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# On the morphological variability of the attachment organ of Lernaeopodidae (Copepoda: Siphonostomatoida)

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**Abstract.** The study of the bulla from 18 lernaeopodid copepod species collected on 15 marine fish species and one freshwater fish species taken mainly from the Gulf of Lions in the Mediterranean Sea reveals a great morphological and structural variability. It is however possible to bring forth three general remarks: - the bulla of Lernaeopodidae parasites of Selachii have a remarkably constant structure probably due to the tegument nature of the attachment substratum; - the bulla of Lernaeopodidae parasites of Teleostei has a morphology influenced by the nature of the attachment tissue; - when species of a same genus (i.e. *Clavellotis*) are attached on a same organ, the shape of the bulla can constitute a taxonomic characteristic.

Lernaeopodidae are parasitic copepods found mainly on marine fish, both Selachii and Teleostei. As often in parasitic copepods, Lernaeopodidae display an exaggerated sexual dimorphism, to the point where only the female is a parasite on the fish host. The small male lives in temporary association, often on the body of its partner. The female presents frequently a characteristic attachment organ, the bulla, unique among parasitic copepods, held by the second maxillae.

The bulla is secreted and formed during the larval stage. At the end of its development, the bulla, attached to the extremities of the second maxillae, implants itself definitely in the tissue of a specific area of the host (Kabata and Cousens 1973, Kawatov et al. 1980, Piasecki 1989). Thus, the adult female is fixed permanently and its movements are limited to rotation around the attachment point of the bulla. The activity area of the parasite mainly of trophic nature is determined by the length of the second maxillae and the cephalothorax. Each of the studied species is localised within a precise microhabitat of the host.

The bulla shows a great variability of shapes among Lernaeopodidae. However, its morphology is remarkably stable within a single species or genus. To determine whether distinct structural types of attachment organs could be differentiated and eventually to establish a correlation either with the substratum in which they implant themselves, or with the taxonomy of the concerned species, we carried out a morphological and histological study of the attachment organ from diversified samples.

## MATERIALS AND METHODS

To achieve our study, we examined several hundred fish belonging to 15 marine species and one freshwater species. Eighteen lernaeopodid copepod species were collected.

**Marine species.** *Alella macrotrachelus* (Brian, 1906) from the gill filaments of *Diplodus sargus* (Linnaeus, 1758) and *D. vulgaris* (Geoffroy Saint-Hilaire, 1817) (Sparidae); *Clavella adunca* (Strøm, 1762) from the gill rakers of *Trisopterus luscus* (Linnaeus, 1758) and *Merlangius merlangus* (Nordmann, 1840) (Gadidae); *Clavella stellata* (Krøyer, 1838) from the skin near pectoral fins of *Merluccius merluccius* (Linnaeus, 1758) (Merlucciidae); *Clavellisa scombri* (Kurz, 1877) from the gill rakers of *Scomber scombrus* Linnaeus, 1758 (Scombridae); *Clavellisa emarginata* (Krøyer, 1837) from the gill rakers of *Alosa fallax* (Lacepède, 1803) (Clupeidae); *Clavellotis fallax* (Heller, 1865)* from the gill rakers of *Dentex dentex* (Linnaeus, 1758) (Sparidae); *Clavellotis sargi* (Kurz, 1877)* from the gill rakers of *Diplodus sargus* and *D. vulgaris*; *Clavellotis strumosa* (Brian, 1906)* from the gill rakers of *Pagellus erythrinus* (Linnaeus, 1758) and *Lithognathus mormyrus* (Linnaeus, 1758) (Sparidae); *Neobrachiella bispinosa* (von Nordmann, 1832) from the buccal cavity of *Trigla lucerna* (Linnaeus, 1758) (Triglidae); *Neobrachiella exigua* (Brian, 1906) from the tip of gill filaments of *Pagellus erythrinus*; *Neobrachiella impudica* (von Nordmann, 1832) from the inner wall of the operculum of *Trigla lucerna* and *Trigloporus lastoviza* (Brünnich, 1768) (Triglidae); *Neobrachiella insidiosa* (Heller, 1865) from the tip of gill filaments of *Merluccius merluccius*; *Neobrachiella merluccii* (Bassett-Smith, 1896) from the gill rakers of *Merluccius merluccius*; *Neobrachiella mugilis* (Kabata, Raibaut et Ben Hassine, 1971)** from the base of pectoral fins of *Liza saliens* (Risso, 1810) (Mugilidae);

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*Pseudocharopinus bicaudatus* (Krøyer, 1837) from the spiracle of *Squalus acanthias* (Linnaeus, 1758) (Squalidae); *Pseudocharopinus malleus* (von Nordmann, 1832) from the inner gill slit of *Torpedo torpedo* (Linnaeus, 1758) (Torpedinidae); *Sparidicola lithognathae* (Kensley et Grindley, 1973) from the inner wall of the operculum of *Lithognathus mormyrus*.

* Taxonomy of the genus after Kabata (1990); ** Taxonomy of the genus after Ho and Takeuchi (1996)

All marine copepod species were collected on fish species taken from Gulf of Lions except *Clavella adunca* collected on *Trisopterus luscus* and *Merlangius merlangus* taken from Bay of Biscay (Atlantic south French coast)

**Freshwater species.** *Tracheliastes polycolpus* von Nordmann, 1832 from the base of anal and dorsal fins of *Leuciscus leuciscus* (Linnaeus, 1766) (Cyprinidae) taken from the Rhone river near Bugey (France).

As a rule, the parasites gathered on fish freshly caught are still alive. They were removed from the fish with the tissue surrounding the attachment area so not to damage the attachment organ. They were then fixed for scanning and transmission electron microscopy in osmic acid, buffered at 2 % according to Palade (1952). Material used for scanning electron microscopy was carefully cleaned and freed of any tissue debris. For the internal structure study, material was embedded in Spurr resin (1969). Observations were carried out on semithin sections stained following the method of Humphrey and Pittman (1974).

**Characteristic structure of a bulla** (Fig. 1). Before carrying out a morphological and structural study of the bulla from the various species observed, we give a characteristic layout of this attachment organ, using as an example *Sparidicola lithognathae*, a parasite of the striped sea bream, localised over the operculum, and more precisely, in the tegument folds between the gill arches.

The bulla is formed principally in two parts; the manubrium and the anchor (Kabata and Cousens 1972). The manubrium, situated at the end of the distal extremity of the maxillary plug, splays out to form an anchor. This anchor is often divided in three parts :

a) a supra-anchoral layer continuing with the manubrium,

b) a central layer, fibrous save for the margins of the anchor, and

c) a subanchoral layer in contact with the host tissue.

The anchor is crossed by canals, visible in histological slides, and often emerging from the subanchoral layer. These canals, according to previous authors, start from the proximal extremity of the manubrium, close to the two spaces which are blocked always by two maxillary plugs.

## RESULTS

### Structural details of the bulla in some species

We found the characteristic organisation of the bulla in every species studied but with considerable variations depending on the implantation site.

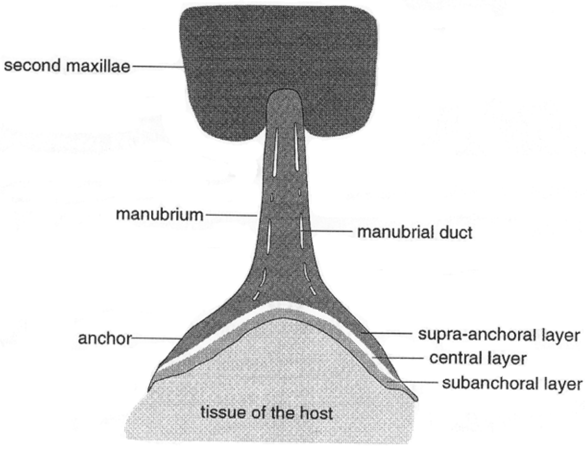


**Fig. 1.** Diagrammatic structure of the bulla.

### Species attached to gills

On the gill filament

*Alella macrotrachelus*. The bulla is held by very short second maxillae whose distal end is formed by a continuous rim still displaying the marks of the maxillary suture (Fig. 2). It has the shape of an elongated bludgeon. Its basal part is formed by a long manubrium prolonged by an anchor almost three times as large with a slight asymmetry due to the contact of this organ with gill cartilage (Fig. 3). The anchoring area is ornamented with a wart-like growth, obliquely lined (Fig. 4). The attachment part penetrates the axial cartilage of the gill filament and is deeply embedded (Fig. 29).

*Neobrachiella exigua*. The distal part of the second maxilla is characterised by the presence of a surrounding festooned bulge. The bulla has the shape of an asymmetrical funnel (Fig. 5). The manubrium is short, the anchor large. The subanchoral area appears spongy due to the presence of pores. The narrow manubrium, perforated by several canals which do not extend to the anchor, can be observed on sagittal sections. The anchor penetrates the fragile gill tissue to flatten its whole surface against the cartilage of the gill's edge. The anchoral matrix is dark and fibrous in its central part attached to the cartilage. Its sides embedded in other gill tissues are of lighter coloured. The supra-anchoral layer is visible as it forms two side strips (Fig. 33).

*Clavella adunca*. The bulla penetrates the end of *Trisopterus luscus* (the bib) gill filament. The manubrium is separated by a constriction from the spherical anchor (Fig. 6) with a corrugated surface (Fig.7).

On the gill arch or the gill rakers

*Clavella adunca*. On *Merlangius merlangus* (the whiting), this species is attached to the gill arch, in which the bulla is completely and firmly embedded. It has an ovoid shape (Fig. 8) and, unlike the bulla on the gill of the bib, it has surface covered with spinules, averaging 3 µm in length (Fig. 9).

*Clavellisa scombri*. The asymmetrical anchor, in the shape of an elongated bludgeon, is mounted on a perfectly cylindrical manubrium (Fig. 10). Its surface displays dense meandering ridges (Fig. 11).

*Clavellisa emarginata*. Also displays a cylindrical manubrium, its difference from *C. scombri* bulla lies in the shape of the anchor, which is less bulky.

*Clavellotis fallax*. The bulla consists of a long manubrium topped by a mushroom-shaped anchor. The surface displays porous microvilli of 0.7 µm in length (Fig. 12).

*Clavellotis sargi*. The bulla is sunken between the ends of two massive second maxillae (Fig. 13). The bulging anchor displays a regular circular line of pores (Fig. 14). These pores correspond with the orifices of several longitudinal canals. The manubrium is relatively long, deeply embedded in the second maxilla while the anchor has its whole surface flattened against the host tissues. The tissues clearly follow the exact shape of the anchor (Fig. 32).

*Clavellotis pagri*. The cylindrical manubrium is clearly visible. It is prolonged by a convex hemi-spherical anchor. As in the previous species, the anchoral area displays a marginal circle of pores.

*Clavellotis characis*. The bulla structure follows that of other studied species from the same genus with the presence of peripheral pores in a row (Fig. 15).

*Clavellotis strumosa*. In this species, the bulla, held by fused short second maxillae (Fig. 16), is very similar to that of *C. characis*, along with the similarity in the shape of the tip of second maxillae (Fig. 17). The circle of pores is further away from the margin of the anchor and has two shallow indentations, indistinctly dividing it into subequal halves (Fig. 18).

*Neobrachiella merluccii*. The bulla (Fig. 19) has the shape of a conical, symmetric spinning top. The ends of the second maxillae form festooned edges surrounding the manubrium, which is not visible. On the surface of the anchor, pores of 6 µm in diameter can be observed.

### Species attached in cavities

In the buccal cavity and throat

*Neobrachiella bispinosa*. The manubrium is circled by two annular outgrowths of the second maxillae. The anchor has the shape of a large bell-mouthed cup with edges displaying regular ribs (Figs. 20, 21). In a longitudinal section, these ribs appear as small teeth. The supra-anchoral and subanchoral layers are very clear, leaving little room for the fibrous central part. The canals starting from the base of the anchor by the ring spread out to the anchoral floor (Fig. 31).

*Pseudocharopinus malleus*. The elongated second maxillae stay separated and unite only at their distal end around the bulla (Fig. 22). The bulla has a reduced manubrium marked by a double maxillary bulge. The anchor has the shape of a wide bell-mouthed cup. The anchoral area is covered by meandering folds (Fig. 23).

In the spiracle

*Pseudocharopinus bicaudatus* The bulla, at the bottom of an infundibulum formed by the ends of both second maxillae, is not very prominent (Fig. 24). The short manubrium is hidden by a surrounding maxillary thickening. The flat and round anchor displays on its surface two large canals with festooned edges, separated by a thick wall. From center of the canals two maxillary plugs emerge (Fig. 25), originally described by Kabata and Cousens (1972). At the end of each maxillary plug, two pores of uneven sizes can be found (Fig. 26).

In longitudinal section, the bulla of *P. bicaudatus* displays a short and large manubrium surrounded by a small collar of maxillary origin. In the disk-shaped anchor, a supra- and a sub-anchoral darker layers can be observed. Between them, the matrix consists of fibres starting from the anchor base where they form a cluster. The manubrium and the proximal part of the anchor are perforated by two large spaces corresponding to the canals from which are issued the maxillary plugs (Fig. 34). The anchor's edge is bordered with a thin dark layer which could be the result of secretion from the copepod (Chandran and Balakrishnan Nair 1979).

The bulla structure of *P. bicaudatus* is similar to those of other congeners such as *P. dentatus* described by Rigby and Tunnel (1971) and Kabata and Cousens (1972), as well as *P. narcinae* (cf. Chandran and Balakrishnan Nair 1979).

### Species attached to the tegument

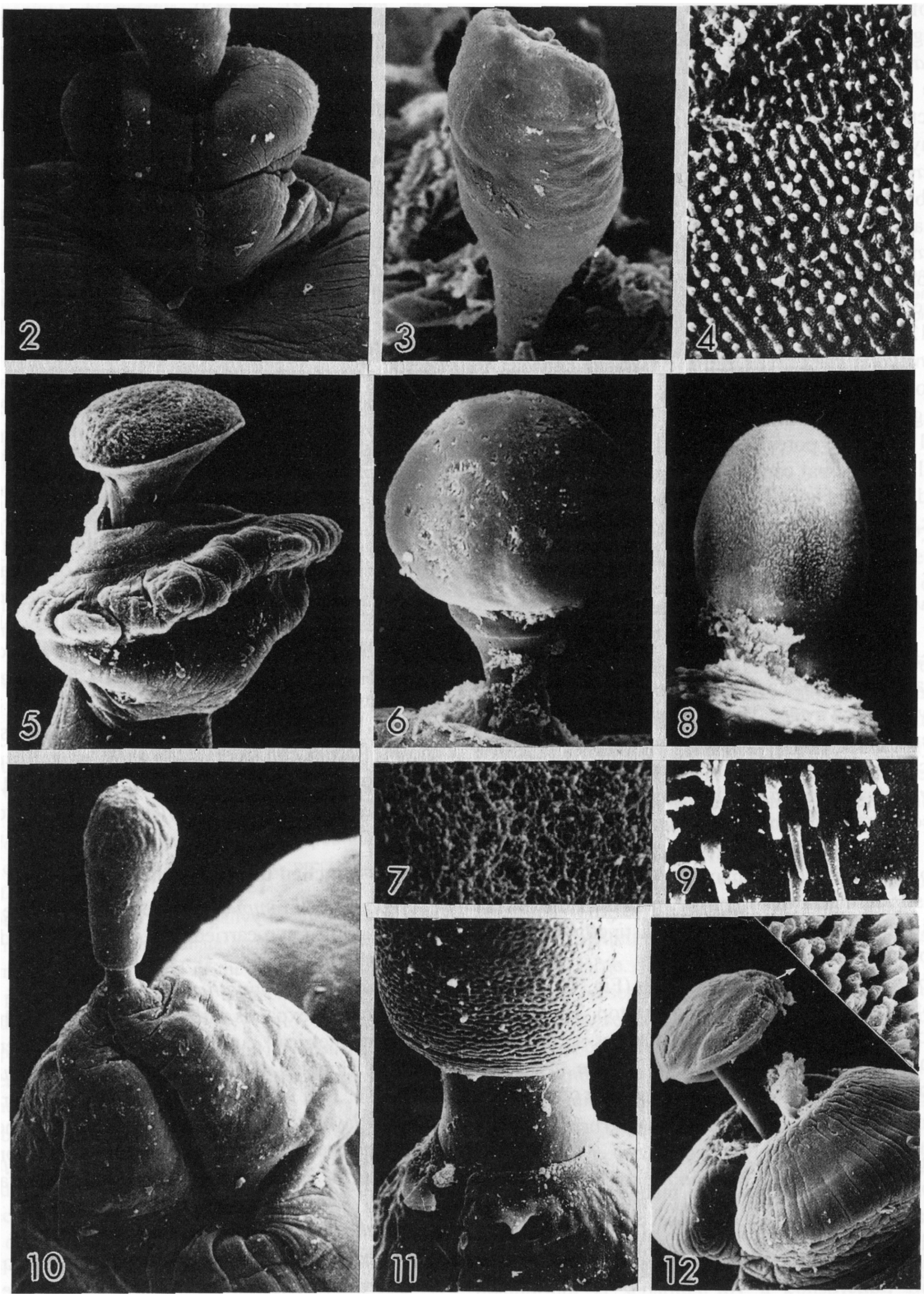
*Neobrachiella impudica*. The anchor has the shape of a bell-mouthed cup carried by a manubrium hidden by a maxillary ruff.

*Sparidicola lithognathae*. The manubrium is long and cylindrical. It expands into an anchor in the shape of a thin asymmetrical cup excavated in the centre and flattened along its whole surface on the operculum tissue (Fig. 28). The Humphrey's stain shows a darker sub-anchoral layer, the rest of the anchoral matrix being of a fibrous nature. Two canals appear in the manubrium and spread to the anchor without piercing its surface (Fig. 28).

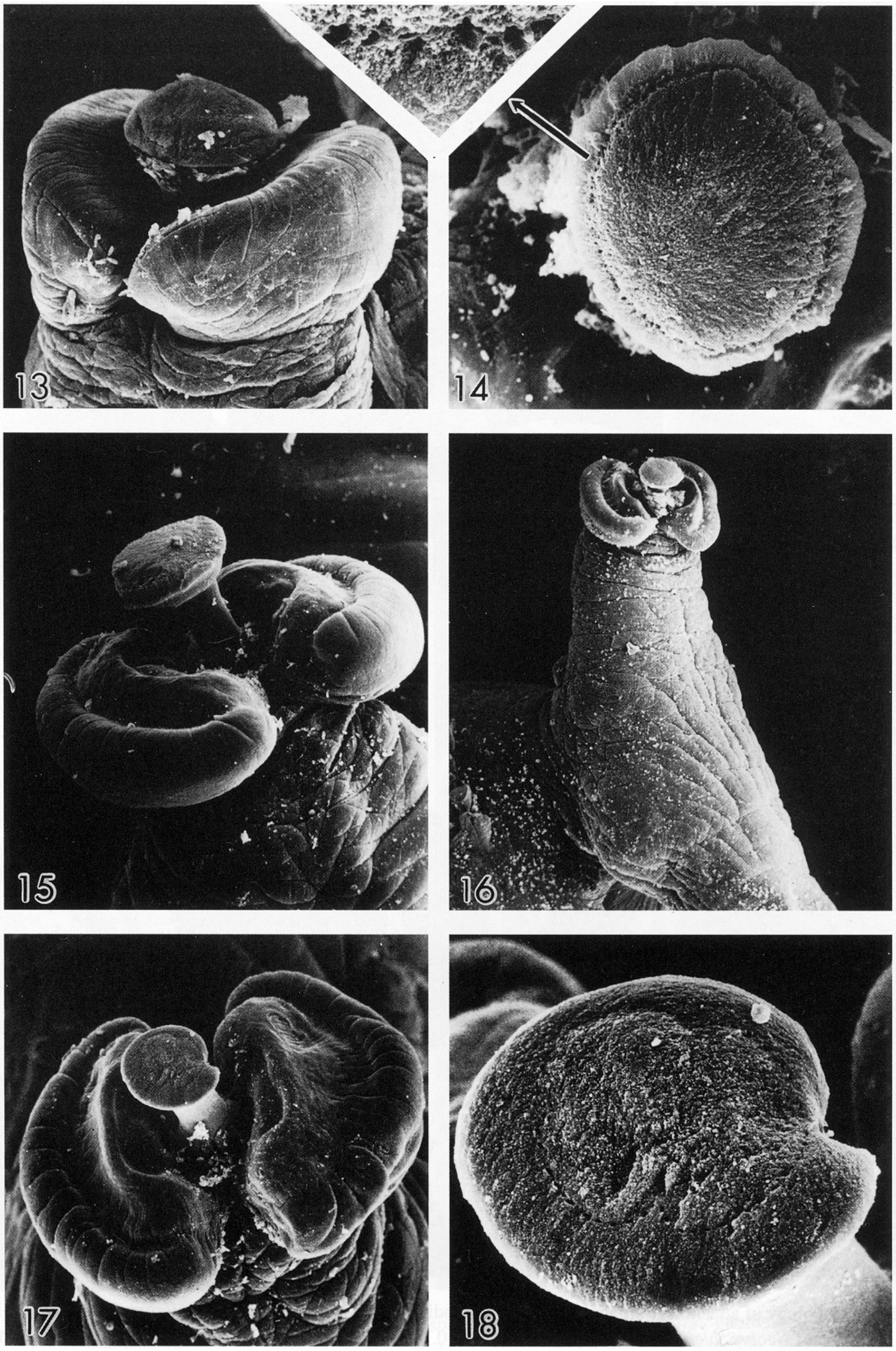
*Clavella stellata*. The anchor with more or less regular edge is attached to the tegument. Its coloration, of lesser density, differentiates it from the darker manubrium. The latter is crossed by several canals displayed in a regular circle (Fig. 30).

### Species attached to the fins

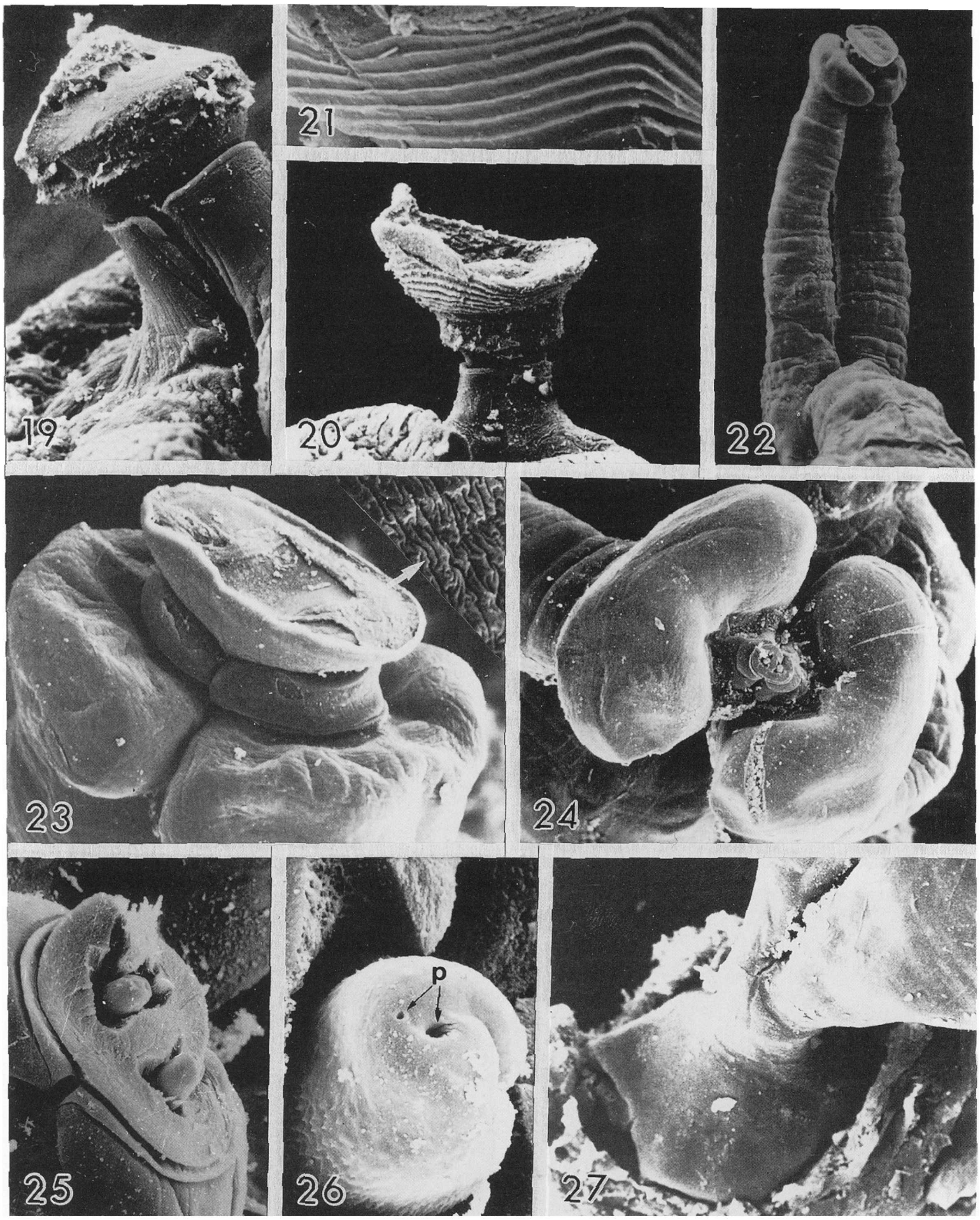
*Tracheliastes polycolpus*. The bulla, carried by two long second maxillae united only at their distal end, is characterised by a short manubrium with a disk-shaped anchor which attaches itself to a fin ray (Fig. 27).



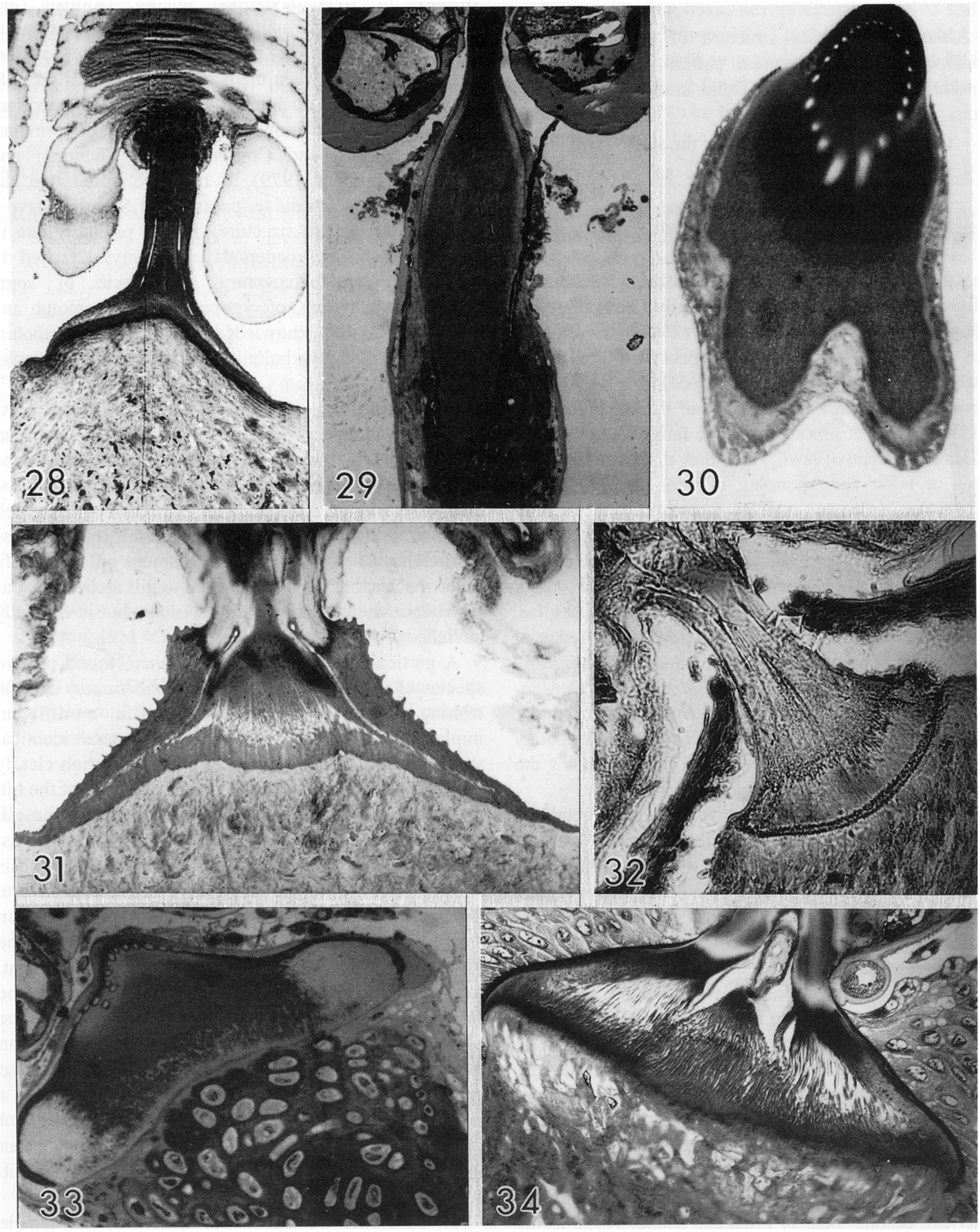
**Figs. 2-12.** Morphology of attachment organ of some lernaeopodid species (scanning electron micrographs). **Figs. 2-4.** *Alella macrotrachelus*. **Fig. 2.** Second maxillae with bulla, × 300. **Fig. 3.** Bulla, × 900. **Fig. 4.** Detail of surface, × 6000. **Fig. 5.** Extremity of second maxillae of *Neobrachiella exigua*, with bulla, × 880. **Figs. 6, 7.** *Clavella adunca* (from gills of bib). **Fig. 6.** Bulla, × 500. **Fig. 7.** Detail of surface, × 8000. **Figs. 8, 9.** *Clavella adunca* (from gill rakers of whiting). **Fig. 8.** Bulla, × 340. **Fig. 9.** Detail of surface, × 5000. **Figs. 10, 11.** *Clavellisa scombri*. **Fig. 10.** Second maxillae with bulla, × 360. **Fig. 11.** Detail of bulla, × 800. **Fig. 12.** Extremity of second maxillae of *Clavellotis fallax*, with bulla, × 380; detail of surface (arrow), × 5400.



**Figs. 13-18.** Morphology of attachment organ of some lernaeopodid species (scanning electron micrographs). **Figs. 13, 14.** *Clavellotis sargi*. **Fig. 13.** Extremity of second maxillae with bulla, × 480. **Fig. 14.** Apical view of bulla, × 1150; detail of pores (arrow), × 5400. **Fig. 15.** Extremity of second maxillae of *Clavellotis characis*, with bulla, × 900. **Figs. 16-18.** *Clavellotis strumosa.* **Fig. 16.** Second maxillae with bulla, × 170. **Fig. 17.** Extremity of second maxillae with bulla, × 360. **Fig. 18.** Apical view of bulla, × 1400.



**Figs. 19-27.** Morphology of attachment organ of some lernaeopodid species (scanning electron micrographs). **Fig. 19.** Extremity of second maxillae of *Neobrachiella merluccii*, with bulla, × 660. **Figs. 20, 21.** *Neobrachiella bispinosa*. **Fig. 20.** Extremity of second maxillae with bulla, × 450. **Fig. 21.** Detail of pellicle flanges, × 1500. **Figs. 22, 23.** *Pseudocharopinus malleus*. **Fig. 22.** Second maxillae with bulla, ×80. **Fig. 23.** Extremity of second maxillae with bulla, × 400; detail of surface (arrow), × 5400. **Figs. 24-26.** *Pseudocharopinus bicaudatus*. **Fig. 24.** Extremity of second maxillae with bulla, × 200. **Fig. 25.** Apical view of the bulla showing two maxillary plugs, × 1200. **Fig. 26.** Tip of maxillary plug with two pores (p), × 6000. **Fig. 27.** Extremity of second maxillae of *Tracheliastes polycolpus*, with bulla attached to a fin ray, × 210.



**Figs. 28-34.** Sections through bullae of some lernaeopodid species. **Fig. 28.** *Sparidicola lithognathae*, × 150. **Fig. 29.** *Alella macrotrachelus*, × 200. **Fig. 30.** *Clavella stellata*, × 380. **Fig. 31.** *Neobrachiella bispinosa*, × 440. **Fig. 32.** *Clavellotis strumosa*, × 500. **Fig. 33.** *Neobrachiella exigua,* × 600. **Fig. 34.** *Pseudocharopinus bicaudatus*, × 340.

## DISCUSSION

Although the bulla structure of female Lernaeopodidae follows a common pattern, its morphology presents a great variability.These modifications appear on:

- the widening or narrowing of the anchor size,
- the change in the anchor shape and in its ornamentation, and
- the lengthening or shortening, or even the disappearance, of the anchor.

Based on a study of the phyletic relations between different genera constituting the family Lernaeopodidae (Kabata 1966), Kabata and Cousens (1972) tried to take into account the morphological aspect of the bulla as a distinctive criterion. They concluded that the morphology appears independent of the phylogenetical position of the copepod within the family, and that it is linked to the type of host. Thus, they distinguished three types of bulla corresponding to three types of hosts: fresh-water Teleostei, marine Teleostei and Elasmobranchii.

The type I includes bullae from species parasitic on freshwater Teleostei with the exception of those belonging to the genus *Tracheliastes* with small bullae. After Kabata and Cousens (1972) "reduction in size of the anchor is characteristic of the genus *Tracheliastes*". For other genera (*Salmincola, Achtheres* and *Coregonicola*), bullae are characterised by a large, circular anchor either lobed or star-shaped. The matrix is spongy and fibrous with the presence of two canals crossing the manubrium and the anchor.

The type II comprises bullae of Lernaeopodidae parasitic on marine teleosts with, generally, a short manubrium and an anchor of small diameter in the shape of a sub-spherical cup or a bludgeon. The canals, starting in the manubrium, branch out and open at the anchor's periphery.

According to our observations on various parasite species from marine Teleostei, it is possible to distinguish inside the type II two large groups of bullae:

(1) large-diameter cups flattened on the host tissues. This is the case for *Neobrachiella bispinosa, N. impudica, N. mugilis* and *Sparidicola lithognathae.* They correspond principally to species attached to the tegument (such as mouth, sub-operculum, base of pectoral fins, skin, scales);

(2) the forms deeply embedded by an anchor of spherical, oblong, pear or bludgeon shape. These forms characterise mainly the gill species except for *Neobrachiella exigua*, the bulla of which corresponds in shape more to those of the first group.

The type III, in Elasmobranchii, is characterised by a short manubrium. Generally, the anchor is small with some exceptions such as *Charopinus dubius*, the female of which, attached to the spiracle of *Raja asterias*, displays a well developed anchor (Raibaut and Maamouri 1975). Usually, it is a disk- or a spindle-shaped structure. The matrix fibres bundle together leaving spaces between them. Two long canals cross to the middle of the anchor. They contain two maxillary plugs. Our observations confirm those of previous authors (Kabata and Cousens 1972, Chandran and Balakrishnan Nair 1979). It must be noted that the bullae of Lernaeopodidae, parasites of Selachii, have a remarkably constant structure. This is probably due to the fact that these copepods are always attached to substratum of tegumentary type (skin of some Hypotremata, cloaca, pterygopods, spiracle, mouth and throat). To our knowledge, no strictly branchial Lernaeopodidae with bulla have been found on Selachii hosts.

To summarise, our observations, associated with those of previous authors, tend to show that the nature of parasitized tissue within which the bulla is embedded has a great influence on the morphology of this singular attachment organ. All species of *Clavellotis* have a well attached bulla in the shape of a mushroom. These species have in common the attachment gill arches. In other species that are also attached to gill arches, such as *Clavellisa*, the bulla has a similar shape but is conically stretched.

A particular case is *Clavella adunca*, found on two species of Gadidae, the bib *(Trisopterus luscus)* and the whiting *(Merlangius merlangus)*, with a different implantation. Scanning has shown a general identical shape for both bullae but with an ornamentation clearly different. Samples attached to the gill filament of the bib have a smooth-surface bulla; those attached to the gill arches of the whiting have a surface with small thorns. We are, therefore, in the presence of an ecomorphosis phenomenon due to the attachment substratum nature. Gill arches are a more resistant implantation area than the gill tissue, from which the difference in the roughness of surface to ensure a good attachment. According to Kabata (1960), there is, at the origin of the ecomorphous differentiation in the gill arches of the whiting (named *Clavella adunca* f. *devastatrix*), an interspecific competition phenomenon: the branchial microhabitat of the whiting is occupied by a monogenean (*Diclidophora merlangi*). This does not seem probable, since we know that a monogenean species of the same genus (*D. luscae*) lives on the bib gills.

To conclude, we think that, generally, the female Lernaeopodidae bulla is characteristic of a taxon as long as all units of the taxon occupy host microhabitats presenting the same histological structure. Evidently, this structure changes according to the nature of the various organs but for a same organ according to the host type. In this manner, the structure of Elasmobranchii tegument is different from that of

Teleostei. In other words, the bulla morphology has indirectly the value of a taxonomic criterion.

However, there are some exceptions to this general rule. For example, species of a same genus have colonised microhabitats anatomically and histologically different and they have, nevertheless, bullae of similar structural types. It is possible, in this case, that the bulla has kept its ancestral structure, characteristic of its first microhabitat, during the conquest of new territories, the conquest which can be followed by speciation.

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