

THE STRUCTURE OF THE COLUMELLAR MUSCLE SYSTEM
IN *CLIO PYRAMIDATA* AND *CYMBULIA PERONI*
(THECOSOMATA, GASTROPODA)

WITH A NOTE ON THE PHYLOGENY OF BOTH SPECIES

by

TRUDY PAFORT-VAN IERSEL & S. VAN DER SPOEL

Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, The Netherlands

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RÉSUMÉ

La relation phylogénétique entre *Clio pyramidata* Linnaeus, 1767 et *Cymbulia peroni* De Blainville, 1818 a été étudiée en se fondant sur la structure de leurs systèmes musculaires. Des spécimens des deux espèces, récoltés dans l'Atlantique Nord et en Méditerranée, ont été coupés à 5 µm d'épaisseur et colorés au Hématoxiline-Eosine, Crossmon ou Azan à des fins histologiques, ou ont été étudiés entiers, soit par dissection, soit après les avoir rendus transparents. Le muscle columellaire et les muscles subectodermiques des parapodies des deux espèces ont été décrits. On en a conclu que *Clio* est néoténique car il se développe sans métamorphoses. L'asymétrie dans l'anatomie a prouvé que *Clio* et *Cymbulia* dérivent tous deux d'ancêtres spiralisés. Pour *Clio*, on a discuté de deux caractères primitifs, qui sont peut-être la conséquence de l'état larvaire de l'adulte, mais qui affirment également la relation possible des mollusques avec un ancêtre du type Coelentéré. Des structures originales trouvées chez *Cymbulia* sont aussi envisagées sous l'aspect d'une relation phylogénétique entre Thécosomes et Coelentérés, et, parmi ces derniers, plus particulièrement les Conulata.

I. INTRODUCTION

Aberrant stages of the opisthobranch pteropod *Clio pyramidata* Linnaeus, 1767, have been described by Van der Spoel (1962, 1967, 1973) as developmental stages characterised by very small, anatomically not differentiated soft parts in full-grown shells. They develop by strobilation, probably as a result of unfavourable environmental conditions (Van der Spoel, 1973).

As far as is known, this strobilation of *Clio* is unique in the phylum Mollusca. The process in *Clio* seems to be comparable to strobilation in Annelida (Van der Spoel, 1973) or Coelenterata (Dr. H. Lemche, pers. comm.). In case strobilation in *Clio* is comparable to that in Annelida or Coelenterata, this may point to a convergence in evolution, a phylogenetic link, between pteropods and

ABSTRACT

The phylogenetic relation between *Clio pyramidata* Linnaeus, 1767, and *Cymbulia peroni* De Blainville, 1818, has been studied with regard to the structure of their muscle systems. Specimens of both species collected from the North Atlantic Ocean and the Mediterranean were sectioned 5 µm thick and stained with Haematoxylin-Eosin, Crossmon or Azan for histological purposes or they were studied as cleared dissected or entire animals. The columellar muscle and subectodermal wing muscles of both species are described. It is concluded that *Clio* shows neoteny since it develops without metamorphosis. The asymmetry in anatomy proves that both *Clio* and *Cymbulia* descend from spiralised ancestors. For *Clio* two primitive characters are discussed which may be due to the "larval stage" of the adult but which also affirm the possible relation of molluscs to a coelenterate-like ancestor. Original structures found in *Cymbulia* are also discussed in the light of a possible phylogenetic relation between Thecosomata and Coelenterata, more in particular Conulata.

annelids or coelenterates, or to an atavism in *Clio*.

It is generally accepted that Annelida and Prosobranchia share a common ancestor (cf. Borradaile et al., 1963; Vagvolgyi, 1967). The thecosomatous pteropods, to which *Clio* belongs, form a rather primitive group with special adaptations to their pelagic way of life, which probably descends from the primitive opisthobranch family Acteonidae (Minichev, 1967). In their turn the Opisthobranchia originated from the Prosobranchia, probably by polyphyletic lines (Purchon, 1968). A confirmation of the phylogenetic relations between *Clio* and Annelida seems to be presented by the process of strobilation.

Strong opposition to the theory that molluscs developed from annelids has been expressed by Beklemishev (1958), Boettger (1959), Hunter & Brown (1965), Odhner (1961) and Steinböck (1963), who argued either that segmentation as found in the mollusc *Neopilina* is a convergence or that *Neopilina* is not at the basis of molluscan phylogeny. Pteropods are not at the root of molluscan phylogeny either, and the arguments given by the above-mentioned authors should also hold good with regard to the phenomenon of strobilation. Vagvolgyi (1967) clearly explains that there exists a relation between molluscs and flatworms, as well as between molluscs and annelids.

Another fact pointing to a phylogenetic link between gastropods and annelids is the pattern of the columellar muscle system in the anterior part of the body of e.g. the opisthobranch *Cylichna* (cf. Lemche, 1956). In this gastropod a cross section of the head parts shows four quadrants each containing parts of the columellar muscle running longitudinally through the body. This situation resembles the structures found in annelids, where a cross section shows four quadrants, each of them with longitudinal muscles (Lemche, 1956). These quadrants are a reflection of the ontogenetical quadrants A, B, C, and D.

The above considerations led to the present study of columellar muscle systems in two thecosomatous species. The two species studied are: the euthecosomatous *Clio pyramidata*, showing strobilation, and the shell-less *Cymbulia peroni* De Blainville, 1810, belonging to the Pseudothecosomata (Van der Spoel, 1976a). The Gymnosomata

are left out of consideration as these are not directly related to the Thecosomata and as the columellar muscle is so strongly reduced here that it is not to be expected to be worth while, from a phylogenetic point of view, to study this muscle in this paper.

Cymbulia has been selected as it was supposed to have a modified columellar muscle, because this species has no shell. The structure of these muscles in Thecosomata can throw light on the problem to what degree characters of the columellar muscle are adaptive. The position of the Pseudothecosomata among the pteropods has often been the subject of discussions because of their deviating features like the pseudoconch and the specialised foot-wing parts. At present it is assumed that the Pseudothecosomata developed from an unknown ancestor through *Peraclis*. This unknown ancestor is also supposed to have given rise to the Euthecosomata through *Limacina* (cf. Tesch, 1946).

In *Clio* two separate longitudinal muscle systems are found, one forming the columellar muscle and the other forming a muscle system in the mantle. In *Cymbulia* the real columellar muscle proved to be absent, while a striated muscle system in the mantle is very strongly developed. In the following description chiefly these two systems are compared and attention is given to the subectodermal muscles of the wings. With regard to the types of cells, three muscle tissues can be recognised (Van der Spoel, 1967), viz.: the smooth muscle tissue of the retractors, the striated subectodermal system and the doubly, obliquely striated intestinal muscle tissues. Pronounced differences in anatomy are linked with the presence or absence of the shell and with differences in wing movements for locomotion which holds especially good for the subectodermal muscle sheets and transversal structures in the wings.

II. ABBREVIATIONS

AF	anchoring muscle filaments
AMM	anterior mantle muscles
CM	columellar muscle
CS	central nervous system
CT	connective tissue threads
CTE	connective tissue envelope
D	diaphragm
E	oesophagus
ECP	envelope of central nervous system and penis
EP	epithelium
G	gonad

I	intestine
IBM	inner body muscle plate
J	jaw
L	liver
LCM	left columellar muscle branch
LDLM	left dorsolateral muscle
LTR	large sustentacular elements
LVLM	left ventrolateral muscle
LWM	longitudinal wing muscle
M	mantle
MDVL	dorsoventral to lateral muscle from the nuchal wall
MDVLPL	dorsoventral to lateral posterior footlobe muscle from the nuchal wall
MDVLR	dorsoventral to lateral muscle running to radula sack
MG	mantle gland
ML	medial connective tissue lamel in wing
MU	mucus
OBM	outer body muscle plate
P	protoconch
PE	penis
PLCM	primary left columellar muscle branch
PMM	posterior mantle muscle
PO	posterior footlobe
PR	penis retractor muscle
PRCM	primary right columellar muscle branch
R	radula
RCM	right columellar muscle branch
RDLM	right dorsolateral muscle
RM	radula muscles
RVLM	right ventrolateral muscle
SLCM	secondary left columellar muscle branch
SRCM	secondary right columellar muscle branch
SUW	subectodermal wing muscles
T	teloconch
TMF	transversal muscle fibres in wings
TMM	transversal mantle muscle
TR	transversal sustentacular elements
TRP	plates of transversal sustentacular elements
TWM	transversal wing muscles
V	visceral mass
W	wing

1-4	PLCM	first to fourth branch of the PLCM
1-4	PRCM	first to fourth branch of the PRCM
1-4	SLCM	first to fourth branch of the SLCM
1-4	SRCM	first to fourth branch of the SRCM

III. MATERIAL AND METHODS

This study is based on adult specimens in either the male or female phase. All specimens (see table I) used for histological and microanatomical studies were preserved in 70% ethanol. Histological staining was executed on transversal, longitudinal and medial serial sections (5 μ m thick). Stains were applied according to the Haematoxylin-Eosin-, Crossmon- and Azan methods. Specimens used for dissecting and for the study of muscles in situ were slightly stained with methylene blue. A polarised light method was developed to investigate muscles, especially those of the columellar system, in situ in complete and in intact animals. The soft parts were slightly stained with Aliserin-RedS-Na₂SO₄, after which the specimens were made transparent with Clove Oil and after dehydration they were embedded in plastic (polyethylene). The polished plastic block with intact animal can be studied under a dissection microscope with polaroid filters. Only the cells of the columellar system and those of the visceral muscles treated in this way become polarising elements. The entire columellar muscle can be traced from its top to the very branches in the wings.

IV. RESULTS FOR *CLIO PYRAMIDATA*

For a description of the general anatomy of this species one is referred to Meisenheimer (1905), Tesch (1946) and Van der Spoel (1967). Muscles in *Clio* are of the normal type also found in coiled Opisthobranchia, though the body is straight. The shell is a straight tube, triangular in cross section. The side where the embryonic shell is found has been called apical, caudal or aboral side, but posterior seems the only correct indication; the oral

TABLE I
Material studied

Species	Expedition	Station	Position
<i>Clio pyramidata</i>	Deep Dump 106 Project	2-2M	38°53'N 72°03'W
<i>Clio pyramidata</i>	Deep Dump 106 Project	3-13B	38°40'N 71°51'W
<i>Clio pyramidata</i>	Ocean Acre Project	several stations	30°N 60°W
<i>Cymbulia peroni</i>	Dana Expedition	3980 ^I	23°26'S 03°56'E
<i>Cymbulia peroni</i>	Tridens Cruise 1972	2	47°N 06°W
<i>Cymbulia peroni</i>	Tridens Cruise 1972	7	39°N 20°W
<i>Cymbulia peroni</i>	U.S.S.I. Mediterranean Cruises ¹⁾	2-5A	41°12'N 07°11'E
<i>Cymbulia peroni</i>	U.S.S.I. Mediterranean Cruises	2-1P	40°44'N 06°20'E

¹⁾ U.S.S.I. = United States Smithsonian Institution.

side then becomes the anterior side. The footparts, transformed into a swimming apparatus at the anterior side of the body, are situated dorsally of the mouth.

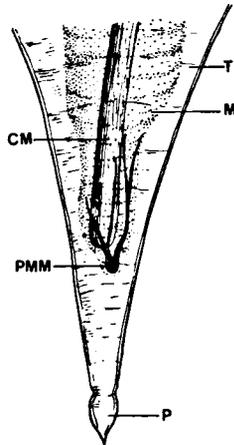


Fig. 1. Posterior shell part of *Clio pyramidata* with attachment of columellar and mantle muscles (for abbreviations see § II).

Columellar muscle

The columellar muscle has its origin in the posterior shell top, where the muscle tissues are fastened by connective tissue (fig. 1). The dorsal point of attachment is usually slightly asymmetrical and anterior to the attachment of the two most ventral mantle muscles. The whole posterior part of the smooth columellar muscle has a retractory function; it is a relatively large cylindrical bundle, dorsally of the visceral mass (fig. 2).

In the nuchal region posterior to the dorsal tentacles and wing bases, the columellar muscle penetrates the inner body and starts to split off branches. One branch runs towards the left wing (LCM) and one to the right wing (RCM) (fig. 3). The LCM and RCM first run parallel to the penis and oesophagus. In the head both muscles show a second dichotomous splitting into the first and second wing muscle at the right and left side (PRCM, SRCM, PLCM, and SLCM, respectively). Distally these muscles split off branches into the posterior footlobe and ventrolateral head wall; these muscles are indicated by the numerals 1 to 4. During the passage through the nuchal wall, when the RCM and LCM become situated in the interior of the neck, some fibres of the RCM and LCM

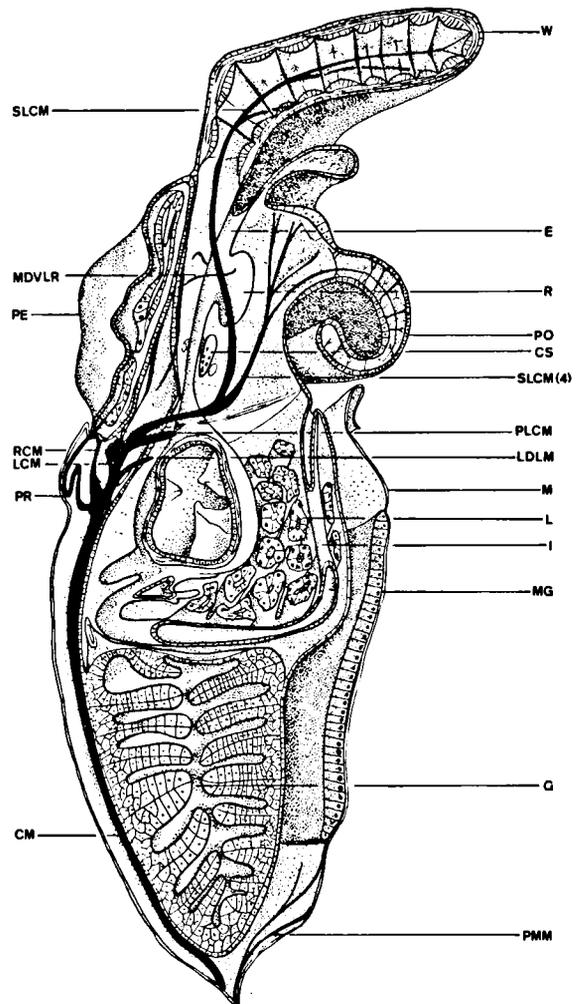


Fig. 2. Diagrammatic longitudinal section through the body of *Clio pyramidata* to show the course of the columellar muscle (for abbreviations see § II).

fuse with the nuchal wall and follow a posterior-anterior course. One group of these fibres takes a laterodorsal position (the LDLM and RDLM) and another group takes a more ventrolateral position (the LVLM and RVLM). At the place where the columellar system penetrates into the body, the character of the muscles in the body wall changes as follows: anteriorly to this place no smooth columellar muscles are found but posteriorly they do occur, as smooth fibres of the columellar muscle here penetrate in between the body-wall muscles.

The anatomy at the left and right side is slightly different because the RCM is larger than the LCM and it penetrates the body more anteriorly than

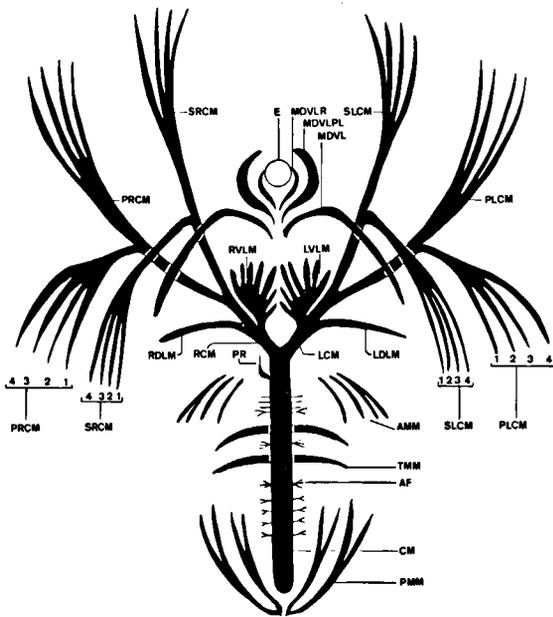


Fig. 3. Diagrammatic representation of the columellar and mantle muscle systems in *Clio* from ventral (for abbreviations see § II).

the LCM. After a rather central course this LCM shifts to the left in the upper nuchal region so that here both branches are running symmetrically (fig. 4A). The exact position of the LCM also depends on the temporary presence of the penis. Directly after penetration of the nuchal region, the muscle crosses the diaphragm.

The posterior part of the columellar muscle is rounded in cross section, but at the point of penetration into the body it becomes a flattened muscle band.

In males the penis is surrounded by a penial sac with muscle filaments of the body wall. However, as the columellar muscle penetrates here into the body, splitting off fibres to the body wall, also a connection between penis sac and columellar muscle is effected. Just before splitting off LCM and RCM, the penis retractor muscle proper splits off and penetrates the bottom of the penial sack to fix to the penis (fig. 2). In *Clio* the penis retractor is much less developed than in e.g. *Cavolinia* and *Cuvierina* (cf. Meisenheimer, 1905; Van der Spoel, 1967). In animals in the female stage the penis is thrown off and the penial sac is empty except for a remnant of the penis retractor at the bottom.

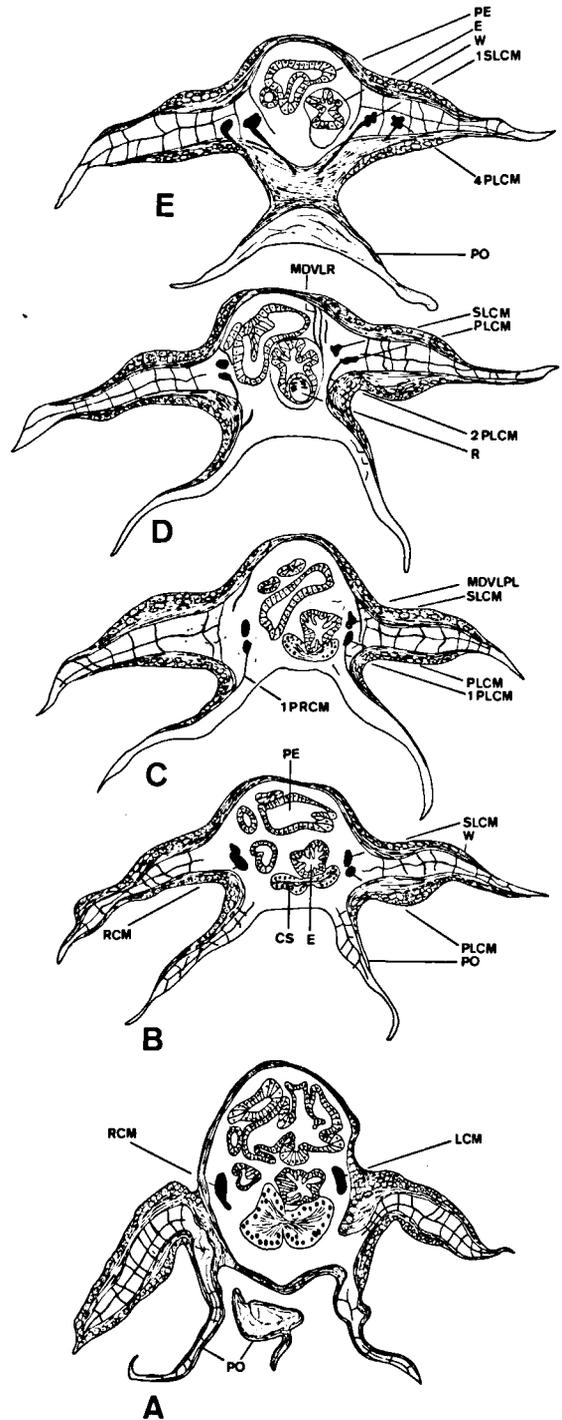


Fig. 4. Five transversal sections (A-E from posterior to anterior) through the posterior part of *Clio pyramidata* (♂) to show the course of the columellar muscles in this region (for abbreviations see § II).

Before entering the real wing lumen, the RCM and LCM each split off a branch, each of which gives off the four separate muscles 1-4. The 1 PRCM bends ventrad and runs to the lateral part of the posterior footlobe (fig. 4C). Some filaments originating from the dorsolateral body wall run parallel to this 1 PRCM. These are probably also filaments of the columellar system which had first penetrated the nuchal wall more posteriorly. These fibres are called the dorsoventral to lateral muscle (MDVL). In total there are three pairs of nuchal wall muscles which will be treated later on.

The second branch of the primary right columellar muscle (2 PRCM) runs nearly directly to the ventrolateral muscles of the wing base and it fixes on the wing epithelium. The third one (3 PRCM) shows the same course as the even more cranial muscle 4 PRCM. The main anterior branch of the PRCM continues its course into the wing lumen towards the wing tip.

Branching of the SRCM occurs more anteriorly than in the PRCM. All four lateral branches (1-4 SRCM) penetrate the subectodermal wall muscles and they attach on the ventrolateral wing epithelium. The 1 SRCM penetrates the right lip, the others run to the wing proper. The main anterior branch of the SRCM enters also the central wing lumen. When fanning out in the wings, the muscle bundles are anchored with numerous muscle cells to the epidermal layers of the wall of the wings (fig. 5).

At the left side nearly the same anatomy is found, though all points of branching are found more anteriorly.

At several places small muscle filaments of the columellar muscle penetrate the neighbouring tissues; this is especially evident along the retractory part beneath the diaphragm (fig. 6). Here a large number of small transversal filaments (AF) form a connection with the mantle integument lateral to the columellar muscle. The splitting off of branches in the penis sac and nuchal wall has been discussed above.

Nuchal wall muscles

The muscles originating from the nuchal wall and showing the cell structure of the columellar muscle cells have already been mentioned. They are proba-

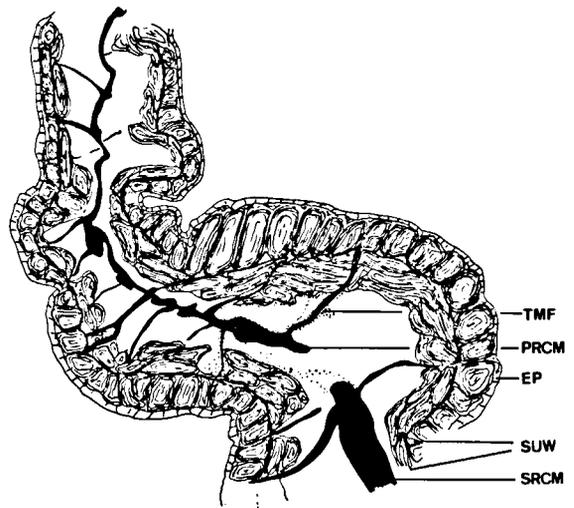


Fig. 5. Slightly diagrammatically drawn cross section through part of the right wing of *Clio pyramidata* (for abbreviations see § II).

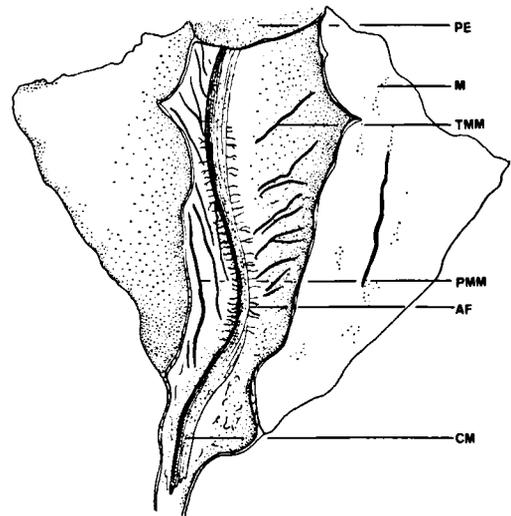


Fig. 6. Posterior part of the columellar muscle of *Clio pyramidata* after removal of the visceral mass to show the transversally running small fibres anchoring the muscle in the tissues (for abbreviations see § II).

bly comparable to the muscles of the cephalic shield in *Philine aperta* (Linnaeus, 1767) (cf. Brace, 1977a). They consist of:

- (1) The dorsoventral to lateral muscle running from the nuchal wall to the lateral parts of the posterior footlobe (MDVL). It originates in the dorsolateral part of the nuchal wall and runs exteriorly to the columellar muscle branches.
- (2) The dorsoventral to lateral muscle running

to the central parts of the posterior footlobe (MDVLPL). It originates in the dorsolateral part of the nuchal wall and runs interiorly to the columellar muscle branches.

(3) The dorsoventral to lateral radula muscle running to the radula sac (MDVLR). It originates from the central part of the nuchal wall and runs laterad of the penis.

These latter two muscles mix up with the muscles in the radula sac (fig. 2). The radula muscles can be considered the buccal retractor which is very weakly developed compared to the situation in other molluscs. In Euthecosomata the radula is reduced as the function of the whole buccal mass in the group has become less important because of the feeding methods applied. Reduction of the retractor is thus explained as well.

Mantle muscles

The system of smooth muscles in the mantle is rather variable in structure. It is always composed of small fibres not comparable to the dimensions of the columellar bundle. Fundamentally one can distinguish three groups which are chiefly concentrated at the ventral side of the mantle. In the posterior top of the mantle two relatively large ventral fibres are found originating in a lump of connective tissue fixed near the shell top (fig. 1). They run to the anterior mantle edge. In *Clio pyramidata* in total eight main mantle fibres are found: two large ventral ones, four smaller left and two smaller right ones (fig. 7). The origin

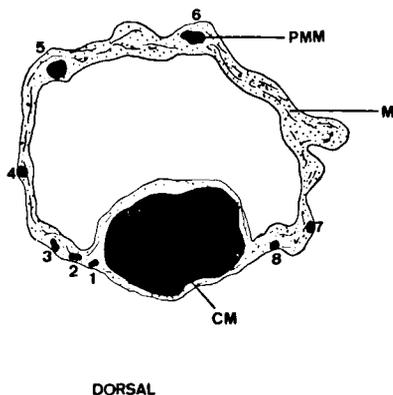


Fig. 7. Cross section through the posterior body tip of *Clio pyramidata* showing the columellar muscle and eight (1-8) mantle muscles (for abbreviations see § II).

of the six small muscles could not be traced exactly, probably the four left ones originate in the integument, and the two right ones may be connected with the columellar muscle. The two larger ventral muscles show constant ramification during their course ventral from the pallial gland to the edge of the mantle. The two muscles at the right side also run to the mantle edge but they ramify less intensively. The four left muscles ramify frequently but they do not run to the mantle edge as their direction becomes a more transversal one.

The second mantle muscle system also consists of muscles running in a longitudinal direction, but they originate near the posterior mantle edge and run halfway down the mantle. In *Clio polita* (Pelseneer, 1888) they are more numerous than in *C. pyramidata*. In *C. polita* five such fibres are found posteriorly at the right and four at the left side. The mantle muscles in *C. polita* all tend to take a more transversally directed course. In this species also a third system is present, probably derived from the normal longitudinal system, consisting of bands running from the median to the left and right side of the mantle.

In all *Clio* species a slight asymmetry in the orientation of mantle muscles is found.

Subectodermal muscles

Dorsally the two wings of *Clio* form a continuous plate which is connected in the middle with the nuchal wall. The ventral side of the wings is interrupted by the mouth with the lips and the posterior footlobe. The wings are thus situated dorsally of the mouth. Both the upper or dorsal and under or ventral wall of the wings are composed of epithelium with inside two well-developed layers of striated muscles. The inner layer runs longitudinally through the wing from the area of the head to the wing tip, the fibres of the outer layer cross the former perpendicularly. These two layers continue into the lateral sides of the posterior footlobe and into the dorsal nuchal area, although less strongly developed.

Muscles of the digestive system

The gizzard, oesophagus and radula are all surrounded by a single system of very compact ring muscles (Van der Spoel, 1967). Around the giz-

zard the transversal ring muscles are strongly developed. Anteriorly, at the ventral side, some small muscle branches which are connected to the radula, split off. Their function is related to the invagination and extrusion of the radula into the oesophagus lumen during feeding (Van der Spoel, 1967).

Besides the muscles from the nuchal wall which form a connection with the radula sac — buccal retractor — and with the posterior footlobe, there are also more diffuse fibres from the nuchal wall connected with the oesophagus, locally providing the digestive system with a stronger muscle layer.

V. RESULTS FOR *CYMBULIA PERONI*

For a general description of the anatomy of *Cymbulia* one is referred to Meisenheimer (1905) and Van der Spoel (1976a). The pseudothecosomatous *Cymbulia* is characterised by the lack of a calcareous shell, the visceral mass is surrounded by a cartilaginous pseudoconch. The wings, fused to a disc-like organ, are found in a horizontal plane above the pseudoconch and visceral mass. For a good understanding it should be pointed out that the tip of the slipper-like protoconch points dorsally, the flagellum between the wings points ventrally, the visceral mass is situated posteriorly or aborally from the swimming plate while the upper side of the plate is oral or anterior.

For a correct understanding of the differences between this and the preceding species, one should realise that the posterior or aboral tip which in *Clio* forms the protoconch tip, is situated in the nuchal wall area in *Cymbulia*. Coiling in the early ontogenetical stage brought this tip very close to the underside of the swimming disc, which resulted in a very anterior position of the origin of the retractor muscle. A complete columellar muscle, however, has not developed in this species which lacks a shell in adults. Yet, the retractor-like muscles found in the mantle are strongly developed; they run from an anterior origin in posterior direction. These muscles, considered by Meisenheimer (1905) to be the columellar muscle, actually are a kind of wing muscles in the mantle. The absence of a shell to attach muscles upon on the one hand, and the anterior position of the

phylogenetic aboral body pole on the other hand, induced the development of another structure for muscle attachment which is the connective tissue structure around the central nervous system, oesophagus and penis sac.

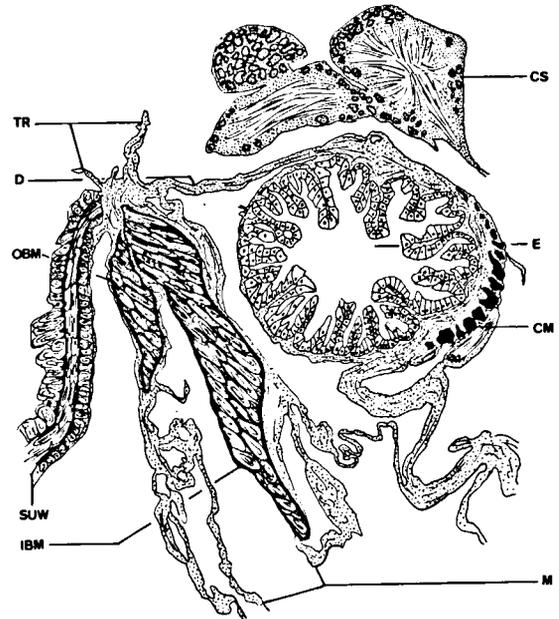


Fig. 8. Longitudinal section through the nuchal area of *Cymbulia peroni* showing the columellar muscle beside the oesophagus and the left two body muscle plates (for abbreviations see § II).

Columellar muscle

The columellar muscle is strongly reduced in *Cymbulia*. The body part consisting of head and wings is separated from the visceral mass by a diaphragm of solid connective tissue. Posterior of the diaphragm no trace of the columellar muscle system is found. Anterior of the diaphragm some columellar bundles run dorsad and dorsolaterad along with the oesophagus (fig. 8). At their aboral side the muscles are attached to the diaphragm and at the other side they split up to penetrate the surroundings of the mouth (fig. 9).

The penis is found in a cavity of the swimming disc and head, at the dorsal and dorsolateral side of the oesophagus. The penial cavity is connected with the diaphragm at the posterior side. At the left dorsolateral side a well-developed band of connective tissue forms a connection between the

penis and the wall of the penis cavity. Just like in *Clio*, bundles of the columellar muscle split off near the diaphragm to form the penis retractor muscle (fig. 10). Along the oesophagus the penis retractor with the columellar muscle form a separate system not directly connected with the wing muscles which are in all probability also derivates from original columellar muscle branches.

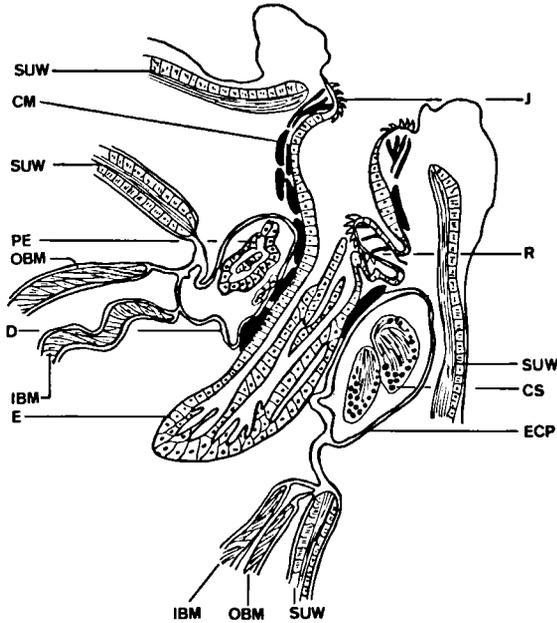


Fig. 9. Longitudinal section in the buccal region of *Cymbulia peroni* (for abbreviations see § II).

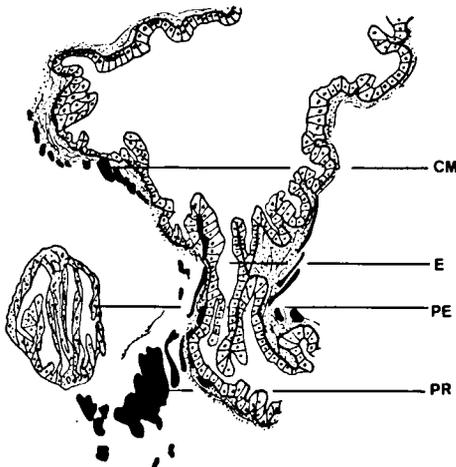


Fig. 10. Cross section through the head parts of *Cymbulia peroni* showing the penis retractor muscle splitting off from the columellar muscle (for abbreviations see § II).

The lumen of the wing disc is filled with thin reticulate connective tissue giving the wing disc its solidity, and being responsible for the anchoring of muscles and nerve fibres. The muscles in this lumen in between the connective tissue are of the same structure as those found alongside the oesophagus. Characteristic of *Cymbulia* is the fact that each muscle fibre is surrounded by a thick sheet of connective tissue. The muscle fibres in the lumen run in a crossing pattern, one system is running from dorsal to ventral, the other from left to right (fig. 11). Distally the muscles are fixed to the wall

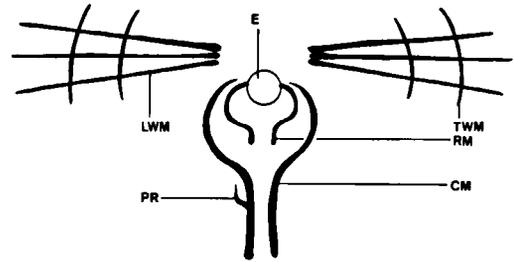


Fig. 11. Diagrammatic representation of the columellar muscle system in *Cymbulia* (for abbreviations see § II).

of the swimming disc. In the centre, near the head, the muscles originate from large supporting bars to which they are fixed (TRP, LTR in fig. 12).

These supporting bars surround the organ system of oesophagus, central nervous system and penis. Two large bars or plates and six somewhat smaller bars are symmetrically placed around the border of the diaphragm. Posteriorly they are inserted in the diaphragm and anteriorly into the subectodermal muscles of the wall of the wing. The supporting bars are composed of muscle filaments surrounded by connective tissue. They have ramifying ends at both sides. Beside the big bars smaller ones are found throughout the entire swimming disc, fixed in the walls aborally and orally. The smaller bars are in the middle also connected with the wing muscles where they touch each other (fig. 13).

Mantle muscles

The mantle integument is situated inside and outside the pseudoconch. As in *Clio* some small smooth muscles were traced in the mantle but they are so weakly developed that no pattern could be

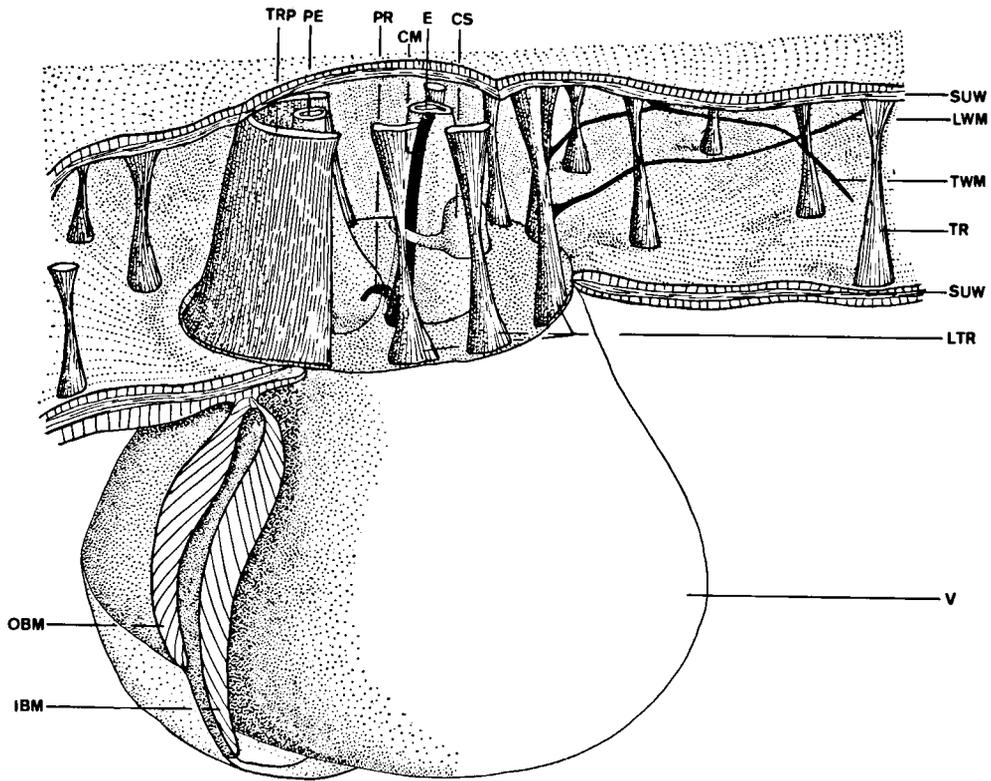


Fig. 12. Diagrammatic representation of the area around the oesophagus after removal of the ventral side of the swimming disc and mantle (for abbreviations see § II).

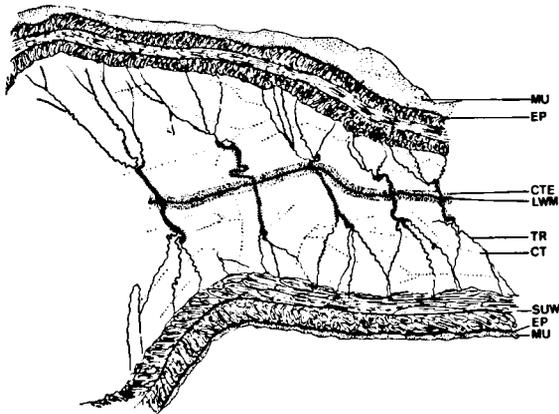


Fig. 13. Slightly diagrammatically drawn cross section through part of the swimming disc of *Cymbulia peroni* (for abbreviations see § II).

discovered. Besides these smaller muscles, however, a very strongly developed muscle system is found in the mantle, of which no homologous structure is found in *Clio*. These are the body muscle plates at the dorsolateral sides of the body. They originate from the most aborally situated

muscle layer in the wing. Both muscle plates form a double structure, probably one part is lying inside and the other outside the pseudoconch. They originate in the same point of the wing wall. The mantle cavity is asymmetrical, for at the right side it occupies a more dorsal position; the body muscle plates are likewise asymmetrical. The left muscle plate is found less dorsally than the right one. The mentioned asymmetry is correlated with the asymmetry of the osphradium which is only present at the right side close to the outer muscle plate, and the asymmetry of the visceral nerves: those at the right (innervating the osphradium) being much thicker than those at the left.

According to Meisenheimer (1905) the body muscle plates belong to the columellar system. The present findings, however, prove this to be incorrect. With regard to their cell structure and anatomy they are derivatives from the subectodermal muscles as discussed below. In a phylogeny based on the columellar muscle system the body muscle plates have to be neglected.

Subectodermal muscles

In *Cymbulia* the wall of the swimming disc consists of two well-developed layers of striated muscles. The structure and histology of these two layers is completely comparable to what is found in *Clio*. In an area of the aboral wall of the swimming disc, however, a third layer is found. This third layer of striated muscle fibres lies outside the two layers already mentioned, thus at the underside of the swimming plate. The body muscle plates originate from this third layer. The muscle fibres of the inner subectodermal layer run parallel to the border of the swimming plate, thus circumorally; the second layer consists of muscles running in radial directions, while the muscle fibres of the small aboral third (outer) layer run parallel to the axis of the visceral mass.

Muscles of the digestive system

The muscles associated with the alimentary duct are identical to those found in *Clio*: around gizzard, oesophagus and radula sac we find one system of circular muscles. Between the circular muscles and the dermis of the oesophagus a thin layer of longitudinal muscles is found. Additionally to this system several stronger muscle fibres (RM) connect the radula sac with the muscles near mouth and lips. The latter muscles, keeping the radula in position, are identical in structure to the columellar muscle bundles dorsally of the oesophagus; probably they belong to the same system but a direct connection between them could not be found.

Connective tissue in wings

In both species described, connective tissue is found in the wings around the muscle fibres. In *Clio* the quantity of this tissue is so small that no special attention has been given to it. In *Cymbulia*, however, the connective tissues are very well developed and at some places even more important than the muscles. This difference is mainly due to the difference in size and locomotive action of the wings in the two species. In *Clio* the relatively small wings execute strong beating during swimming. Muscles are strongly developed to enable the rigorous beats of more than 180°; at the same time the thick muscles, merely by their volume, keep the wing in shape. In *Cymbulia* the wings

are relatively thin and large and during locomotion the wings do not beat but they merely undulate. For this undulating movement no strong muscles are required, but to keep the large swimming disc in shape a strong sustentacular system of connective tissue is necessary. This system is realised by the thick connective tissue envelope around the smooth muscle fibres running longitudinally in the wing lumen and around those in the wing bars (fig. 14).

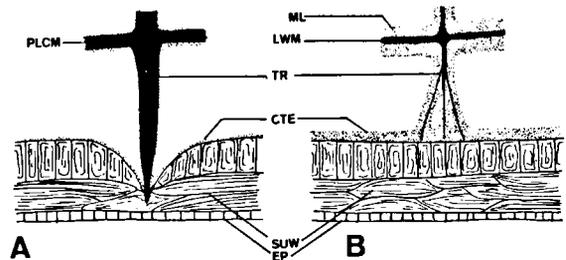


Fig. 14. Diagrammatic representation of a bar in the wing of *Clio pyramidata* (A) and of *Cymbulia peroni* (B) (for abbreviations see § II).

VI. DISCUSSION

Clio pyramidata

The mantle muscles and columellar muscle of *Clio pyramidata* are of the same histological structure and belong to the same system. The mantle muscles are attached posteriorly to the origin of the columellar muscle, which is a normal situation in spiralisated species, as shown by *Cylicbna* (cf. Lemche, 1956). It points to spiralisation in the ancestors of *Clio*. At the aboral side near the apex, shifted to the left, eight mantle muscles are present. The two large ventral mantle muscles are attached to the shell, the origin of the other six mantle muscles is not clear, possibly some of them originate from the columellar muscle as is also known for other Opisthobranchia (Brace, 1977a; Lemche, 1956). The muscles in the mantle have a retractor function while a more transversal course at some places may be related to the protection of organs like heart and kidney. The mantle muscles also promote the water current in the mantle cavity (Eales, 1949; Brace, 1977a).

Below the diaphragm, the dorsoanterior part of the strongly developed columellar muscle has a retractor function. Due to the straight shell, the retractor part is symmetrically situated with regard to body and shell.

There are few features in the anatomy of *Clio* pointing to an origin from spiralised ancestors. However, the asymmetry of the columellar muscle bundles in the nuchal region is one of these. In the wings and head parts no sign of asymmetry is found, which corresponds with spiralised species, where the asymmetrical organisation of the body does not influence the head parts (Eales, 1949).

In the head a ramifying pattern of eight columellar muscle bundles is found. Two ramifications fan out into each wing, while the other four bundles terminate in the posterior footlobe near the mouth. This division of muscles very strongly resembles the division of muscles over four body quadrants as found in coelenterates and worms. Besides having a retractor function, the sections of the muscle in the wing also contribute to the swimming movements, while the bundles in the head and posterior footlobe participate in food collecting. The subdivision into some smaller bundles in the head region increases the mobility in that part of the body (Brace, 1977a), which has also a positive effect on food collecting.

Anchorage of the columellar muscle by thin muscle filaments, originating from the columellar muscle and terminating in mantle integument, body wall and wing wall, is comparable with similar structures in other opisthobranchs like *Philina* (cf. Brace, 1977a) and *Cylichna* (cf. Lemche, 1956). The anchoring has a double purpose: all parts of the body become connected with the retractory system by these filaments, and the muscle is kept in position. In opisthobranchs there is a stronger development of body-wall musculature than in other gastropods, while the importance of the columellar muscle decreases. Especially in pteropods, considered to be the best swimming opisthobranchs, the striated musculature of the wing wall is very strongly developed (cf. Thompson, 1976) and in *Cymbulia* these muscles even take over the function of the columellar system.

As to conclude from the structure of the columellar system, *Clio* develops without metamorphosis. The full-grown still shows its larval muscles and larval stage. This conclusion is supported by the orientation of the mantle muscles somewhat left from the middle, and of the columellar muscle somewhat to the right in the nuchal

region of the body, and by the place of its origin in the shell. The mantle muscles have to be considered as the original right retractor muscle in the veliger of Opisthobranchia (Brown, 1934), which is turned to the left in Cavoliniidae by the 180° rotation of the body (Meisenheimer, 1905; Tesch, 1913; Bonnevie, 1914). In the same way the columellar muscle of *Clio*, orientated slightly to the right, resembles the left retractor muscle in the veliger of Opisthobranchia, running to the velum and operculum (into wings and posterior footlobe, respectively). It is also evident that the wings are homologous with the velum and not with the foot, from the fact that the wings are found apically and dorsally of the mouth, which would be impossible if foot structures were concerned. The sculpture of the shell also points to a direct development from a larval stage without metamorphosis. The fact that the full-grown adult is still in a larval stage can be considered a logical consequence of the identical pelagic behaviour of larva and adult (Van der Spoel, 1976a).

The asymmetrical orientation of the two columellar muscle ramifications in the nuchal region, the origin of the columellar muscle above the fastening of the mantle muscles and the trace of spiralisation in the soft parts of the larvae (Van der Spoel, 1967), point to the presence of spiralisation in the ancestors of *Clio*. Therefore, the external symmetry is an adaptation to the pelagic way of life and consequently of secondary nature. Thus there is no reason to doubt the commonly accepted theory, that within the Euthecosomata, Limacinidae-like species are the ancestors of the Cavoliniidae (Pelseneer, 1892; Tesch, 1904; Meisenheimer, 1905; Bonnevie, 1914; Van der Spoel, 1967; Minichev, 1967).

Cymbulia peroni

Distinctly different from *Clio* is the other genus studied: *Cymbulia*. The present investigations prove the lack of a columellar muscle aboral to the diaphragm. In *Cymbulia*, as is normal in Opisthobranchia, the loss of the shell is coupled with the loss of the retractory and attaching part of the columellar muscle (Lang, 1900). The forming of a secondary gelatinous shell did involve the development of secondary attaching muscle systems,

the body muscle plates. These body muscle plates develop from an outer striated muscle layer of the wing wall. They are not attached to the pseudoconch, but terminate in the mantle integument (Meisenheimer, 1905; Van der Spoel, 1976b). The body muscle plates are doubly folded; the median parts are situated inside the pseudoconch, the lateral parts probably outside, in the external mantle integument. Some bundles of rudiments of the columellar muscle still present above the diaphragm run from the diaphragm dorsally along the oesophagus towards the mouth region, as in the tectibranch *Philine* (Brown, 1934; Hurst, 1965; Brace, 1977a) and in *Berthella* (cf. Brace, 1977c) where these bundles are considered buccal retractor muscles. Like in *Clio* the penis retractor ramifies from this part of the columellar system. Obviously the part of the columellar muscle close to the oesophagus is functionally involved in the internal food transport.

Part of the columellar system runs in the wing lumen enclosed between the walls of the wing, contributing to the swimming locomotion of *Cymbulia*. The columellar muscle filaments in the wings are connected with numerous supporting bars in between the walls of the wings. The latter maintain the shape of the large wing disc. Two little plates of supporting bars found lateral to the penis have besides a supporting function, probably also something to do with the evagination of the penis, because of their relatively large quantity of muscle filaments. These supporting "walls" and the large supporting bars are ventrally and laterally attached to the diaphragm, forming a protecting envelope around oesophagus, ganglia and penis, also separating the wing disc from the rest of the body.

The strongly developed striated muscles of the wall of the wing disc contain anteriorly two layers and posteriorly three layers. The body muscles originate from the third posterior layer.

In *Cymbulia* a metamorphosis occurs during which, among other changes, the larval shell is thrown off (Thiriott-Quévieux, 1970). There are no strong indications that the reduced columellar muscle system did develop from a larval system, as supposed for *Clio*. However, in *Cymbulia* too, there is no difference between the pelagic way of life of larva and adult.

Some features also point in the direction of spiralised ancestors; for *Cymbulia*, the external symmetry is secondary. For example, on the right side the mantle cavity penetrates further dorsally (Meisenheimer, 1905); the position of the body muscle plates is asymmetrical; one osphradium is present on the right side; the embryonic shell is ultra-dextral (Pelseener, 1891). The present investigations do not contradict the commonly accepted theory that the ancestor of *Cymbulia* is a *Peraclis*-like species (Meisenheimer, 1905; Bonnevie, 1914; Tesch, 1948; McGowan, 1968).

Phylogeny

In *Clio* the columellar muscle is a strongly developed larval muscle system, whereas in *Cymbulia* the columellar muscle is reduced, greater parts have even disappeared.

It seems that the adaptation to a pelagic way of life of adults in Thecosomata has been realised in two different ways. In *Clio* adaptation consists of the absence of real metamorphosis (neoteny) with retention of the shell. In *Cymbulia* the adaptation is realised by replacement of the calcareous shell by a gelatinous pseudoconch together with retention of metamorphosis. The loss of a real columellar muscle in the latter is a consequence of the loss of the shell. Changes in body shape also influence the columellar system and in *Cymbulia* the head-foot parts have been shifted into a position perpendicular, dorsoventral, to the body axis so that the columellar muscles no longer could follow one united straight course. *Clio* and *Cymbulia* represent different lines of development; the Pseudothecosomata seem to be more adapted to pelagic life and thus they represent the most progressive group among the Thecosomata. The Euthecosomata and Pseudothecosomata are supposed to be related by means of an unknown ancestor which gave rise to *Limacina*- and *Peraclis*-like groups, respectively (Meisenheimer, 1905; Tesch, 1913, 1948; Van der Spoel, 1976b). The unknown ancestor could very well have been a very small opisthobranch without gills, as postulated by Brace (1977b).

In *Clio pyramidata* two facts need special attention. First there is the strobilation, comparable with the strobilation in Annelida and Coelenterata. Secondly we see in both mantle and head a pattern of eight muscles of the columellar system. The

posterior parts can be divided into four ontogenetical quadrants, each with two ramifications of the columellar muscle (right wing, left wing, right part of posterior footlobe, left part of posterior footlobe). This situation resembles that in *Cylichna* (cf. Lemche, 1956) and suggests a phylogenetic relation with the Coelenterata. According to Lemche (1966), the eight (larval) muscles show that the molluscs must be derived from a primitive tetracyclomeric type of organism like a coelenterate and that "from Molluscan-like ancestors Arthropods and Annelids have evolved independently". In *Clio pyramidata* the primitive features affirm the possible relation to a coelenterate-like ancestor. It may be due to the "larval stage" persisting in the adult that these primitive features appear in *Clio*. The reduced muscle system of *Cymbulia* shows no such primitive characters and nothing points to a relation with coelenterate-like forms as far as the proper columellar muscle system is concerned; derivatives from this muscle however, also show tetracyclomeric traces.

The Coelenterata hypothesis

As explained above, Thecosomata are primitive in structure, but phylogenetically strongly adapted and specialised animals. Fossils of Thecosomata are only known from younger geological periods, not older than Oligocene, which may agree with their highly evolved status. Much older than the Thecosomata are the Conulata and it is noteworthy that these Conulata have long been considered to belong to the Pteropoda. Presumably, the resemblance between the two groups is more than haphazard, and it was the late Dr. Lemche who focussed our attention on this problem (Lemche, 1966, 1971). The subclass Conulata is at present considered as a division of the Scyphozoa (e.g. Hyman, 1940) and a relation between the Thecosomata and Conulata would be an affirmation of the hypothesis that Mollusca could be derived from Coelenterata.

Sessile and pelagic forms of Conulata are shell-bearing. This shell, the epiderm, is flexible and consists of a laminate structure composed of chitin, calcium phosphate and chitinophosphate. In juvenile thecosomatous pteropods, shells with closely resembling structures are common (Van der Spoel,

1967). The colour of the Conulata shell, reddish, reddish-purple or bluish-gray is also found in shells of Thecosomata. In both Conulata and Pteropoda the shell is an ectodermal product. In Conulata the shell is tetrapyramidal in shape but in straight Thecosomata it seems to be tripyramidal. This three-sided pyramidal shape, however, is not fundamental in Thecosomata. (The spirally coiled Thecosomata *Limacina* and *Peraclis* are not directly comparable with the Conulata but they are so closely related to the straight, bilateral symmetrical forms that for the moment no special comparison with these two genera will be given.) The dorsal rib in e.g. *Clio pyramidata* is no original rib but only a bending of the dorsal side, and in some species like *Clio recurva* (Children, 1823) and *C. polita* this rib is absent. The ventral side is usually one uninterrupted surface. The lateral ribs are no ribs, but, though very small, lateral sides. In *Clio pyramidata* forma *convexa* (Boas, 1886) and *C. recurva* such clear structural lateral sides are present. Fundamentally the shell in *Clio* is therefore tetrapyramidal, and so is the mantle. The shell sculpture is probably of little phylogenetic importance, but Conulata and Thecosomata share the same sculpture pattern of transversal striae with a median line on each side.

Very uncommon among Mollusca is the active shedding of the protoconch and the formation of a closing membrane as found in Cavoliniidae. As far as we know closing membranes of this type, outside the molluscs, are only found in freelifving planktonic Conulata, and there the formation is identical to what is found in Cavoliniidae. In *Hyalocypris*, *Diacria*, *Cuvierina* and *Cavolinia* smooth convex closing membranes identical to those in Conulata are formed.

The wing musculature consists of two systems as discussed above, a columellar system and a subectodermal system. When we compare the wings and posterior footlobe, or swimming disc, in Thecosomata with the umbrella of e.g. *Nausithoe* (Scyphozoa, Coronata) resemblance is obvious. The scyphozoan coronal muscles and the radial ones together with the delta muscle are identical to the crossing system of subectodermal muscles in Thecosomata, if radial is considered directed oral and if circular is considered circum-oral. The radial

muscles are found directly under the ectoderm, the circum-oral ones are situated inside the circular ones. If the swimming disc in Thecosomata is identical to the scyphozoan umbrella it should also have a tetradial structure. The swimming disc is composed of four lobes indeed: the left and right wing and the left and right half of the posterior footlobe. In many Thecosomata (e.g. in *Limacina*, *Hyalocypris*, *Desmopterus* and some species of *Clio*) the posterior footlobe is divided into two parts by a median fold or marginal incision, and both halves are served always by their own branches of the columellar system. In *Desmopterus* there are actually four and not five lobes as the central posterior lobe can not be homologous to an umbrellar quadrant. This lobe has to be considered a tentacle as it lacks the radial muscles, being only crossed by the coronal muscle. The two posterior wing tentacles in *Desmopterus* and the two wing tentacles in *Peraclis* are radial in position and they can be considered homologous to umbrellar tentacles. So for *Desmopterus* and probably *Cymbulia* three tentacles could be traced, the fourth could not be found.

Posterior to the swimming disc two paired sensory organs are found in Thecosomata, viz.: the optical tentacles and the statocysts, which may be considered homologous to the rhopalium organs in Scyphozoa, also being interradial in position. The statocysts are in origin outer tentacles. This is proved by the fact that they are connected with the body wall by a loop of connective tissue, which causes them to lie outside the connective tissue of the body wall.

The mouthparts (the lip disc) should be tetradial with septal lobes as in Conulata and other Scyphozoa and this is the actual situation in Thecosomata. The two lateral lips are septal in between the wings and the posterior footlobe. The cephalic lobe, considered as a quadrant of the lip disc, is septal in between the two wings and the median lip, and it is exactly opposite to the posterior footlobes. The fact that no columellar branch or crossing muscle system is found in the lips corresponds well to the scyphozoan structure where no radial, coronal or septal muscles are found in the funnel.

In *Cymbulia* eight large supporting bars are found around the oesophagus which also is an

indication for the tetradial structure of this part of the body. The direction of these bars is anterior-posterior and as such they can be considered to belong, two by two, to a quadrant. The bars are composed of smooth muscle cells and thereby they are to be considered as derivatives from septal muscles.

It has already been mentioned that the columellar muscle in *Clio* shows a tetradial structure. The eight branches correspond with the eight septal muscles of Conulata and other Scyphozoa. In these groups the septa are T-shaped which explains the number of eight columellar muscles in *Clio* as well as the eight bars in *Cymbulia*.

The mantle muscles in *Clio* show a tetradial structure of smooth cells as discussed above. The mantle can very well be considered as umbrellar in nature. In *Lucernaria* (Stauromedusae) the septal muscles continue in the umbrella as four separate branches. It can be assumed that the mantle is a posteriorly shifted part of the umbrella with part of the columellar system, thus with part of the septal muscles. The fact that the mantle muscles do neither connect with each other nor with the columellar muscle may indicate that these mantle muscles are dislocated anterior branches of the septal muscles that became detached. If the mantle is a posteriorly shifted part of the umbrella indeed, its obvious tetradial structure in Cavoliniidae with septal lobes is not difficult to explain. The mantle in aberrant specimens develops after the wings have grown out and it originates from the same region as the wings. This also indicates that the mantle may be considered, just as the wings, as of umbrellar origin.

In behaviour there is also a similarity between Coelenterata and Thecosomata. *Aurelia* (Scyphozoa) for example, feeds chiefly on small plankton organisms collected on the exumbrellar surface, where they become entangled in mucus before they are passed by flagellar action to the lappets where they are collected as eight masses in the centre of the lappets. The manubrium tentacles pick up these masses to pass them into the stomach. Though this way of feeding is not the most common among scyphozoans it resembles almost perfectly to what is found in *Clio* where feeding is executed by the wings and mantle (both of umbrellar origin) by

sticking particles in mucus and ciliary transport of mucus to the lips (of manubrium origin). Locomotion by swimming is normal in all Thecosomata and it is a quite common primitive behaviour in juvenile molluscs. Swimming is a natural consequence of feeding in juvenile Gastropoda and adult Thecosomata, since in order to feed, the animal has to swim in the same way as *Aurelia*.

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