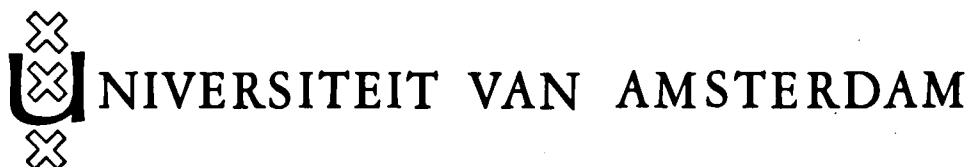


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ARE PTEROPODS REALLY PTERO-PODS? ¹⁾

(MOLLUSCA, GASTROPODA, PTEROPODA)

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ABSTRACT

The columellar muscle system consists anteriorly of a high number of longitudinal branches surrounding a hydrocoel, which forms higher up two lateral, one ventral and four smaller dorsal bundles. These bundles enter the muscular envelope of head and nuchal region, which is formed out of the wing-wall muscles. The two lateral bundles proceed farthest apically to insert on the buccal appendages; the four dorsal fibres fuse with the walls of buccal organs and oesophagus, while the ventral muscles run into the posterior and lateral footlobes. The wings are attached to the body by an extra right and left muscle neither derived from the columellar nor from the wing-wall muscle system. So the posterior and lateral footparts are mesopodal, the wings epipodal and the buccal appendages propodal, or velar, in origin.

INTRODUCTION

In thecosomatous pteropods, such as *Clio* and *Cymbulia*, the "wings" are homologous with the velum and not with the foot, as is evident from the fact that the wings are found apically and

dorsally to the mouth (Pafort-van Iersel & Van der Spoel, 1979).

The position of the "wings" in gymnosomatous pteropods, such as *Clione* studied in this paper, is ventral and anterior to the mouth suggesting that they might be footparts. However, judging from the muscle system, the wings in Gymnosomata are neither comparable to footparts nor to the velum. As a consequence, there are no pteropods which have real ptero-(wing)

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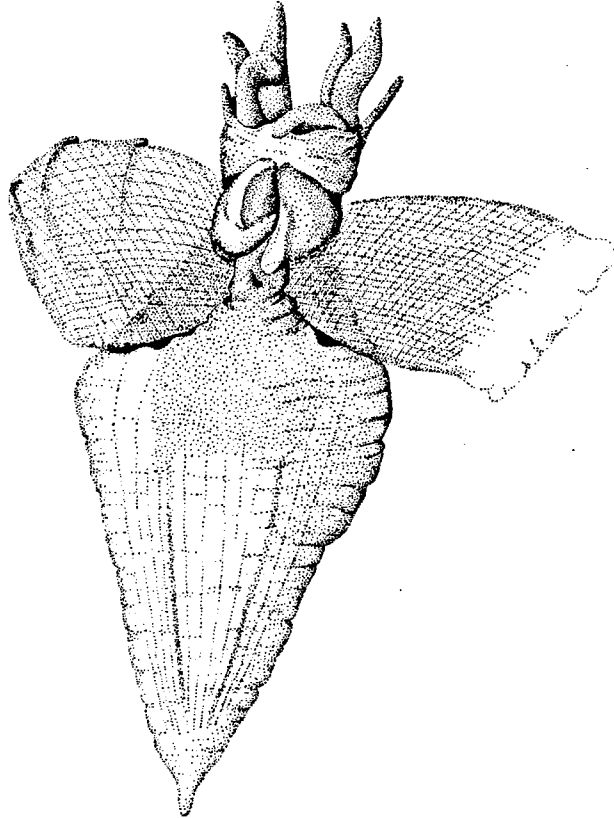


Fig. 1. *Clione limacina* forma *minuta*, ventral view.

poda(feet).

The present description is based on *Clione limacina* (Phipps, 1774) forma *minuta* Pruvot-Fol, 1926, collected by the 1980 Amsterdam Mid North Atlantic Plankton Expedition at station 10 haul 4. The author is very much indebted to Mr. A.F. de Fluiter for preparing the histological slides of an additional specimen from the Dana Expeditions station 4206 IV, 53°38'N 29°41'W, 0-100 m.

DESCRIPTION OF THE MUSCLE SYSTEM

In Gymnosomata the wings are anterior and ventral to the mouth with in between one posterior and two lateral footlobes (fig. 1). The strongly developed buccal organs consist of a buccal mass with radula and jaws, two lateral hook-sacks and, depending on the family concerned, apically buccal cones, bladders or arms. To conclude from the columellar muscle structure the wings are epipodial.

There are four groups of longitudinal mus-

cles in *Clione*: two lateral (LM & RM), one ventral (VM) and one dorsal (DM) group (fig. 2). These four bundles are considered the real columellar muscle of a larval type. It is noteworthy that this system consists of four parts and more remarkable is that the four bundles completely split in a dichotomous way anteriorly. The dorsal muscles usually do not fuse to form one band, so that the four small muscles remain separated (DM figs. 2 & 3). This is probably the reason why Meisenheimer (1905) and Tesch (1913) did not notice this part of the muscle system.

The mentioned four-four arrangement is also found in Thecosomata, and is considered an indication of the phylogenetic relation of the Mollusca with the tetrameric group of Coelenterata (Pafort-van Iersel & Van der Spoel, 1979). In contrast to what is found in the Thecosomata, the columellar muscle in Gymnosomata does not penetrate the wings. This makes one consider these wings only homologous with those of Thecosomata and of epipodial origin.

The mentioned structure is also in agreement

with Tesch (1913): "Die Muskulatur der beiden Flossen steht weder mit einander noch mit der Körper Muskulatur in Verbindung." Meisenheimer (1905), however, already described a connection of body and wings by muscles, but did not assess the correct position with regard to the muscle system. The connection is formed by an extra muscle on each side (LW & RW) not related to the columellar muscle and not derived from the wing-wall muscle system (WI). From the left wing lumen a muscle runs anteriorly to the right body side and a similar one runs from the right wing to the left side. These muscles cross ventrally just below the nuchal region and turn slightly dorsally. These two muscles do not connect with any other muscle system, they only insert in the wings on the central septum. The area where these two muscles are

found slightly resembles the situation in *Cymbulia* where the body muscle plates are found (Pafort-van Iersel & Van der Spoel, 1979) but the present muscles are of an entirely different origin as they do not come from the wing-wall muscles as in *Cymbulia*.

The wing-wall muscles form an envelope of the wing lumen and they surround the buccal and nuchal regions as well. Diagrammatically the wing-wall muscles thus form two cylinders, one horizontal, representing the wings, and one vertical, dorsad to the horizontal one, surrounding the head region (fig. 2). The vertical cylinder is open at both ends. The crossing muscles connecting the wings leave through the caudal opening to enter the body. The longitudinal columellar muscles first run, caudally, outside of the nuchal part of the envelopment and

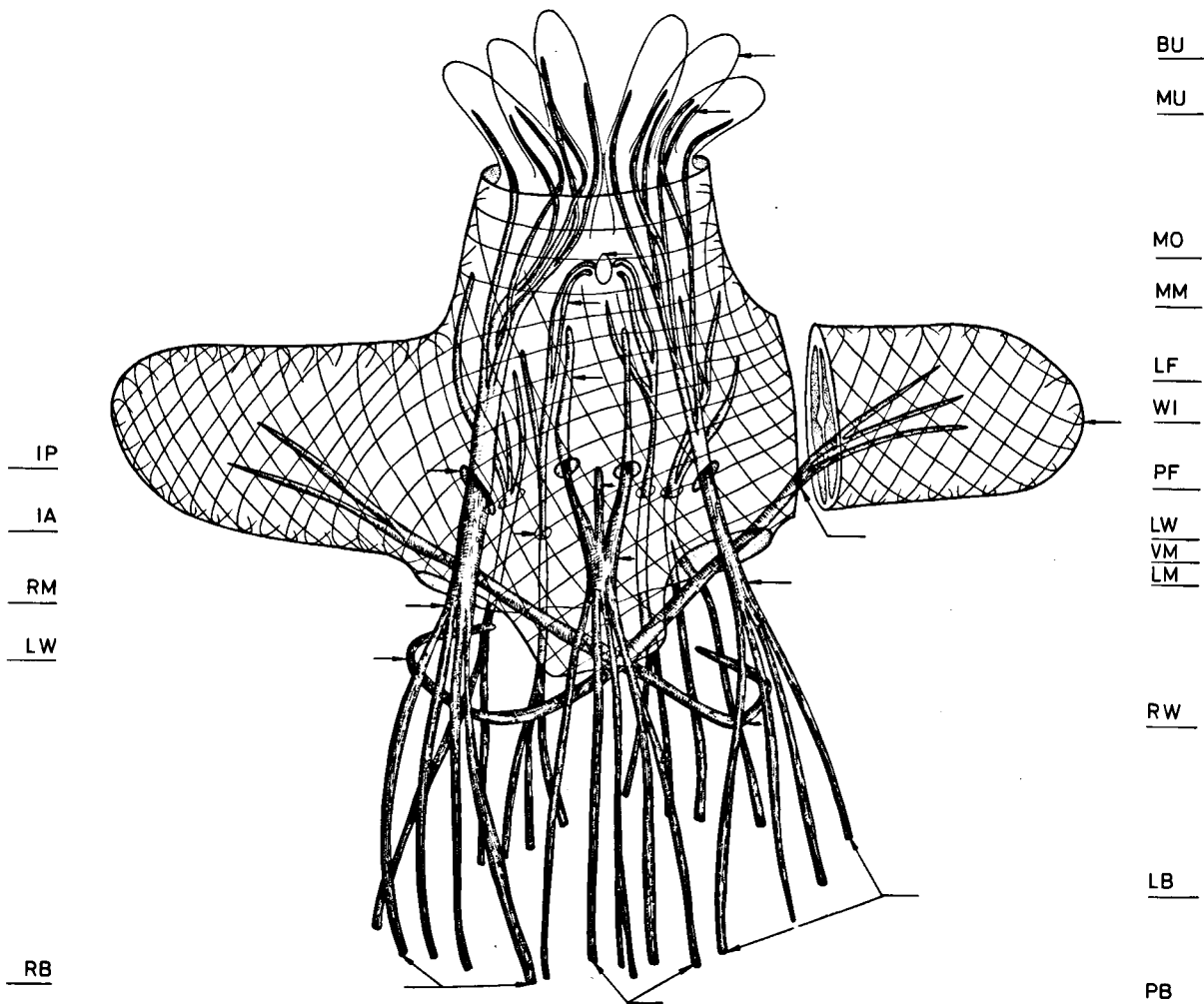


Fig. 2. Diagrammatic representation of the muscles in the apical half of *Clione limacina forma minuta*, ventral view; for legenda see fig. 3.

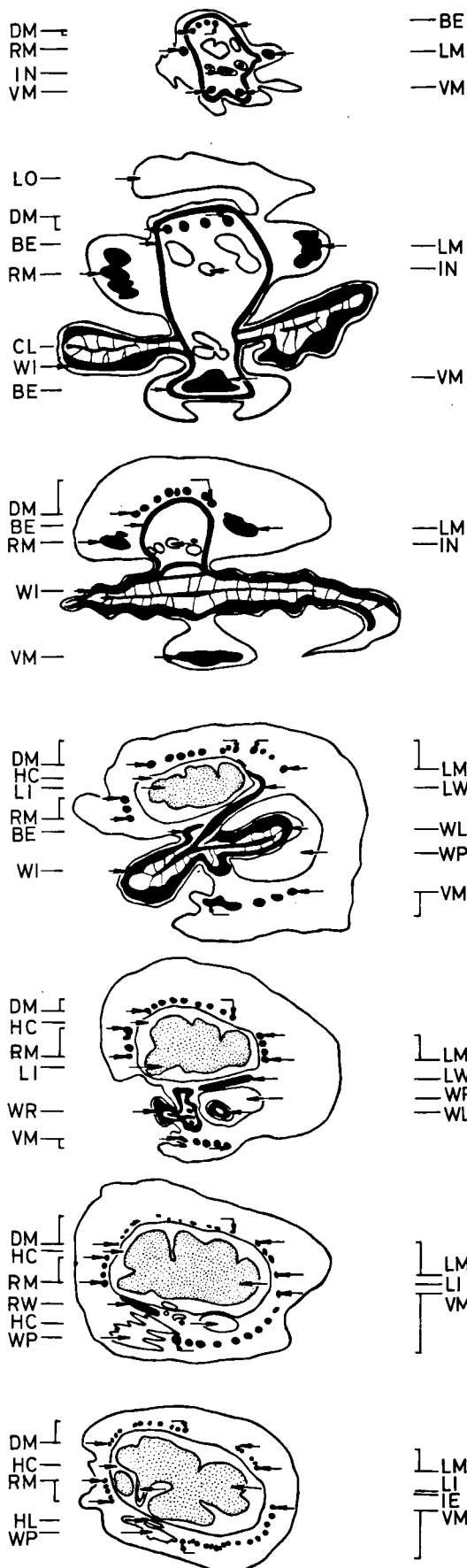


Fig. 3. Seven schematic cross-sections of *Clione limacina* forma *minuta*, the uppermost one made just below the buccal cones, the lowest one just below the posterior footlobes, muscles in black.

- BE-enveloement of buccal mass
- BU-buccal cones
- CL-central wing septum
- CM-columellar muscle
- DM-branches of dorsal muscle
- HC-hydrocoel
- HK-heart-kidney complex
- IA-anterior entering of muscles
- IE-intestine-liver transition
- IN-intestine
- IP-posterior entering of muscles
- LB-branches of left muscle
- LF-muscle to left footlobe
- LI-liver
- LM-left muscle
- LO-lobe of body integument
- LW-left crossing wing muscle
- MM-muscle of mouth
- MO-mouth
- MU-buccal cone muscles
- PB-branches of ventral muscle
- PF-muscles of posterior footlobe
- RB-branches of right muscle
- RL-muscle to right footlobe
- RM-right muscle
- RW-right crossing wing muscle
- VM-ventral muscle
- WI-wing-wall muscle sheet
- WL-left wing
- WP-wing pocket
- WR-right wing

penetrate it at the level of the buccal mass. These columellar muscles are inserted posteriorly on the oesophageal wall and buccal organs (the dorsal fibres), in the buccal appendages (the lateral fibres), and in the posterior and lateral footlobes (the ventral fibres). The posterior footlobe has a function as sucking organ in all Gymnosomata and in some genera it bears an accessory penal or copulatory sucker (Boas, 1886; Pruvot-Fol, 1926). These lobes are therefore comparable with the mesopodium, or creeping foot. The buccal appendages are provided with columellar muscle bands from the two lateral stems and consequently they are comparable to velar or propodal labial palps, according to Hyman (1967): "The velar lobes regress and are cast off or resorbed except in cases where their bases remain as the oral veil or labial palps".

The musculature of the wing-wall muscles is comparable to the structure found in the Thecosomata, consisting of two layers of crossing muscles under the integument and connected with the central wing septum by some connective tissue bars. The external shape of the wings is spatulate in Gymnosomata and more or less bilobate in Thecosomata, which also indicates that the wings in Gymnosomata are not related to a dichotomous branching system like the columellar muscle, as they are in Thecosomata.

Anteriorly the columellar muscle does not attach to a shell, but it ends in the caudal integument of the shell-less body. Still, the animal has some rigidity and the columellar muscle is able to retract the posterior body parts. The "skeleton" of *Clione* is a hydrocoel filling the entire anterior part of the body caudad of the diaphragm. The wings also contain a hollow space completely separated from the body hydrocoel. It is the body fluid in the body hydrocoel and in the wings which forms the animal's stiff axis.

Comparing Euthecosomata, Pseudothecosomata and Gymnosomata (fig. 4) a reduction of the columellar muscle system of the mantle is seen parallel to the disappearance of the mantle and a reduction of the columellar muscles in the wings. In Pseudothecosomata and Gymnosomata an extra muscle developed to provide a connection between wings and body.

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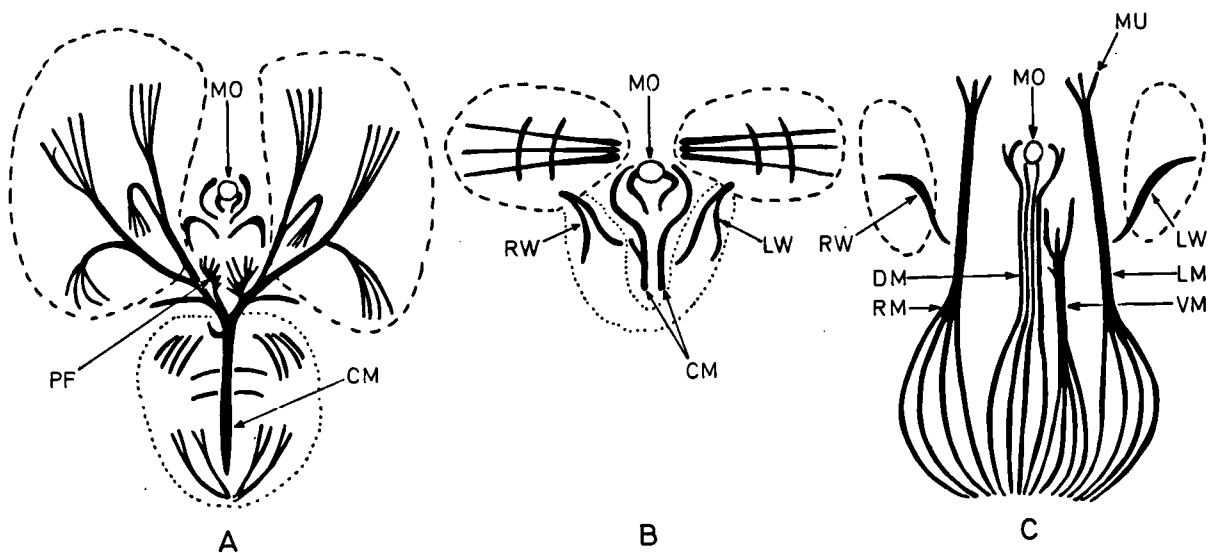


Fig. 4. Diagram of the muscle system of *Clio* (A), *Cymbulia* (B) and *Clione* (C). The circle represents the mouth, dotted contours mark the mantle, broken-line contours mark the wings.

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