalists have erroneously taken it for the penis (the penis of *Cuvierina* is situated in the same position as that of other Cavoliniidæ, and is of the same form); but it seems probable that it is an accessory copulatory organ, and assists the two individuals *in coitu* in maintaining their attachment to each other. The somewhat frequent absence of this appendage and its variable degree of development lead me to think that it is a temporary organ.

The Nervous System of *Cuvierina* is on the whole constituted like that of other Cavoliniidæ. The cerebral and pedal ganglia resemble those of *Clio*, and give origin to the same nerves.

The pedal ganglia show clearly a small second commissure in front of the first (Pl. III. fig. 1, *e*).

The pleural ganglia, which were discovered in *Clio* by transverse sections of the nervous system, are here recognisable externally, as distinct from the three other ganglia of the same side (Pl. II. fig. 10, *c*).

The visceral ganglia, which in *Clio* were seen to form a mass, composed of two asymmetrical but not separate halves, form here two ganglionic masses, closely approximated but still distinct, as in *Limacina*, with this difference, that the larger ganglion is on the left and the smaller on the right.

The large ganglion corresponds to the larger half of the visceral ganglionic mass of *Clio*; in fact the same nerves issue from it: the left pallial nerve (Pl. III. figs. 1, *4*), and the nerves of the "abdominal" ganglion (genital, *3*, and visceral, *2*); whilst from the right ganglion issues only the right pallial nerve (*1*) which also supplies the osphradium.

There are no differences in the form and position of the otocysts and the osphradium between *Cavolinia* and *Clio*.

3. *Cavolinia.*

It has already been pointed out that this genus consists of two groups:—(A) formed by *Cavolinia trispinosa* and *Cavolinia quadridentata*; (B) including the other six species admitted in the systematic portion of this Report. These two groups, although agreeing in their essential characters, differ in certain points to which allusion will afterwards be made.

The Head, in all species of *Cavolinia*, resembles that of *Clio* (*s. str.*). Both tentacles are well developed, the right especially attaining large dimensions.

The Foot is of different form in the two groups. In group A (*Cavolinia trispinosa* and *Cavolinia quadridentata*) the fins are like those of *Clio* (*s. str.*), as also the posterior lobe of the foot, which is long.

In group B (typical *Cavolinia*) the fins are not so narrow dorso-ventrally, and they form a muscular surface, almost undivided, with the posterior lobe of the foot. This latter is very short and almost as broad as the united fins, from which it is scarcely separated.

The Mantle in *Cavolinia* has a form quite peculiar to the genus, which gives it its most striking character, and is reflected in the disposition of the shell.

The mantle-opening is narrow dorso-ventrally; morphologically indeed it extends as far as the posterior extremity of the lateral slits of the shell, for it is up to this point that the opening of the latter extends. The margins of the mantle, however, are united together by a narrow transverse membrane, as far as in front of the closing apparatus of the shell. These margins are prolonged beyond this united membrane, and may extend outwards by the lateral slits in the shell, just as the separate margins extend through the anterior aperture of the shell, in such a way as to cover during the life of the animal almost the whole external surface of the shell (in the typical *Cavoliniæ*, *e.g.*, *Cavolinia tridentata*).

Besides this in the *Cavoliniæ*, in a restricted sense (that is, excluding *Cavolinia trispinosa* and *Cavolinia quadridentata*), there arises between the margins of the mantle thus prolonged beyond the uniting membrane, on either side posteriorly, a very extensile appendage, which may be double or triple according to the species and according to the state of development, and may float out behind. These appendages possibly correspond to the two symmetrical appendages on the margins of the mantle of *Cuvierina*.

Cavolinia trispinosa and *Cavolinia quadridentata*, which do not possess these symmetrical appendages, are provided on the left side with a lateral lobe (balancer) like that of *Clio*.

The pallial gland, symmetrical as in all the Cavoliniidæ, presents transverse opaque and transparent bands of unlike histological nature. The columellar muscle, which is rather broad, is situated dorsally as in all the Cavoliniidæ, and only directed ventrally at the anterior portion where it bifurcates, passing on either side of the œsophagus to be distributed to the fins and posterior lobe of the foot. This muscle, however, is not really symmetrical, that is to say, situated exactly in the median line; it is oblique, and this is especially visible in *Cavolinia longirostris* (Pl. III. fig. 2), where the insertion of the muscle into the shell, instead of being in the centre of the posterior truncation, is in its right hand angle.

The Digestive Tract.—The anterior portion (buccal mass, œsophagus) resembles that of the other Cavoliniidæ already examined. The stomach, like that of *Clio*, possesses a fifth large triangular masticatory plate, situated behind the four others, and on the ventral side.

All the species of *Cavolinia* have a posterior gastric cæcum, such as has already been described in some species of *Clio*.

The liver in the typical *Cavoliniæ* is like that of the preceding genus in shape, and its duct opens at the right side of the hinder portion of the stomach. In the group A (*Cavolina trispinosa* and *Cavolinia quadridentata*, Pl. III. fig. 3) this organ has an arrangement unique among the Thecosomata; it is composed of two lobes, quite separated, and having each its own duct. These two lobes of the liver are placed to the right and left of the stomach, and their ducts open separately on either side of the gastric cæcum, the duct of the right lobe being much longer than that of the left.

In all *Cavoliniæ* the anus opens almost dorsally, quite behind the liver. Close to the anus is a flattened anal gland, as in other members of the family.

The Circulatory and Excretory Organs.—The heart is situated on the right beside the genital gland. The kidney is towards the ventral aspect of the latter and behind it, disposed almost transversely. In *Cavolinia* the kidney is not at all spongy; its structure is the same as that found in other Cavoliniidæ.

In all the typical *Cavoliniæ* (*i.e.*, the six species included in group B) there is a gill, as Boas[1] has already pointed out. In *Cavolinia inflexa* it is smaller than in the other forms.

The form and structure of this organ are well known, since Souleyet described and figured it in *Cavolinia tridentata*. I will only remark that the gill of *Cavolinia* is not symmetrical, as might be imagined. The right hand portion is more developed than the left, for it extends farther forwards, besides which it is more dorsal in position. It corresponds to the anterior part of the gill in the Gastropoda.

The Generative Organs.—A consideration of the generative organs as a whole shows that some differences exist between the typical Cavoliniidæ and the two species included in group A.

In the latter the genital gland is quite ventral in position, and it is developed equally on the right and left sides. In the typical *Cavoliniæ*, on the other hand, the gland is quite asymmetrical, and largely developed on the left side.

The genital duct in group A presents an elongated swelling on its course, which is lacking in the typical forms; these, however, are provided with a vesicula seminalis which has the form of a long cæcum, without any dilatation at its extremity, and coiled several times upon itself (Pl. III. fig. 2, *h*). *Cavolinia inflexa* has an ovoid vesicula

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[1] Spolia atlantica, p. 207.

seminalis, with a very short duct (Pl. III. fig. 4, *c*). *Cavolinia longirostris* appears to form a transition between this arrangement and that observed in the other typical *Cavolinia*, for in this species the vesicula seminalis has the form of a long cæcum, towards the extremity of which is a swelling, which is wanting in the other species of *Cavolinia* (*s. str.*).

On the other hand, there are in all *Cavoliniæ*, at the distal extremity of the genital duct, the same accessory glands as in other Thecosomata; a large muciparous gland and smaller albumen-gland close together. In group A, however, there is a pyriform receptaculum seminis at the end of a long duct, a little in front of these glands.

The genital aperture (Pl. III. fig. 4, *e*), the ciliated seminal groove (*f*), and the orifice of the penis, are situated as are the corresponding parts of other Cavoliniidæ. The penis encloses a horny stylet (*e.g.*, in *Cavolinia trispinosa*, Pl. III. fig. 5), which Souleyet[1] did not notice in the genus.

The Nervous System.—In *Cavolinia*, as in all other Thecosomata, the cerebral ganglia are situated at the sides of the œsophagus, and connected by a long supraœsophageal commissure. They are in reality cerebro-pleural ganglia, for each encloses a pleural centre within it.

The pedal ganglia, as in *Cuvierina*, and probably all other Thecosomata, have a second small anterior commissure, which is readily visible in a series of transverse sections of the central nervous system.

As in the case of *Clio* the visceral mass is formed of two asymmetrical halves, the right being the smaller of the two. All the figures, therefore, which represent this mass as symmetrical are incorrect.

Thus in the typical *Cavoliniæ* the visceral ganglia are disposed as in *Clio*, and the nerves take origin in the same manner. The two pallial nerves (*1* and *4* in the figures of the nervous system) are very strong in this species, in correlation with the presence of the pallial appendages and of the extensible margins of the mantle. In *Cavolinia inflexa* the two halves of the visceral ganglionic mass are rather further separated, but still asymmetrical.

In the forms included in group A (*Cavolinia trispinosa* and *Cavolinia quadridentata*) the ganglionic elements of the visceral commissure are clearly separated, as in *Cuvierina*, into two asymmetrical ganglionic masses (the right being the smaller), but to a less extent than in *Cuvierina*. The nerves take origin in a manner similar to that described in the latter genus.

This clear separation of the ganglia in group A shows beyond doubt that these species are the most archaic of the living forms of this genus—a view which is supported by the presence of the balancer, as in *Clio*, and the less specialised character of the foot.

On the other hand, the absence of a gill, the characters of the mantle, of the genital

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[1] Voyage de la Bonite, Zoologie, t. ii. p. 186.

organs, and of the embryonic shell, show also that these two species are most nearly allied to *Clio*, which is a more ancient genus than *Cavolinia*. Finally, the presence of a liver divided into two separate lobes distinguishes them from the other typical species of *Cavolinia*.

These differences, upon which I did not lay sufficient stress in my systematic Report on the Thecosomata, lead me to regard the group A as a subgenus of *Cavolinia*, and the name *Diacria*, Gray, 1842, created for the species *Cavolinia trispinosa*, appears to me suitable for it.

Family III. CYMBULIIDÆ.

The animals of this family differ greatly, in appearance at least, from those contained in the two preceding families. The disposition of the various parts of the body, as compared with other Thecosomata, has already been explained.[1]

When a member of the Family Cymbuliidæ and another form, one of the Cavoliniidæ for example, are placed in corresponding positions, it is easy to see that their organisation is similar in all essential respects.

The three genera of this family will now be examined in succession.

1. *Cymbulia*.

The Head, as we have had occasion to indicate when speaking of *Peraclis*, differs from that of the above-mentioned Thecosomata, in the fact that it is distinct, situated at the dorsal side of the fin, and flattened down upon this latter without being free, as in *Gleba*.

It is further characterised by its two symmetrical tentacles, of equal size and with no sheath at their base, as well as by the position of the orifice of the copulatory organ, which is in the middle line of the dorsal surface of the head, a little behind the tentacles.

As regards the latter, Gegenbaur[2] throws doubt upon the existence of a nerve in the interior of these sensory organs. As we shall see, however, a nerve is distributed there, and terminates in a little ganglionic enlargement.

The Foot is in the form of a large undivided natatory disc, extending ventrally as far as the head, which is bent backwards.

The ventral lash-like appendage is not homologous with the posterior pedal lobe of the Cavoliniidæ and Limacinidæ. This latter, which also bears the operculum in the Limacinidæ, corresponds to the posterior operculigerous part of the foot of the Gastropoda. On the contrary, the filiform appendage of *Cymbulia* and of the larva of *Gleba* is

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[1] Zool. Chall. Exp., part lxv. pp. 96, 97.

[2] Untersuchungen uber Pteropoden und Heteropoden, p. 45.

situated *in front* of the lobe which bears the operculum.[1] (It has already been remarked that the larval *Cymbuliæ* have an operculum.[2])

So far as I can judge, this appendage seems to be most properly comparable with the middle part of the foot of the Heteropoda which carries the sucker, and is called by Grobben[3] "rudimentär Sohle des Protopodiums." These two portions occupy strictly corresponding situations.

I do not, however, agree with Fol[4] that this appendage of the Cymbuliidæ corresponds with the posterior lobe of the foot of the Gymnosomata. I think rather that this last is homologous with the central and posterior parts of the foot of the Aplysioidea.

The Mantle extends ventrally, and also a little dorsally, much further than in the Cavoliniidæ, in order to form the cartilaginous "shell," which is in fact nothing more nor less than an induration of the subepithelial dermic layer of the mantle.

The pallial gland (Pl. III. fig. 8, *a*; Pl. IV. fig. 7), which is a modification of the internal epithelial layer of the mantle, differs from that of the Cavoliniidæ in being obviously asymmetrical, the right portion being the larger. It is divided into anterior and posterior parts by a transparent band, which is itself asymmetrical (see Pl. III. fig. 8).

Since *Cymbulia* does not possess a true shell, the columellar muscle, corresponding to that of the Limacinidæ and Cavoliniidæ is entirely wanting.

The space between the fin and the "shell" (Pl. IV. fig. 1, *d*) is freely open and leads into the pallial cavity. On removing or cutting through the fin (Pl. III. fig. 7, *e*) the opening of the mantle-cavity is seen to be asymmetrical, thus differing from that of the Cavoliniidæ; this opening is in fact decidedly turned to the right.

In consequence of the reduction of the dorsal surface of the animal the pallial cavity appears to extend along the dorsal side to just below the heart (Pl. IV. fig. 1, *n*) between the kidney and the visceral mass (*h*) (digestive and generative organs),[5] which appears to hang freely into the mantle-cavity. It must be noticed that the aboral extremity of this visceral mass almost corresponds to the ventral prominence of the same mass in *Cavolinia gibbosa*, for example, where there is a tendency to the dorso-ventral elongation so pronounced in *Cymbulia*.

Thus the ventral surface of *Cymbulia* reaches a little further than this aboral extremity of the visceral mass.

On either side of the visceral mass there may be seen on the inner wall of the mantle rather large muscular bundles, arising where the fin joins with the visceral mass and

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[1] Krohn, Beiträge zur Entwickelungsgeschichte der Pteropoden und Heteropoden, pl. i. fig. 13, d.

[2] Zool. Chall. Exp., part lxv. pl. ii. fig. 14.

[3] Zur Morphologie des Fusses der Heteropoden, *Arb. Zool. Inst. Wien*, t. vii. p. 224.

[4] Sur le développement des Ptéropodes, *Arch. d. Zool. Expér.*, sér. 1, t. iv. p. 183.

[5] This is clearly shown in fig. 1 of my systematic Report on the Thecosomata (Zool. Chall. Exp., part lxv. p. 97).

extending into the mantle. These muscles are probably constrictors of the pallial cavity; and they have perhaps an influence on the successive dilatations of the kidney. It was these muscles which van Beneden[1] took for gills; but, as will subsequently appear, *Cymbulia*, like *Clio*, is destitute of these organs.

The Digestive Tract.—The mouth is not as in the Cavoliniidæ and Limacinidæ (except *Peraclis*) bordered by lateral lips; here the lips are dorsal and ventral, and are produced along the sides of the proboscis to unite and become continuous with the dorsal margin of the fin.

The horny portions of the buccal mass have already been described, notably by Troschel; it is only necessary to note that the two jaws are situated more ventrally than in the Cavoliniidæ.

Into the buccal cavity open the two salivary glands (Pl. IV. fig. 2, *c*) which, though readily visible, have not been noticed by any previous author.

The œsophagus is very large (Pl. IV. fig. 2, *d*), and scarcely distinctly separable from the stomach (*e*). This latter contains within it the same large masticatory plates as in the Cavoliniidæ; the fifth posterior plate, though still triangular, differs a little in form, being very elongated.

The stomach does not present at its posterior extremity a true cæcum like that of *Cavolinia* and some species of *Clio*, but only a large and not very deep *cul de sac*. The intestine does not arise at the posterior extremity of the stomach but a little anterior to it.

The liver is constituted like that of the typical *Cavolinias*; according to Gegenbaur[2] it opens into the stomach by from three to six canals. I have only been able to see, however, two of these hepatic ducts. This multiplicity of ducts among the Thecosomata is an archaic character, which the Cymbuliidæ have retained.

The intestine is longer and more coiled than in the preceding forms of Thecosomata, but morphologically the curvature is the same as in the Cavoliniidæ. The intestine is entirely enveloped in the liver, only the extreme portion of the rectum being free. The anus is not situated so far to the left as in the Cavoliniidæ, scarcely passing the median line, but the terminal part of the intestine is directed distinctly towards the left side.

The Excretory and Circulatory Organs.—The kidney is situated on the dorsal aspect of the visceral mass, at the bottom of the pallial cavity. It is almost symmetrical in form and extends along the mantle, across both sides of the visceral cavity, in such a manner that when looked at in profile by reason of its transparency the lumen appears almost circular (Pl. IV. fig. 1, *h*). The walls of this organ are exceedingly thin and transparent as in *Clio*. It opens into the pallial cavity by an oval aperture (*m*) surrounded

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[1] Exercices Zootomiques, pl. i. fig. xii. *b*.

[2] Untersuchungen über Pteropoden und Heteropoden, p. 48.

by a sphincter, on the right side. On the other hand it opens into the pericardium as in all Mollusca.

The heart (Pl. IV. fig. 1, *n*), within its large pericardium, lies at the base of the pallial cavity under the penis, above the kidney, and on the dorsal surface of the visceral mass.

As was remarked above, gills are entirely wanting. Very probably in the Cymbuliidæ, as in all the abranchiate Thecosomata (*Clio*, *Cuvierina*, &c.), respiration is carried on by some parts of the integument.

The Generative Organs.—The genital gland (Pl. III. fig. 9, *a*) is slightly asymmetrical, its left side being more developed than the right; it is somewhat excavated in front to receive the accessory glands and the genital duct. This latter (*b*), very thin at its origin, enlarges rapidly throughout its middle portion, and then narrows again till it reaches the accessory glands. It is not very long and surrounds these latter.

They form a large mass situated anteriorly and a little to the right, and include a large muciparous gland (*d*) and a small albuminiparous gland (*e*) on the right side of the duct. These two glands, along with an ovoid receptaculum seminis (*c*) with a short duct, open into the distal enlarged portion of the genital duct.

The genital aperture (*f*) is situated in front on the right of the visceral mass (Pl. IV. fig. 1, *j*). A spermatic groove, ciliated, proceeds from it towards the dorsal surface on the right side; a little posterior to the genital opening, this groove becomes transformed into a canal by the fusion of its margins (Pl. IV. fig. 1). This canal opens into the cavity occupied by the copulatory organ.

This latter, as I have already had occasion to remark, is situated on the dorsal surface of the head. It has the same structure as in other Thecosomata; but the position of its orifice is different, being situated in the middle line of the dorsal surface of the head (*k*), a little behind the tentacles.

The Nervous System.—The central nervous system (Pl. IV. fig. 1, *o*) is placed a little farther back than in the preceding forms.

As regards the cerebral and pedal ganglia the central nervous system of *Cymbulia* resembles that of other Thecosomata (compare figs. 1 and 10, Pl. III.), as was recognised by van Beneden, Gegenbaur, and Souleyet. That is to say—

1. The cerebral ganglia are situated at the sides of the œsophagus (Pl. III. fig. 11, *a*), and united by a long supraœsophageal cerebral commissure (*c*).

2. The pedal ganglia (*b*) are situated below the œsophagus, approximated to each other and to the cerebral ganglia; they are not fused with the visceral ganglia, however, as is represented in the figure of von Jhering.[1]

These latter have been the subject of great disagreement among the four anatomists who have studied the genus *Cymbulia*, and especially between the figures and description of one of them.

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[1] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, pl. v. fig. 19.

The figure of the nervous system of *Cymbulia* given by Souleyet[1] shows three ganglionic enlargements on the visceral commissure, whilst the text states only that "la disposition du système nerveux est la même que chez les autres Ptéropodes testacés."[2] Now it has been shown that in these latter the ganglia of the visceral commissure form a mass composed of two asymmetrical halves, more or less clearly separated.

On the other hand, von Beneden[3] describes the elements of the visceral commissure as "une paire de ganglions," whilst Gegenbaur[4] agrees with Souleyet in saying that the nervous system of *Cymbulia* resembles that of typical Thecosomata. Finally, von Jhering, the last who has studied these organs, describes and figures[5] the elements of the visceral commissure as fused with the pedal ganglia in such a way as to form two large symmetrical infraœsophageal ganglionic masses, upon which the otocysts are placed.

The investigation which I have made of the nervous system of *Cymbulia*[6] has shown that Souleyet's figure is by no means complete with respect to the nerves which proceed from the visceral ganglia, but it is *absolutely accurate* as regards the number and disposition of the ganglionic enlargements, that is to say, that there are three closely placed visceral ganglia, separated only by constrictions, and of which the outer are approximated to the cerebral ganglia (Pl. III. fig. 10, *c*, *d*, *e*).

The two outer ganglia are symmetrical, the median is the largest (fig. 10, *d*). It may further be seen (figs. 10 and 11) that the visceral ganglia are quite distinct from the pedal ganglia (*b*), in contradiction to what is stated by von Jhering. The central nervous system of *Cymbulia*, seen from the ventral surface, can only present the appearance attributed to it by the last-named author, before the surrounding connective-tissue has been removed from it.

The nerves which arise from the visceral ganglia are four in number, as follows,—one springs from each lateral ganglion (*1* and *4*), and two (not one only as depicted by Souleyet) which issue from the unpaired median ganglion (*2* and *3*). The stronger of these latter proceeds from the left of the ganglion, the more slender on the right side.

The nerves of the lateral ganglia (*1* and *4*) supply the mantle; the nerves from the median ganglion proceed to the genital (*3*) and to the circulatory and excretory organs (*2*).

The nerves from the other ganglia are distributed in the following manner:—

From each cerebral ganglion arise three nerves (and not two as I stated formerly[7]); an incipient transverse segmentation, which recurs more clearly expressed in *Gleba*, may be observed in the cerebral ganglia (Pl. III. fig. 11). From the dorsal segment proceeds

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[1] Voyage de la Bonite, Zoologie, Mollusques, pl. xv. bis, fig. 38.

[2] *Ibid.*, t. ii. p. 239.

[3] Exercices Zootomiques, p. 11.

[4] Untersuchungen über Pteropoden und Heteropoden, p. 44.

[5] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 117.

[6] *Loc. cit.*, pl. v. fig. 10.

[7] *Ibid.*, pl. iv. fig. 13.

the tentacular nerve (the existence of which was doubted by Gegenbaur); the two nerves from the ventral segment supply the cephalic region (proboscis, lips, &c.).

From each pedal ganglion two large cords proceed laterally to innervate the fin, within which they are very widely ramified.

The enteric or stomato-gastric system is constituted as follows:—The buccal ganglia (Pl. IV. fig. 2, *g*) are connected to the cerebral ganglia by very short cords, in contradiction to the condition figured by von Jhering.[1] These ganglia are closely approximated, and not separated by a long commissure as is indicated by the figure of this author.

The buccal ganglia give off in front and at the sides threads which innervate the buccal mass and the salivary glands. Posteriorly, a strong nervous cord ("nerf stomacal" of Lacaze Duthiers) extends over the œsophagus as far as the stomach (Pl. IV. fig. 2, *h*), where these two nerves form a gastric plexus (*i*).

This exhibits considerable regularity, and is composed of two nervous rings, one on the anterior and one on the posterior portion of the stomach; these are united by four threads passing between the four masticatory plates. At the points of junction between these threads and the rings there are small ganglionic enlargements.

This regular gastric plexus probably exists in all the Thecosomata, but the small size of the stomach in other species renders its demonstration difficult, whilst in *Cymbulia*, where the stomach is larger and the nerves thicker, it is much more easily seen.

An identical arrangement has recently been recorded in the Tectibranchiate Opisthobranchs by Lacaze Duthiers.[2] In these animals (*e.g.*, *Philine*) the two "nerfs stomacaux" lead to the regular gastric plexus formed by an anterior and a posterior gastric nervous ring, which are united by threads passing between the masticatory plates.

The otocysts are situated posteriorly on the ventral surface of the pedal ganglia. Formerly I stated[3] that von Jhering was in error in representing an auditory nerve leading from the otocyst to the cerebral ganglion. I now recognise that I was mistaken; since that time I have had an opportunity of studying the same species as von Jhering, *Cymbulia peroni*, in which the otocysts are deeply coloured with dark brown pigment, which extends along the auditory nerve, and thus renders it very easy of detection.

2. *Cymbuliopsis*.

In the sum total of its external characters (form of the fin, proboscis, &c.) this genus resembles *Gleba* rather than *Cymbulia*, but the shape of the hardened portion of the mantle differs widely from the corresponding part of *Gleba*.[4]

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[1] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, pl. v. fig. 19.

[2] Considérations sur le système nerveux des Gastéropodes, *Comptes rendus*, t. ciii. p. 685.

[3] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 116, note 5.

[4] Compare the systematic Report on the Thecosomata, Zool. Chall. Exp., part lxv. fig. 2, p. 100 (*Cymbuliopsis*), and fig. 3, p. 102 (*Gleba*).

The Mantle.—The pallial gland, so far as I was able to observe on the badly preserved specimen at my disposal, presents the same appearance as that of *Gleba*. It is clearly asymmetrical, and is divided by a transverse band, also asymmetrical, as in the other Cymbuliidæ.

The aperture of the pallial cavity also exhibits the asymmetrical disposition already noticed in *Cymbulia*, and the pallial cavity has the same extent as in this latter genus.

The Digestive and Generative Organs.—As in *Gleba*, neither a buccal mass nor horny structures in the mouth are to be found. The digestive and generative organs are similar on the whole to those of *Gleba*, and consequently to those of *Cymbulia*. The terminal portion of the intestine is clearly directed towards the left side of the median line.

The visceral mass, which as in these two genera is suspended freely in the pallial cavity, presents at its aboral aspect a rather thin prominent ring. It resembles a sucker in form, and I am unable to give any adequate explanation of its function.

The Circulatory and Excretory Organs.—The heart and the kidney have the same situation and mutual relations as in the other genera of the family.

The Nervous System also is disposed as in *Cymbulia* and *Gleba*, that is to say, the visceral commissure is composed of three closely-placed ganglia. This special conformation of the visceral commissure, then, is a very definite character of the family Cymbuliidæ, and is only shared by the genus *Peraclis*.

The cerebral ganglia are slightly segmented as in *Cymbulia*, and the pedal ganglia do not differ from those of this genus. The otocysts too are disposed in the same manner, and the innervation of the various organs is quite similar.

3. *Gleba*.

The Head differs from that of *Cymbulia* in being free, and projecting in the form of a more or less elongated proboscis in front of the fin. The tentacles are quite similar to those of *Cymbulia*, and are situated in the same position, so that in those forms which have an elongated proboscis they are a long way behind the mouth.

As in the preceding genera, the opening of the copulatory organ is situated a little posterior to the tentacles and in the middle line in the adult, whilst in very young individuals it is placed a little towards the right side (Pl. III. fig. 12, *h*).

The Foot forms a very large natatory disc with even margins, and having neither a space devoid of muscular fibres at the lateral extremity of the dorsal margin, as in *Cymbulia*, nor a ventral appendage. During development this appendage exists and is very long, but it becomes much reduced in the older larvæ (Pl. III. fig. 12, *c*), and disappears entirely in the adult.

The Mantle has on the whole the same disposition as in *Cymbulia*, except that the hardened portion, commonly known as the "cartilaginous shell," is neither so much developed nor so thick.[1]

The pallial gland is asymmetrical (Pl. IV. fig. 3, *a*) and divided into an anterior and a posterior portion by an asymmetrical transparent band, which presents near its middle a narrow more opaque band.

Neither buccal mass, jaws, radula, nor salivary glands are to be found; the œsophagus is very extensile. As regards the rest of the visceral anatomy, all that has been noticed in *Cymbulia* holds good here also, and I have nothing to add to what has been published by previous authors (van Beneden, delle Chiaje, and chiefly Gegenbaur).

The Central Nervous System (Pl. IV. fig. 4) is constructed on the same plan as that of *Cymbulia*, but it may be noted that the segmentation of the cerebral ganglia (*a*) is more marked than in this latter genus. Besides this, each of the two segments has on its posterior aspect a little globular swelling, of the same structure as the superficial layer of the ganglia, that is to say, composed of large nervous cells. No nerves arise from these swellings.

The ganglionic elements of the visceral commissure (*c*, *d*) are disposed in the same manner as in the typical genus of the family, there being three closely approximated ganglia.

The innervation is quite similar to that of *Cymbulia*. From each cerebral ganglion a nerve (*i*) passes to the tentacle, where it expands into an olfactory or rhinophoral ganglion. From each pedal ganglion are given off laterally the two large nerves which ramify in the fin, and anteriorly a more slender nerve (*h*) which innervates the retractor muscle of the proboscis.

Finally, the nerves from the visceral ganglia are disposed as in *Cymbulia* (*3*, *4*).

Phylogenetic Relations of the Thecosomata to Each Other.

From a comparative study of the organisation of the different Thecosomata we ought to be able to ascertain which form has preserved the most traces of the primitive structure of the group, that is, which of the recent species is the most nearly related to the ancestral form from which all the other Mollusca of the group Thecosomata have been derived.

It is our ignorance of this actual primitive form which has led to false conclusions regarding the affinities of the Pteropoda. The knowledge of this form will permit us to attempt the solution of the problem (which we shall do in the second part of this Report)—which of the recent Mollusca are the most nearly related to those forms which have given origin to the group Thecosomata.

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[1] Compare the systematic Report, Zool. Chall. Exp., part lxv. fig. 1, p. 97 (*Cymbulia*), and fig. 3, p. 102 (*Gleba*).

The most primitive form among the living Thecosomata has scarcely been sought for in any special manner, and opinions differ very greatly on this subject; some think that it is to be found among the Cavoliniidæ (*Clio*, subgenus *Creseis*), others are of opinion that it belongs to the family Limacinidæ.

In order to arrive at a positive result on this question we shall study the mutual relations of the three groups of Thecosomata (Limacinidæ, Cavoliniidæ, Cymbuliidæ), comparing their organisation.

These relations are not very easy to explain, taking into consideration the great apparent differences presented by the three above-named families—differences which have not been sufficiently considered hitherto in the relationships which the three groups bear to each other.

1. If in the first place we consider the Cymbuliidæ, we find that their affinities are very obscure. Boas[1] seems to regard them as specialised Cavoliniidæ, and for my own part, before I had had the opportunity of studying the organisation of the genus *Peraclis*, I was in a state of the most complete uncertainty regarding their relationships. The knowledge of this genus, however, has thrown some light upon their affinities.

Apart from the presence of the "cartilaginous shell," which has no homology with the calcareous shells of other Thecosomata, we may see that the Cymbuliidæ differ from the Cavoliniidæ by very definite characters, particularly in the shape of the head, which, in the former, is very distinct and quite symmetrical as regards the tentacles, which have no sheath, and in the arrangement of the central nervous system, which has three visceral ganglia instead of two closely placed as in the Cavoliniidæ.

On the other hand, we have seen that among the Limacinidæ, *Peraclis*, which, in all other respects resembles the Cymbuliidæ quite as much as does any of the Cavoliniidæ, has a distinct head agreeing with that of the older larvæ of the Cymbuliidæ in its general form and also in the symmetry of its tentacles, which are further devoid of a sheath; besides this the nervous system is constructed on the same type and has three visceral ganglionic masses arranged in the same manner.

Of all other Thecosomata, then, *Peraclis* is the one which most closely resembles the Cymbuliidæ, and with which this family has the closest affinity.

2. On the other hand, the Cavoliniidæ, as well as the Cymbuliidæ, have undoubted affinities to the Limacinidæ, but these are with the genus *Limacina*, which presents numerous resemblances to the subgenus *Creseis* of *Clio*. The head is indistinct and has the same asymmetrical arrangement as regards the tentacles and penis; besides which the fins in *Creseis* present the small tentacular lobe which is found in many *Limacinæ*.

If, however, the Cavoliniidæ and Cymbuliidæ, which are not directly connected with each other, have each of them close affinities with the Limacinidæ (*Limacina* or *Peraclis*), these relations between the straight Thecosomata (Cavoliniidæ and Cymbuliidæ),

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[1] Spolia atlantica, p. 166.

and the coiled Thecosomata (Limacinidæ) are not rendered any the less easy of explanation, in consequence of the fundamental difference existing between the two groups: namely, that the pallial cavity is dorsal in the coiled and ventral in the straight forms, and that the anus is on the right side in the former and on the left side in the latter.

Souleyet[1] and Grobben[2] have endeavoured to explain these differences by the coiling of the Limacinidæ, but this explanation is insufficient, for if one imagine a *Clio* of the subgenus *Creseis* coiled in the same manner as a *Limacina*, the relative position of the dorsal surface of the head and the pallial cavity cannot change.

Huxley[3] foresaw that the difference is not so great as it appears, when he said, "I cannot think that any real variation will be found to occur among closely allied forms, in a matter so fundamentally connected with their whole structure and mode of development." He had not, however, quite grasped the real cause, for he thought that the displacement of the pallial cavity to the dorsal surface in the Limacinidæ is only a continuation of the process which carries the anus to the left in the Cavoliniidæ.

Boas[4] was the first to give a clear and simple explanation of this apparently deep-seated difference. His explanation may be summarised as follows:—

The anterior or cephalic part (including the buccal mass, central nervous system, genital aperture, and copulatory organ) is so disposed to the other part in one of these great groups that it would require to be twisted through 180 degrees in order to assume the position found in the other.

By this means all the differences which exist between the straight and the coiled Thecosomata are readily explicable, and the two groups themselves may be referred to a common type.

In favour of this hypothesis of "partial rotation" several arguments have been adduced by Boas, and I am able to add others which render the explanation still more satisfactory. Indeed, the sum total of these arguments allows us to demonstrate with almost mathematical certainty the above-mentioned rotation.

In fact we may see (Pl. III. fig. 6) that—

1. The pallial cavity, which is dorsal in the Limacinidæ, is on the opposite aspect, that is to say, is exactly ventral, in the straight Thecosomata.

2. The lobe of the mantle-margin, which is at the right side in the Limacinidæ, is on the left in those straight Thecosomata which possess it.

3. The osphradium (olfactory organ of Spengel) is situated on the right in the straight Thecosomata and on the left in the Limacinidæ.

4. The retractor (columellar) muscle, which is dorsal in the straight Thecosomata,

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[1] Voyage de la Bonite, Zoologie, t. ii. pp. 209–210.

[2] Morphologische Studien über den Harn- und Geschlechtsapparat sowie die Leibeshöhle der Cephalopoden, *Arb. Zool. Inst. Wien*, t. v. p. 63.

[3] On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 43.

[4] Spolia atlantica, p. 184.

is ventral in the Limacinidæ (the Cymbuliidæ, in which the calcareous shell falls off at the end of embryonic development, have of course no retractor muscle.)

5. The fifth large gastric plate, which is dorsal in the Limacinidæ, is ventral in all the straight forms.

6. The aperture of the bile-duct, which is at the right in all the straight Thecosomata, is at the left in the Limacinidæ.

7. The intestine, which ends at the right of the pallial cavity in the Limacinidæ, ends at the left of the same cavity in the straight forms.

8. The genital duct, which arises from the dorsal edge of the gland in the straight Thecosomata, springs from the ventral side in the Limacinidæ.

9. The shell, in those straight forms which have any curvature, is bent towards the dorsal surface, whilst in the Limacinidæ the shell is twisted ventrally.

Thus on comparing these two groups it appears that, taking one of them as a standard, the anterior part of the other has rotated upon the posterior part through a half revolution (180 degrees) upon the longitudinal axis or *vice versâ*.

Now since we have seen that each of the two families of straight Thecosomata has clear affinities with the Limacinidæ, without their exhibiting any relationship to each other, we have still to show which of the three families is the most primitive, and what has been the line of their descent.

I. As regards the Cymbuliidæ and Limacinidæ, there can be no doubt that the Limacinidæ are the more primitive and have given origin to the Cymbuliidæ. The development of the latter furnishes in support of this view excellent arguments which have not hitherto been sufficiently appreciated:—

1. The embryonic shell of the Cymbuliidæ is a coiled one, whence these forms are classed by Fol[1] among his "Campyloconques" in opposition to the Cavoliniidæ, which he terms "Orthoconques"; but neither Krohn[2] nor Fol[3] state whether the shell is dextral or sinistral, and it is impossible to ascertain this from the figures given by Krohn.[4] I have seen many embryonic shells both of *Cymbulia* and *Gleba*,[5] and all were sinistral like the shells of the Limacinidæ.
2. In the older embryos, which yet bear shells, the pallial cavity is dorsal[6] and the anus to the right,[7] just as in the coiled Pteropods.
3. These same embryos then carry an operculum on the foot, which is multispiral as has already been pointed out by Krohn,[8] who, however, did not notice the direction of the spire. The examination of numerous specimens with the operculum *in situ* enables me to affirm that its spire is always sinistral. Now this

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[1] Sur le développement des Ptéropodes, *Arch. d. Zool. Expér.*, sér. 1, t. iv. p. 178.

[2] Beiträge zur Entwickelungsgeschichte der Pteropoden und Heteropoden.

[3] *Loc. cit.*

[4] *Loc. cit.*, pl. i. figs. 12, 14.

[5] Zool. Chall. Exp., part lxv. pl. ii. figs. 14, 17.

[6] Krohn, *loc. cit.*, p. 19.

[7] Krohn, *loc. cit.*, p. 20.

[8] Krohn, *loc. cit.*, pl. i. fig. 15.

is precisely what is observed in *Peraclis*, whose operculum closely resembles that of the young Cymbuliidæ.

4. Besides this it has been pointed out that the older larvæ of the Cymbuliidæ, in which the proboscis is not yet reflexed in front of the fin, have the head shaped exactly like that of *Peraclis* (compare for example *Gleba*, Pl. III. fig. 12); it is quite symmetrical as regards the tentacles, with the same small prominent proboscis, the penis even being also situated on the right side. Further, in *Peraclis*, as in all the Cymbuliidæ, the central nervous system has three visceral ganglia.

We may say then that the Cymbuliidæ have descended from "Limacinoid" ancestors, and that among the recent Limacinidæ *Peraclis* is the form which most closely resembles those ancestors.

II. It now remains, then, for us to ascertain which of the two families, Limacinidæ and Cavoliniidæ, is the more primitive; that is to say, are the Cavoliniidæ descended from the Limacinidæ or have they given origin to them? Very numerous arguments speak in favour of the former hypothesis, and show that the rotation of 180 degrees, which has been alluded to above, has taken place from right to left in a Limacinoid type to give rise to the Cavoliniidæ, whilst the converse is impossible.

1. Let us consider first the relations of the digestive tract and genital duct. We see (Pl. I. fig. 3) that in the Limacinidæ the duct arises on the ventral side of the gland and passes directly to the right side of the body, making a quarter of a revolution (90 degrees) round the digestive tract (see Pl. III. fig. 6). In the Cavoliniidæ (Pl. II. fig. 1) the duct arises on the dorsal edge of the genital gland, and instead of proceeding directly to the right side of the body where the genital aperture is situated, it passes by the left side, then ventrally, and finally reaches the right side, having thus made three-quarters of a revolution (270 degrees) around the digestive tract (see Pl. III. fig. 6). It is clear that of these two routes the shorter (that is, 90 degrees) is the more primitive. It follows then that in the Cavoliniidæ, considering the genital aperture which is in the head as fixed, the visceral portion where the genital gland is situated along with the origin of the genital duct, has made a half rotation from right to left around a longitudinal axis, which explains why the genital duct makes a half revolution (180 degrees) round the tube more than in the Limacinidæ.

2. A large number of events in the development prove beyond all possibility of contradiction that the Cavoliniidæ spring from Limacinoid ancestors by the relative displacement of the visceral and cephalic portions of the body.

   A. In stating his theory of rotation in the Cavoliniidæ, Boas remarks that the anterior or cephalic portion has performed a rotation of 180 degrees relatively to the posterior part, or *vice versâ*. This manner of expressing the process does not seem to me quite accurate, although it indicates correctly the practical result of it. The truth is rather that each part (cephalic or visceral) has performed a quarter of a rotation around the longitudinal axis, the cephalic portion from left to right and the visceral portion in the contrary direction. A study of the retractor muscle shows that such has been the case.

In somewhat advanced larvæ of Cavoliniidæ this muscle may be seen to be inserted at the right side of the shell. In the adult condition it is always inserted dorsally close to the middle line, in such a manner that then the muscle is entirely dorsal and parallel to the axis of the body, whilst in the larvæ it is very oblique. According to Boas, of the two subdivisions of the retractor muscle, that which passes on the right side of the œsophagus would be a new formation.[1] The examination of Fol's figure above referred to shows that it is nothing of the kind, and that this right branch is the more primitive, since it passes to the right side of the head and to the *two* fins, whilst the left branch, which passes along the other side of the œsophagus and only supplies the left side of the head, is secondary.

B. The pallial cavity originates on the right side;[2] in the adults it is quite ventral.

C. The anus is displaced towards the left;[3] in the adult it is situated quite at the left.

D. The shield (pallial gland), which is quite symmetrical in the adult Cavoliniidæ, is still asymmetrical and oblique in the older larvæ,[4] its right side being the more developed, which indicates that it originates on this side and is displaced towards the left.

E. The embryos of the Cavoliniidæ, on the appearance of the apex of the shell, curve in order to follow the more rapid development of the right side; there is then a tendency towards the sinistral coiling of the Limacinidæ,[5] a coiling which still appears in the development of the Cymbuliidæ, in which the uncoiling is not brought about so soon as in the Cavoliniidæ.

3. Facts are observed even in the adults which prove the rotation which has brought about the difference between the coiled and the straight Thecosomata—

A. The dorsal groove of *Clio* (*Styliola*) *subula*. This groove is not parallel to the axis of the shell, but oblique; it commences at the left and terminates in the middle line dorsally; it thus describes a quarter of a circle and consequently indicates all the successive positions of the dorsal side during the quarter of a rotation performed by the visceral portion of the body from left to right (regarding the animal from the dorsal side).

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[1] Spolia atlantica, p. 185, note 3.

[2] Fol, *loc. cit.*, p. 175.

[3] *Ibid.*, p. 146.

[4] *Ibid.*, pl. v. fig. 2, *mb*

[5] *Ibid.*, p. 197.

B. The columellar muscle of *Cavolinia longirostris* (Pl. II. fig. 3). This muscle is not inserted in the middle line of the dorsal side of the shell but at the right hand angle of its truncature.

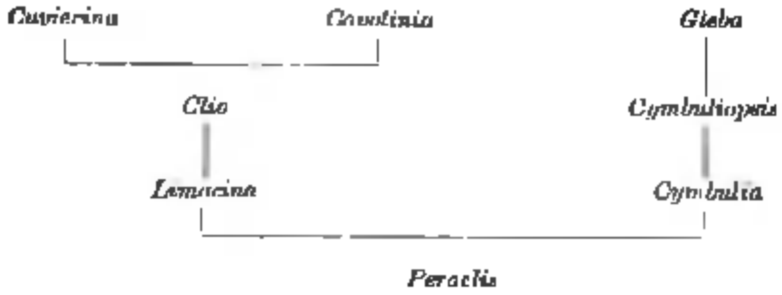
C. The central nervous system of *Limacina* (Pl. I. figs. 7, 8). We have already remarked that in this genus the ganglionic elements of the visceral commissure are united into two asymmetrical masses: the right large and the left small. This asymmetry is easily explained by the fact that the "abdominal" ganglion (the fused posterior visceral ganglia) has united with the "supra-intestinal" ganglion (right anterior visceral); the cause of the union is that in the asymmetrical Thecosomata it is the right-hand half of the visceral portion which is the best developed, that side of each set of organs having alone persisted. On examining the central nervous system of the Cavoliniidæ it is seen on the contrary that the left-hand portion of the single ganglionic visceral mass, or the left half, if the two halves are distinguishable, is the larger (*Cuvierina*, Pl. III. fig. 1); this latter mass encloses the abdominal ganglion and the subintestinal (left anterior visceral), and in fact gives origin to the nerves of the "abdominal" ganglion, which arise in *Limacina* from the large right ganglion. Thus the abdominal ganglion has followed the viscera which it innervates (genital gland, kidney, heart, &c.) in their rotation from right to left (regarding the animal from the ventral surface).

It is impossible, then, to deny the existence of this rotation converting the Limacinoid type into straight Thecosomata, or the descent of these latter from the coiled Thecosomata.

In the Cymbuliidæ the rotation has not been so complete as in the Cavoliniidæ. The pallial cavity is not so decidedly ventral, its aperture being less symmetrical, a little oblique and more open towards the right side (Pl. III. fig. 7), showing clearly that it has originated on this side and been displaced towards the left. Besides, the anus has been transported not so far to the left as in the Cavoliniidæ, and is situated only a little to the right of the middle line. The shield (pallial gland), like the orifice of the pallial cavity, is still asymmetrical (Pl. III. fig. 8), as in the Limacinidæ, and not symmetrical, as in the Cavoliniidæ.

Supposing, then, for a moment, that the cephalic portion has remained immovable, the visceral portion of the Cymbuliidæ has made a little less than a half rotation about its longitudinal axis. From this point of view, then, the Cymbuliidæ are a little less specialised than the Cavoliniidæ.

The phylogenetic relations of the different genera of Thecosomata may be expressed graphically by means of the following table:—



1. We have thus explained the affinities of the Cymbuliidæ and *Peraclis*. We may say, then, that the Cymbuliidæ arise from Limacinidæ resembling *Peraclis* which have lost their calcareous shell towards the end of embryonic development, and the two halves of which (cephalic and visceral) have each performed in opposite directions a little less than a quarter of the rotation about their antero-posterior axis, and, lastly, which have acquired by a subepithelial thickening of the pallial integument a "cartilaginous shell," which makes up for the loss of the calcareous shell.

Gleba is more specialised than *Cymbulia* and *Cymbuliopsis*, and in its development passes through a stage closely resembling *Cymbulia*, with a short proboscis and long appendage to the foot; this appendage shortens and disappears, whilst the proboscis elongates; further, in passing from *Cymbulia* to *Gleba* the cartilaginous shell diminishes in importance.

In the same way *Cymbuliopsis* is more specialised than *Cymbulia*, as shown in its more prominent proboscis and the disappearance of the pedal appendage. The shell has retained more importance than in *Gleba*.

2. *Limacina* is more specialised than *Peraclis*; the head has become less distinct, and the tentacles have lost their symmetry; the nervous system is more concentrated, the abdominal ganglion, which is quite distinct and separate in *Peraclis* (Pl. I. fig. 12, *d*), having fused with the "supra-intestinal" ganglion (Pl. I. fig. 8). The *Limacinæ* have become specialised in two different directions—firstly, by elongating the spire of the shell in such a manner as to attain the extreme form of *Limacina bulimoides*.

This mode of specialisation cannot, however, be very favourable, the most advantageous arrangement for a swimming animal being perfect symmetry, which cannot be realised by a coiled shell. Hence, specialisation in another direction is brought about—the uncoiling of the spire in such a way as to give rise to the straight forms, which, though symmetrical only as regards their external appearance, are thus adapted better for pelagic life. Their symmetry is thus secondary, for their primitive asymmetry remains real, complete, and profoundly impressed upon all their internal organisation.

This uncoiling must have acted like that of the caducous embryonic shell of *Gleba*, a large part of which is straight and separated from the spire.[1] This uncoiling must have

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[1] Zool. Chall. Exp., part lxv. pl. ii. fig. 17.

been accompanied by the loss of the operculum; in the large adult *Limacinæ* (in *Limacina helicina*, for example) the tendency is already observed to lose the operculum, and even the partially uncoiled embryonic shell of *Gleba* has none, nor have the embryonic shells of the Cavoliniidæ.

3. The most primitive of the straight Thecosomata (subgenus *Creseis* of *Clio*) are circular in section, and have retained certain traits of the *Limacinæ*; thus *Clio virgula* has the initial part of the shell coiled dorsally, indicating a former coiling. These forms of *Clio* have also on the dorsal margin of each fin the same small tentacular lobe as is found in certain *Limacinæ*. It is easy to see how the forms compressed dorso-ventrally and with lateral keels (*Clio* properly so called) have originated from these species of *Clio* which are circular in section.

4. From these latter the *Cuvierinæ* have arisen by constriction behind the aperture, and by the formation of a diaphragm about the middle of the shell, behind which the initial part of the shell may become lost.

5. Finally, those forms of *Clio* which are compressed dorso-ventrally, in which (as in *Clio cuspidata*, for example) the lateral margins have diverged almost in opposite directions, the aperture being produced into a narrow slit at either side, have given rise to the most primitive *Cavoliniæ*, which, as in the case of *Cavolinia trispinosa* and *Cavolinia quadridentata*, still retain some of the characters of *Clio* or other primitive characters, such as a well-marked embryonic shell, fins distinct from the rather narrow ventral lobe of the foot, ganglionic elements of the visceral commissure still separated into two halves, &c.; and from these forms the passage is easy to all the other *Cavoliniæ*. Embryology confirms the view that the *Cavoliniæ* are the most specialised in this sense; in fact Fol[1] remarks in this connection, ". . . les Hyaléacées sont un extrême."

This account of the phylogeny of the Thecosomata, drawn up from comparative anatomy and based upon embryology, is also found to agree with palæontology, which gives it additional support. We find *Limacina* in the most ancient Tertiary deposits, and also forms resembling *Clio*, with circular transverse section (*Euchilotheca*), as well as nearly related forms which lead on to *Cuvierina* (*Tibiella*). *Clio*, properly so called, however, and *Cavolinia*, do not appear until the Miocene. As for the Cymbuliidæ, it is hardly possible that their "cartilaginous shells" should be preserved.

As regards the fossils considered to be Primary Thecosomata (*Creseis*, *Cleodora*, &c.), and the larval shells of Cymbuliidæ described by Ehrenberg, we shall soon see the slender basis on which rests the systematic position assigned to them.

From what has been stated above, it is easy to see the importance of the position occupied by the Limacinidæ in the morphology of the Thecosomata. By means of the knowledge of *Peraclis* they enable us to understand the relations of the Cymbuliidæ, which were extremely difficult. Wagner[2] even considered them as the most primitive

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[1] *Loc. cit.*, p. 206.

[2] Die Wirbellosen des weissen Meeres, Bd. i. p. 118.

of the Pteropods, and as derived from the Heteropods! On the other hand, *Limacina* explains the relations of the Cavoliniidæ, which if the Limacinidæ no longer existed would never have been understood, in spite of the existence of fossil Limacinidæ; for the morphological results obtained from the study of fossil shells are exceedingly small, and render those who devote themselves exclusively to this study liable to singular misconceptions.

Finally, thanks to the Limacinidæ, it will be possible, as we shall shortly see, to trace out the affinity of the Thecosomata to the other Molluscs, and to determine their phylogenetic origin.

SUMMARY ON THE THECOSOMATA.

The Thecosomata possess only one pair of cephalic tentacles.

The fins embrace the head as far as its dorsal surface.

The mantle presents on the floor of the pallial cavity a large pallial gland.

All the Thecosomata, except *Gleba* and *Cymbuliopsis*, have a radula, the formula of which is 1 : 1 : 1, two jaws placed laterally, and, contrary to the assertions of Gegenbaur, a pair of short salivary glands.

The stomach is a masticatory gizzard with muscular walls, and exhibits four large symmetrical masticatory plates (never two, as stated by Huxley,[1] and copied from him by Woodward and Tryon), a fifth posterior plate, and generally eight small anterior plates. The liver does not pour its secretion into the gizzard, but into the posterior part of the stomach, into which it opens by a very small number of apertures.

At the anus is generally situated an anal gland.

The copulatory organ is situated on the anterior dorsal part of the head near the tentacles.

The cerebral ganglia are situated at the sides of the œsophagus and united by a long supraœsophageal commissure; the pleural ganglia close beside the cerebral, and seem united with them.

II. GYMNOSOMATA.

As may be seen from the systematic Report upon this group,[2] I divide these animals into five families, one of which (Pneumonodermatidæ) includes three genera, whilst the others (Clionopsidæ, Notobranchæidæ, Clionidæ, and Halopsychidæ) include only one each.

Of the family Notobranchæidæ I was not able to obtain a single specimen for anatomical investigation, so that my researches refer only to the other divisions.

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[1] On the Morphology of the Cephalous Mollusca, p. 48, *Phil. Trans.*, 1853.

[2] Zool. Chall. Exp., part lviii. p. 11.

Family I. PNEUMONODERMATIDÆ.

The three genera which make up this family resemble each other very closely in their general internal organisation, since their principal zoological differential characters are external, taken from the buccal acetabuliferous appendages and the gills.[1] I think, therefore, that the best course will be to examine these three genera simultaneously rather than separately, in order to avoid numerous repetitions; I shall mention in each case, however, the points in which I have observed differences between *Dexiobranchæa*, *Spongiobranchæa*, and *Pneumonoderma*.

The Head in the Pneumonodermatidæ is somewhat elongated. It presents anteriorly the buccal opening, dorso-ventral in direction, and the two anterior or labial tentacles, situated on either side of it and dorsally rather than ventrally. These tentacles are more or less elongated; those of *Spongiobranchæa* are more elongated than in others. They are not the seat of a special sense but of general sensibility; their distal extremity encloses elongated nervous cells.

On the dorsal surface of the cephalic region, near the middle of its length, is a pair of posterior or nuchal tentacles, which are quite symmetrical but only slightly prominent. Each of them receives two cerebral nerves, each of which is swollen at its distal extremity within the tentacle, an arrangement which perhaps led Souleyet to believe that they are bifid.[2]

These tentacles are difficult to discover when retracted in preserved specimens, but are readily found from within owing to the presence of the nerves. We shall shortly see that these are the optic and olfactory nerves, and their distal enlargements are the rudimentary eye and the olfactory ganglion or rhinophore.

The Foot is similarly shaped in all three genera, as has been already described in the systematic portion of this Report. The plicated tubercle at the base of the posterior lobe is glandular in function. All the ventral surface of the foot is ciliated.

The visceral envelope, continuous with that of the head, has several kinds of sparse unicellular glands scattered all over it. The most considerable are aggregated in the middle line on the dorsal surface, where they form a depression known as the dorsal patch. A transverse section through this (Pl. IV. fig. 7) shows the presence of two kinds of glands—(1) the peripheral or lateral glands (*b*), which are very large cells; (2) the median glands (*c*), small in size and whose secretion is of a bright colour.

The Digestive Tract.—The anterior portion from the mouth, as far as the buccal mass, constitutes an evaginable proboscis of the acrembolic type. This has been figured in three genera in the systematic part of this Report; it is least developed in *Dexiobranchæa*.

On the anterior part of the retracted proboscis (posterior part when it is evaginated) are

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[1] Compare the systematic Report on the Gymnosomata, Zool. Chall. Exp., part lviii. pp. 11–32.

[2] Voyage de la Bonite, Zoologie, t. ii. p. 256.

situated the acetabuliferous appendages, and I wish to lay special stress on the fact that they originate on the proboscis and have no connection with the foot. The form of these appendages varies in different genera, as was shown in the systematic Report on the Gymnosomata. In the different known species of Pneumonodermatidæ these appendages have attained different degrees of development, varying from the condition in which the suckers are directly inserted on the proboscis (*Dexiobranchæa simplex*) to that in which they are carried on two long symmetrical stems (*Spongiobranchæa* and *Pneumonoderma*).

The structure of these suckers has been studied by Niemiec,[1] and by myself; it differs essentially from that of the suckers of Cephalopods, also studied by Colasanti,[2] by Niemiec, and by Paul Girod.[3]

At the posterior end of the proboscis is the buccal mass, in such a manner that it is carried quite forwards, along with the horny pieces which it encloses, when the proboscis is evaginated.

In this buccal mass (Pl. IV. fig. 6) are contained, as we have seen, two jaws united in the middle line (*b*), a powerful radula (*c*), and the organs known under the name of hook-sacs; these last are also seen of all degrees of development in the Pneumonodermatidæ, from *Dexiobranchæa* where they form only two small depressions enclosing short hooks (*a*), to *Pneumonoderma* where they form long evaginable sacs (*a'*) with a wall covered with hooks.[4]

From the fact that the proboscis is evaginable, it follows that when it is expanded it must contain the anterior part of the œsophagus doubled up within it; this latter then must increase in length with the proboscis, always being longer than it. The œsophagus is rather extensible and ciliated throughout its whole length as in other Pteropods. It is rather short and traverses a membranous diaphragm like that which we have seen in the Thecosomata (*Cuvierina*, &c.), and which we shall also find in all the Gymnosomata. This diaphragm divides the general body-cavity into a cephalic portion, enclosing the buccal mass, the central nervous system, the penis, &c., and a posterior visceral portion.

The œsophagus, in its passage through this diaphragm, is accompanied by the salivary glands, which open in the usual position, are much elongated, and do not present a marked separation between the secreting and conducting portions. They have been figured by van Beneden[5] as united by their posterior parts. I have always found, however, both in the various species of *Pneumonoderma* which I have examined, and in other genera, that the two salivary glands are free and distinct throughout their whole extent.

The stomach forms a large pouch, with slightly muscular walls, entirely surrounded by the liver, which pours its secretion into it by numerous apertures; this arrangement is observed in all Gymnosomata.

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[1] Recherches morphologiques sur les ventouses dans le règne animal, *Recueil Zool. Suisse*, t. ii. 1885.

[2] Ricerche anatomiche e fisiologiche sopra il braccio dei Cefalopodi, *Atti R. Accad. d. Lincei*, ser. 2, t. iii. pt. 2, 1876.

[3] Recherches sur la peau des Céphalopodes, *Arch. de Zool. Expér.*, sér. 2, t. ii., 1884.

[4] Compare the Systematic Report on the Gymnosomata, Zool. Chall. Exp., part lviii. fig. 1, p. 6, 7.

[5] Recherches anatomiques sur le Pneumodermon violaceum, d'Orb., *Mém. Acad. Sci. Bruxelles*, t. xi. pl. i. figs. 4, 9.

The intestine arises from the posterior part of the stomach; it is short and passes directly without any flexure to the right side, where the anus is situated. Thus the curvature of the digestive tract is lateral and to the right, and not neural. If it appear a little ventral this is in consequence of the great reduction of the pedal surface. It opens into a cloacal depression, like that of *Clionopsis* (Pl. IV. fig. 10), where is also found the opening of the kidney.

The Respiratory and Excretory Organs.—The situation and structure of the gills have been already described in three genera in the systematic portion of this Report. The primitive gill is the lateral one, which also is nearest to the auricle of the heart, this latter being posterior. For the rest the heart is shaped as in the Thecosomata. The arterial system is more easily followed than in these latter; but it does not present any special or interesting disposition.

The kidney, whose existence was suspected by Gegenbaur,[1] is an organ with thin walls, not very obvious, and difficult to demonstrate by dissection. It is made up, as in *Clionopsis* and *Clione*, of a flattened sac, situated between the visceral mass and the lateral gill, and opening anteriorly into the cloacal depression near the anus.

The Generative Organs.—The genital gland (Pl. IV. fig. 8, *a*) occupies the posterior part of the visceral cavity. It forms a compact mass, presenting lobes more or less distinctly separated. The genital duct (*b*) arises from the anterior part of the gland, a little ventrally; it is rather thin at its origin, but dilates as it proceeds as far as the middle of its course.

This duct, somewhat coiled, reaches the accessory genital glands, which are situated ventrally at the anterior end of the visceral mass; among these may be distinguished a coiled muciparous gland (*c*), and a small albumen gland (*d*), situated on the back of the other and to some extent embedded in it.

After these two glands the genital duct presents a receptaculum seminis (*e*) rather long and ovoid in shape; then it opens on the right side of the cervical region behind the posterior margin of the fin of that side. At the genital aperture (*f*) commences a ciliated spermatic groove, parallel to the fin, and passing forwards in front of the anterior border of the fin to the orifice of the penis, which is situated on the anterior aspect of the right side of the foot. The penis, which is coiled up in a cavity of the head, is rather long, and has the same form as in the other Gymnosomata, such as *Clione*.[2]

The Nervous System.—The only information we possess regarding the nervous system of the Pneumonodermatidæ is derived from the researches of Cuvier,[3] van Beneden,[4] Souleyet,[5] and Gegenbaur,[6] and is based upon the study of the genus *Pneumonoderma* alone.

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[1] Untersuchungen über Pteropoden und Heteropoden, p. 86.

[2] Zool. Chall. Exp., part lviii. p. 47.

[3] Mémoire sur l'Hyale et le Pneumoderme, *Ann. Mus. Hist. Nat. Paris*, t. iv. p. 228, pl. lix. B, fig. 9.

[4] Recherches anatomiques sur le Pneumodermon violaceum, d'Orb., *Mém. Acad. Sci. Bruxelles*, t. xi. p. 43, pl. i. fig. 2.

[5] Voyage de la Bonite, Zoologie, t. ii. p. 267, pl. xv. figs. 28–38.

[6] Untersuchungen über Pteropoden und Heteropoden, p. 97.

The first two authors have limited themselves to a description of the ganglia, without noticing the various nerves which proceed from them; the last has given no figure. Cuvier recognised the four pairs of ganglia which make up the central nervous system of *Pneumonoderma*; but nothing further is to be learned from his description and figure. Van Beneden has given a better figure of the central nervous system, without, however, distinguishing the cerebro-pleural and cerebro-pedal connectives, which he regards as forming only a single trunk. Gegenbaur confines himself to a very brief description, in the course of which he remarks that the acetabuliferous appendages are innervated by the pedal ganglia! Lastly, the description of Souleyet is much more exact, and my own researches on the nervous system of *Pneumonoderma* have shown that his figures are exceedingly accurate.

On the other hand, the comparative examination which I have made of the genera *Dexiobranchæa*, *Spongiobranchæa*, and *Pneumonoderma* has demonstrated that the central nervous system is essentially similar in composition in these three genera; so much so, indeed, that to describe one of them is to describe all.

The cephalic portion of the Pneumonodermatidæ being somewhat elongated (see Pl. V. fig. 1), as also the anterior part of the digestive tract, the central nervous system is situated relatively farther back than in the other Gymnosomata. As in all these it is composed of eight ganglia (Pl. V. fig. 1) disposed in pairs. For information regarding the form and relative dimensions of these ganglia I may refer to the figures, from which it may be obtained more readily than from even a long description.

Three of the pairs of connectives—cerebro-pleural (Pl. V. fig. 1, *e*), cerebro-pedal (*f*), and pleuro-visceral (*g*) are here rather long, in such a manner that the four pairs of ganglia are less concentrated than in other families. It is in *Dexiobranchæa* that the connectives (especially the cerebro-pleural and cerebro-pedal) are the longest, and that the concentration of the ganglia is least marked; this agrees well with the other archaic characters of this genus.

I. The cerebral ganglia (Pl. V. fig. 1, *a*) are slightly elongated transversely, and almost in apposition. In *Spongiobranchæa* there is a small cerebral commissure, more appreciable than in *Pneumonoderma*.

From each cerebral ganglion issue three connectives—cerebro-pleural (Pl. IV. fig. 9, *f*), cerebro-pedal (*g*), and cerebro-buccal (*i*), the first being the strongest. The last is the most slender, and arises from the œsophageal face of the ganglion (see Pl. IV. fig. 9, *i*, and Pl. V. fig. 3, *j*), whilst the cerebro-pleural and cerebro-pedal connectives issue from the lateral surface, one behind the other, the latter being the anterior.

The anterior part of each cerebral ganglion gives rise to three nerves, or more correctly to two, for the two lateral nerves (Pl. V. fig. 1, *j* and *k*) arise by a common trunk.

1. The median nerve (*l*) passes to the proboscis, the buccal opening, and the lips.

2. The lateral nerve, which is the strongest of those springing from the cerebral ganglion, divides almost immediately into two branches—

(i.) The one nearer the middle line (*j*) innervates the suckers situated on the wall of the proboscis (whether they be disposed as in *Dexiobranchæa* or as in the other genera of the family), and ramifies in the sucker-bearing appendages.

(ii.) The lateral branch (*k*) supplies the anterior or labial tentacle.

3 and 4. Two nerves (Pl. V. fig. 1, *h* and *i*) spring from the dorsal surface of the cerebral ganglion, and proceed to the posterior or nuchal tentacle of each side.

The more anterior and median of these nerves (*h*), which is also the stronger, is the tentacular nerve properly so called, or olfactory nerve (it has been wrongly regarded as the optic nerve by van Beneden). This nerve ends in a ganglionic enlargement, the olfactory ganglion or rhinophore, from which arise many small very ramified nerves, distributed to the terminal surface of the tentacle.

As for the true optic nerve, it is the second dorsal nerve (*i*), which arises more posteriorly and to the side, near the origin of the pedal connective. At the origin of this nerve there is found, as in many Gastropods, a small ganglionic enlargement, which I have seen especially well marked in *Spongiobranchæa*. The rudiment of the eye forms, at the extremity of the optic nerve, an enlargement almost contiguous to the rhinopore.

In a large number of Gastropods the tentacular (olfactory) nerve arises by a common trunk with the optic nerve. In the present case each has its own origin, but they show an anastomosis which recalls the condition seen in some Gastropods (for example, *Truncatella*).[1]

Finally, there arises at the side of the optic nerve, still nearer to the origin of the pleural and pedal connectives, a slender nerve which passes ventrally between the two connectives just mentioned to the otocyst. I have observed this disposition very clearly in *Spongiobranchæa* (Pl. V. fig. 3, *z*),[2] and I cannot doubt that it exists also in other genera.

II. The pedal ganglia (*b*) are united by a strong posterior and by a second anterior commissure (Pl. IV. fig. 9, *l*), more difficult of observation, which I have found in all Gymnosomata, but which has not hitherto been recorded. The homologue of this second commissure is found in a large number of Opisthobranchia (*Aplysia*,[3] for example), where it arises near the nerves of the foot, or even from one of those nerves.

Each pedal ganglion is united to the corresponding cerebral ganglion by a connective (*g*) which arises from its lateral part. The pleuro-pedal connective is invisible, the pleural ganglion being in close juxtaposition to the pedal.

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[1] Vayssière, Étude sur l'organisation de la Truncatella truncatula, *Journ. de Conchyl.*, 1885, pl. xiii. fig. 18, *S*.

[2] I am indebted to Professor Spengel for the specimens of *Spongiobranchæa* which I have dissected.

[3] Compare von Ihering, Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, pl. iv. fig 14, pa. pa. co.

The pedal ganglia are the largest of all, and somewhat triangular in form. A large number of nerves arise from them—seven in *Pneumonoderma* (Pl. IV. fig. 9)—two anterior, two lateral, and three posterior.

1. The more median of the anterior nerves (I) passes forward and innervates the foot.

2. From the ventral surface of the ganglion, near the anterior margin, arises the large nerve (II) which passes to and ramifies in the fin.

3 and 4. The two lateral nerves (III and IV), of which the anterior is the stronger, pass forward to innervate the parts situated between the foot and the integuments of the head.

5, 6, and 7. The three posterior nerves (V, VI, and VII) proceed to the part of the envelop of the body situated dorsally to the foot, behind the head, and in front of the visceral sac. These nerves are also found with the same distribution in the other Gymnosomata, and are incontestably homologous with those which Lacaze Duthiers has described under the name "nerfs cervicaux."[1]

The outermost of these nerves (V) anastomoses with the nerve (*j*) which springs from the pleural ganglion. Elsewhere I have only observed this anastomosis in *Aplysia* where it was not noticed by Lacaze Duthiers.[2] I have found it in all the typical Gymnosomata, in which it has not hitherto been seen except in *Pneumonoderma* by Souleyet.[3]

The plexus formed by these two nerves contributes to the innervation of the so-called "cervical" region. The details of its composition may vary according to the genus and even according to the species; its general disposition is, however, always the same.

To the posterior border of the pedal ganglion, near the origin of the middle cervical (VI) and near the point where the pedal ganglion is approximated to the pleural ganglion, is situated the otocyst (Pl. V. fig. 3, *h*), which is just in contact with the pleural ganglion; as has been mentioned above, its nerve (*i*) is derived from the cerebral ganglion.

III. The pleural ganglion (*c*) is the smallest of those which make up the central nervous system, and is ovoid in form. It gives origin laterally to the nerve (Pl. IV. fig. 9, *j*) which unites with the outermost of the cervico-pedal nerves (V) in order to form the cervical plexus above described. The law of Lacaze Duthiers, according to which the pleural ganglion never gives off nerves,[4] must therefore be restricted to the aquatic *Pulmonata*.

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[1] Du système nerveux des Gastéropodes pulmonés aquatiques, *Arch. d. Zool. Expér.*, sér. 1, t. i. p. 493, 6°.

[2] Système nerveux des Gastéropodes (type Aplysie), *Comptes rendus*, t. cv. pp. 878–882.

[3] Voyage de la Bonite, Zoologie, Mollusques, pl. xv. fig. 37.

[4] Du système nerveux des Gastéropodes pulmonés aquatiques, *loc. cit.*, p. 494, 12°.

From the anterior extremity of the pleural ganglion issues the cerebro-pleural connective, and from its posterior extremity the pleuro-visceral connective (somewhat elongated in *Pneumonoderma*), which leads to the corresponding ganglion of the fourth pair.

IV. This fourth pair is composed of two ganglia (Pl. IV. fig. 9, *d*) in close apposition and almost spherical. Hitherto we have seen in the nervous system of the Pneumonodermatidæ an absolute symmetry in the size of the two ganglia of the same pair (cerebral, pleural, and pedal ganglia), and in the number of nerves which they give off. Now, however, this symmetry ceases.

An attentive examination shows that these two ganglia are slightly unequal, the left being the larger. But the asymmetry becomes more striking when we consider the nerves given off from them. The right ganglion only gives origin to one nerve, while three spring from the left hand one, a lateral nerve and two posterior almost median nerves. This asymmetry is found in all the Gymnosomata, and has only been noticed by Souleyet, who, however, did not attach any importance to it. Spengel[1] is wrong in attempting to modify Souleyet's figure so as to render the visceral nerves symmetrical in their origin.

1. The nerve from the right visceral ganglion (*1*), which is symmetrical with the lateral nerve of the left ganglion, supplies the right half of the visceral sac and the osphradium. This is constituted as in *Clionopsis* (Pl. IV. fig. 10, *a*) by a ganglionic pad occupying the antero-lateral angle of the cloacal depression; a divided branch of the nerve (*1*) passes to it.

2 and 3. The two posterior nerves of the right ganglion (*2* and *3*) innervate the viscera (genital organs, heart, kidney) and the gills.

4. Finally, the lateral nerve of the left ganglion (*4*) arises near the connective, and supplies the left half of the visceral sac.

V. The buccal ganglia, seen for the first time by van Beneden, are situated below the œsophagus, between the two hook-sacs, a little behind the point where the salivary glands open. They are in close juxtaposition, and each of them gives origin anteriorly to a filament on which is situated an accessory ganglion; these threads innervate the salivary glands.

The other nerves which arise from the buccal ganglia are five in number, as is shown in the figures of Souleyet and van Beneden—one azygous anterior nerve arising from the point where the two buccal ganglia are in contact, and innervating the radula; and also a lateral and a posterior nerve from each ganglion. The former supplies the walls of the buccal mass, and the latter the hook-sacs.

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[1] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. pl. xvii. fig. 10.

The proboscis of the Pneumonodermatidæ being rather elongated, the anterior part of the digestive tract is capable of considerable displacement. The cerebro-buccal connectives are also long in this family (Pl. IV. fig. 9, *i*).

Family II. CLIONOPSIDÆ.

The family includes only the single genus *Clionopsis*.

The Cephalic Region is less elongated in this family than in the preceding. The anterior or labial tentacles are short and shaped as in all the Gymnosomata. The posterior or nuchal tentacles are more conspicuous than in most of these, and are especially well developed in *Clionopsis krohni*. Like those of the Pneumonodermatidæ, they each receive two nerves, each terminating in an enlargement.

The Foot of *Clionopsis* is characterised by the absence of a posterior lobe; it presents, however, a plicated tubercle, having the same structure as in other Gymnosomata.

The Visceral Sac exhibits also the glandular dorsal patch, already described in the case of the preceding family.

The Digestive Tract.—As regards these organs, *Clionopsis* only differs from the Pneumonodermatidæ in its anterior portion. Indeed the stomach, liver, and intestine are disposed identically in the two families, and the anus also opens into a cloacal depression near the aperture of the kidney; this depression is limited anteriorly and to the right by the osphradium (Pl. IV. fig. 10).

The anterior part, however, of the digestive tract of *Clionopsis* is characterised by the great elongation of the proboscis and of the œsophagus (the evaginated proboscis of *Clionopsis* has been figured in the systematic portion of this Report).[1] The elongation of the œsophagus is a necessary consequence of that of the proboscis, since it has to be folded up within the latter when it is everted.

The proboscis is further characterised by the absence of buccal appendages, which is explained by the law of compensation in the organs; the growth of the proboscis in length renders useless the presence of organs of prehension at its base.

The Respiratory Organs consist, as I have already stated in my systematic Report, of a terminal gill in the adult state, almost analogous to that of *Pneumonoderma;* the lateral gill is absent.

The Excretory and Circulatory Organs.—Of all the Gymnosomata, *Clionopsis* is the one in which the form of the renal apparatus and its relations with the central circulatory organ are the most readily recognisable, owing to the transparency of the integument. Its structure and relations have already been accurately described by Gegenbaur.

The Generative Organs of the Clionopsidæ are quite similar to those of the Pneumonodermatidæ (Pl. IV. fig. 8).

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[1] Zool. Chall. Exp., part lviii. pl. iii. fig. 1.

The Nervous System of *Clionopsis* has been described and figured by Troschel[1] and by Gegenbaur,[2] but only in a summary fashion.

Troschel represents the nervous system as formed of three pairs of ganglia, which may be regarded as cerebral, pedal, and visceral. He did not observe the pedal commissure,[3] and only saw nerves issuing from the cerebral ganglia. Among these is to be noted as a curiosity a nerve which, according to Troschel, runs from the posterior or nuchal to the anterior or labial tentacle. Gegenbaur was the first to see the pleural ganglia of *Clionopsis*, but as regards the nerves he only saw some issuing from the pedal ganglia.

According to my own observations[4] the central nervous system of *Clionopsis* is constituted in the same manner as that of *Pneumonoderma*; that is to say, it is composed of four pairs of ganglia, disposed as in this last, the pleuro-pedal connective being quite evanescent as in all Gymnosomata.

The cerebral ganglia are close together, and are shaped like those of the Pneumonodermatidæ. As regards the nerves given off from these ganglia, the chief difference from the preceding forms is dependent upon the absence of the buccal appendages. From the anterior side of each ganglion proceed two large nerves.

1. The lateral, which passes to the anterior tentacle.
2. The median, which soon ramifies freely, and is distributed to the large proboscis, and then to the buccal opening and the lips.

3 and 4. From the dorsal surface of the ganglion arise, as in the preceding genera, two nerves for the posterior or nuchal tentacles. These two nerves were seen and figured by Troschel, but he erroneously represented the left optic nerve as anterior to the olfactory nerve. As for Troschel's nerve from one tentacle to the other, I can positively assert that it does not exist, and suppose that the retractor muscle of the anterior tentacle has been taken by him for a nervous thread.

The description given of the pedal and pleural ganglia of Pneumonodermatidæ is also applicable to the Clionopsidæ. The pedal ganglia also have the second small commissure, and the lateral cervical nerve also anastomoses with the nerve of the pleural ganglion in order to contribute to the innervation of the neck.

The two visceral ganglia are characterised, as in all the typical Gymnosomata, by their asymmetry; that of the right side is smaller than the other, and only

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[1] Beiträge zur Kenntniss der Pteropoden, *Archiv f. Naturgesch.*, Jahrg. xx. p. 226, pl. x. fig. 9, v.

[2] Untersuchungen über Pteropoden und Heteropoden, p. 70, pl. v. fig. 12.

[3] It is strange that the pedal commissures of the Gymnosomata, which are the only true commissures, for the cerebral ganglia as well as those of the visceral commissures are in juxtaposition, have passed unnoticed, even where they are especially strong. Thus Cuvier has not figured the pedal commissures in *Clione*, nor has Souleyet in *Halopsyche*, nor Gegenbaur in *Clionopsis*.

[4] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. pp. 102–104, pl. iv. fig. 5.

gives origin to one, whilst three nerves spring from the left ganglion, which are distributed in a manner precisely similar to the corresponding nerves in the Pneumonodermatidæ. The nerve from the right ganglion innervates the right side of the visceral sac, one of its branches subdivides to supply the osphradium, which has the form of a ciliated nervous band, situated in the antero-lateral angle of the cloacal depression (Pl. IV. fig. 10).

There is no difference between the stomato-gastric nervous system of *Clionopsis* and that of the Pneumonodermatidæ.

Family III. CLIONIDÆ.

The Head of the Clionidæ differs from that of the Pneumonodermatidæ and the Clionopsidæ in its anterior extremity, which is swollen and separated from the body by a "neck." The anterior tentacles are long, and have the same structure as those of the Pneumonodermatidæ. The posterior are situated on the margin of the distended portion of the head towards the neck, and are shaped as in the two preceding families.

The buccal aperture is capable of opening widely, and its margins separate when the anterior portion of the digestive tract is evaginated (Pl. V. fig. 4). When the evaginable parts are retracted, the margins of the buccal opening close upon each other like two half hoods over the buccal cavity.[1]

The Foot is shaped almost exactly as in the Pneumonodermatidæ, but does not exhibit the plicated tubercle at the base of the posterior lobe. The visceral sac has no dorsal glandular patch as in the preceding families.

The Digestive Tract.—The anterior evaginable portion or proboscis is much shorter than in the Gymnosomata already examined (see Pl. V. fig. 4, *a*). At the base of this evaginable proboscis are conical buccal appendages (to the number of two or three pairs, symmetrically disposed on either side), and known as buccal cones or cephaloconi (Pl. V. fig. 4, *c*). I have already[2] described their structure, and now limit myself to mentioning the points which were then demonstrated:—

1. That they do not bear suckers of any kind.

2. That they present special nervous terminations, and enclose in their interior long unicellular glands collected into follicles.

I must add, however, that my sections were made from contracted cones from specimens killed in alcohol, so that the groups of columnar epithelial cells surrounding

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[1] See Pelseneer, The cephalic appendages of the Gymnosomatous Pteropoda, *Quart. Journ. Micr. Sci.*, 1885, vol. xxv. pl. xxxv. figs. 4, 8.

[2] *Ibid.*, pp. 495–500, pl. xxxv. figs. 11–22.

the nervous terminations are pressed closely against each other, whilst in the living animals these groups are spaced as shown in the following figure:—

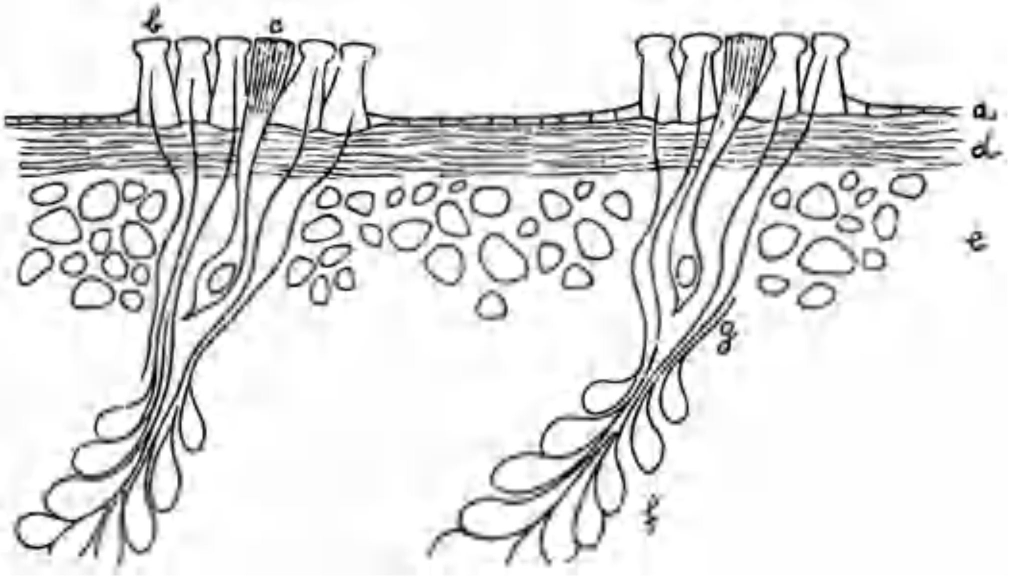

Fig. 1.—Diagrammatic representation of a part of one of the cones of *Clione*. *a*, epithelium; *b*, elongated epithelial cells surrounding the nervous termination (*c*); *d*, longitudinal muscular fibres; *e*, circular muscular fibres; *f*, unicellular glands, the secretion of which (*g*) spreads outwards, through the elevated epithelial cells (*b*).

The secretion of the glands contained in the cones serves to attach the prey of *Clione*, as has been observed by Wagner.[1]

At the base of the buccal cones the digestive tract, that is the anterior portion of the retracted proboscis, is contracted by two symmetrical lip-like pads, which I have called false lips; they close the alimentary canal when the two halves of the cephalic hood are turned back, in order to uncover the buccal cones.

The radula is shaped on the same plan as in the preceding families. There are no jaws. The hook-sacs, which are small in *Clionopsis* as in *Dexiobranchæa*, are here similar to those of *Spongiobranchæa*.[2]

The remainder of the digestive tract (including the accessory glands) is comparable with that of the Pneumonodermatidæ, except that the salivary glands do not exhibit the swelling prior to their termination observed in this latter family. The anus opens in the same place, but not in a cloacal depression common to it and the orifice of the kidney as in the preceding genera.

Several of the visceral openings are very difficult to distinguish from the exterior in *Clione*. Pl. V. fig. 5 shows the various orifices in their relative positions.

In addition to the diaphragm traversed by the œsophagus there is another posterior

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[1] Die Wirbellosen des weissen Meeres, Bd. i. p. 63.

[2] Compare Pl. V. fig. 4, *n*, with fig. 2 on p. 39 of the systematic Report on the Gymnosomata, Zool. Chall. Exp., part lviii.

to the viscera, separating the visceral cavity from a third cavity, which occupies the caudal region.

Gills are entirely absent in *Clione*. According to Wagner the body-wall presents a hollow space in its thickness, in which the venous blood probably becomes oxygenated, and whence it may return into the auricle by an orifice, which would place this latter in communication with the space in question. I have never seen this orifice, but perhaps it is very difficult to discover it in preserved specimens.

The kidney occupies the same position as in the Pneumonodermatidæ and Clionopsidæ, and its relations with the pericardium are similar. Wagner[1] has been unable to find the reno-pericardial orifice, which may, nevertheless, be discovered by examining serial transverse sections of the kidney. The external opening of this organ is near the anus (Pl. V. fig. 5, *f*), but it does not occupy a common depression with the latter.

The Generative Organs are disposed as in the two preceding families, and do not offer special characters.

The Nervous System of *Clione limacina* has been particularly studied by Eschricht,[2] Souleyet,[3] von Jhering,[4] and Wagner.[5] Cuvier's contribution to this particular subject is almost nothing; his figure shows three pairs of ganglia, of which the median (corresponding to the pedal ganglia) are not united by a commissure, whilst the other two pairs (cerebral and visceral) are said to be both united by *subœsophageal* commissures.

Eschricht's description is equally brief, but more correct. His figure is too small, and in some points inexact.

Souleyet's figures are undoubtedly better; unfortunately they have no explanatory letters, and the accompanying text refers only to the cerebral and buccal ganglia.

As to the drawing given by von Jhering, no less than twenty years after that of Souleyet, it is a complete anachronism, being incomplete, inaccurate, and highly diagrammatic.

Lastly, the illustrations published by Wagner are very detailed, but they indicate several arrangements which my researches[6] seem to me to refute.

The general arrangement of the nervous system of *Clione* resembles that of all the preceding genera, the pleural ganglia being paired, in contradiction to what is stated by von Jhering.

The nerves given off by each cerebral ganglion are five in number; three springing from the anterior and two from the dorsal part.

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[1] Die Wirbellosen des weissen Meeres, Bd. i. pl. ix. fig. 2, *x*.

[2] Anatomische untersuchungen über die Clione borealis, p. 6, pl. iii. fig. 28.

[3] Voyage de la Bonite, Zoologie, t. ii. p. 283, pl. xv. bis figs. 16, 17.

[4] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 238, pl. v. fig. 20.

[5] Die Wirbellosen des weissen Meeres, Bd. i. pp. 98–105, pl. xi. fig. 4, pl. xii. fig. 1.

[6] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. pp. 96–101, pl. iv. figs. 1–4.

1. Of the three first named the one nearest the middle line is directed forwards and divides into two principal branches which innervate the dorsal and middle cones.
2. The middle nerve as soon as it issues from the ganglion gives origin to a strong thread passing to the anterior tentacle. Farther on a more slender branch springs from this nerve and gives off two branches, which innervate the lateral parts of the head and the retractor muscles of the buccal cones and of the anterior tentacle.

   The main trunk further gives off a branch distributed to the hood covering the head, to the lips, and finally to the ventral cone; before entering which it exhibits an anastomosis with the nerve to the middle cone.

   Von Jhering describes the nerves of the buccal cones as having each a ganglion united by commissure with the nerves of the two neighbouring cones; that is to say, they have a disposition identical with that observed in the brachial nerves of the Cephalopoda. This is, however, quite erroneous; not one of the nerves to the cones presents a ganglion on its course. As for the "commissures" said to exist between these ganglia, I have never been able to observe anything more than the anastomosis indicated above between the ventral and middle cones; this is oblique and has none of the characters of a regular commissure.
3. The lateral nerve, more slender than the preceding, passes round the buccal mass, and innervates the false lips, a pair of swollen pads situated at the base of the buccal cones.

4 and 5. The two nerves which arise from the dorsal surface of the cerebral ganglion and pass to the posterior tentacle, behave like the corresponding nerves of other Gymnosomata; that is, they are optic and olfactory nerves, each ending in an enlargement.

   Wagner[1] regards the terminal enlargement of the optic nerve as the olfactory ganglion. Now the constitution of the swelling at the end of the other nerve shows that it is the olfactory ganglion or rhinophore; in fact it gives rise to a rather large number of small nerves which become lost in the extremity of the nuchal tentacle; this is well known to be a character of the olfactory ganglion of the Gastropoda. On the other hand, the other swelling is comparable with the corresponding enlargement in the other Gymnosomata, in which, especially in *Pneumonoderma*, may be recognised the component parts of a rudimentary eye.[2]

The pedal ganglia are constituted as in the preceding Gymnosomata. Their second

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[1] Die Wirbellosen des weissen Meeres, Bd. i. pl. xii. fig. 9, gn.e

[2] Pelseneer, The Cephalic Appendages of the Gymnosomatous Pteropoda, *Quart. Journ. Micr. Sci.*, 1885, pp. 494, 496.

anterior commissure arises at the base of the median nerve of the foot. The cervical plexus formed by the anastomosis of the cervical nerve and the nerve from the pleural ganglion agrees with that of the preceding genera. The pleural ganglia are paired as in all Gymnosomata.

The visceral ganglia resemble those of all the other genera hitherto studied, being characterised by the asymmetry of their nerves.

Eschricht and von Jhering have represented these nerves as symmetrical, and Wagner has figured[1] one of them as taking origin between the two ganglia, which is quite contrary to fact.

As a matter of fact, and as Souleyet alone has accurately depicted, though without description, only one nerve springs from the right ganglion, whilst three nerves issue from the left,—a lateral one, corresponding to the nerve from the right ganglion, and two others almost median.

According to Wagner[2] the lateral nerve of the left ganglion *sometimes arises from the pedal ganglion!* I have never observed such an arrangement in any one of the numerous specimens of *Clione* which I have dissected, and it seems to me almost impossible.

The nerve from the right ganglion behaves like the corresponding nerve in other Gymnosomata. One of its branches supplies the osphradium, situated between the anus and the genital aperture (Pl. V. fig. 9). The osphradium is circular in form and its structure recalls the corresponding organ of the Thecosomata, for it is formed of a mass of ganglionic cells, covered by columnar ciliated epithelium (Pl. V. fig. 7).

The buccal ganglia do not present any characters different from those of other genera; the cerebro-buccal connective always arises from the œsophageal face of the cerebral ganglia, and never, as in von Jhering's figure,[3] from their anterior border by a trunk common to the cerebral nerves.

Family IV. HALOPSYCHIDÆ.

The specimens which I had the opportunity of studying were not in a condition favourable to delicate anatomical investigation. The alcohol had not penetrated well through the thick envelop of the body, so that the viscera were badly preserved.

Hence, as regards a large portion of the visceral anatomy, I have only been able to control and confirm the greater part of the brief description of Souleyet, and to rectify some of his statements which were incorrect.

The Head is cylindrical and very small in proportion to the body of the animal. In

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[1] Die Wirbellosen des weissen Meeres, Bd. i. pl. xii. figs. 1, 12.

[2] *Ibid.*, p. 100, pl. xi. figs. 4, 11.

[3] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, pl. v. fig. 20, 1.

my systematic Report on the Gymnosomata, I have stated[1] how in *Halopsyche* the absence of a cephalic hood, shaped like that of *Clione*, is due to the great development of the buccal appendages; and how, in consequence of this, the buccal opening of *Halopsyche* corresponds with the false lips of the latter genus and the anterior tentacles are situated upon a common base with the buccal appendages. As regards the posterior tentacles, I may refer to the same work.

I have also, in that part of my Report, described the form of the foot, which exhibits the same parts as the corresponding organ in other Gymnosomata. Its two antero-lateral symmetrical lobes, situated ventrally to the mouth, were regarded by Souleyet,[2] Owen,[3] and others as tentacles. But since they are innervated by the pedal ganglia, they clearly belong to the foot, as Huxley[4] was the first to point out.

The envelop of the body presents a thickening which has neither the same structure nor the same morphological value as that which is known as the "cartilaginous shell" in the Cymbuliidæ, since it is situated in the visceral sac and not in the mantle, which is entirely wanting in *Halopsyche* as in all the Gymnosomata. From this point of view, therefore, as from any other, there is nothing to justify an approximation of Halopsychidæ to the Cymbuliidæ.

The Digestive Tract.—The absence of the proboscis is explained by the great development of the buccal appendages in the same way as the contrary fact is explained in *Clionopsis*. The mouth opening leads then directly into the buccal mass, which is constructed on the same plan as in other Gymnosomata, except as regards the hook-sacs, whose absence is due to the lack of the proboscis.

The salivary glands, somewhat elongated, appear in transverse sections of the head. The stomach resembles in form that of all the Gymnosomata, and has no masticatory organs whatever, a fact which shows clearly that *Halopsyche* has no relation with the Thecosomata. The intestine is a little longer than in the preceding genera, but ends on the right side[5] in the same position as in them.

The Respiratory and Circulatory Organs.—Souleyet regarded the buccal appendages as two gills, but as a matter of fact, branchiæ are entirely wanting in *Halopsyche* as in *Clione*. I suppose that respiration must be brought as in *Clione* according to Wagner, for the structure of the body wall, as seen in transverse sections, is the same as he represents in the case of *Clione*.[6]

The heart, according to Souleyet,[7] is situated in the middle line, at the base of the cephalic appendages, which he regarded as gills. Nothing of the kind is the case. On

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[1] Zool. Chall. Exp., part lxv. p. 63.

[2] Voyage de la Bonite, Zoologie, t. ii. p. 243, pl. xv. fig. 3, *t*.

[3] Mollusca, Encyclopædia Britannica, 9th ed., vol. xv. p. 381, fig. 40, *d*.

[4] On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 41, pl. iv. fig. 3, *m*.

[5] Not on the left side, as said by Huxley, *loc. cit.*, p. 41.

[6] Die Wirbellosen des weissen Meeres, Bd. i. pl. x. fig. 3.

[7] Voyage de la Bonite, Zoologie, t. ii. p. 247.

the right side, a little further forward than in the Pneumonodermatidæ, are certain very delicate organs (which I was not able completely to isolate in the badly preserved specimens examined) which I regard as the heart and kidney.

The Generative Organs.—These resemble those of all the other Gymnosomata, the genital gland and duct being disposed in the same fashion. The hard body situated on the right of the visceral mass, whose relations Souleyet was not able to make out, is nothing else than the muciparous-gland, which, as in some other Mollusca, becomes strongly hardened by alcohol. The receptaculum seminis is like that of other genera.

The genital aperture, as may be demonstrated by transverse sections, is situated in the usual position, behind the base of the right fin, and not as represented by Souleyet,[1] who probably mistook the opening of the penis for it. This latter opens at the base of the right lateral lobe of the foot, and for the rest does not differ from that of other Gymnosomata.

The Nervous System of *Halopsyche* is very difficult to study by dissection. The ganglia are so exceedingly small (the length of the whole animal being scarcely more than 4 mm.), that they are crushed by the points of the finest needles, and can only be properly distinguished by the aid of compound lenses of short focus.

Further, of the three zoologists who have treated of the organisation of *Halopsyche*,[2] two have not mentioned the nervous system. Souleyet is the only one who has described and figured it, and even he does so inaccurately, his representation being defective—

1. In the number of commissures (he shows only the pedal commissure);
2. In the number of ganglia (he records eight, whilst in reality there are only seven).

The arrangement of this nervous system, like the rest of the organisation, supports the view that the genus *Halopsyche* belongs to the Gymnosomata, for it is constructed on a plan very different from that of the Thecosomata, whilst it agrees in its general disposition with that of the Gymnosomata.

The cerebral ganglia, instead of being placed at the sides of the œsophagus and connected by a long supraœsophageal commissure, as in the Thecosomata (Pl. I. fig. 7; Pl. II. fig. 10; Pl. III. fig. 11), are approximated to each other and situated above the œsophagus (Pl. V. figs. 9, 10, 11, *a*).

Each of them gives origin to two principal nerves:—

1. A lateral nerve (Pl. V. fig. 10, *f*), soon swelling into an elongated ganglion, which occupies the nuchal tentacle. The optic and olfactory nerves of the preceding Gymnosomata are not then to be distinguished in the present instance, a fact which is due to the atrophy of the eye.

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[1] Voyage de la Bonite, Zoologie, Mollusques, pl. xv. fig. 3, *a'*.

[2] Huxley (On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 40); Macdonald (On the Anatomy of Eurybia gaudichaudi, *Trans. Linn. Soc. Lond.*, vol. xxii. p. 245); Souleyet (Voyage de la Bonite, Zoologie, t. ii, p. 250). Von Ihering (Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 242) only republishes, in a few lines, the data of Souleyet, including the inaccuracies.

2. A median nerve (*e*) innervating the buccal appendage (which Souleyet regarded as a gill, and to which he attributed a visceral innervation[1]) and the anterior tentacle.[2]

Each cerebral ganglion is connected to two infraœsophageal ganglia. The more anterior of the two is united with it by a rather short connective, which is easily distinguished by its transparence from the opaque white ganglia; the posterior ganglion is almost in contact with the cerebral ganglion.

The anterior subœsophageal ganglion (Pl. V. fig. 10, *b*) is the pedal ganglion. It is connected with its fellow by a commissure as short as that which connects the cerebral ganglia. In addition to this principal commissure, which does not appear in Souleyet's figure, there is a second very slender one (Pl. V. figs. 8, 9, *f*) analogous to the second pedal commissure observed in the preceding families.

Each pedal ganglion gives origin to three nerves (Pl. V. fig. 8, *l*, *m*), which supply the foot and the fins. On the posterior margin of the pedal ganglia are situated the otocysts (*i*).

The smaller of the two subœsophageal ganglia (*c*) which are connected to either cerebral ganglia is connected posteriorly with a large azygous median subœsophageal ganglion. It follows hence that this little ganglion must be either the pleural ganglion or perhaps a ganglion of the visceral commissure.[3]

It cannot, however, be the pleural ganglion, for the pedal ganglion of the same side is not united to it by a connective; on the contrary it is quite separated from it (see Pl. V. figs. 8, 10); it is, therefore, a ganglion of the visceral commissure, as is shown also by the nerves which arise from it and innervate the visceral envelope.

The azygous median ganglion (*d*) is elongated transversely and is larger than the two lateral ganglia (*c* and *e*). The two nerves which spring from it supply the viscera.

The buccal ganglia (Pl. V. fig. 9, *c*), which were not observed by Souleyet, are situated under the œsophagus. The cerebro-buccal connective (*e*) is rather strong, and arises from the posterior margin of the cerebral ganglion on its œsophageal surface. The two buccal ganglia are close together, and situated between the œsophagus and the pedal ganglia.

The arrangement of the nervous system of *Halopsyche*, as I have described and figured it, differs in some particulars from Souleyet's account, especially as regards the constitution of the visceral commissure.

In his description Souleyet supplied "par l'analogie" those details which he could

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[1] Voyage de la Bonite, Zoologie, t. ii. p. 260.

[2] Compare the disposition of the buccal appendage and the anterior tentacle in the systematic Report on the Gymnosomata, Zool. Chall. Exp., part lviii. p. 53, fig. 4.

[3] I differ from Lacaze Duthiers in not regarding the pleural ganglia as a part of the visceral commissure. The distinctive character of the components of this commissure in the asymmetrical Mollusca is that they are devoid of symmetry, that is to say, they are individually unpaired even when the visceral commissure is paired as regards the number of its ganglia, or they are asymmetrical even when they are in pairs. The pleural ganglia, on the other hand, are always in pairs and equal to each other.

not clearly make out;[1] hence he mistook the smallest of the ganglia connected with the cerebral for the homologue of the pleural ganglion of other Gymnosomata, and figured it as connected with the pedal ganglion; in the same way he indicates two large ganglia between these two small ganglia, and at their left side he makes three nerves proceed from them as in *Pneumonoderma* and *Clione*. Nothing of the kind, however, exists in *Halopsyche*.

My drawings were made after the examination of a large number of specimens, and in order to control my dissections I made a series of transverse sections of the central nervous system. The sections, which pass through the visceral ganglia (Pl. V. fig. 11), show beyond all doubt that these are three in number (*b*, *c*, *d*).

SUMMARY ON THE GYMNOSOMATA.

The Gymnosomata possess two pairs of cephalic tentacles—the anterior or labial and the posterior or nuchal, to which the optic and olfactory nerves are distributed.

The fins, or lateral margins of the foot, are separated from its middle portion (ambulatory sole), and do not enclose the cephalic region.

The mantle is entirely wanting, and consequently the shell and pallial cavity.

The anterior part of the digestive tract is evaginable (except in *Halopsyche*) in such a way as to produce a proboscis of the acrembolic type. The outer part (in evagination) is tegumentary in origin; it extends as far as the jaws, radula, and hook-sacs, which mark the commencement of the digestive tract. At the anterior part of this proboscis (except in *Clionopsis*) there are buccal appendages, which are innervated by the cerebral ganglia, and carry suckers or sensory and secretory organs. On the wall of the proboscis two longer or shorter evaginable sacs are developed, the surface of which bears horny hooks. These organs were taken for jaws by Eschricht, and by Lankester for an appendage of the "fore foot." Krohn showed by a study of their development that they are evaginations of the œsophageal wall.[2]

The jaws (except in *Clione*, where they are wanting) are united ventrally in the middle line.

The salivary glands are long, with no distinction between the duct and the gland.

The stomach is an entirely unarmed digestive sac, and is entirely surrounded by the acini of the liver, which open into it by numerous apertures.

The intestine is short, as in all carnivorous animals, and has a straight course from the stomach to the anus; it opens to the right and dorsally with respect to the foot.

The penis is situated anteriorly, and issues at the right side of the foot.

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[1] Voyage de la Bonite, Zoologie, t. ii. p. 281.

[2] Beiträge zur Entwickelungsgeschichte der Pteropoden und Heteropoden, p. 7.

The central nervous system is formed of eight ganglia, except in *Halopsyche*, where there are only seven. The cerebral ganglia are closely approximated to each other, and are the only supraœsophageal ones; I lay stress on this point, because so recently as 1877 Garner has stated[1] that *Clione* possesses six ganglia, of which, in contradistinction to the arrangement in *Pneumonoderma*, four are *above* the œsophagus. The pleural ganglia, distinct from the cerebral, are close to the pedal.

III. SUMMARY ON THE PTEROPODA.

In the Pteropoda the lateral portions of the foot are all modified into fins. The jaws are lateral and paired. There are salivary glands. The stomach has "horny" plates in the adult condition, or only during the larval stages (Gymnosomata). The radula has in the same transverse row lateral teeth, which resemble each other in form, differing only in size.

The flexure of the intestine is not neural, but resembles that of the Gastropods, which is improperly called dorsal, and would be more correctly termed lateral.

The heart is lateral and the excretory organ azygous. The pericardium is isolated from the circulation. This is a statement of importance, because even in 1882 Claus[2] stated that water enters the circulatory system by the kidney and pericardium; and because this same author states that in the Pteropoda the blood goes from the respiratory organs to the heart by way of the pericardial "sinus," even though so long since as 1857 Herman Müller showed the absence of corpuscles in the fluid of the pericardium.

The hermaphrodite genital gland has a single efferent duct and a single common genital aperture, from which a seminal groove leads to the copulatory organ, situated in the cephalic region.

The nervous system is characterised by the asymmetry of the visceral portion. The pedal ganglia have a double commissure.

The Pteropoda are thus essentially characterised by the asymmetry of their internal organisation, combined with the symmetry of their external form.

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[1] Malacological Notes, *Ann. and Mag. Nat. Hist.*, ser. 4, vol. xix. pp. 372, 373.

[2] Grundzüge der Zoologie, t. ii. p. 31, 1882.

II. AFFINITIES AND PHYLOGENETIC RELATIONSHIPS OF THE PTEROPODA.

I. HISTORICAL.

Although the Pteropoda have been known for a considerable period,[1] it is only during the present century that their systematic position has been seriously studied.

The opinions on this head may be divided into two principal groups :—

1. The Pteropoda form a distinct class among the Mollusca, of the same value as the Cephalopoda, Gastropoda, Scaphopoda, and Pelecypoda.

2. They may be placed within one of two out of these four classes of Mollusca (Cephalopoda or Gastropoda).

1. Since the time of Cuvier,[2] who established the "classe des Ptéropodes," the former view has always been the more in credit, and it is still the most widely spread at the present day. Indeed, we find it adopted in the general text-books of zoology which now serve for the elementary education of naturalists, thanks to the numerous translations which have been made.[3]

Further, the "class" Pteropoda is generally placed, in the systematic arrangement, beside the Cephalopoda, and stress is generally laid upon the affinity which these two groups bear to each other; and when it happens that the author who emphasises these "affinities" has himself studied the Pteropoda (as in the case of Gegenbaur), the opinion acquires by this means additional weight.

The view, then, that the Pteropods and Cephalopods are intimately related is a very deep-rooted one, and there is scarcely a general zoological text-book or a special treatise on the Mollusca in which it is not stated.

Von Jhering, who was formerly an active supporter of this theory,[4] has since abandoned it,[5] but he still considers the Pteropoda as constituting a distinct class.[6]

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[1] So early as 1676 Martens described and figured a Pteropod which was no other than *Clione limacina* (Spitzbergische oder grönlandische Reisebeschreibung, p. 169, pl. P, fig. *f*).

[2] Mémoire sur l'Hyale et le Pneumoderme, *Ann. Mus. Hist. Nat. Paris*, t. iv. p. 232.

[3] Huxley, A Manual of the Anatomy of Invertebrated Animals, 1877, p. 434; Gegenbaur, Grundriss der vergleichenden Anatomie, 2 ed., 1878, p. 335; Claus, Grundzüge der Zoologie, 4 ed., 1882, t. ii. p. 66.

[4] Vergleichende anatomie des Nervensystemes und Phylogenie der Mollusken, p. 278, &c., 1876.

[5] Ueber die Verwandtschaftsbeziehungen der Cephalopoden, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. p. 4, 1880.

[6] Gibt es Orthoneuren?, *Zeitschr. f. wiss. Zool.*, Bd. xlv. p. 525, 1887.

2A. But it is in the second group of interpretations of the systematic position of the Pteropoda—that is to say, among those which place them along with some other Molluscan class—that we find the idea of their connection with the Cephalopoda carried to the furthest extreme. This view consists in regarding the Pteropoda as Cephalopoda, and in simply ranking them within this group. It was long since defended by Oken[1] and by Eschscholtz.[2] More recently it has been adopted by Ray Lankester.[3]

2B. We now come to the third hypothesis, according to which the Pteropoda should be placed among the Gastropoda.

In this connection it is interesting to point out that Cuvier, who established the "class" Pteropoda, remarked in his memoir on *Clio borealis*[4] that this animal exhibits "aucun des caractères des Céphalopodes," but that on the contrary it "offre beaucoup de rapports avec les Gastéropodes." In 1800, in his Leçons d'anatomie comparée, he even placed *Clio* (= *Clione*) among the Gastropoda, which, however, did not prevent him four years later from creating a distinct class for the Pteropoda.

It must be noted, however, that certain important points in the morphology of the Pteropoda were incompletely understood by Cuvier; thus he misunderstood the foot (that is the median part of the foot) of the Gymnosomata. This organ was comprehended only by de Blainville, who with remarkable insight affirmed that the relations of the Pteropoda were with the Opisthobranchia ("Bulléens"), at the same time reducing the group Pteropoda to its proper rank, and abstracting from it the foreign forms (Heteropoda, Nudibranchia, Cœlenterata) which had been introduced by Péron and Lesueur, with the exception of *Phylliroë*.[5]

I must admit, however, that the two hypotheses which I have placed in the second main group have not had very favourable receptions. I have already stated that Oken's interpretation, that the Pteropoda are Cephalopoda, is only defended at the present day by Ray Lankester. De Blainville's interpretation, that the Pteropods are Gastropods nearly related to the Bulloidea, which was so ably defended by the lamented Souleyet,[6] who died in 1852, has also fallen into oblivion.

Spengel, however, in his study of the nervous system of the Mollusca, places the Pteropoda among the Euthyneurous Gastropoda, as a group of the same rank as the Opisthobranchia and Pulmonata,[7] though still with a certain amount of reservation.[8]

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[1] Lehrbuch der Zoologie.

[2] Zoologischer Atlas.

[3] Mollusca, Encyclopædia Britannica, 9th ed., vol. xvi.

[4] *Ann. Mus. Hist. Nat. Paris*, 1802.

[5] It was Souleyet and not Leuckart who first recognised the true affinities of *Phylliroe*. His work dates from 1846 (*Comptes rendus*, t. xxii. p. 473), whilst that of Leuckart was only published in 1851 (*Archiv f. Naturgesch.*, Jahrg. xvii. p. 139).

[6] Voyage de la Bonite, Zoologie, t. ii., 1852.

[7] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. p. 373.

[8] *Ibid.*, p. 381.

Grobben[1] also affirms that the Pteropoda ought to be included in the class Gastropoda, but without deciding to which group they are related.

In 1885 I pointed out, when treating of the cephalic appendages, that the affinities of the Pteropoda are with the Euthyneura (Pulmonata and Opisthobranchia),[2] and since then I have defended their precise affinities with the Opisthobranchia,[3] and especially with the Tectibranchia.[4]

Lastly, Boas, in the morphological introduction to a work systematic in the main,[5] has followed out rigorously the view of de Blainville, and it is to be regretted that this part was not more extensive, and that he did not give at full length a demonstration of the affinities of the Pteropoda with the Tectibranchiate Opisthobranchs, and of the genealogical relations of the two groups.

There are no other instances of avowed adhesion to this view. The "class" Pteropoda still keeps its position everywhere; and its so-called affinities with the Cephalopoda are maintained by the powerful support of timid souls, who not being able to make up their minds to modify the Cuvierian system, and having really no opinion of their own, retain the generally received ideas as a matter of prudence.

From this rapid historical sketch, it appears that there are three different theories regarding the systematic position of the Pteropoda.

1. They form a distinct class.
2. They are Cephalopods.
3. They are Gastropods.

We must therefore attempt to answer the following questions:—

1. Are the Pteropods Cephalopods?
2. Are the Pteropods Gastropods?

If we obtain a negative answer to these two questions, then we must clearly retain the Pteropoda as a distinct class, but if either of them be answered in the affirmative, the "class" Pteropoda must be abandoned.

In order to answer the two questions we shall compare the Pteropods successively with the Cephalopoda and the Gastropoda, on the basis of those anatomical characters which are common to the Thecosomata and Gymnosomata.

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[1] Morphologische Studien über den Harn- und Geschlechtsapparat sowie die Leibeshöhle der Cephalopoden, *Arb. Zool. Inst. Wien*, Bd. v. p. 245.

[2] On the Cephalic Appendages of the Gymnosomatous Pteropoda, *Quart. Journ. Micr. Sci.*, vol. xxv., N. S., p. 506.

[3] Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 197.

[4] Description d'un nouveau genre de Ptéropode Gymnosome, *Bull. Sci. Dép. Nord*, 1886, p. 226.

[5] Spolia atlantica, &c., *K. dansk. Vidensk. Selsk. Skriv.*, 6 Raekke, Bd. iv. p. 19.

II. ARE THE PTEROPODA CEPHALOPODA?

In the organisation of the Pteropoda certain points may be seen which indicate a resemblance to the Cephalopoda.

1. The ventral position of the pallial cavity of *certain* Thecosomata (Cavoliniidæ and Cymbuliidæ).

2. The "ventral" flexure of the alimentary canal in the same groups.

3. The presence of acetabuliferous appendages in some Gymnosomata (Pneumonodermatidæ).

It is impossible, however, to show, as Hyatt[1] maintains, that "the general aspect, the arrangement and position of the oral region, and *the disposition of the internal organisation* are similar in both" (Pteropods and Cephalopods). This is, indeed, a heresy, and one must never have dissected a Pteropod to be able to make such an assertion.

It has been said that there are three points in which resemblance may be traced between the Cephalopoda and Pteropoda. We shall soon see how much foundation these resemblances have; but in the meantime it may be remarked that in *not a single point of their organisation* can a true resemblance be found which would justify the assertions which have been made regarding the affinities of the two groups, nor even explain the position which has been assigned to the Pteropods in the neighbourhood of the Cephalopods.

A. *The digestive tract* and its appendages may be first examined:—

- *a. Retractile Proboscis.*—This organ, so well developed in the Gymnosomata, does not exist in the Cephalopoda.
- *b. Radula.*—Woodward,[2] speaking of the Cephalopoda, remarks—"The odontophore somewhat resembles that of the Pteropods"—a statement which, though quite incorrect, has been copied into other text-books of Conchology.

  As a matter of fact this radula of the Cephalopoda is characterised by its uniformity; it always has the formula 3–1–3, or more accurately 1–2–1–2–1, that is to say, there is a central tooth, and, on either side, two lateral teeth and a marginal tooth; this last differs from the two lateral teeth by its general form and by its narrower basilar piece. The only exceptions known to this formula, 3–1–3, are *Gonatus* (belonging to the family Onychii) and *Nautilus*. The former has no

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[1] On the parallelism between the individual and orders in Tetrabranchiate Cephalopoda, *Mem. Boston Soc. Nat. Hist.*, vol. i. pt. ii. p. 203.

[2] A Manual of the Mollusca, p. 448, 1866.

marginal teeth, and, according to Sars,[1] its formula is 2–1–2; whilst in *Nautilus*, according to Keferstein,[2] there are two marginal teeth on each side, so that the radular formula is 2–2–1–2–2.

In the Pteropoda, on the other hand, the radula varies within wide limits (the extreme formulæ being 1–1–1 and 17–1–17), and besides is characterised by the uniformity of all the lateral teeth, which differ only in their respective dimensions, their form not distinguishing, among them, so-called marginal teeth.

c. *Mandibles.*—In all the Cephalopoda these are dorsal and ventral; in the Pteropoda, on the other hand, they are lateral, sometimes situated ventrally side by side (Gymnosomata).

d. *Salivary Glands.*—In the Cephalopoda there are generally two pairs of these, which consist of two distinct portions, viz., the distended glandular mass and the narrow excretory duct. In the Pteropoda there is never more than one pair of salivary glands, which vary in length and do not exhibit any distinction between duct and gland.

e. *Œsophagus.*—A crop is present in the Cephalopoda but not in the Pteropoda.

f. *Stomach.*—This organ in the Cephalopoda never possesses any masticatory plates, even in the embryonic condition; on the contrary, the Thecosomatous Pteropoda have them always, and according to Krohn[3] the Gymnosomata have them during their larval development. The Cephalopoda have a gastric cæcum into which the ducts of the liver open; upon these latter is situated the gland commonly known as a "pancreas." The Pteropoda have neither such a cæcum nor "pancreas."

g. *Intestine.*—In the Cephalopoda this organ terminates in the middle line, whilst in the coiled Thecosomata (Limacinidæ) and in the Gymnosomata it ends on the right side (in the Gymnosomata it appears to be ventral in consequence of the reduction of the pedal face; in reality it would be quite lateral if this last were of larger size); in the straight Thecosomata (Cavoliniidæ and Cymbuliidæ) it terminates on the left side, in consequence of the rotation which was explained at the end of the first part of this anatomical Report.

B. If we consider the *organs of circulation*, *respiration*, and *excretion*, we see that in the Pteropoda the heart is asymmetrical, as is also the gill when it exists, whilst in the Cephalopoda these organs (heart and gills) are quite symmetrical. In the same manner

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[1] Mollusca regionis arcticæ Norvegiæ, pl. xvii. fig. 2; see also Steenstrup, *Oversigt k. Dansk. Vid. Selsk. Forhandl.*, 1880, p. 10.

[2] Die Klassen und Ordnungen des Thierreichs, Bd. iii. pl. cxv. figs. 2, 3.

[3] Beiträge zur Entwickelungsgeschichte der Pteropoden und Heteropoden, pp. 8, 14.

the kidney of the Pteropoda is azygous and asymmetrical, whilst in the Cephalopoda there are two (four in *Nautilus*) symmetrical kidneys, isolated or in communication.

C. As regards the *genital organs*, we may first remark that the Cephalopods are diœcious, whilst the Pteropods are hermaphrodite.

The genital ducts differ very widely in the two groups—in the Cephalopoda the genital gland is isolated in a kind of cœlomic space, and has no direct continuity with the genital duct, which is only continuous with the wall of the cavity just mentioned. In the Pteropoda, on the contrary, the genital duct is continuous with the envelope of the gland, and, further, these animals have only a single asymmetrical genital duct, whilst in the Cephalopoda there are numerous indications of paired symmetrical ducts—in *Nautilus* in both sexes,[1] in the females of the Octopoda and of *Ommatostrephes*; and finally in *Rossia* and *Spirula*, the oviduct is on the right (as is the functional oviduct in *Nautilus*), whilst in the other Decapoda it is on the left, which proves that originally it was bilaterally symmetrical.

Lastly, the copulatory organ of the Pteropoda is situated on the head, far from the genital aperture, and is not morphologically comparable with the penis of the Cephalopoda.

D. *Nervous System.*—The nervous system of the Pteropoda differs from that of the Cephalopoda mainly in the absence of symmetry in the visceral portion. When there is an apparent symmetry in the disposition of the ganglionic visceral nervous elements, there is real asymmetry in the origin of the nerves. Furthermore, there is in the Cephalopoda a concentration of the central nervous system, so great that the commissures and connectives have almost disappeared; and there exists in all these animals a pair of "brachial" ganglia which are entirely wanting in the Pteropoda. As regards the nervous system, as in other groups there is no indication of direct relation between the Pteropods and Cephalopods.

The osphradium (Spengel's olfactory organ) is paired in those Cephalopoda which possess it;[2] it is unpaired in the Pteropoda.

The otocysts of the Cephalopoda (except *Nautilus*) enclose a single otolith; in all the Pteropoda there are many otoliths.

E. The Cephalopoda have two symmetrical columellar muscles (formed by the union of the retractor capitis and retractor pedis of either side), whilst the Pteropoda have only a single median columellar muscle.

F. *Ontogeny.*—If after examining the adult animal we consider its ontogenetic development comparatively in the two groups, we find constant and clear differences. The segmentation of the ovum, which is complete in the Pteropoda, is only partial in the Cephalopoda. In the original development of the Pteropoda there is observed at the commencement the primitive symmetry of all Mollusca, but during the whole larval

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[1] Ray Lankester and Bourne, On the Existence of Spengel's Olfactory Organ and of Paired Genital Ducts in the Pearly Nautilus, *Quart. Journ. Micr. Sci.*, vol. xxiii., N. S., p. 346.

[2] *Ibid.*, p. 340; see also Zernoff, Ueber das Geruchsorgan der Cephalopoden, *Bull. Soc. Nat. Moscou*, 1869, p. 71, pls. i., ii.

life the complete asymmetry is very distinct; and if in the adult we have an apparent external symmetry, there is a real internal asymmetry. And, on the contrary, in the Cephalopoda the complete primordial symmetry never disappears for a moment from the youngest embryonic stage to the perfect adult state.

It is not, however, only in the above facts (anatomical and embryological) that we fail to find traces of affinities between the two groups. Even in the three points already mentioned, as indicating resemblances between them, we shall show that the likenesses are not real but merely superficial.

1 and 2. The flexure of the intestine and the position of the pallial cavity certainly constitute one of the most important and most often quoted arguments in favour of the relation between the Pteropoda and Cephalopoda.[1] It is asserted that the flexure is "neural" in the Cavoliniidæ and in the Cymbuliidæ, and that the anus opens in them, as in the Cephalopoda, into a ventral pallial cavity.

The form of the argument is perfectly fair, but yet the conclusion is entirely false, because of the inaccuracy of the premises. The flexure of the intestines and the position of the pallial cavity in the straight Thecosomata, though apparently similar to those of the Cephalopoda, are really due to quite a different process, and that which is primitive in the Cephalopoda is secondary in the Pteropoda, as Grobben[2] perceived, so that the two are not strictly comparable.

The fact is, that a truly primitive neural flexure of the intestine and a primitive ventral pallial cavity only exist in the three classes—Cephalopoda, Scaphopoda, and Pelecypoda. This flexure is brought about by a displacement (considerable in the Cephalopoda and Scaphopoda) of the posterior part of the body—a displacement resulting, in its turn, from a partial rotation in the neural direction about a transverse axis.

As regards a hæmal flexure, it may be said with truth not to exist. In the Gastropods, where the pallial cavity is dorsal, the flexure of the intestine is always *lateral*, in consequence of a movement of rotation (quite different from that observed in the Cephalopoda) of the posterior part about a short dorso-pedal axis, which has been especially studied by Spengel.[3] Further, the terminal branch of the digestive tract may end either above the œsophagus (as in many Gastropods), which gives the appearance of a hæmal flexure, or on the same level with it (as in a good many Opisthobranchs), or even below the œsophagus, which would bring about almost a neural, but still always lateral, flexure.

As regards the Pteropoda, they have the same lateral flexure of the intestine as the Gastropods, the anus opening on the right, below the œsophagus in the Gymnosomata, in consequence of the reduction of the pedal surface, and about on the same level with it, or

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[1] Huxley, On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 44; Gegenbaur, Grundriss der vergleichenden Anatomie, p. 378, fig. 190, 1878.

[2] Morphologische studien, &c., *Arb. Zool. Inst. Wien*, Bd. v. p. 241.

[3] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv.

a little above in the Limacinidæ. Even if the flexure appear neural in the straight Thecosomes (the figure of *Creseis* given by Gegenbaur[1] is inaccurate in this particular), it is always in reality lateral, since the anus opens to the left; and we have seen that this difference from the Limacinidæ has been caused by the process of rotation already explained, and that among the Thecosomata the primitive form is the *lateral* flexure found in the Limacinidæ, as also in the Gymnosomata, and differing in both from the true neural median flexure of the Cephalopoda.

In the same way, as regards the pallial cavity of the Thecosomata, it has been shown that the primitive form is the dorsal cavity of the coiled Thecosomata, and that the ventral position of the pallial cavity in the straight forms is due to a process quite different from that which has brought about the analogous situation in the Cephalopoda, and hence that the two arrangements are not at all comparable.

Consequently there is no proof to be found here of any connection between the Cephalopods and the Pteropods.

3. The majority of authors have traced a homology between the buccal appendages of the Gymnosomata and the arms of the Cephalopoda. I may specially mention R. Leuckart,[2] Lovén,[3] von Jhering,[4] Gegenbaur,[5] Grenacher,[6] Brooks,[7] Ray Lankester,[8] and Grobben.[9] Huxley alone,[10] even when declaring himself in favour of this interpretation, has maintained a certain reservation regarding the innervation of the appendages of the Gymnosomata.

If, however, these authors agree as to the homology of these two sets of organs, they differ entirely regarding their morphological value.

Huxley[11] and Ray Lankester[12] consider them to belong to the foot, whilst, on the other hand, von Jhering[13] and Grobben,[14] &c., regard them as cephalic organs.

Now, I have shown from their innervation that the appendages of the Gymnosomata are cephalic in their nature.

What, then, is the morphological value of the arms of the Cephalopoda? This question, which has been so often discussed, is of great importance. Indeed, it is upon the pretended homology between the appendages of the Gymnosomata and the arms of

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[1] Untersuchungen über Pteropoden und Heteropoden, pl. ii. fig. 1, g.

[2] Ueber die Morphologie und die Verwandtschaftsverhältnisse der wirbellosen Thiere.

[3] Bidrag til Kännedom om utveckling af Mollusca Acephala Lamellibranchiata, *K. Svensk. Vetensk. Akad. Handl.*, 1848.

[4] Vergleichende anatomie des Nervensystemes und Phylogenie der Mollusken.

[5] Grundriss der vergleichenden Anatomie.

[6] Zur Entwickelungsgeschichte der Cephalopoden, *Zeitschr. f. wiss. Zool.*, Bd. xxiv.

[7] Development of the Squid, Loligo Pealii, *Anniv. Mem. Boston Soc. Nat. Hist.*, 1880.

[8] Mollusca, Encyclopædia Britannica, 9th ed. vol. xvi.

[9] Zur Kenntniss der Morphologie und der Verwandtschaftsverhältnisse der Cephalopoden, *Arb. Zool. Inst. Wien*, t. vii.

[10] On the Morphology of the Cephalous Mollusca, *Phil. Trans.*, 1853, p. 40.

[11] *Loc. cit.* pl. v. fig. 5.

[12] Mollusca, Encyclopædia Britannica, 9th ed. vol. xvi. p. 664.

[13] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 269.

[14] Zur Kenntniss der Morphologie und der Verwandtschaftsverhältnisse der Cephalopoden, *Arb. Zool. Inst. Wien*, vii. p. 71.

the Cephalopoda that reliance has generally been placed in classing these two groups near together (Claus, Fischer, &c.), or even including them in the same class (Ray Lankester).

This question of the morphological value of the arms of the Cephalopoda has always been the subject of animated discussion. It may be laid down at the outset that there are two hypotheses to be considered:—

1. The arms are pedal in nature; this is especially the opinion of the English naturalists, Huxley, Ray Lankester, &c.

2. The arms are cephalic in nature; a view maintained particularly by naturalists of the German school (Grenacher, von Jhering, Grobben).

In investigating this disputed point we may adopt the following methods:—(1) comparative anatomy, (2) embryology.

(1) If the arms of the Cephalopoda are, like the appendages of the Gymnosomata, cephalic in origin, their nerve supply ought at once to make this clear to us.

Topographically there is no difference of opinion regarding the part of the nervous system which gives off nerves to the arms of the Cephalopoda; viz., the anterior infraœsophageal or brachial ganglia ("ganglion de la patte d'oie" of Cuvier).

But as regards the morphological value of these ganglia there is the same difference of opinion as regards the arms.

These are pedal ganglia, say the English naturalists.

They are cerebral or cephalic, maintain the Germans.

The solution of the question as to the morphological value of the arms is to be found then by solving this other question:—What is the morphological value of the brachial ganglia of the Cephalopoda?

A few words are necessary here to explain how such differences of opinion can exist regarding an organ whose topographical anatomy is so well known.

The central nervous system of the Cephalopoda is entirely concentrated in the head, around the œsophagus, and resting in the cephalic cartilage in the Dibranchia; a little less protected in the Tetrabranchia.

In spite of the great concentration of the component parts the following separate elements may be recognised externally in this central nervous system:—

1. A supraœsophageal mass.
2. A subœsophageal mass, including:—
    - (i.) An anterior mass.
    - (ii.) A middle mass.
    - (iii.) A posterior mass.

The supraœsophageal mass gives off the optic and olfactory nerves, and innervates the whole cephalic region; there is no disagreement regarding its nature, all recognising in it the fused cerebral ganglia.

The anterior subœsophageal mass gives off the nerves to the arms, and hence has been called "brachial."

The middle subœsophageal mass, from which arise the nerves of the siphon, has been universally regarded as constituted by the pedal ganglia.

Lastly, the posterior subœsophageal mass innervates the mantle and the viscera; hence it corresponds with the combined visceral ganglia of other Mollusca.[1]

The supraœsophageal mass (cerebral ganglia) is united to the infraœsophageal masses by two connectives on either side; the anterior is rather thin and passes to the brachial ganglion; the posterior is very large and thick, and joins the cerebral ganglion to the two posterior infraœsophageal masses, that is the pedal and visceral ganglia.

It has already been stated that all observers are agreed as to the interpretation of the supraœsophageal and the two posterior subœsophageal masses. The disagreement relates only to the brachial ganglia, which are regarded by one party as pedal and by the other as cerebral. We shall now proceed to discuss this point.

Those zoologists who maintain that the brachial ganglia are part of the cerebral ganglia explain their position below the œsophagus by saying that on either side a part of the cerebral ganglia has been displaced from the upper to the lower surface of the œsophagus, still remaining united to the cerebral ganglion, and that these two nervous masses have fused below the œsophagus and formed the brachial ganglia. In this manner the brachial ganglia are cerebral in origin, and the arms which they innervate are similarly cephalic.

Against this interpretation the following arguments may be adduced:—

I. It is eminently unlikely that in order to innervate the crown of arms which surrounds the buccal aperture on *all* sides (*lateral* and *dorsal* as well as ventral) a portion of the cerebral ganglia should have descended on either side to the lower aspect of the œsophagus, and that it should be just this particular part of the cerebral ganglia situated entirely below the œsophagus that innervates the arms situated dorsally to and at either side of the latter.

If the arms were really cephalic in origin, the nervous mass which innervates them would not have descended *entirely* to the lower surface of the digestive tract, and those arms, which are situated above the œsophagus, would surely be supplied directly from the supraœsophageal cerebral mass, even if all were not so innervated as in the case of the six cones of *Clione*.

If the muscular mass of the arms had all been displaced from the upper aspect of the head in order to locate itself entirely below the mouth, then it would be reasonable to suppose that a portion of the cerebral ganglia had followed this movement, and descended on either side of the digestive tract. But nothing of the kind is the case. On the

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[1] See Paul Pelseneer, Recherches sur le système nerveux des Ptéropodes, *Arch. de Biol.*, t. vii. p. 191.

contrary, the dorsal half of the mass of the arms is sometimes more voluminous than the ventral mass (compare, for example, *Nautilus*), but, nevertheless, the nervous centre which innervates the *whole* brachial mass is situated *exclusively on the lower surface* of the œsophagus. This shows clearly that the brachial mass does not originate from the dorsal, but in the ventral parts of the animal (that is from the foot), and that its two halves have been fused above the head; this view is confirmed, as we shall see in the sequel, by the embryology of these organs.

II. Grobben[1] states that the arms of the Cephalopoda were primitively lateral to the mouth, as are the cones of *Clione*. In the latter, however, all the cones, both ventral and dorsal, are innervated by the supraœsophageal ganglia. If, then, the arms of the Cephalopoda and the cones of *Clione* were morphologically homologous, it would be impossible to understand why, the disposition of these organs being similar, the disposition of their innervating organs should be different. But I have shown that the cones of *Clione* and the buccal appendages of the other Gymnosomata are organs formed on the inner wall of the evaginable proboscis, which is made up of the anterior portion of the digestive tract, and whose cephalic nature is therefore indisputable. The relation of the arms of the Cephalopoda to the anterior part of the digestive tract is entirely different.

Supposing, however, that the arms are really cephalic appendages, primitively situated at the sides of the buccal opening, we might compare them with the absolutely identical arrangement which we see in *Ampullaria*. Here we find on either side of the mouth (not more dorsally than ventrally) a large conical appendage, elongated, voluminous, and relatively as large as several arms of a Cephalopod.

How then are these appendages innervated? By the supraœsophageal or *cerebral* ganglia.[2] These appendages probably correspond with the labial palps of certain Pulmonata (*Helix*, *Glandina*, &c.), whilst the appendage situated in front of the eye corresponds with the nuchal tentacle or rhinophore of the *Euthyneura*, inasmuch as it encloses the highly ramified olfactory nerve.[3]

III. In *Vermetus*, on the other hand, we find between the mouth and the foot two long appendages (buccal tentacles of d'Orbigny; tentacular or antibuccal filaments of Quoy and Gaimard), which stand precisely in the same position as the ventral arms of the Cephalopoda, and as far separated from the pedal disc as these arms are from the funnel, upon the pedal origin of which no doubt has ever been thrown.

How then are these appendages innervated? By the anterior subœsophageal or *pedal* ganglia, as has been shown by Lacaze Duthiers,[4] and as I have been able to convince myself in the case of *Vermetus gigas*.

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[1] Zur Kenntniss der Morphologie, &c., *loc. cit.*, pp. 68, 70.

[2] Anatomie von Ampullaria urceus, *Archiv f. Naturgesch.*, Jahrg. xi. p. 200, pl. viii. fig. 3, *b*.

[3] *Ibid.*, pl. viii. fig. 3, *a'*.

[4] Mémoire sur l'anatomie et l'embryogénie des Vermets, *Ann. d. Sci. Nat.*, Zoologie, sér. 4, *t.* xiii. p. 238, pl. vi. fig. 4, *t*.

If it be admitted that cephalic appendages may surround the buccal aperture and unite below the alimentary canal (as is demanded by the arguments of von Jhering and of Grobben), then it ought also to be allowed that pedal appendages, such as those of *Vermetus*, may encroach upon the sides of the mouth and unite above the œsophagus, and embryology teaches us that this is what must have taken place in the case of the Cephalopoda.

IV. If, now, these appendages should undergo great development, it is natural that a pair of special ganglia (the brachial ganglia) should be formed for their innervation at the expense of the pedal ganglia. The formation of accessory ganglia in consequence of the great development of certain organs is often observed in the Mollusca, and here we find a case almost identical with that of the Cephalopoda.

In two groups of Gastropoda we find that the head carries a muscular mass as large in proportion as the brachial mass of the Cephalopoda; these are the Bullidæ ("Acères" of Cuvier) and the Naticidæ.

1. In the Bullidæ there is a "cephalic hood," which seems to be analogous to the hood of the *Nautilus* and to the dorsal arms of the Dibranchia; it arises from the fusion of the four tentacles (two labial and two nuchal) of the *Euthyneura*, and assists these animals in digging. The cephalic nature of the hood is thus beyond doubt.

Is then the nervous system of the Bullidæ similar to that of the Cephalopoda, and do we find there in front of the pedal ganglia other subœsophageal ganglia which innervate this cephalic mass? By no means. Here, as in *Ampullaria*, the innervation of this mass has its source in the supraœsophageal or cerebral ganglia.

On other grounds, too, it is impossible to regard the arms of the Cephalopoda as similar in origin to the cephalic tentacles of the Gastropoda. For even if the tentacles do not any longer exist in the adult Dibranchia, I may point out that they are still present in *Nautilus* (which is incontestably more primitive), though their homology has not hitherto been perceived. The structures in question are the ophthalmic tentacles, situated in front of and behind each eye; as a matter of fact these tentacles are innervated by the supraœsophageal ganglia,[1] whilst all the other appendages (whose mass corresponds morphologically to the arms of the Dibranchia) are innervated by the anterior infraœsophageal ganglia, which also give off the nerves to the funnel.

2. In *Natica* the muscular mass which covers the head can be reflected in front so as to expose the buccal opening. It is the anterior part of the foot, but physiologically is the same part as the cephalic hood of the Bullidæ, and like it aids in burrowing.

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[1] Valenciennes, Nouvelles recherches sur le Nautile flambé, *Archives Mus. Hist. Nat. Paris*, t. ii. p. 288, pl. viii. figs. 2, 3, 6 and 7. It is inaccurate to state, as does von Jhering (Vergleichende Anatomie, &c., p. 262), that the anterior ophthalmic tentacle is innervated by the anterior infraœsophageal ganglion, as also the olfactory organ. Its nerve issues from the extreme lateral part of the supraœsophageal ganglion. Compare the figures of Valenciennes above quoted.

We find in *Natica* that the disposition of the anterior subœsophageal ganglia resembles that seen in the Cephalopoda. In front of each pedal ganglion, in the position occupied by the brachial ganglion of the Cephalopoda, there is another corresponding subœsophageal ganglion, and this propedal ganglion innervates the voluminous mass which covers the head. I may here remark that the figures of the nervous system of *Natica* given by Souleyet,[1] which are the only original figures known to me, are inverted, that is to say that the upper (dorsal) surface is indicated as the lower (ventral) surface, and *vice versa*. It follows from this that the peculiarity of the nervous system of *Natica* in possessing propedal ganglia has not hitherto been observed.

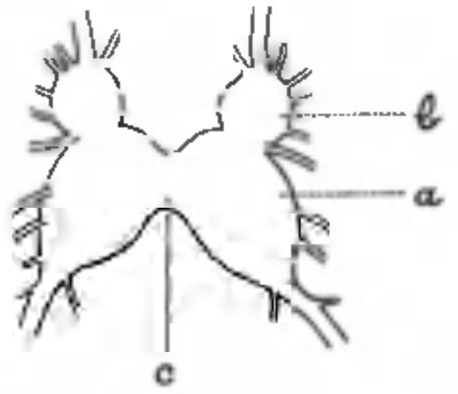

Fig. 2.—The pedal ganglia of *Natica*. *a*, pedal ganglia; *b*, propedal ganglia; *c*, pedal commissure.

The formation of these propedal ganglia and their separation from the pedal ganglia are evidently due to the great development of the anterior part of the foot, which has become transformed into a cephalic shield. Something of the same kind must have taken place in the Cephalopoda, where the formation of the brachial ganglia has been brought about by the great development of that part of the foot which has entirely surrounded the head and produced the arms.

It must not be concluded from what has just been said that I regard the shield of *Natica* and the arms of Cephalopods as exactly homologous; I only wish to draw from these facts the following conclusions:—In *Natica* we observe the formation of a pair of propedal ganglia in consequence of great development of the anterior part of the foot; in Cephalopoda we observe the same propedal ganglia; we may conclude, therefore, that the organs which they innervate are a portion of the foot situated anteriorly, which has taken on considerable development.

In *Natica* this anterior part of the foot covers the head by its anterior border, hence the coalescence with the head could not proceed further, because the mouth could not have remained open. In the Cephalopoda, on the other hand, it is the lateral margins of the foot which have invaded the head, leaving the buccal opening free; the two halves have met on the dorsal aspect of the head, concrescence has taken place, and the head has thus become entirely surrounded by a pedal mass.

Where, then, is the head? asks von Jhering.[2] The postero-lateral portions of it are to be seen in *Nautilus*, with the eye, the olfactory groove, and the two tentacles; and between the pedal appendages is seen the buccal mass. If the head be to a large extent concealed, it is not therefore non-existent.

V. We have already seen how those naturalists who defend the views which regard

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[1] Voyage de la Bonite, Zoologie, Mollusques, pl. xxxvi. figs. 13, 14.

[2] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 266.

the arms of Cephalopods as cephalic structures, interpret the nervous system, and especially the brachial ganglia of the animals. We will now examine the value of this interpretation.

From the point of view of these zoologists, which was briefly stated above, it is evident :—

1. That the union of each brachial ganglion to the corresponding pedal ganglia is a secondary disposition.

2. That the cerebro-brachial connective must be a primitive structure, since it would represent the means by which the brachial ganglion would remain in connection with the cerebral ganglion from which it arose.

We will now consider each of these conclusions separately.

1. If, instead of regarding the nervous system of the Decapod Dibranchiates such as *Sepiola* and *Ommatostrephes*, which, so far as the present question is concerned, form the end of the series, we refer to the nervous system of the Octopoda, we shall find that in *Octopus* the brachial ganglia are only separated from the pedal ganglia by a very slight external constriction; and in *Cirroteuthis*, which in certain respects (notably in the presence of fins) is a more primitive Octopod than *Octopus*, the brachial ganglia are in such close contact that the nerves to the funnel (which in *Octopus* arise from the pedal ganglia) have their origin quite close to that of the nerves to the ventral arms[1] (which in *Octopus* spring from the brachial ganglia).

And if, in addition to what has been stated above, we do not confine ourselves to a macroscopic examination of the exterior of the nervous system of the Cephalopoda, but study it also, as I have done, by serial microscopic sections, we shall find that in *Octopus* the central substance formed by the prolongations of the cells and giving origin to the nerves is quite continuous between the pedal and brachial ganglia.

If now we pass to the Decapoda and study not only the adults but also the embryos in all stages of development (in *Sepia* for example), we shall see that in the youngest forms the central substance of the pedal and brachial ganglia is in free communication, and that it is only little by little, in the subsequent stages, that they become separated as in the adult, where their central masses only communicate by a very slender bridge.[2]

From this point of view then, the Decapod central nervous system passes in the course of its development through an Octopod stage. These facts show clearly that the brachial ganglion results from the transverse segmentation of the pedal ganglion, and consequently that the union of each brachial ganglion with the corresponding pedal ganglion is not a secondary disposition.[3]

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[1] Reinhardt og Prosch, Om Sciadephorus Mülleri, *K. dansk. Vidensk. Selsk. Afhandl.*, t. v. p. 19, pl. v. fig. 2.

[2] Stieda, Untersuchungen über den Bau der Cephalopoden, *Zeitschr. f. wiss. Zool.*, Bd. xxiv. pl. xiii. fig. 6.

[3] This subject will be treated at greater length and with illustrations in a paper which I propose to publish in the *Arch. d. Biol.*, t. viii., under the following title,—"Sur la valeur morphologique des bras des Céphalopodes et sur la composition de leur système nerveux central."

2. The cerebro-brachial connective may be either (i.) adventitious or (ii.) primitive.

   (i.) It is impossible to deny the tendency of neighbouring ganglia, when they are homonymous or successive, to become united by nervous threads. On considering, for example, a large number of Streptoneura, it will be seen that the left anterior visceral ganglion (subintestinal, left pallial, or parietal ganglion) is united by a connective to the right pleural ganglion, with which it has really nothing to do (*e.g.*, *Cassidaria*).[1]

   In *Natica* the propedal ganglion is not united to the cerebral ganglion; in the female *Nautilus* the ganglion which innervates the internal labial tentacles[2] (which does not represent, it is true, the whole brachial ganglion of a Dibranchiate, but nevertheless corresponds to a part of it) has also no cerebral connective. It might possibly be said, then, that the cerebro-brachial connective of the Dibranchia is only an adventitious arrangement.

   (ii.) This connective may, however, be a primitive structure, and represent an anterior part of the original cerebro-pedal connective, which the brachial ganglion has carried along with it on its separation from the pedal ganglion.

   Grobben[3] regards this connective as a detached part of the primitive cerebro-pedal connective, and I share his opinion; but I may remark that there is a contradiction in Grobben's view, according to which the brachial ganglion should be a detached part of the cerebral ganglion, since then two parts of the cerebral ganglion would be joined by a *cerebro-pedal* connective.

   If, however, I regard the union of the brachial and cerebral ganglia of a Dibranchiate as primitive in the same way as the union of the brachial and pedal ganglia, I must remember that the first union is brought about by a simple connective and the second by the central ganglionic substance, which is a very different matter.

VI. Great importance has been attributed to the supraœsophageal commissure which connects the two brachial ganglia in *Eledone*,[4] and it has been regarded as a clear proof that the brachial ganglia were primitively supraœsophageal.[5]

This commissure has only been recorded by Dietl, and only in *Eledone*. I have seen it neither in *Sepia*, *Loligo*, nor other Decapoda; and I may further remark that the infraœsophageal commissure between the brachial ganglia existing in *all* Cephalopoda is much

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[1] Spengel, Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. pl. xvii. fig. 4, *s*.

[2] Owen, Memoir on the Pearly Nautilus, pl. vii. fig. 1, 8.

[3] Zur Kenntniss der Morphologie und der Verwandtschaftsverhältnisse der Cephalopoden. *Arb. Zool. Inst. Wien*, Bd. vii. p. 69.

[4] Dietl, Untersuchungen über die Organisation des Gehirns wirbelloser Thiere, *Sitzungsb. d. k. Akad. Wiss. Wien*, Bd. lxxvi. pl. v. fig. 23, *etc.*

[5] Grobben, *loc. cit.*, p. 69.

more important by reason of its volume than the thin supracœsophageal thread mentioned by Dietl in *Eledone* alone.

I will also add that probably in all the Opisthobranchia (Bullidæ,[1] Umbrellidæ,[2] Pleurobranchidæ,[3] Aplysiidæ,[4] many Nudibranchia,[5] &c.), as well as in the Gymnosomatous Pteropoda,[6] there is an infracœsophageal cerebral commissure, which von Jhering has called subcerebral. It is much more slender than the supracœsophageal cerebral commissure, but no one has ventured to suggest in consequence of this, that in the Opisthobranchia the cerebral ganglia were primitively subœsophageal.

So far as I can see, the supracœsophageal brachial commissure of *Eledone* is of no more morphological value than the subœsophageal cerebral commissure of the Gastropods just mentioned.

Nothing is further from complete demonstration than the hypothesis according to which the brachial ganglia are cerebral in origin. On the other hand, many proofs show that they are only a segmented part of the pedal ganglia.

Such transverse segmentations of ganglia are not rare among the Mollusca. In addition to the instance already quoted of the pedal ganglia of *Natica* and those of the Marseniidæ,[7] we may mention the siphonal ganglia of *Cypræa*,[8] the tentacular ganglion of *Pleurobranchus*,[9] the siphonal ganglion of many Pelecypoda, &c. Even in the Decapod Cephalopoda, too, there is an instance of the division of the cerebral ganglia, quite comparable to that of the pedal ganglia which has led to the formation of the brachial ganglia. Chéron[10] has shown, and his statement has not been disputed, that the ganglion known as the "superior buccal," and still called by that name by Stieda[11] and Bobretzky,[12] is nothing else than the anterior part of the cerebral ganglia. I am able to state further that in the embryos of *Sepia* the formation of these "buccal" ganglia and their separation from the cerebral ganglia takes place in a manner quite parallel to that which has been advanced above as regards the formation of the brachial from the pedal ganglia.

It might be objected that in *Ommatostrephes*, for example,[13] the brachial ganglia are

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[1] Vayssière, Recherches anatomiques sur la famille des Bullidés, *Ann. d. Sci. Nat.*, Zoologie, sér. 6, t. ix. pl. vi. fig. 46 (*Gastropteron*), pl. viii. fig. 69 (*Doridium*), pl. ix. fig. 81 (*Philine*), pl. xi. fig. 101 (*Scaphander*), pl. xii. fig. 114 (*Bulla*).

[2] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *Ann. Mus. Marseille*, t. ii. pl. vi. fig. 149.

[3] Vayssière, *ibid.*, p. 144.

[4] Vayssière, *ibid.*, pl. iv. fig. 94.

[5] Von Jhering, Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 283.

[6] Wagner, Die Wirbellosen des weissen Meeres, Bd. i. pl. xii. fig. 1.

[7] Bergh, Die Marseniaden, *Zool. Jahrbücher*, Bd. i. p. 188, fig. 1.

[8] Von Jhering, *loc. cit.*, pl. viii. fig. 35.

[9] Von Jhering, *ibid.*, pl. xi. fig. 8.

[10] Recherches pour servir à l'histoire du système nerveux des Céphalopodes dibranchiaux, *Ann. d. Sci. Nat.*, Zoologie, sér. 5, t. v.

[11] Studien über den Bau der Cephalopoden, *Zeitschr. f. wiss. Zool.*, Bd. xxiv.

[12] Observations on the development of the Cephalopoda, *Proc. Soc. Friends of Nat. Hist. Anthrop. and Ethnogr. Moscow*, 1876 (Russian).

[13] On the Nervous System of Ommastrephes todarus, *Ann. and Mag. Nat. Hist.*, ser. 2, vol. x. pls. i., ii.

very widely separated from the pedal. To this I should reply that in the Dibranchiate Cephalopoda, as has already been said, we may observe, in the degree in which the brachial ganglia are separated from the pedal, a whole series of successive stages (*Ommatostrephes*, *Sepiola*, *Loligo*, *Sepia*, *Octopus*), in which the brachial ganglia are gradually less and less distinctly separated, and in the last-named form a single mass, and are only marked off by a slight constriction.

I may further remark that this gradual separation of the brachial from the pedal ganglia, which is seen in passing from *Octopus* to *Ommatostrephes*, corresponds to an equivalent separation between the "superior buccal" and cerebral ganglia, the former separating from the latter even more than the brachial ganglia separate from the pedal. Whatever be the separation of the brachial and pedal ganglia, the pedo-brachial connective always remains much more important than the cerebro-brachial.

Thus then the great removal of the brachial and pedal ganglia (in *Ommatostrephes*) is not a primitive arrangement. It is adventitious, and due to the cause which separates at the same time all the anterior portion of the main mass of the central nervous system, as well supraœsophageal as subœsophageal.

Primitively, the brachial and pedal ganglia of the same side must have been in close apposition, as is shown by the observation of the development of the Decapoda (alluded to above) and as appears still to be the case in *Cirroteuthis*, according to the figures of Reinhardt and Prosch.[1]

In *Nautilus*, which is the most primitive of all, this separation of the brachial from the pedal ganglion has not yet taken place; in the female,[2] however, there is found a small ganglion corresponding to a part of the brachial ganglion, which innervates the internal labial appendages. But all the appendages of the male and the other appendages of the female are innervated directly by the anterior subœsophageal ganglionic ring, and the nerves to the funnel are seen to issue at the side of the last ventral "tentacular" nerves.

Some have desired to see in this anterior subœsophageal ring, which corresponds to the brachial and pedal ganglia of the Dibranchia, an external pedal portion and an internal cerebral portion. But in this case the latter would be only lateral and would not extend below the œsophagus (compare the figure of von Jhering[3]). This part would then innervate the tentaculiferous appendages; in this way it is sought to prove the cephalic nature of these latter.

This division is, however, quite imaginary, and it has remained invisible to those zoologists who have not been prejudiced by attempting to prove the cephalic nature of the appendages (Owen, Valenciennes, &c.). In reality this ring is entirely pedal, and

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[1] Om Sciadephorus Mülleri, *K. dansk. Vidensk. Selsk. Afhandl.*, p. 18, pl. v. fig. 2.

[2] Owen, Memoir on the Pearly Nautilus, pl. vii. fig. 6.

[3] Vergleichende anatomie des Nervensystemes und Morphologie der Mollusken, p. 262, fig. 14.

exactly corresponds to the pedal and brachial ganglia of the Dibranchia; it innervates the funnel and all the appendages.

It is inaccurate to state, as does Grobben,[1] that there are nerves to the appendages which arise from the cerebral ganglia above the optic nerve. The three nerves figured in this position by von Jhering[2] are the nerves which pass to the cavity situated at the posterior extremity of the cephalic cartilage, and which were regarded by Valenciennes[3] as auditory nerves.

(2) If, on the other hand, we seek in the ontogenetic development for some light on the morphological value of the arms of the Cephalopoda, we see that, the embryo resting with its ventral face on the surface of the vitellus, the arms appear on either side of the mantle against the vitellus, advance successively towards the anterior extremity, and finally meet in front of the mouth (compare the lucid figures of Kolliker[4]).

From what has been said above, we may conclude:—

1. The arms of the Cephalopoda are pedal in origin;

2. The buccal appendages of the Gymnosomata and the arms of the Cephalopoda are not homologous structures.

Ray Lankester[5] has insisted on the fact that in the Pteropoda a part of the foot comes to surround the cephalic region, and it is principally on this that he relies in support of his opinion that the Pteropoda should be classed along with the Cephalopoda.

As regards the Gymnosomata we have already done full justice to this argument by showing that their cephalic appendages have absolutely nothing in common with the foot. But as regards the Thecosomata it is true that a certain portion of the foot (the two fins) comes from either side to surround the head and advances as far as its dorsal aspect, in a manner analogous to that in which the arms of the Cephalopoda (whose pedal nature we have just demonstrated) envelop the head.

Here we have a resemblance which I should not think of disputing, and which Ray Lankester only weakens when he compares the fins of the Pteropods, not to the arms of the Cephalopods, but to their funnel. If, however, we rely upon this solitary resemblance (which is true only of the Thecosomata) to unite the Pteropoda and Cephalopoda, we frame an artificial classification.

A single resemblance, based upon an adaptive modification of a single organ, the foot, which is true only of the Thecosomata among the Pteropoda, cannot invalidate the numerous proofs drawn from all points in the organisation of the entire group, both

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[1] Zur Kenntniss der Morphologie, &c., *Arb. Zool. Inst. Wien*, Bd. vii. p. 68.

[2] *Loc. cit.*, fig. 14, p. 269.

[3] Nouveau mémoire sur le Nautile flambé, *Archives Mus. Hist. Nat. Paris*, t. ii. pl. viii. fig. 2, 3.

[4] Entwickelungsgeschichte der Cephalopoden, pl. ii. figs. 17–27.

[5] Mollusca, Encyclopædia Britannica, 9th ed., p. 684, fig. 75.

of Pteropoda and Cephalopods. We might find numerous instances of very dissimilar animals, in which a homologous organ is modified in an analogous manner without proposing to unite them on that account, if the sum total of their organisation showed them to be distinct. In this way we ought to deal with the Cephalopoda and Pteropoda.

On the other hand, a natural classification based upon a comparative examination of the whole organisation of the two groups must show, as we have demonstrated in the preceding pages, that there is no direct relation between the Pteropoda and Cephalopoda, and that they have nothing in common except inasmuch as they belong to the same Molluscan phylum.

The high position which has been accorded to the Pteropoda arises rather from their external form than from their structure, as has already been pointed out by Garner.[1] The adaptation to pelagic life has brought about in these animals a symmetrical exterior[2] in order to insure the perfection of natation. But this symmetry has proceeded no further; and what clearly separates the two groups is the complete asymmetry of the organisation of the Pteropoda as opposed to the perfect symmetry of the Cephalopoda.

III. ARE THE PTEROPODA GASTROPODA?

In the Pteropoda as in the asymmetrical Gastropoda—

1. The jaws are paired and lateral.

2. The flexure of the intestine is lateral, what has been improperly called dorsal or hæmal in the Gastropoda, for the intestine does not bend dorsally in a sagittal median plane in the same way as it curves ventrally in the Cephalopoda.

3. The heart is lateral and has only one auricle; the kidney is unpaired and lateral.

4. The unpaired genital gland has only one asymmetrical unpaired genital duct.

5. The nervous system is asymmetrical as regards the ganglionic masses of the visceral commissure and the nerves which spring from it; the osphradium (olfactory organ of Spengel) is unpaired and lateral.

6. A consideration of the development of the Pteropoda shows that as in the asymmetrical Gastropoda the pallial cavity of the Thecosomata is formed to the right of the anus,[3] and that the Pteropoda like the Gastropoda are asymmetrical even in the larval condition.[4] The first stages of the embryo show the primitive symmetry of all Mollusca; this is soon followed by asymmetry, and in the adult animal, though only as regards the external form, there is an adaptive return to the former symmetry, necessitated by pelagic habits.

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[1] Malacological Notes, *Ann. and Mag. Nat. Hist.*, ser. 4, vol. xix. p. 373.

[2] Grobben (Morphologische Studien, &c., *Arb. Zool. Inst. Wien*, Bd. v. p. 240) also interprets the symmetry of the Pteropoda in the same way.

[3] Fol, Sur le développement des Ptéropodes, *Arch. d. Zool. Expér.*, sér. 1, t. iv. p. 108.

[4] Fol, *Ibid.*, p. 127.

In conclusion, as has been said by Fol,[1] the embryonic characters are not sufficient to justify the separation of the Pteropoda from the Gastropoda.

We see then that the Pteropoda possess the principal general characters of the Gastropoda and especially the visceral asymmetry which results from the unilateral development of the visceral organs and characterises the specialised, that is to say the most numerous, Gastropoda.

But if we seek out from among the Gastropoda those forms with which the Pteropoda have the greatest affinity, we find the common characters still more numerous.

1. In the Pteropoda, as in the Tectibranchia,[2] a partition, or species of diaphragm, divides the body-cavity into a posterior visceral and anterior or cephalic portion, this latter enclosing the buccal mass, the central nervous system, and the copulatory organ.

2. The salivary glands of the Pteropoda, like those of the Tectibranchia (*e.g.*, Bulloidea and Aplysioidea) do not exhibit a duct differentiated off from the secretory portion.

3. The stomach in the Thecosomata at all ages and in the larval Gymnosomata has masticatory plates, as in the great majority of the Tectibranchia. The adult Gymnosomata in consequence of their diet have an unarmed stomach like that of the carnivorous Tectibranchia (*e.g.*, *Doridium*).[3]

4. The liver of the Pteropoda is disposed like that of the Tectibranchia, the Gymnosomata resembling *Gastropteron*, the Thecosomata the Bullidæ in this respect.

5. The generative gland of the Pteropoda is hermaphrodite like that of the Tectibranchia; as in the Aplysioidea and Bulloidea it possesses a single undivided efferent duct with a single orifice. As in these two the genital aperture is connected by a spermatic groove with the copulatory organ which is situated in the head.

6. The pedal ganglia both of the Thecosomatous and Gymnosomatous Pteropoda have two commissures like those of the above-mentioned Tectibranchia, Aplysioidea, and Bulloidea (the second commissure figured in *Cuvierina* and also seen in *Cavolinia* has probably escaped notice in the other genera on account of its small size).

The Pteropoda are thus clearly separated from all the other classes of Mollusca, whilst they present all the characters of the "typical" (asymmetrical but not primitive) Gastropoda.

Further, among the Gastropoda their whole organisation (hermaphroditism and the structure of the nervous system) separates them from the Streptoneura (Prosobranchia

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[1] Fol, *ibid.*, pp. 197, 198.

[2] Vayssière, Recherches anatomiques sur la famille des Bullidés, *Ann. d. Sci. Nat.* (Zool.), sér. 6, t. ix. p. 78.

[3] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *Ann. Mus. Marseille*, t. ii. p. 44.

and Heteropoda), and unites them closely with the Euthyneura (Opisthobranchia and Pulmonata), which de Blainville had previously designated as the "Paracéphalophores monoïques," including indeed the Pteropoda among them.[1] The Euthyneura differ much more from the Streptoneura than from the Pteropoda. These latter must then be placed in the group Euthyneura as was formerly done by de Blainville and more recently by Spengel.[2]

On the other hand, among the Euthyneura the Pteropoda present such resemblances to the "Opisthobranchia" that they are much more closely related to them (by the respiratory, circulatory, and generative organs) than these latter are to the Pulmonata. The Pteropoda must, therefore, be incorporated among the Opisthobranchia.

Now, as regards the two groups of the Opisthobranchia, Nudibranchs and Tectibranchs, the characters of the digestive tract (gastric armature), of the undivided genital duct, and of the spermatic groove, separate the Pteropoda much less from the Tectibranchs than these differ from the Nudibranchs. Hence the Pteropoda are, as regards their anatomical characters, Tectibranchia.

Among these, too, they have undoubtedly much more affinity for the forms which have been called in recent classifications[3] Cephalaspidea and Anaspidea (that is to say, the Bulloidea and Aplysioidea respectively) than for the group known as Notaspidea (that is the Pleurobranchoidea), and the former of these groups differs in its organisation much less from the Pteropoda than from the Pleurobranchs.

We shall now inquire what are the special affinities which the two subdivisions (Thecosomata and Gymnosomata) have respectively for those Tectibranchia which are their nearest relations among the Gastropoda.

IV. SPECIAL AFFINITIES OF THE THECOSOMATA AND GYMNOSOMATA.

We have just seen (1) that the Pteropoda are Gastropods; (2) that they belong to the group Euthyneura; (3) that they must be classed among the "Opistobranchia"; (4) that they must be placed with the Tectibranchia, and more particularly in the group formed by the Cephalaspidea and Anaspidea (Bulloidea and Aplysioidea).

These conclusions, however, were reached by reasoning on the basis of those characters which are common to the two groups, Thecosomata and Gymnosomata. If now we

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[1] Manuel de Malacologie, pp. 447, 460. H. Milne-Edwards (Note sur la Classification naturelle des Mollusques Gastéropodes, *Ann. d. Sci. Nat.* (Zool.), sér. 3, t. iv. p. 112) criticises de Blainville's classification of the Gastropoda, because it is based only on the generative organs, whilst the "natural" classification which he proposes is based only on the respiratory organs; besides it unites the Opisthobranchia and the Prosobranchia in a group opposed to the Pulmonata, which is much less natural than de Blainville's classification. As regards the name "Opisthobranchia," von Jhering has already proposed to abandon it because it is inaccurate. It is true that several animals of this group have not the auricle behind the ventricle but on the same level (as for example in *Gastropteron*); in *Actæon* the auricle is actually in front of the ventricle, as in *Limacina*. However, seeing that a new name might in its turn prove to be inaccurate, I preserve the term "Opisthobranchia," the group to which it is applied being quite a natural one.

[2] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. p. 373.

[3] Fischer, Manuel de Conchyliologie, p. 550.

consider each group separately, taking its own special characters into account, and if in this way we inquire with which of the Tectibranchs each group has the greatest affinity, we shall arrive at the conclusion that the two groups are not so closely related to each other as they are to the particular forms of Tectibranchs for which they have each the closest affinity.

This is an impression which must have been produced upon every zoologist who has examined, even in a cursory manner, the organisation of these animals, for the two groups exhibit such clearly marked differences, and each forms such a homogeneous whole, that it is quite impossible to derive one of them from the other, or to find for them an immediate common ancestor.

It is only by limiting oneself to the study of a single form (as Wagner has done in the case of *Clione*,[1] and attempting thence to construct the phylogenetic history of the Pteropoda, that one can regard the Thecosomata as the ancestors of the Gymnosomata.[2] It is true that by following this method one arrives at the strange result that the Pteropoda have been derived from the Heteropoda, and have given origin to the Cephalopoda.[3]

Boas was the first to formulate the opinion of the separate origin of the Thecosomata and Gymnosomata, and to assert that the two groups are "independent of each other."[4]

There is no need to recapitulate here the distinctions between the two divisions; they have been sufficiently expounded in the Report on the Gymnosomata,[5] and in the Summaries on the Thecosomata and on the Gymnosomata (pp. 37 and 55). But I must dwell for a few moments on the statement made by Boas,[6] "that the fins are not homologous in the two groups." This is an opinion which I do not share. The fins, both of the Gymnosomata and Thecosomata, are the modified lateral margins of the foot, and the differences which they present are almost the same as those which exist between the Bulloidea and the Aplysioidea.

In the Bulloidea the pedal surface is continuous with the natatory lobes, *e.g.*, *Acera* and *Gastropteron*), and there is no special creeping surface. In the Aplysioidea, on the other hand, these natatory lobes are distinct from the rather narrow creeping surface, which is clearly marked off (*e.g.*, *Aplysia*, *Notarchus*, *Oxynoe*, &c.).

The Gymnosomata also present an arrangement analogous to that of the Aplysioidea, but carried to an extreme; the natatory lobes are quite separated from the portion of the foot corresponding to the creeping surface.

Embryology shows further that these organs (the fins) are homologous in the Gymnosomata and Thecosomata. Fol[7] has shown that the fins of the Pteropoda cor-

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[1] Die Wirbellosen des weissen Meeres, Bd. i. p. 119.

[2] Von Jhering, on the other hand, regards the Thecosomata as the descendants of the Gymnosomata (Vergleichende Anatomie des Nervensystemes, &c., p. 273), whilst Grobben holds that the Limacinidæ (Thecosomata) are the most primitive Pteropoda (Morphologische Studien, &c., *Arb. Zool. Inst. Wien*, Bd. v. p. 240).

[3] Wagner, Die Wirbellosen des weissen Meeres, Bd. i. p. 22.

[4] Spolia atlantica, &c., *loc. cit.*, p. 179.

[5] Zool. Chall. Exp., part lviii. pp. 4–6.

[6] Spolia atlantica, &c., *loc. cit.*, p. 178.

[7] Sur le développement des Ptéropodes, *Archives de Zool. Expér.*, sér. 1, t. iv. p. 193.

respond to the lateral parts of the embryonic pedal disc, and are comparable to the whole lateral portion of the foot of the Gastropoda.

De Blainville and Boas have pointed out that it is the Bulloidea among the Tectibranchiata that the Thecosomata approach the most nearly, and we shall see that this view is quite justified. These authors, however, confine themselves to this mere statement without attacking the question whether the Thecosomata are descended from the Bulloidea or *vice versâ*, and without trying to ascertain by what course the passage has been made.

Further, Boas is unable to point out for which group of the Opisthobranchia the Gymnosomata have the greatest affinity.

We must then enquire what are the special affinities of the Gymnosomata, and whether the Pteropoda are a primitive or a derived group as regards the Tectibranchia; and, further, according to the answer obtained we must endeavour to show for each group of Pteropods (Thecosomata and Gymnosomata) to which group of Tectibranchs it is most nearly related, and how the passage from the one to the other has been brought about.

A. THECOSOMATA.

If it were necessary to investigate the relationships of the Thecosomata by reference only to the organisation of the Cavoliniidæ, the task would present great difficulties, for, as we have seen, these animals have undergone an anomalous transformation, which quite masks the aspect they would otherwise present, and renders them very different from animals to which they are very closely related.

This is the cause which has led to the affinities of the Pteropoda having been for so long misunderstood:—the Cavoliniidæ have been taken as types of the Pteropoda, and as they could not be classed along with other Mollusca, they have been erected into an independent group.

Fortunately the Limacinidæ still exist in our seas, and we have been able to show that they are the most primitive Thecosomata, whilst the Cavoliniidæ have been derived from them by a process which we have indicated above. It is then upon the Limacinidæ and not upon the Cavoliniidæ that we must rely in endeavouring to trace out the affinities of the Thecosomata.

Considering for a moment the *operculum* of the Limacinidæ, we see that *Actæon*, one of the Bulloidea, is the only operculate Tectibranch, and that its operculum is precisely similar to that of *Limacina*—elongated, semi-lunar, and with few coils. The reversed coiling of its spire arises from the reverse coiling of the animal and of the shell; *Actæon* is coiled in the direct (right-handed) way, and has an operculum with a sinistral spire; *Limacina*, which is coiled in a retrograde direction, has an operculum with a dextral spire.

Mantle.—At the place where the "shield" of the Thecosomata is situated, the roof of the pallial cavity of the Bulloidea also exhibits a pallial gland (*Bulla*, Pl. II. fig. 3, *d*; *Scaphander*, &c.). This pallial gland of the Bulloidea presents different degrees of development; and in *Actæon* (Pl. I. fig. 6, *a*), where it is rather large, it is quite identical both in form and position with the shield of Limacinidæ (Pl. I. fig. 5, *a*). The situation of this pallial gland in the Bulloidea close to the gill shows that it (and consequently also the "shield" of the Thecosomata) is nothing else than the hypobranchial gland of the Gastropods, which has become asymmetrical in the adult straight Thecosomata in consequence of an adaptive return to the primitive external symmetry.[1]

The margin of the mantle in the Bulloidea is continued on the right side by a large lobe (Pl. II. fig. 3, *f*) which corresponds to the right lobe of the mantle in the Limacinidæ, often called the "balancer" (Pl. I. fig. 1, *g*).

The Digestive Tract. 1. *Radula.*—In the Tectibranchia systematists distinguish marginal and lateral teeth. In reality all the teeth of the same transverse row (except the central tooth) are similar in form, and pass insensibly from the innermost to the outermost by diminishing in size and the gradual loss of the marginal denticulations.

In the Bulloidea, properly so called, there are only a small number of teeth on either side of the central one, for example in *Cylichna* and in some species of *Tornatina* (*Tornatina truncatula* = *Cylichna truncata*[2]); Fischer[3] is wrong in denying a radula to the Tornatinidæ; the outer teeth are here very much reduced in size (these are the so-called "marginal" teeth), whilst the inner ("lateral") tooth on either side of the median one remain well developed, thus exhibiting a formula which, by degeneration and loss of the marginal teeth, comes into agreement with that of the Thecosomata;[4] this formula (1–1–1) is in fact exhibited by some of the Bulloidea—*Scaphander* (Sars),[5] *Amphisphyra* (Lovén),[6] *Runcina*.[7]

The form of the teeth in the Bulloidea is the same as that in the Thecosomata, especially the most primitive ones, the Limacinidæ.

2. *Salivary Glands.*—In *Scaphander*[8] these have precisely the form and structure of those of the Thecosomata, short, ovoid, and with no differentiated duct.

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[1] Schiemenz (Ueber die Wasseraufnahme bei Lamellibranchiaten und Gastropoden, *Mitth. Zool. Stat. Neapel*, Bd. v. p. 627) has already recognised the relations between the "shield" and the "mucous" (hypobranchial) gland of Gastropoda, but he identifies it also with the ink-bag of the Cephalopoda. This homology does not hold, for the hypobranchial gland exists in the Cephalopoda, and as there are two gills so there are two hypobranchial glands, which have been long known under the name of spleen ("Milz"). Joubin, who has studied these organs (Structure et développement de la branchie de quelques Céphalopodes des Côtes de France, *Arch. d. Zool. Expér.* sér. 2, t. iii. pp. 115–119), has not recognised their homology for want of comparison.

[2] Formula—4–1–1–1–4; see Forbes and Hanley, History of the British Mollusca and their Shells, pl. vv. fig. 4a.

[3] Manuel de Conchyliologie, p. 555.

[4] In the genus *Cylichna*, also, the reduction of the number of "marginal" teeth is clearly visible. See Sars, Mollusca regionis arcticæ Norvegiæ, pl. xi. figs. 3 (*Cylichna alba*, Brown, 6–1–1–1–6), 4 (*Cylichna cylindracea*, Penn., 3–1–1–1–3), 5 (*Cylichna propinqua*, M. Sars, 2–1–1–1–2).

[5] *Loc. cit.*, pl. xi. figs. 13, 14.

[6] Malacozoologi, *Öfversigt k. Vetensk.-Akad. Förhandl.*, 1847, pl. iii.; Forbes and Hanley, *loc. cit.*, pl. UU, fig. 2, *c*.

[7] Gray, Guide to the Systematic Distribution of the Mollusca in the British Museum, part i. (1857), fig. 114, p. 205.

[8] Vayssière, Recherches anatomiques sur la famille des Bullidés, *loc. cit.*, pl. x. fig. 87.

3. *Gizzard or Stomach.*—Almost all the Bulloidea have a stomach armed with horny plates, usually three in number, almost symmetrical (one dorsal, and a lateral one on either side). This number is, however, variable, as is also the symmetry of the plates. Thus in *Scaphander* the three plates are irregular, the dorsal being very narrow. In *Acera* there are nine such plates, and in *Runcina* (= *Pelta*) four symmetrically disposed as in the Thecosomata,[1] so that in this respect the Bulloidea differ much more among themselves than *Runcina* differs from the Thecosomata.

Besides this there are in many Bulloidea in front of the three large symmetrical plates twice as many smaller plates, just as in the Thecosomata (*Bulla hydatis*,[2] *Bulla striata*,[3] *Haminea cornea*,[4] &c.).

4. *Liver.*—*Philine* and *Bulla* are said to have two hepatic ducts;[5] the less specialised *Cavoliniæ* (*Cavolinia trispinosa*[6] and *Cavolinia quadridentata*, Pl. III. fig. 4, *h*, *j*) have also two.

5. *Anal Gland.*—The gland which is found in the Cavoliniidæ (*Clio*, *Cavolinia*) to the left of the visceral cavity at the extremity of the rectum, almost symmetrically with respect to the osphradium, exists also in the Bulloidea; I have seen it in *Bulla striata*, *Haminea hydatis* (Pl. II. fig. 3, *h*), and *Haminea cornea*; in *Scaphander* it occupies a prolongation of the mantle which accompanies the visceral sac for several turns of the spire (as Vayssière[7] has already observed); in *Actæon* the arrangement is similar to that of *Scaphander*, but the extension formed by the gland is much longer and reaches as far as the first coils of the spire.

The Generative Organs.—In *Philine*[8] and *Doridium*[9] there is a vesicula seminalis comparable to that of certain species of *Cavolinia* (*e.g.*, *Cavolinia tridentata*).

The Nervous System.—The cerebral ganglia are separated from each other and connected by a long supraœsophageal commissure, both in the Bulloidea and the Thecosomata. The pleural ganglia are fused with the cerebral in the Thecosomata to form a single mass which is usually undivided externally. This is also the case in *Actæon* (Pl. II. fig. 11); in all the other Bulloidea the pleural ganglia are situated near to the cerebral ganglia, so that the cerebro-pleural connectives are either very short or not discernible. We have further seen that in the Thecosomata, *e.g.*, in *Cymbulia* (Pl. IV. fig. 2), the stomato-gastric nervous system has the same arrangement as in the Bulloidea (*Philine*): an anterior and a posterior ring connected by threads passing between the horny stomacal plates.

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[1] Vayssière, Recherches anatomiques sur les genres Pelta et Tylodina, *Ann. d. Sci. Nat.* (Zool.), sér. 6, t. xv. pl. i. fig. 4.

[2] Vayssière, Recherches anatomiques sur la famille des Bullidés, *loc. cit.*, pl. xii. fig. 111.

[3] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *loc. cit.*, pl. i. fig. 4.

[4] *Ibid.*, pl. i. fig. 11.

[5] Vayssière, Recherches anatomiques sur la famille des Bullidés, *loc. cit.*, p. 68.

[6] Souleyet, Voyage de la Bonite, Zoologie, t. ii. pl. ix. fig. 20.

[7] Vayssière, Recherches anatomiques sur la famille des Bullidés, *loc. cit.*, p. 90.

[8] *Ibid.*, pl. x. fig. 23.

[9] *Ibid.*, pl. viii. fig. 68.

Hence it appears that the Thecosomata resemble the Bulloidea more than the Gymnosomata.

We must now inquire what are the special affinities of these latter, that is to say, what are the Tectibranchia to which they are most nearly related?

B. Gymnosomata.

As in the case of the Thecosomata we have based our inquiry on the most primitive of the group, that is, mainly on the Pneumonodermatidæ, and especially on *Dexiobranchæa*. We have already shown in the Report on the Gymnosomata[1] that the Pneumonodermatidæ are the most primitive of the naked Pteropoda, and that *Dexiobranchæa* is the least specialised among them. Wagner[2] is quite wrong in regarding *Clione* as more primitive than *Pneumonoderma*, and the latter as derived from the former.

a. In most Tectibranchs there is a proboscis of the acrembolic type, that is, produced by the evagination of the anterior part of the œsophagus, like the rather short one of *Dexiobranchæa* and *Clione* (Pl. V. fig. 4, *a*), the somewhat longer one of *Pneumonoderma*[3] and *Spongiobranchæa*,[4] and the very long one of *Clionopsis*.[5] Among the Anaspidea (Aplysioidea) we find a similar rather short proboscis in *Aplysia*, *Notarchus*,[6] &c.

b. Like the Gymnosomata the Aplysioidea have two pairs of cephalic tentacles (*Aplysia*, *Notarchus* (Fig. 4, on p. 83), *Dolabella*, &c.); the anterior pair correspond to the labial pair of the Gymnosomata, and the second pair to the nuchal tentacles of these latter, for the olfactory nerve terminates in their interior and the optic nerve at their base. In the Bulloidea, on the other hand, we know that the cephalic tentacles fuse to form the shield which is of so much importance in connection with the burrowing habits of these animals.

c. The fins of the Gymnosomata are comparable to those of the Aplysioidea.

Von Jhering[7] refuses to admit the homology of the parapodia of *Gastropteron* and the other Tectibranchia with the "pteropodia" of the Pteropoda. If these organs are absolutely homologous with the epipodia of the Prosobranchs which the French school of the Sorbonne (Lacaze Duthiers and his pupils) regard as *pallial* in nature, that is a point which I should not like to affirm; nevertheless, I regard these latter as also pedal in origin.[8] I maintain, however, that the parapodia of the Tectibranchs and the fins of the Pteropods are strictly homologous.

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[1] Zool. Chall. Exp., part lviii. p. 67.

[2] Die Wirbellosen des weissen Meeres, Bd. i. p. 118.

[3] Zool. Chall. Exp., part lviii. p. 6, fig. 1, 4.

[4] *Ibid.*, p. 18, fig. 2, 1.

[5] *Ibid.*, pl. iii. fig. 1.

[6] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *loc. cit.*, p. 63.

[7] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 249.

[8] Paul Pelseneer, Sur la valeur morphologique de l'épipodium des Gastropodes rhipidoglosses, *Comptes rendus*, t. cv. p. 578.

On dissecting an *Aplysia* and a *Pneumonoderma* it will be seen that the fins of the latter and the parapodia of the former are innervated in exactly the same manner, similar nerves pass to them, issuing from the same points in the pedal ganglia.

In the Bulloidea, the parapodia (specially developed in *Gastropteron*, *Acera*, &c.) are continuous with the plantar or creeping surface of the foot, and form with it an uninterrupted surface. In the Aplysioidea the more ventral portion of the parapodia serves as a part of the visceral wall (Fig. 3, B), so that their origin appears to be separate from the plantar surface; a similar arrangement is found in the Gymnosomatous Pteropoda, where, in consequence of the reduction of the plantar surface, the parapodia or fins seem still further separated from the latter.

Fig. 3.—Diagrammatic transverse sections, A, of one of the Bulloidea, B, of one of the Aplysioidea; a, creeping surface of the foot; b, parapodium or natatory lobe of the foot.

Among the Aplysioidea are found different degrees of freedom of the parapodia relatively to the visceral sac, which lead gradually to the Gymnosomatous type. Thus in *Aplysia leporina* the parapodia are largely united behind; in *Aplysia punctata* they are less so; in *Aplysia fasciata* they are for the most part free.

In all these, however, the plantar surface is fused with the visceral mass, to the posterior extremity of which it extends, and the parapodia reach to the same point as the plantar surface. In *Notarchus*, on the other hand (Fig. 4), the plantar surface has no connection with the visceral sac, and the two parapodia are united dorsally above this latter, being fused throughout their whole length except a small tract anteriorly; they form thus a sac in which floats the visceral mass. In the same manner in the Gymnosomata the foot has no connection with the visceral sac; but here the plantar surface being reduced to the anterior part of the body, the parapodia or fins are also reduced to the same portion.

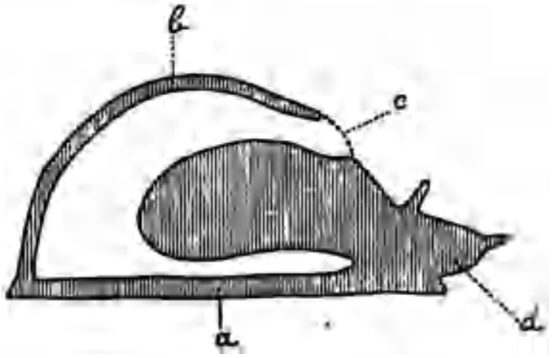

Fig. 4.—Sagittal section of *Notarchus*; a, creeping surface of the foot; b, parapodia united so as to form a sac around the visceral mass; c, aperture of the sac; d, head with anterior and posterior tentacles.

If, however, the fins of the Gymnosomata are homologous with the parapodia of the

Aplysioidea, then these must be indisputably so with those of the Bulloidea, for they pass insensibly from one into the other by transitional stages. On the other hand the fins of the Thecosomata correspond with the parapodia of the Bulloidea, and like these latter are continuous with the plantar surface of the foot, and also continuous with the posterior or ventral lobe of the foot. Hence it follows that, contrary to the opinion of Boas,[1] the fins of the Thecosomata and those of the Gymnosomata are strictly homologous.

d. If we consider the digestive tract:—

(i.) *Radula.*—The teeth of the Gymnosomata resemble in form those of a large number of Tectibranchs, *e.g.*, *Aplysia*. As in this case it is seen that, in the same transverse row of the radula, all the teeth except the median one are identical in form and only differ by decreasing in size from the innermost to the outermost.

Furthermore, we have seen that in the Gymnosomata the number of lateral teeth increases with age.[2] In *Aplysia*,[3] and probably in all the other Anaspidea, the state of matters is exactly the same.

(ii.) *Jaws.*—All the Gymnosomata are provided with paired jaws, which meet in the middle line ventrally. *Clione* alone is without them, as are certain carnivorous Tectibranchs, *e.g.*, *Actæon*, *Doridium*, *Lobiger*.

But in addition to the jaws united upon the floor of the buccal cavity in front of the radula, the Gymnosomata, except *Halopsyche*, possess hook-sacs, the homologies of which are not clearly explained.

When Eschricht published the anatomical description of *Clione*[4] the horny buccal organs of other Gymnosomata were not known. Eschricht, finding in this Gymnosome a radula and no jaws, but two hook-sacs, regarded these latter as representing morphologically the jaws of other Molluscs.[5] Since then, however, the study of the Gymnosomata has shown that they possess, in addition to the hook-sacs found in *Clione*, two jaws approximated in the ventral median line which are wanting in this latter.

The homologies of the hook-sacs are thus still unknown.

They are not, however, entirely new structures which are not found elsewhere. On the contrary, and in fact in the Aplysioidea (*Notarchus*, *Dolabella*, &c.), there may be observed an arrangement in which it is easy to see the origin of the hook-sacs of the Gymnosomata. This arrangement, to which attention was first called by Vayssière,[6] consists in the presence on

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[1] Spolia atlantica, p. 178.

[2] Zool. Chall. Exp., part lviii. pp. 6, 13.

[3] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *loc. cit.*, p. 61.

[4] Anatomische Untersuchungen über die Clione borealis, 1838.

[5] *Ibid.*, p. 10.

[6] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, i. Tectibranches, *loc. cit.*, p. 90.

the roof (superior or dorsal wall) of the buccal cavity of an armature of rather strong and somewhat recurved hooks (Pl. IV. fig. 5).[1] I have satisfied myself of the existence of this armature in *Notarchus punctatus* and *Dolabella neapolitana*.[2]

On comparing this armature, not with the hook-sacs of *Pneumonoderma*, which present the most highly specialised form of these organs, but rather with those of *Dexiobranchæa* (Pl. IV. fig. 6), which actually present the primitive condition, it is easy to understand that it is not a great step from the dorsal buccal wall, covered with hooks, to the small depressions filled with hooks found in *Dexiobranchæa*.

What, however, is the morphological value of this armature of hooks in *Notarchus* and *Dolabella* and of the hook-sacs of the Gymnosomata?

The comparative study of the horny buccal pieces other than the radula is attended with peculiar difficulties, for these pieces have never been the subjects of systematic investigation as has the radula. The knowledge of these organs which we possess is then very fragmentary, and there are scarcely any synthetic documents relating to them.

The only attempt to treat these pieces systematically was made by Mörch more than twenty years ago.[3] But this author, besides including among the extra-radular pieces organs which have no place there (*e.g.*, the pickaxe-like organs of *Conus*, which correspond morphologically to the radula), multiplies the number of different species which, according to him, may be distinguished among these organs, so that he by no means facilitates the systematisation and homologisation of these extra-radular pieces.

These horny extra-radular pieces are wanting in certain Gastropod Mollusca—Toxoglossa (*Conus*, *Pleurotoma*, &c.), Pyramidellidæ, Eulimidæ, many Trochidæ, Heteropoda, *Gadinia*, *Amphibola*, Testacellidæ, many Nudibranchs (*Doridopsis*, *Hermæa*, *Tethys*), *Phyllidia*, Pellibranchia, certain Tectibranchs (*Actæon*, *Utriculus*, *Scaphander*, *Doridium*, *Lobiger*). But the great majority of the Mollusca called "Odontophora" possess horny buccal pieces other than the radula.

As regards the relative position of these organs, we may state in the first place that the radula is always situated posteriorly to every other horny

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[1] *Ibid.*, pl. iv. fig. 90.

[2] *Dolabella neapolitana*, delle Chiaje, seems to me to be identical with *Aplysia petalifera*, Rang, *Aplysia webbii*, van Beneden, *Aplysia depressa*, Cantraine, and *Dolabella ornata*, Deshayes; on the other hand, however, it appears to constitute a genus (*Aplysiella*) distinct from *Aplysia* and *Dolabella*. It will probably be necessary therefore to call this species *Aplysiella petalifera* (Rang).

[3] On the Homology of the Buccal Parts of the Mollusca, *Ann. and Mag. Nat. Hist.*, ser. 3, vol. xvi. p. 73.

piece which may be present in the buccal cavity; sometimes these may be near the radula, but they are never behind it.

Furthermore, the radula is always situated in the inferior (ventral or neural) part of the alimentary canal, whilst the extra-radular horny pieces may be at any point whatever of the circumference of the buccal cavity—dorsally, ventrally, or laterally.

To these various situations of the extra-radular horny pieces must certainly be attributed the diversity of the organs which have been distinguished among them, as well as the confusion which reigns among the names which have been applied to them.

The extra-radular horny pieces are inserted directly into the wall of the digestive tract, and can only be removed along with it; the radula, on the contrary, forms an independent mobile ribbon, capable of extensive displacements, and actuated by a muscular and cartilaginous mechanism.

Finally, as to the physiological rôle of the extra-radular horny pieces: by reason of their situation being usually anterior, they have for special duty the retention of the prey, or of such portion of it as they have seized, whilst the radula discharges the function of dividing and comminuting it.

All the extra-radular horny pieces, however diverse their forms and the names by which they have been designated, appear to me on an ultimate analysis to be referable to jaws. The primitive form of these latter organs must have been a horny ring, situated in front of the radula towards the anterior portion of the buccal cavity; the origin of this ring has been the cuticularisation of this latter cavity at the place where it is most exposed.

This annular form may still be seen in a few Molluscs (*e.g.*, in *Umbrella*), where the ring is divided vertically into two lateral halves. By a transverse division into dorsal and ventral portions, the mandibles of the Cephalopoda have taken origin.

The two lateral halves of this ring are also found in the lateral mandibles of nearly all Gastropoda. These horny pieces may have remained as a single united surface, or may have become scaly or covered with spines, which might finally become isolated and independent; lastly, the separate portions may subdivide and reunite in various ways, and give rise to the numerous types of extra-radular horny pieces found among the Gastropoda.

As regards the special case of the Aplysioidea and the Gymnosomata, the scaly jaws (which are approximated in the median ventral line) and the dorsal hooks of *Notarchus* (which have become specialised into the hook-sacs of the Gymnosomata) would represent the modified remains of the primitive horny ring.

(iii.) *Salivary Glands.*—These organs in the Gymnosomata closely resemble the corresponding organs of the Aplysioid Tectibranchia; they are narrow and elongated, and extend, gradually diminishing in diameter, from the distal extremity to their termination in the buccal mass, without any separation into a proper glandular portion and a distinct duct.

(iv.) *Stomach.*—In the adult Gymnosomata this is unarmed. This absence of masticatory plates in the stomach is probably due to the exclusively carnivorous diet of the Gymnosomata. Indeed the most carnivorous of the Bulloidea (*e.g.*, *Doridium*) are also without gastric plates.

e. The Respiratory Organs.—The most primitive of the Gymnosomata (Pneumonodermatidæ) have a lateral gill (on the right side), the position and relations of which leave no doubt as to its homology with the gill of the Aplysioidea and of all the Tectibranchs (the posterior gill of *Pneumonoderma*, *Spongiobranchæa*, *Clionopsis*, and *Notobranchæa* being a new formation). This lateral gill, although simpler than that of the Aplysioidea, is analogous to it in its structure, for in *Pneumonoderma* it is also formed by the folding of a single lamella.

f. The Generative Organs.—The hermaphrodite genital gland of the Gymnosomata is arranged like that of all the Tectibranchs. The conformation of the genital duct in the Aplysioidea is exactly identical with that of the duct in the Gymnosomata, the accessory genital glands (albuminiparous and muciparous glands) and the receptaculum seminis being situated towards its extremity. The structure and position of the copulatory organ also are the same both in the Aplysioidea and the Gymnosomata.

g. The Nervous System.—There is almost absolute identity between the central nervous system of a Gymnosome (*e.g.*, *Spongiobranchæa*, Pl. V. fig. 3) and that of certain Aplysioidea, such as *Notarchus*[1] or *Dolabella* (Pl. V. fig. 2), and the central nervous system of other Aplysioidea only differs from that of the Gymnosomata in the elongation of the pleuro-visceral connectives and the displacement backwards of the visceral ganglia.

In the Gymnosomata and in all the Aplysioidea the cerebral ganglia are closely approximated on the dorsal aspect of the œsophagus; the pleural ganglia are close to the pedal ganglia, so that the cerebro-pleural connectives are almost as long as the cerebro-pedal, and the pleuro-pedal connectives scarcely exist. A long and slender sub-œsophageal cerebral commissure (subcerebral commissure of von Jhering) also exists in both groups.

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[1] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, *loc. cit.*, pl. iv. figs. 24, 25.

As regards the visceral ganglia, they are asymmetrical in the Aplysioidea (*Aplysia*, *Notarchus*,[1] *Dolabella rumphii*,[2] *Dolabella neapolitana*, &c.) as in the Gymnosomata; the right ganglion is larger than the left, and gives origin to three principal nerves (right pallial and two visceral nerves), whilst the left ganglion only gives rise to the left pallial nerve.

In the Aplysioidea (*Aplysia*, &c.) I have observed the same pleuro-pedal anastomoses (cervical plexus) as has been above described in all the Gymnosomata.

The situation of the osphradium is the same both in the Aplysioidea and the Gymnosomata—between the genital opening and the aperture of the kidney, a little ventrally (compare the figure of *Clione*, Pl. V. fig. 5, *j*, with that of *Aplysia* published by my esteemed teacher Professor E. Ray Lankester[3]).

The careful comparison of the Gymnosomata and the Gastropoda shows then that the former have very close affinities with the Aplysioidea; that they differ less from them than from the Thecosomata; and that, on the other hand, the Aplysioidea differ less from the Bulloidea than from the Gymnosomata.

V. DO THE PTEROPODA CONSTITUTE A PRIMITIVE OR A DERIVED GROUP?

The view has often been expressed that the Pteropoda constitute a primitive group in the phylum Mollusca. Haeckel[4] in his phylogeny of the Mollusca shows that Pteropods are situated at the base of the two groups Cephalopoda and Gastropoda.

In the same way von Jhering[5] considered that Pteropods are the ancestors of the Cephalopods; but he has since abandoned the idea of the affinity between these two groups. Wagner, on the other hand, points to the Pteropoda as the probable source of the Cephalopods.[6] Lastly, several zoologists still regard the Pteropods as primitive in consequence of the simplicity which is observed in certain parts of their organisation, as for example the circulatory apparatus (Roule,[7] &c.).

To the question at the head of this chapter we have now to reply:—No, the Pteropods are not primitive Molluscs; on the other hand, they constitute a derived group among the Mollusca.

In support of this view, arguments may be adduced from—(1) comparative anatomy, (2) embryology, (3) palæontology.

1. A. The profound asymmetry of the organisation of the Pteropods indicates a group

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[1] *Ibid.*, pl. iv. figs. 94, 95.

[2] Amaudrut, Le Système nerveux de la Dolabella Rumphii, *Bull. Soc. Philom. Paris*, sér. 7, t. x. p. 70.

[3] Mollusca, in Encyclopædia Britannica, 9th ed., vol. xvi. p. 657, fig. 63, *m*, between *k* and *e*.

[4] Natürliche Schöpfungsgeschichte, ed. 3, p. 476; Generelle Morphologie, t. ii. p. cxiii, and pl. vi.

[5] Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken, p. 249.

[6] Die Wirbellosen des weissen Meeres, Bd. i. p. 117.

[7] Recherches histologiques sur les Lamellibranches, *Journ. Anat. et Phys.*, 23e année, p. 79.

which has already undergone numerous modifications, and has become widely separated from the primitive symmetrical Archimollusc.

B. The concentration of the nervous centres indicates a very specialised and highly differentiated group.

2. In the course of their development the Pteropods pass through a stage even more asymmetrical than the adult. This fact indicates clearly that they arise from ancestors more asymmetrical than themselves, and that their apparent symmetry has been acquired in the course of time by adaptation to their natatory habits.

Comparative anatomy and embryology indicate then that the Pteropoda are not primitive Mollusca, and furthermore, that they are derived from ancestors which themselves are not primitive, but on the contrary already specialised. Some naturalists entirely misunderstand the degree of specialisation of the Gastropoda; thus Boutan[1] regards as the most primitive those Gastropods which he calls typical, that is to say those in which the asymmetry is carried to the highest pitch, and he criticises the opinion of Spengel, who regards the Fissurellidæ as primitive Gastropoda. Among the asymmetrical Gastropoda, *Fissurella* and its allies are in fact the most primitive, as is shown by the conformation of some of their organs (*e.g.*, those of circulation and excretion); such is the inaccurate point of view which Boutan has adopted and from which he has been led to confound the judicious conclusions of Spengel with the rash generalisations of von Jhering.

3. The organisms from the Primary formations, which are usually referred to the Pteropoda, have no affinities with these latter, as I shall show further on. In the Secondary rocks there are no traces of Pteropods, the first undoubted remains of this group being found in the lower Tertiaries. They are then of recent origin.

We are consequently justified in saying:—The Pteropoda do not form a primitive group, but on the contrary a recent and specialised one—a terminal group. The greater part of the characters of terminal groups, as formulated by my esteemed teacher, Professor Giard,[2] are entirely applicable to the Pteropoda:—

(1) They are profoundly modified in adaptation to a special mode of existence.

(2) They exhibit very slight variability.

(3) They include only a small number of species.

VI. POLYPHYLETIC ORIGIN OF THE PTEROPODA.

We regard it then as proved that the Pteropoda (both Thecosomata and Gymnosomata) are derived animals and of recent origin, and by no means primitive Mollusca.

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[1] Recherches sur l'anatomie et le développement de Fissurella, *Archives de Zool. Expér.*, sér. 2, t. iii. bis, pp. 150, 151.

[2] Observations . . . (sur les mammifères ovipares), *Bull. Scient. Départ. Nord*, 1886, p. 416.

On the other hand, we have seen that each group has different affinities—those of the Thecosomata being with the Bulloidea, those of the Gymnosomata with the Aplysioidea. We must conclude therefore that the Pteropoda are polyphyletic in origin.

We shall now endeavour to show in the case of each group what has been the line of descent.

A. Origin of the Thecosomata.

Hitherto those authors who have believed that the affinities of the Pteropoda are with the Tectibranchia (de Blainville and Boas) have contented themselves with indicating the proximity of the Thecosomata to the Bulloidea, but without going further and trying to ascertain whether the Thecosomata are phylogenetically derived from these latter, and in what way this descent may have taken place.

It may be most confidently affirmed that the Thecosomata are descended from ancestors resembling the Bulloidea, and that the cause of the modifications which they have undergone is to be found in the increase of natatory habits and the adaptation to pelagic life.

If now we try to ascertain by what process the passage from one group to another has taken place, and by what successive modifications a Bulloid has become a Thecosomatous Pteropod, we are met at first by an apparent difficulty, in the fact that the most primitive Thecosomata, the Limacinidæ, are sinistrorsal, whilst all the existing Bulloidea are dextrorsal. But is this a real difficulty? Is there in fact a great morphological difference between a dextrorsal and a sinistrorsal animal?

Of what importance is the direction of the spiral? It is of scarcely any value, for we see among the species of a single genus (*Neptunea*, *Pyrula*, *Vertigo*, &c.), or among the genera of a single family (*Lanistes* and *Ampullaria*), forms coiled in opposite directions.[1] If this be the case with forms so nearly related, there is *a fortiori* no reason for astonishment that the same thing should happen in the case of the Bulloidea and Limacinidæ.

The examples just quoted show that it is very natural and simple that among the Bulloidea there should have arisen in course of time sinistrorsal forms, which, however, have preserved the dextrorsal asymmetry of their internal organisation; that is to say, that in these animals the "sinistrorsity" has only affected the coiling of the visceral sac and the shell, and these sinistral forms would bear to some of the Bulloidea the same relation that *Lanistes* bears to *Ampullaria*. (Bouvier[2] has shown that *Lanistes* is not sinistral as regards its organisation, and that it differs from *Ampullaria* only by the contrary twisting of its visceral sac.)

These forms, which are still unknown to us, are the extinct ancestry of the Lima-

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[1] In the Pyramidellidæ we have a case in which in the same specimen the first coils are sinistral and the subsequent ones dextral.

[2] Sur le système nerveux typique des Prosobranches dextres ou sénestres, *Comptes rendus*, t. ciii. p. 1276.

cinidæ. We know that in these latter also the sinistrorsity has only affected the coiling of the spire.

It is easy to explain the transition from a creeping Bulloid to a swimming Limacinid. Even among the Bulloidea we observe a great tendency to natatory habits; the margins of the foot (parapodia) extend laterally so far that they can be reflected over the shell, and assist by their movements, in a natation at first imperfect then gradually more complete, in the forms which have become more specialised (*Acera*, &c.), and even carried out to a very high degree in *Gastropteron*.

It is quite comprehensible how, among animals having such tendencies, forms should have arisen having the mantle and shell well developed and with sinistral coiling, which by gradual specialisation have become exclusively pelagic animals, the first rough sketch, as it were, of the Limacinidæ.

If we examine the whole series of the Bulloidea (or Cephalaspidea), living and fossil, we shall find that the most ancient are forms resembling *Actæon* (these are probably the most ancient of the Opisthobranchia, and their importance with respect to the phylogeny of the Gastropoda cannot be overrated); the organisation of the recent *Actæon* (especially its nervous system, generative organs, and operculum), and its possible relations with the Pyramidellidæ, show that it may be not very far removed from the common stock of the Streptoneura (Prosobranchs and Heteropods) and the Euthyneura.

The genus *Bulla*, however, properly so called, scarcely appears before the Cretaceous period.

The presence of an operculum in the most primitive Thecosomata (Limacinidæ and the larvæ of the Cymbuliidæ) shows that they are descended from operculate ancestors. *Actæon* still retains this operculum (it is the only Opisthobranch which does not lose it in the adult state), and all the fossil Actæonidæ certainly possessed it. The earliest Bullidæ—*sens. lat.*, *i.e.*, comprising the Scaphandridæ and the Tornatinidæ—(derived from the Actæonidæ) must have possessed it also, and the animals of this family will only have lost it subsequently in the adult condition. It is from some of these operculate forms, intermediate between *Actæon* and *Bulla*, that the first Thecosomatous Pteropods have arisen.

If for example we consider such forms as *Globiconcha* or *Hydatina*; if we allow that some of them have become coiled sinistrally whilst retaining the dextrorsal asymmetry in their organisation (as happens in some Gastropods, *e.g.*, *Lanistes*); lastly, if in these animals the lateral margins of the foot, already strongly developed, become still more specialised, we shall have the first Limacinidæ.

A sinistral shell from one of the forms above quoted would, in fact, closely resemble a short-spired shell of one of the Limacinidæ, such as the earliest Eocene *Limacinæ*. On the other hand, owing to more and more exclusive adaptation to pelagic life, the shell of the Bulloidea must have become more delicate, and have acquired a structure very similar to that of *Limacina*, as in the case of the shells of the living *Haminea* and

Acera; and since these Bulloidea probably resembled *Acera*, we may still find a feature of resemblance in the "proboscis" of this latter and that of *Peraclis* and the young Cymbuliidæ.

I have said that the Thecosomatous Pteropods must have arisen towards the end of the Cretaceous or in the early part of the Tertiary epoch. Indeed, in the Secondary period there exists no Pteropod analogous to the Tertiary Thecosomata; and, as I have already said, I cannot admit among the Thecosomata the so-called Primary "Pteropoda."

There exists a considerable number of these fossils (more than a hundred species), which, not being assignable to any other group, have been placed among the Pteropoda on account of certain apparent resemblances.

The absence, which has been already mentioned, of any organic remains in the Secondary rocks which could possibly be attributed to the Pteropoda, and the enormous interval of time which consequently separates these fossils from the true Tertiary Thecosomata, is of itself an argument against the interpretation which has been given by palæontologists of these organisms.

The only so-called "Pteropods" in the Secondary rocks are two species of *Conularia* analogous to those of the Primary formations—*Conularia* sp., Bittner,[1] from the Trias, and *Conularia cancellata*, Argeliez, from the Lias.

In spite of the distance in time which separates the Primary "Pteropoda" from the true Thecosomata of the Tertiary period, the former have hitherto been always ranged among the latter, although only a small number of them show an external resemblance to certain species of *Clio* of the subgenera *Creseis* and *Hyalocylix*.

The fossils which exhibit this supposed resemblance to the existing Cavoliniidæ are as follows:—

1. The "*Creseis*" and "*Styliola*" of the Silurian and Devonian. These are fossils which are not very well preserved, have no embryonic shell like that of *Clio*, and often exhibiting a longitudinal striation such as is seen in no existing species of *Clio*. No real affinity can be found between these organisms and the genus *Clio* (*Creseis*); on the other hand, the great size of these Primary fossils separates them from all known forms of Pteropoda in the same manner as they are separated by stratigraphical considerations, for from the Devonian to the lower Tertiary there is no fossil which could be referred to an extinct Thecosome of this group.

As to the supposed specimens of *Creseis* of small size described by Ehrenberg,[2] their strong regular curvature, their oblique mouth, their apex without any distinct embryonic shell, separate them entirely from all the known Thecosomata, and render it impossible to unite them with the subgenus *Creseis* of *Clio*.

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[1] *Verhandl. k. k. geol. Reichsanst.*, 1878, p. 281.

[2] Ueber massenhaft jetzt lebende oceanische und die fossile ältesten Pteropoden der Urwelt, *Monatsber. d. k. preuss. Akad. d. Wiss. Berlin*, 1861, figs. 19–21.

2. *Tentaculites.*—These are the only Primary "Pteropods" on which one might found arguments in favour of an apparent resemblance to the subgenus *Hyalocylix* of *Clio.* Their external surface, indeed, presents grooves or rather transverse rings. Nevertheless, the comparison of median longitudinal sections of a *Tentaculites* and a *Clio* shows at once that the resemblance is only superficial, and that in reality the two organisms are quite dissimilar in structure.

The Thecosomatous Pteropods such as *Clio* have a shell of almost constant thickness, and distended at the extremity (embryonic shell of Fol). *Tentaculites*, on the other hand, ends in a sharply pointed extremity, and the thickness of the shell gradually increases from the aperture towards the apex.[1]

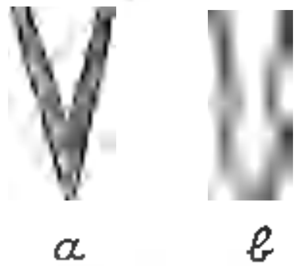

Fig. 5.—Longitudinal section of the apex, *a*, of *Tentaculites*, *b*, of *Clio*.

In the same way the supposed Devonian *Cleodora* (=*Clio*), described by Ludwig,[2] has the apex like that of *Tentaculites*, and not at all like that of *Clio*.

Among the other Primary "Pteropods" three principal groups may be distinguished—(1) *Conularia*, (2) *Hyolithes*, (3) the Cymbuliidæ described by Ehrenberg, *Ecculiomphalus*, Portlock (=*Phanerotinus*, Sowerby; this was ranged by Bronn[3] among the Pteropods, but is really a Gastropod allied to the Solariidæ).

1. *Conularia.*—These differ from all the Thecosomatous Pteropoda hitherto known in their quadrangular shell and contracted aperture; even the structure of their shell separates them entirely from the Thecosomata. They have been placed along with these by d'Archiac and Verneuil, who, not being zoologists, were unacquainted with the organisation of the Pteropoda; and in consequence merely of this allocation all palæontologists have continued to class *Conularia* among the Pteropods.[4]

2. *Hyolithes.*—These are distinguished from all the Pteropoda by their triangular form, their partitions, and their operculum, which in no respect resembles that of any operculate Mollusc. I must also here allude to the case of *Calceola sandalina*, which was so long referred to the Brachiopoda, and which is only an operculate Polyp. Without committing myself to any opinion regarding *Hyolithes*, which I have not had the opportunity of studying personally, I may ask whether it may not be possible that this also is a species of operculate Polyp.

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[1] Ludwig, Pteropoden aus dem Devon und Oligocän in Hessen und Nassau, *Palæontographica*, Bd. xi. pl. 1. 3*b*.

[2] *Ibid.* I must mention that the elongated Primary fossils with an initial dilatation resemble Dentaliidæ as much as if not more than Thecosomatous Pteropoda (compare M. Sars, Malakologiske Jagttagelser, *Forhandl. Vid. Selsk.*, 1864, pl. viii. figs. 49–51, and G. O. Sars, On some Remarkable Forms of Animal Life, &c., i. 1872, pl. iii. figs. 14, 15). Some similar Dentaliidæ have been found in the Challenger soundings. This would furnish an argument in favour of the views of Grobben, who regards the Scaphopoda as very primitive forms (Morphologische Studien, &c., *loc. cit.*).

[3] Die Klassen und Ordnungen des Thierreichs, Bd. iii. p. 646.

[4] Lindström (On the Silurian Gastropoda and Pteropoda of Gotland, *K. Svensk. Vetensk. Akad. Handl.*, Bd. xix. No. 6, p. 40) insists that the septa of *Conularia* furnish a proof of its Pteropod nature, whereas not one of the living Thecosomata has septa of this character.

3. Cymbuliidæ.—The Silurian fossils described by Ehrenberg[1] under the name of ***Panderella***, and regarded as larval shells of Cymbuliidæ,[2] are coiled in a plane, and are bilaterally symmetrical like those of *Bellerophon* or *Oxygyrus*.

As to the fossils referred with a "?" to larval shells of *Cymbulia*[3] and *Tiedemannia* (=*Gleba*),[4] they are entirely uncoiled, the turns of the spire not being in contact; and in most cases they are coiled in one plane, neither spire nor umbilicus being visible. There is thus no connection between these fossils and the larval shells of Cymbuliidæ.

To sum up, we see that in the case of all these Primary so-called "Pteropoda" there is no reason whatever to regard them as Thecosomata. One palæontologist even has recognised the improbability of the organisms being referable to the Pteropoda: Hoernes,[5] in speaking of *Conularia* and ***Hyolithes***, says that they "perhaps form a group distinct from the Pteropods and of unknown affinities."

I am strongly inclined to believe that among these Primary "Pteropods" there are organisms belonging to different groups, but I am unable to decide which; and perhaps, even after a prolonged study, it would be impossible to class them with any known living organisms. What I can definitely assert, however (and Boas, whose authority on this point cannot be doubted, has arrived at the same opinion[6]), is that not one of them has the least affinity of any kind whatever with the Pteropoda, and that these latter are only to be discerned with certainty at the beginning of the Tertiary period.

B. Origin of the Gymnosomata.

We have already shown that the Gymnosomata are closely related to the Aplysioidea. Just as we consider that the Thecosomata are descended from the Bulloidea, so we are persuaded that the Gymnosomata have arisen from Aplysiid ancestors, and we have already expressed this opinion several times.[7]

In the present instance we cannot, as with Thecosomata, call palæontology to witness. The shell of the Aplysioidea is quite rudimentary, scarcely calcified, and but little adapted to fossilisation; and in the Gymnosomata both mantle and shell have entirely disappeared in the adult.

In *Notarchus* among the Aplysioidea, the mantle is already extremely reduced, and the shell has become microscopic, being lodged a little behind the anus.[8] Thus this form

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[1] Ueber massenhaft jetzt lebende oceanische und die fossile ältesten Pteropoden der Urwelt, *Monatsber. d. k. preuss. Akad. d. Wiss. Berlin*, 1861, p. 434. Ueber die Obersilurischen und Devonischen microscopischen Pteropoden, Polythalamien und Crinoiden bei Petersburg in Russland, *Ibid.*, 1862, pp. 599, 600.

[2] Ueber massenhaft jetzt lebende, &c., *loc. cit.*, figs. 1–9.

[3] *Ibid.*, figs. 10, 11.

[4] *Ibid.*, figs. 12–16.

[5] Manuel de Paléontologie, p. 375.

[6] Spolia atlantica, pp. 94, 95.

[7] Description d'un nouveau genre de Ptéropode Gymnosome, *Bull. Scient. Dép. Nord*, 1886, p. 226; and Zool. Chall. Exp., part lviii. p. 67.

[8] Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, I. Tectibranches, *loc. cit.*, p. 66, fig. 81.

leads on to a stage which is found in the Gymnosomata. Furthermore, there are in *Notarchus* many structures in which the whole organisation of the Gymnosomata may be foreseen.

The foot is entirely separated from the visceral sac, as in the Gymnosomata. The parapodia (lateral margins of the foot) have become greatly developed, but owing to a special modification their free borders have fused dorsally, forming around the body a large "epipodial" or parapodial sac, open only in front above the neck, so that swimming is performed in *Notarchus* by the parapodia it is true, but in a manner which recalls the propulsion of the Cephalopoda, the water contained in the parapodial sac being expelled by its contraction.

On the other hand the palatine roof, armed with hooks, of *Notarchus* indicates, as we have seen, the first origin of the hook-sacs of the Gymnosomata, and the lateral gill is homologous with that of the Pneumonodermatidæ. Finally, the conformation of the nervous system is identical in *Notarchus* (and also in the *Dolabella neapolitana*) and the Gymnosomata.

If, then, we assume a form nearly related to *Notarchus*, in which the free margins of the parapodia have not fused; in which the creeping foot has become shortened by disuse; in which the small rudiments of mantle and shell seen in *Notarchus* have entirely disappeared; in which the covering of hooks found on the palatine arch has been divided into symmetrical halves located in two depressions of the wall of the digestive tract (thus becoming transformed into hook-sacs like those of *Dexiobranchæa*); in which on the ventral wall of the proboscis there have been formed prehensile organs similar to the primitive suckers of *Dexiobranchæa*; and lastly, in which the gill has been somewhat simplified in its structure,—we shall have a type very close to the most primitive Pneumonodermatidæ.

In the systematic Report on the Gymnosomata (Relations of the Gymnosomata to each other[1]) I have shown how all the living forms of Gymnosomata may be derived from this primitive type. We are therefore justified in saying that the Gymnosomata are specialised Aplysioidea, adapted to extremely natatory habits, and to an entirely pelagic mode of life.

VII. SUMMARY.

A. The Pteropoda do not constitute among the Mollusca a class of the same value as the Cephalopoda, Gastropoda, Scaphopoda, and Pelecypoda.

B. The Pteropoda are not primitive Mollusca, but are a derived and recent group.

C. They have no affinity with the Cephalopoda.

D. They are Gastropoda in which the adaptation to pelagic life has so modified their external characters as to give them an apparent symmetry.

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[1] Zool. Chall. Exp., part lviii. pp. 67–69.

E. Among the Gastropoda they do not constitute a distinct subclass, nor even an order.

F. They belong to the Euthyneura, and among these to the Tectibranchiate Opisthobranchs. They differ less from the Tectibranchs than these differ from the other Opisthobranchs. The different families which make up the Pteropoda must be distributed among the families of the Tectibranchia according to their special affinities.

G. The Pteropoda are polyphyletic in their origin; in other words, the Thecosomata and Gymnosomata are two independent groups: they have not a common origin and they differ more from each other than each one differs from a group of Tectibranchs to which it is most closely allied.

H. The Thecosomata have descended from the Bulloidea.

I. The Gymnosomata have descended from the Aplysioidea.

VIII. GENERAL CONCLUSIONS.

I have shown that the Pteropoda differ less from the Euthyneurous Gastropoda of the Tectibranchiate Opisthobranch group than these differ from the other Opisthobranchs, and that the different forms which have hitherto been united in one "class" Pteropoda find their natural places besides certain families of Tectibranchs. Furthermore, I have shown that the "Pteropoda" as a whole differ less from those Tectibranchs which are known as Cephalaspidea and Anaspidea (or Bulloidea and Aplysioidea respectively) than these together differ from the third group of Tectibranchs, Notaspidea (or Pleurobranchoidea).

In conclusion then I may say:—The Heteropoda were formerly regarded as a distinct class like the Pteropoda. But for a long time now they have been placed among the Gastropoda, the affinities having been recognised which they bear to the Streptoneura (or Prosobranchia), of which, to use the expression of Spengel, they are forms "modified by adaptation to a pelagic mode of life."[1]

I am strongly in favour of this mode of classifying the Heteropoda according to their natural affinities. Yet the Heteropoda are Gastropoda much more specialised in their organisation than are the Pteropoda; and they exhibit differences from all the Streptoneura *much greater* than those which separate the Pteropoda from the Euthyneurous Gastropoda of the Tectibranchiate Opisthobranch group.

Henceforth, therefore, we should abstain from making a distinct class of the Pteropoda, but we should rather distribute the animals which have been called by this name among other groups, according to their natural affinities.

The table on the following page shows the manner in which I propose to classify the Pteropoda.

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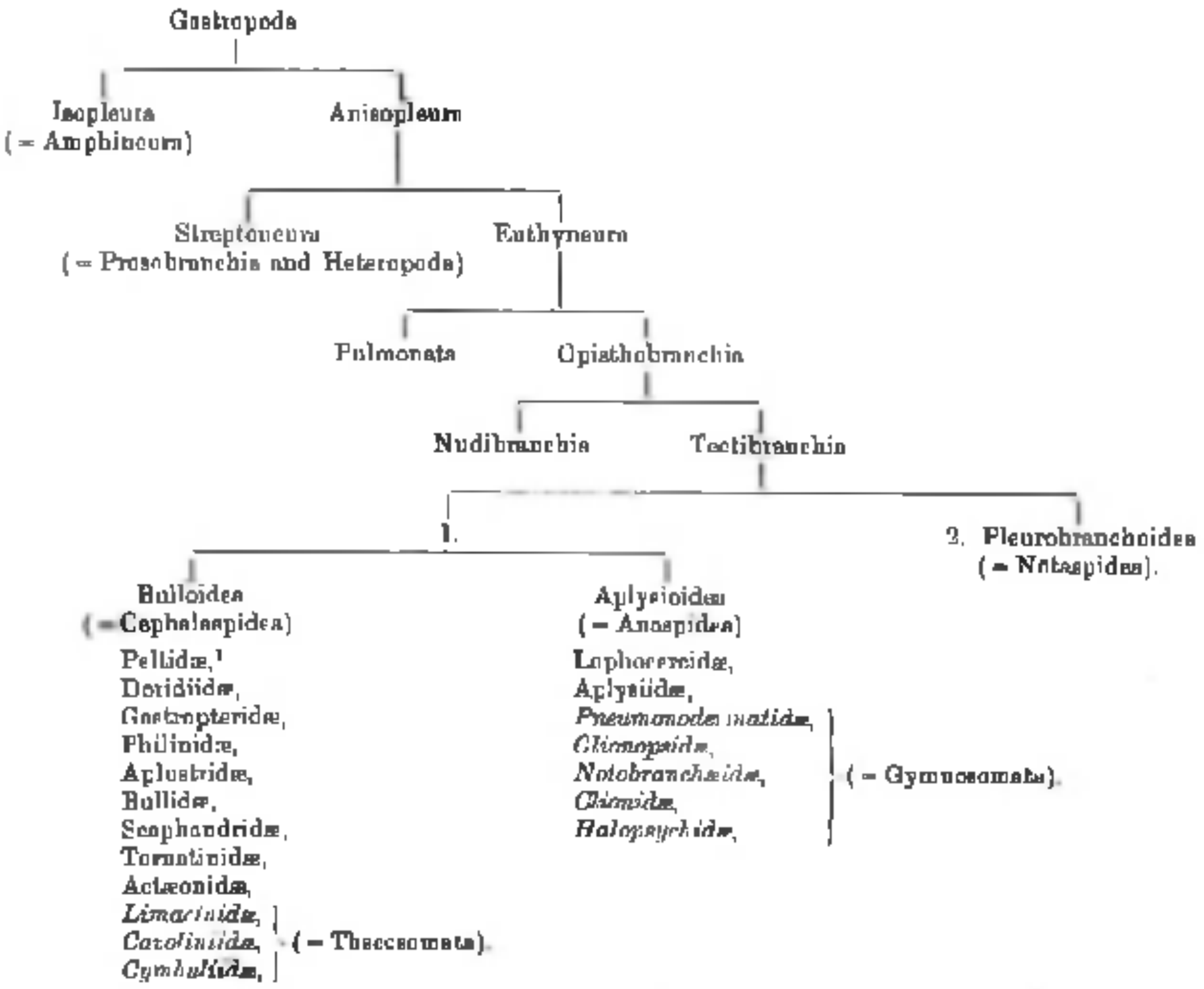
[1] Die Geruchsorgane und das Nervensystem der Mollusken, *Zeitschr. f. wiss. Zool.*, Bd. xxxv. p. 343.

TABLE SHOWING PROPOSED CLASSIFICATION OF PTEROPODA.



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[1] All the authors who allude to this family (Woodward, A Manual of the Mollusca, p. 187; Bronn, Die Klassen und Ordnungen des Thierreichs, Bd. iii. p. 795; Vayssière, Recherches zoologiques et anatomiques sur les Mollusques Opistobranches du Golfe de Marseille, *loc. cit.*, p. 104; Fischer, Manuel de Conchyliologie, p. 573) have regarded these Mollusca as Pleurobranchidæ. They are, however, true Bulloidea, as is shown by the conformation of the head, of the generative organs, and of the nervous system.

PLATE I.

Fig. 1. *Limacina helicina.*

Fig. 1. Head seen from the right side; *a*, right tentacle; *b*, fin; *c*, tentaculiform lobe of the fin; *d*, posterior lobe of the foot; *e*, columellar muscle; *f*, mantle; *g*, "balancer," or lateral lobe of the mantle; *h*, genital opening; *i*, seminal groove.

Fig. 2. *Limacina lesueuri.*

Fig. 2. Dorsal view, with the penis (*c*) evaginated; *a*, the head, with two tentacles and the seminal groove; *b*, "balancer"; *c*, penis.

Fig. 3. *Limacina helicina.*

Fig. 3. View from the right side, the mantle, as also the heart and kidney, having been removed from that side; *a*, fin; *b*, posterior lobe of the foot; *c*, buccal mass; *d*, œsophagus; *e*, one of the four large stomachal plates; *f*, the posterior dorsal azygous plate; *g*, intestine; *h*, anus; *i*, gonad or genital gland; *j*, genital duct; *k*, accessory genital glands; *l*, seminal groove; *m*, columellar muscle; *n*, pallial cavity; *o*, central nervous system.

Fig. 4. *Limacina lesueuri.*

Fig. 4. The evaginated penis, seen from the right side.

Fig. 5. *Limacina helicina.*

Fig. 5. Dorsal view; *a*, "shield" or pallial gland; *b*, kidney; *c*, heart, visible owing to the transparency of the mantle.

Fig. 6. *Actæon tornatilis.*

Fig. 6. Dorsal view; *a*, *b*, *c*, as in fig. 5; *d*, cephalic hood.

Figs. 7, 8. *Limacina helicina.*

Fig. 7. Central nervous system, seen from the left side; *a*, buccal mass; *b*, œsophagus; *c*, cerebral ganglion; *d*, cerebral commissure; *e*, pedal ganglion; *f*, right visceral ganglion; *g*, left visceral ganglion; *h*, otocyst; *i*, tentacular nerve; *j*, nerve to the fin; *2*, *3*, visceral nerves; *4*, left pallial nerve.

Fig. 8. Central nervous system, seen from the ventral side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, right visceral ganglion; *d*, left visceral ganglion; *e*, otocyst; *f*, nerve to the fin; *1*, right pallial nerve; *2*, *3*, visceral nerves; *4*, left pallial nerve.

Figs. 9–12. *Peraclis reticulata.*

Fig. 9. Dorsal surface of the head; *a*, head with the tentacles; *b*, fin; *c*, posterior lobe of the foot; *d*, operculum.

Fig. 10. Pallial gland seen from within.

Fig. 11. Distal extremity of the genital duct, seen from the right side; *a*, genital aperture; *b*, muciparous gland; *c*, albuminiparous gland; *d*, vesicula seminalis.

Fig. 12. Central nervous system, seen from the ventral surface; the cerebral commissure having been divided and the cerebral ganglia reflected ventrally; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, right visceral ganglion; *d*, azygous median visceral or abdominal ganglion; *e*, left visceral ganglion; *f*, otocyst; *g*, cerebral commissure; *h*, cephalic nerve; *i*, nerve to the fin; *1*, right pallial nerve; *2*, *3*, visceral nerves; *4*, left pallial nerve.

PLATE II.

Fig. 1. *Clio striata.*

Fig. 1. View from the right side, the mantle, as also the heart and kidney, having been removed from that side; *a*, fin; *b*, posterior lobe of the foot; *c*, right tentacle; *d*, pallial cavity; *e*, buccal mass; *f*, œsophagus; *g*, one of the anterior gastric plates; *h*, posterior azygous gastric plate; *i*, intestine; *j*, bile duct; *k*, genital gland; *l*, genital duct; *m*, accessory genital glands; *n*, distal part of the genital duct; *o*, genital aperture; *p*, penis; *q*, orifice of the penis; *r*, position occupied by the liver.

Fig. 2. *Clio pyramidata.*

Fig. 2. Pallial gland, seen from behind.

Fig. 3. *Bulla (Haminea) hydatis.*

Fig. 3. Dorsal aspect, the mantle having been split and reflected to the left side; *a*, cephalic head; *b*, parapodium; *c*, point up to which the mantle has been divided along the dotted line; *d*, pallial or hypobranchial gland; *e*, gill; *f*, lateral lobe of the mantle; *g*, anus; *h*, anal gland; *i*, spermatic groove; *j*, genital aperture.

Fig. 4. *Clio striata.*

Fig. 4. Pallial gland, seen from behind.

Fig. 5. *Clio acicula.*

Fig. 5. Stomach opened along the dorsal side; *a*, œsophagus; *b*, the eight small anterior gastric plates; *c*, the four large plates; *d*, the posterior azygous ventral plate; *e*, commencement of the intestine.

Fig. 6. *Cuvierina columnella.*

Fig. 6. The cervical region opened from below; *a*, fin; *b*, posterior lobe of the foot; *c*, buccal mass; *d*, central nervous system; *e*, œsophagus; *f*, diaphragm.

Figs. 7, 8. *Clio pyramidata.*

Fig. 7. Anterior portion, seen from the left side; *a*, fin; *b*, posterior lobe of the foot; *c*, left tentacle; *d*, accessory genital gland; *e*, anus; *f*, anal gland; *g*, intestine; *h*, liver.

Fig. 8. Ventral aspect of the heart and kidney, the latter having been reflected towards the left side; *a*, ventricle; *b*, auricle; *c*, pericardium; *d*, kidney; *e*, opening from the kidney into the pallial cavity; *f*, communication between the kidney and pericardium.

Fig. 9. *Clio.*

Fig. 9. Transverse section through the central nervous system; *a*, cerebral ganglion; *b*, pleural ganglion; *c*, visceral ganglionic mass; *d*, otocyst with otoliths; *f*, œsophagus.

Fig. 10. *Cuvierina columnella.*

Fig. 10. Central nervous system, seen from the left side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, left visceral ganglion; *e*, otocyst; *f*, cerebral commissure; *g*, tentacular nerve; *h*, *i*, visceral nerves; *k*, left pallial nerve.

Fig. 11. *Actæon tornatilis.*

Fig. 11. Central nervous system, seen from the dorsal side; *a*, cerebro-pleural ganglion; *b*, pedal ganglion; *c*, right anterior visceral or supraintestinal ganglion; *d*, abdominal or posterior visceral ganglion; *e*, left anterior visceral or subintestinal ganglion; *f*, genital (accessory) ganglion; *g*, osphradium; *h*, buccal or stomato-gastric ganglion; *i*, cerebral commissure; *j*, cerebro-pedal connective; *k*, cerebro-pleural connective; *l*, pedal commissure; *m*, second pedal commissure; *n*, nerve to the penis.

PLATE III.

Fig. 1. *Cuvierina columnella.*

Fig. 1. Central nervous system, from the ventral surface; *a*, pedal ganglion; *b*, right visceral ganglion; *c*, left visceral ganglion; *d*, otocyst; *e*, second pedal commissure; *1*, right pallial nerve; *2*, *3*, visceral nerves; *4*, left pallial nerve.

Fig. 2. *Cavolinia longirostris.*

Fig. 2. Ventral aspect, the mantle having been removed from this side; *a*, retractor or columellar muscle; *a'*, its left anterior branch; *b*, fin; *c*, œsophagus; *d*, stomach; *e*, intestine; *f*, liver; *g*, genital gland; *h*, vesicula seminalis; *i*, accessory genital glands; *j*, genital duct.

Fig. 3. *Cavolinia quadridentata.*

Fig. 3. Ventral aspect of the digestive tract; *a*, buccal mass; *b*, salivary gland; *c*, œsophagus; *d*, stomach; *e*, cæcum; *f*, intestine; *g*, right lobe of the liver; *h*, its duct; *i*, left lobe of the liver; *j*, its duct.

Fig. 4. *Cavolinia inflexa.*

Fig. 4. Generative organs, seen from the right side; *a*, genital gland; *b*, genital duct; *c*, vesicula seminalis; *d*, accessory genital glands; *e*, genital orifice; *f*, spermatic groove.

Fig. 5. *Cavolinia trispinosa.*

Fig. 5. Horny spicule from the penis.

Fig. 6. Limacinidæ and Cavoliniidæ.

Fig. 6. Comparative diagrams of the organisation of the Limacinidæ and Cavoliniidæ, the animals being seen from the cephalic extremity.—A, Limacinidæ; B, Cavoliniidæ. The following letters have the same significance in the two diagrams; *a*, œsophagus; *b*, stomach; *c*, bile duct; *d*, posterior azygous gastric plate; *d'*, anus; *e*, origin of the genital duct; *f*, genital orifice; *g*, pallial gland (shield); *h*, pallial cavity.

Fig. 7. *Cymbulia peroni.*

Fig. 7. Anterior aspect, the fin having been cut through ventrally and laterally; *a*, head with the two tentacles; *b*, fin; *c*, "shell"; *d*, pallial cavity; *e*, visceral mass and anus; *f*, pallial gland (shield).

Figs. 8–11. *Cymbulia.*

Fig. 8. *a*, Pallial gland; *b*, outline of the shell.

Fig. 9. Ventral aspect of the generative organs, the accessory glands being reflected to the left side; *a*, genital gland; *b*, genital duct; *c*, receptaculum seminis; *d*, muciparous gland; *e*, albuminiparous gland; *f*, genital orifice.

Fig. 10. Ventral aspect of the central nervous system; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, right visceral ganglion; *d*, posterior visceral or abdominal ganglion; *e*, left visceral ganglion; *f*, otocyst; *g*, nerves to the fin; *1*, right pallial nerve; *2*, *3*, visceral nerves; *4*, left pallial nerve.

Fig. 11. Lateral view of the central nervous system; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, right visceral ganglion; *d*, posterior visceral or abdominal ganglion; *e*, cerebral commissure; *f*, otocyst; *g*, nerves to the fin; *h*, œsophagus; *1*, left pallial nerve; *2*, *3*, visceral nerves.

Fig. 12. *Gleba cordata.*

Fig. 12. Anterior view of the larva; *a*, buccal aperture; *b*, penis; *c*, posterior lobe of the foot.

PLATE IV.

Figs. 1, 2. *Cymbulia.*

Fig. 1. Central part of the animal, seen from the right side as a transparent object; *a*, "shell"; *b*, truncated fin; *c*, posterior appendage of the fin, cut short; *d*, space between this appendage and the shell; *e*, pallial gland; *f*, entrance of the pallial cavity; *g*, mouth; *h*, visceral mass; *i*, anus; *j*, genital orifice, followed by the spermatic groove leading to the penis; *k*, aperture of the penis; *l*, lumen of the kidney; *m*, aperture leading from the kidney into the pallial cavity; *n*, heart; *o*, central nervous system; *p*, pallial cavity.

Fig. 2. Stomato-gastric nervous system, seen from the left side; *a*, mouth; *b*, buccal mass; *c*, salivary gland; *d*, œsophagus; *e*, stomach; *f*, intestine; *g*, buccal ganglion; *h*, œsophageal nerve leading to *i*, the gastric plexus.

Figs. 3, 4. *Gleba.*

Fig. 3. *a*, Pallial gland; *b*, outline of the shell.

Fig. 4. Central nervous system, seen from the left side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, left visceral ganglion; *d*, posterior visceral or abdominal ganglion; *e*, cerebral commissure; *f*, otocyst; *g*, nerves to the fin; *h*, nerve to the retractor muscle of the proboscis; *i*, tentacular nerve; *j*, œsophagus; *3*, visceral (genital) nerve; *4*, left pallial nerve.

Fig. 5. *Notarchus.*

Fig. 5. Sagital section of the buccal mass, from a sketch kindly presented by Dr. Vayssière; *a*, palatine teeth; *b*, right jaw; *c*, radula; *d*, mouth; *e*, œsophagus.

Fig. 6. *Dexiobranchæa.*

Fig. 6. Diagramatic sagittal section of the buccal mass; *a*, hook-sac; a', hook sac as found in *Pneumonoderma*; *b*, jaw; *c*, radula; *d*, mouth; *e*, œsophagus.

Fig. 7. *Pneumonoderma.*

Fig. 7. Transverse section of the dorsal patch; *a*, epithelium; *b*, large glandular cells; *c*, small central glandular cells.

Fig. 8. *Spongiobranchæa.*

Fig. 8. Dorsal view of the generative organs; *a*, genital gland; *b*, genital duct; *c*, muciparous gland; *d*, albuminiparous gland; *e*, receptaculum seminis; *f*, genital orifice.

Fig. 9. *Pneumonoderma.*

Fig. 9. Ventral view of the central nervous system, the cerebral commissure having been divided and the cerebral ganglia reflected ventrally; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, right visceral ganglion; *e*, buccal ganglion; *f*, cerebro-pleural connective; *g*, cerebro-pedal connective; *h*, pleuro-visceral connective; *i*, cerebro-buccal connective; *j*, nerve from the pleural ganglion; *k*, pedal commissure; *l*, second pedal commissure; i., nerve to the foot; ii., nerve to fin; iii., iv., lateral pedal nerves; v., vi., vii., cervical nerves; *1*, nerve from the right visceral ganglion; *2*, *3*, median nerves from the left visceral ganglion; *4*, lateral nerve from the left visceral ganglion.

Fig. 10. *Clionopsis.*

Fig. 10. Ventral view of the osphradium; *a*, osphradium; *b*, nerve ramifying in the osphradium; *c*, anus; *d*, opening of the kidney; *e*, cloacal depression.

PLATE V.

Fig. 1. *Pneumonoderma.*

Fig. 1. **Dorsal view of the central nervous system**; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, visceral ganglion; *e*, cerebro-pedal connective; *f*, cerebro-pleural connective; *g*, pleuro-visceral connective; *h*, olfactory nerve; *i*, optic nerve; *j*, nerve to the acetabuliferous appendage; *k*, nerve to the anterior tentacle; *l*, labial nerve.

Fig. 2. *Dolabella neapolitana.*

Fig. 2. Central nervous system, seen from the right side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, right visceral ganglion; *e*, cerebro-pedal connective; *f*, cerebro-pleural connective; *g*, pleuro-visceral connective; *h*, œsophagus.

Fig. 3. *Spongiobranchæa.*

Fig. 3. Central nervous system seen from the left side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, left visceral ganglion; *e*, cerebro-pedal connective; *f*, cerebro-pleural connective; *g*, pleuro-visceral connective; *h*, otocyst; *i*, auditory nerve; *j*, cerebro-buccal connective; *3*, genital nerve; *4*, lateral nerve from the left visceral ganglion.

Fig. 4. *Clione limacina.*

Fig. 4. Ventral aspect of the anterior portion; *a*, evaginated proboscis; *b*, evaginated hook-sacs; *c*, buccal cone; *d*, anterior tentacle; *e*, fin; *f*, lateral lobe of the foot; *g*, posterior lobe of the foot.

Figs. 5–7. *Clione.*

Fig. 5. Anterior region, seen from the right side, in order to show the visceral openings; *a*, anterior tentacle; *b*, head; *c*, foot; *d*, fin cut off at its origin; *e*, anus; *f*, aperture of the kidney; *g*, genital aperture; *h*, spermatic groove; *i*, orifice of the penis; *j*, osphradium.

Fig. 6. Osphradium and its nerve supply, seen from the right side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, pleural ganglion; *d*, right visceral ganglion; *e*, osphradium; *f*, œsophagus; *g*, anus; *h*, opening of the penis; *i*, lateral lobe of the foot; *j*, posterior lobe of the foot.

Fig. 7. Transverse section of the osphradium; *a*, osphradial nerve; *b*, its sheath, continued by the connective envelope of the osphradium; *c*, ganglionic cells of the osphradium; *d*, sensory epithelium.

Figs. 8–11. *Halopsyche gaudichaudi.*

Fig. 8. Ventral aspect of the central nervous system; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, right visceral ganglion; *d*, posterior visceral or abdominal ganglion; *e*, left visceral ganglion; *f*, second pedal commissure; *g*, cerebral commissure; *h*, cerebro-pedal connective; *i*, otocyst; *j*, nerve to the buccal appendage; *k*, nerve and ganglion of the nuchal tentacle; *l*, nerves to the fin; *m*, nerve to the foot; *1*, *2*, *3*, *4*, visceral nerves.

Fig. 9. Oral view of the central nervous system; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, buccal ganglion; *d*, cerebro-pedal connective; *e*, cerebro-buccal connective; *f*, second pedal commissure; *g*, nerve and ganglion of the nuchal tentacle; *h*, nerve to the buccal appendage; *i*, nerve to the foot; *j*, nerves to the fin.

Fig. 10. Central nervous system, seen from the left side; *a*, cerebral ganglion; *b*, pedal ganglion; *c*, left visceral ganglion; *d*, posterior visceral ganglion; *e*, nerve to the buccal appendage; *f*, nerve and ganglion of the nuchal tentacle; *g*, nerves to the fin; *h*, otocyst; *3*, *4*, visceral nerves.

Fig. 11. Transverse section of the central nervous system passing through the visceral ganglia; *a*, cerebral ganglion; *b*, right visceral ganglion; *c*, posterior visceral or abdominal ganglion; *d*, left visceral ganglion; *e*, cerebral commissure; *f*, œsophagus.

ERRATUM IN PART LXVI.

Page 2, line 23, *for* "Opisthobranchiate" *read* "Tectibranchiate," and *vice versâ.*

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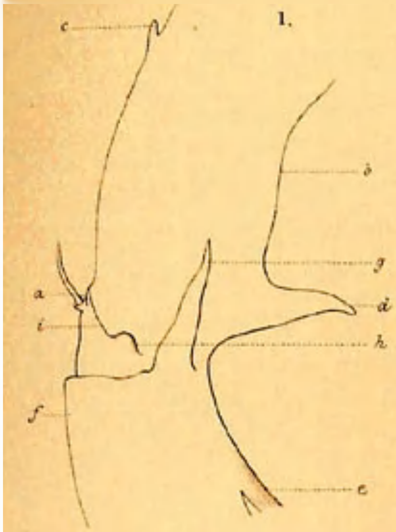

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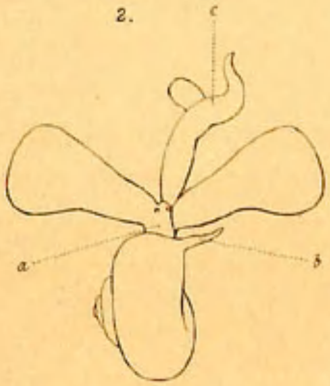

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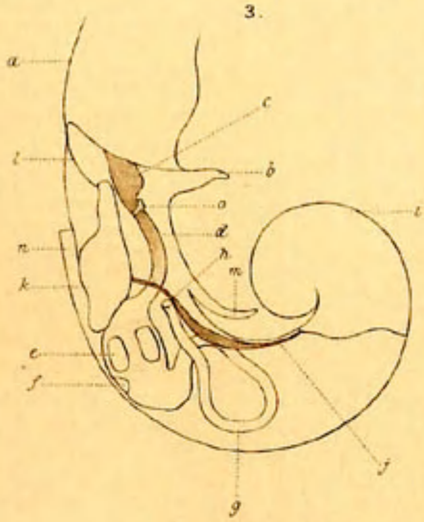

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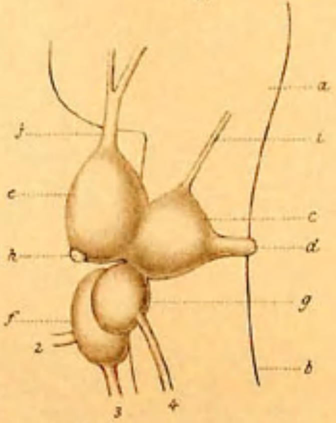

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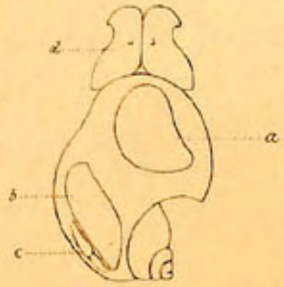

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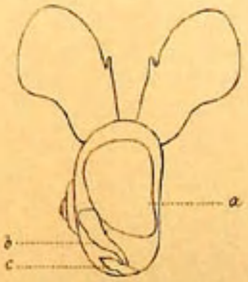

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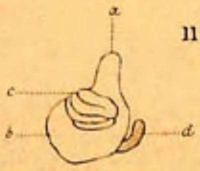

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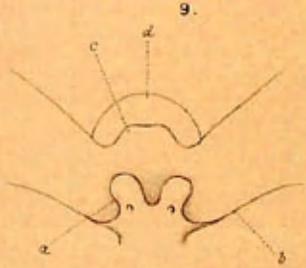

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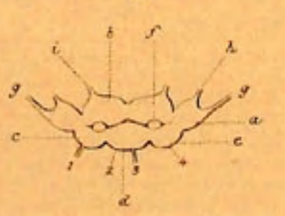

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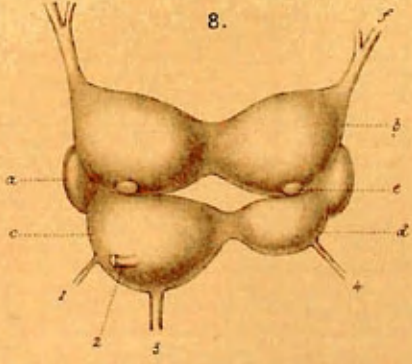

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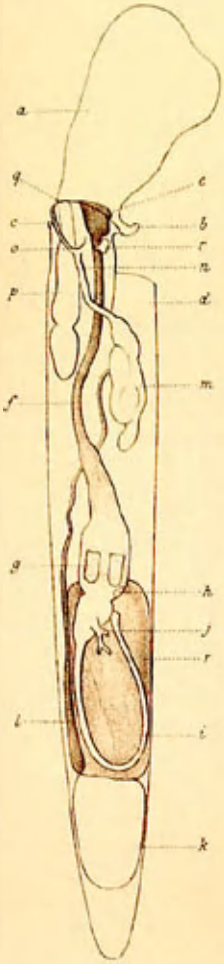

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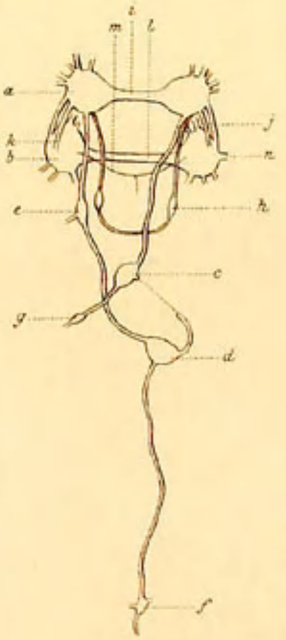

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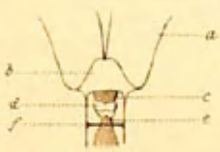

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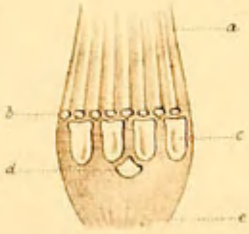

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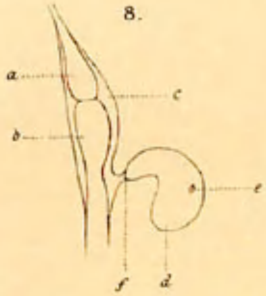

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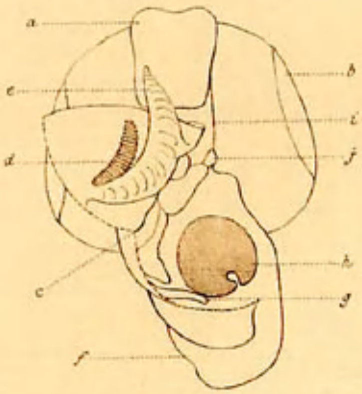

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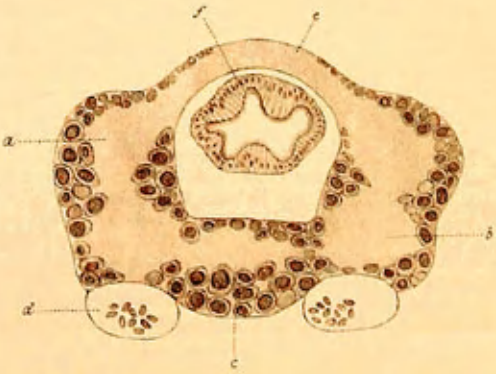

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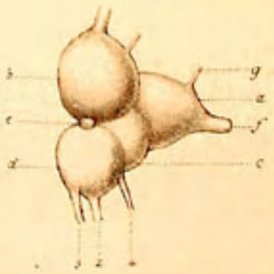

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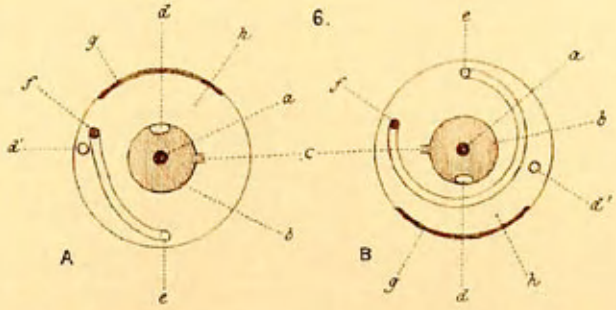

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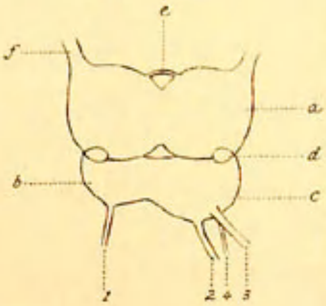

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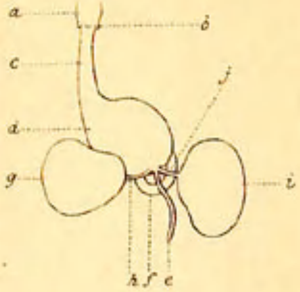

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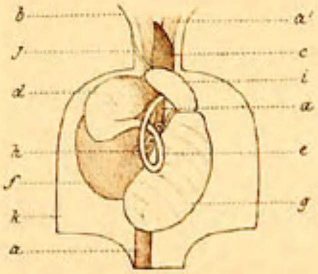

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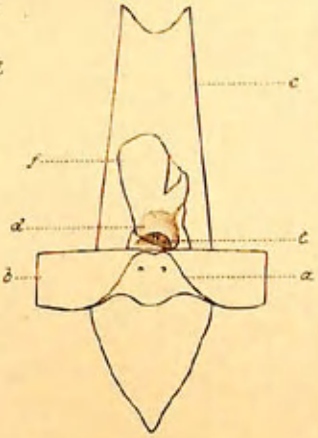

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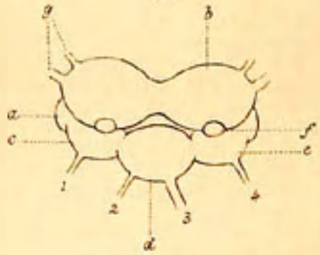

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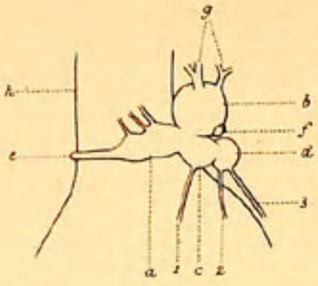

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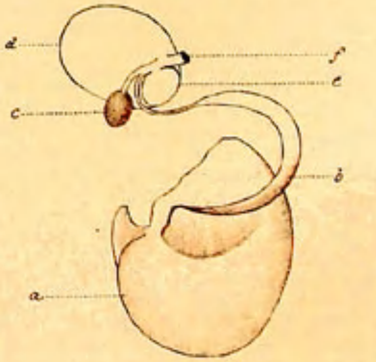

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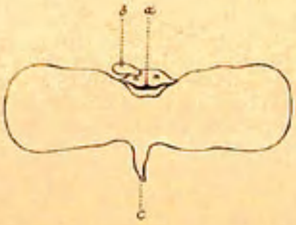

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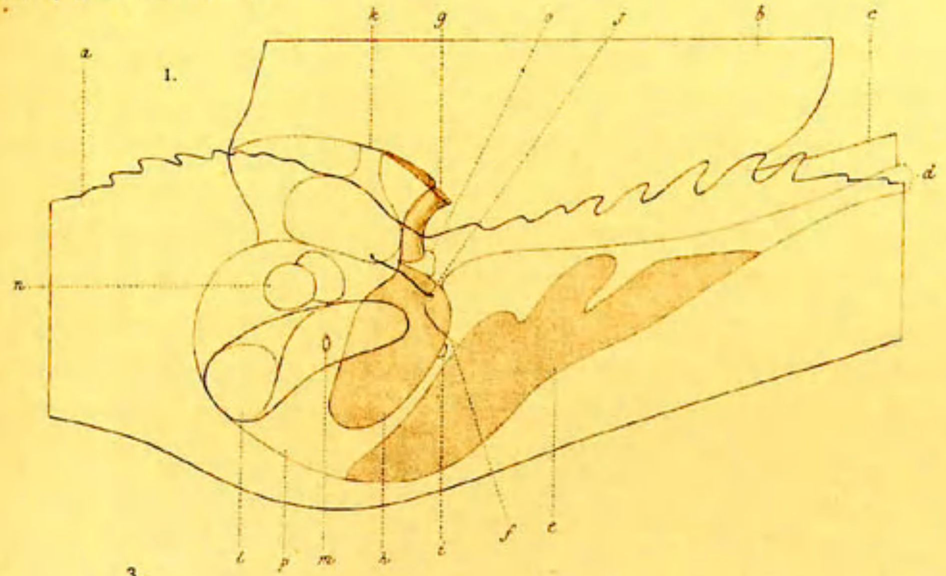

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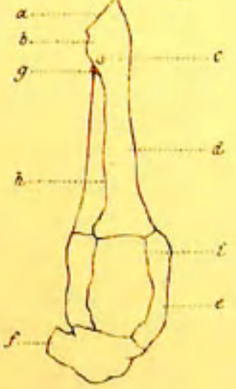

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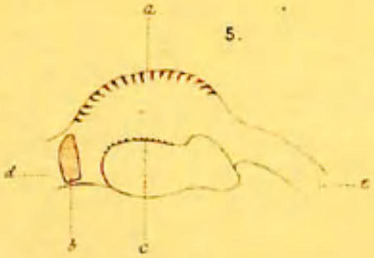

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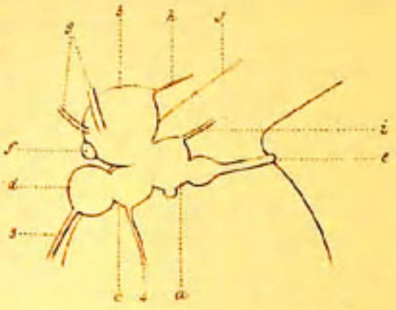

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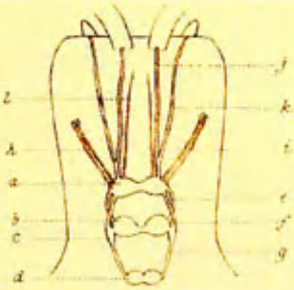

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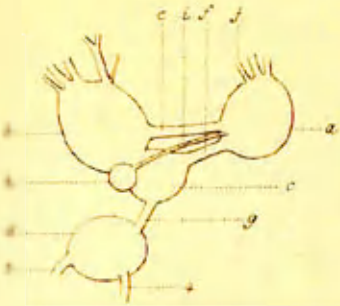

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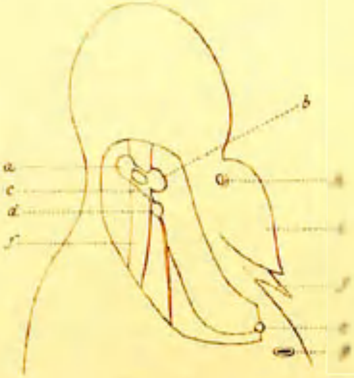

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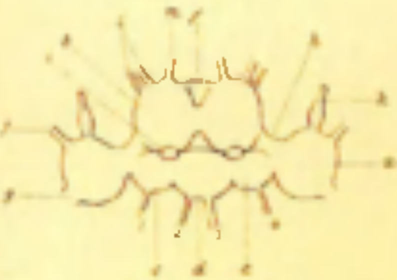

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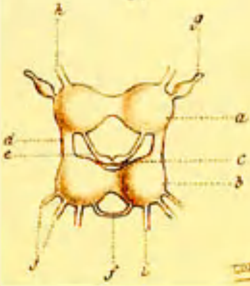

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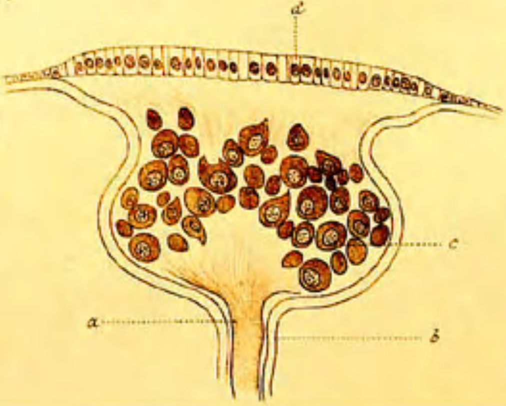

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