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Functional morphology of the foregut of *Lophogaster typicus* and *L. spinosus* (Crustacea, Mysidacea, Lophogastrida)[1]

Laetitia DE JONG
Laboratoire de Biologie Animale (Plancton), Université de Provence
13331 Marseille Cedex 3 - France
E-mail: bioplank@newsup.univ-mrs.fr - Fax: (33) 4 91 10 60 06

Abstract: The foreguts of two *Lophogaster* species (Crustacea, Mysidacea, Lophogastrida), one benthic and another pelagic, are described. Their morphology is characteristic of the genus and does not seem related with the ecology of the species, as it would be expected. The foregut is very different from that observed in other Lophogastrida (*Eucopia* and *Gnathophausia*). Indeed, the cardiac chamber is followed by a large alimentary pouch occupying half the length of the cephalothorax, and which probably corresponds to the dorsal pyloric chamber. Such storage system is original among crustaceans exhibiting the caridoid facies (Mysidacea, Euphausiacea and Decapoda). As the dorsal pyloric chamber is posteriorly closed by this pouch, the junction between the stomach and the intestine takes place at the level of the ventral pyloric chamber, instead of the dorsal one as in other Mysidacea. The gastric mill also is original, since the lateral teeth look like mandibles owing to their morphology and internal musculature. Lastly, at the junction with the stomach, the very small size of the lumen of the intestine probably do not allow the passage of coarse particles, contrary to what occurs in other Mysidacea, Euphausiacea and Decapoda.

Résumé : *Morphologie fonctionnelle du stomodeum chez Lophogaster typicus et L. spinosus (Crustacea, Mysidacea, Lophogastrida.*
L'estomac de deux espèces de *Lophogaster,* l'une benthique et l'autre pélagique, a été étudié. Sa morphologie est caractéristique du genre et ne semble pas reliée à l'écologie des espèces, comme on aurait pu s'y attendre. L'estomac est très différent de celui observé chez d'autres Lophogastrida (*Eucopia* et *Gnathophausia*). En effet, la chambre cardiaque se prolonge par une vaste poche alimentaire qui occupe en longueur la moitié du céphalothorax. Elle correspond probablement à la chambre pylorique dorsale. Ce système de réserve est original parmi les crustacés ayant un faciès caridoïde (Mysidacés, Euphausiacés et Décapodes). En raison du développement de cette poche, la jonction entre l'estomac et l'intestin se fait au niveau de la chambre pylorique ventrale, alors que chez les autres Mysidacés, elle se fait au niveau dorsal. Le moulin gastrique aussi est original, dans la mesure où les dents latérales ressemblent à des mandibules par leur forme et la présence de muscles internes. Enfin, à la jonction avec l'estomac, la lumière intestinale est si étroite qu'elle ne permet vraisemblablement pas le passage de grosses particules, à l'inverse de ce qui s'observe chez les autres Mysidacés, les Euphausiacés et les Décapodes.

Keywords : Foregut, morphology, Crustacea, Mysidacea, Lophogastrida, *Lophogaster*.

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Introduction

Sparse information about the digestive system of the suborder Lophogastrida is available and there is no information

in the literature on the foregut of the genus *Lophogaster*. This genus belongs to one of the two families of the sub-order Lophogastrida, the Lophogastridae, including all the other genera but *Eucopia*, which constitutes the family Eucopiidae.

This study describes, for the first time, the foregut of two species of *Lophogaster*, *L. typicus* M. Sars, 1857, a benthic species, and *L. spinosus* Ortmann, 1906, a pelagic one. Previous investigations on *Eucopia* (De Jong & Casanova, 1997a) and *Gnathophausia* (De Jong & Casanova, 1997b), two other Lophogastrida genera are also complemented. Electron microscopy has been used to investigate the functional morphology of both foregut and intestine.

Materials and methods

The specimens of *Lophogaster typicus* used for scanning electron microscopy were collected off Gibraltar (35°45'0 N - 5°17'0 W, 17/06/84, at a depth of 280-300m) and those of *Lophogaster spinosus* off Morocco (28°16'0 N - 16°06'2 W, 29/03/68, at a depth of 1000m); their number were 8 and 2 respectively. Animals were preserved in 70% ethanol solution. They were dissected under a binocular microscope and the foreguts carefully cleaned for observations. For binocular microscope observations, stomachs were: (1) washed in 0.5% sodium hypochlorite solution; (2) washed in ethanol solution with 1.5% lactic acid; (3) stained with chlorazol black in 50% ethanol solution at 40°C (Casanova *et al.*, 1993). For scanning electron microscopy, empty opened stomachs were critical point-dried, sputter-coated with gold and examined with a (JEOL, JS M35C) SEM microscope. For transmission electron microscopy, juvenile specimens of *Lophogaster typicus* collected in the Gulf of Lions (43°05'50 N - 5°13'0 E, 1/04/96, at a depth of 590m) were fixed in a solution of 2% glutaraldehyde - 1% paraformaldehyde - 30% filtered sea water in 0.2 M sodium cacodylate buffer, at 4°C, with a final pH of 7.3 (final osmolarity of the solution around 1200 mosm), then washed in the same buffer and postfixed in buffered 1% osmium tetroxide (Arnauld *et al.*, 1988). Thin sections obtained from Epon embedded material were stained with uranyl acetate and lead citrate (Reynolds, 1963) and examined with a JEOL 100C Transmission electron microscope. Epon semi-thin sections, 1 µm thick, were stained with 50% unna blue for light microscopy and direct comparison with thin sections.

Results

Foregut

The entire foregut is lined with a chitinous cuticle. It consists of a vertical oesophagus and an elongated stomach that is functionally divided into an anterior cardiac and a posterior pyloric regions by a pair of cardio-pyloric valves (Figs. 1A, 1B). Moreover, a pair of lateral simple folds, fringed with very long setae, separates the stomach into two distinct dorsoventral regions: the upper dorsal region or food channel, which consists of a large alimentary pouch, and the lower ventral region or filter region (Figs. 1A, 1B). At the junction between the oesophagus and the stomach there is no oesophageal cardiac valve (Fig. 1B). The primary filter of the cardiac chamber, which is composed of the ventral cardiac ridge, the ventrolateral filter channels and the ventrolateral cardiac ridges (Fig. 1B), is similar to those of *Eucopia* (De Jong & Casanova, 1997a) and *Gnathophausia* (De Jong & Casanova, 1997b). However, the ventrolateral cardiac ridges are laterally more developed to form a pair of lateral plates ornamented with small sharp spines (Figs. 1B, 2A). In *L. spinosus*, some of these spines exhibit an apical aperture, which might be regarded as a pore (Fig. 2B).

The ventrolateral walls of the cardiac chamber form a pair of strong lateral teeth, looking like mandibles (Fig. 1B). Muscles are attached inside the teeth and reach their tips (Fig 2C). The teeth are ornamented with tiny scales at their tips (Fig. 2G) and fringed with very long serrulated setae at their bases (Figs. 1B, 2D). These setae exhibit a true apical pore (Fig. 2E). Some slight variations in shape of these teeth have been observed in different specimens of *L. typicus*, but the general feature is that presented in figures 1B and 2D. An apical aperture has been found in one of these teeth, but it still remains unclear if it is a real aperture or just the consequence of a damage (Fig. 2F). Behind the lateral teeth, there is a small fold provided with very long serrulated setae (Fig. 2D). These small folds might correspond to the second pair of lateral teeth occurring in *Eucopia* and *Gnathophausia*. The roof of the cardiac chamber bears an unpaired anterodorsal tooth (Fig. 1B). Its tip is globular and armed with serrulated spines (Figs. 1B, 2H). Dorsally, the cardiac chamber is followed by a very large posterior expansion, which forms an alimentary pouch (Fig. 1A) occupying half the length of the cephalothorax and which belongs to the pyloric chamber. The gastric mill, consisting of the strong lateral teeth and the anterodorsal tooth, protrudes into the anterior part of this alimentary pouch. It is situated at the beginning of the cardiac chamber, right above the oesophagus opening (Figs. 1A, 1B).

The pyloric chamber is longer than the cardiac one (Fig. 1A). Its ventral part constitutes the secondary filter of the foregut, which is more important than the primary filter of the cardiac chamber. It exhibits the same features as in other Lophogastrida: a ventral pyloric ridge, ventrolateral filter channels and ventrolateral pyloric ridges (Fig. 1B). Thus, its functional morphology and setal system arrangement are also homologous. However, the setae of the ventrolateral pyloric ridges of *L. spinosus* are serrulated and flattened

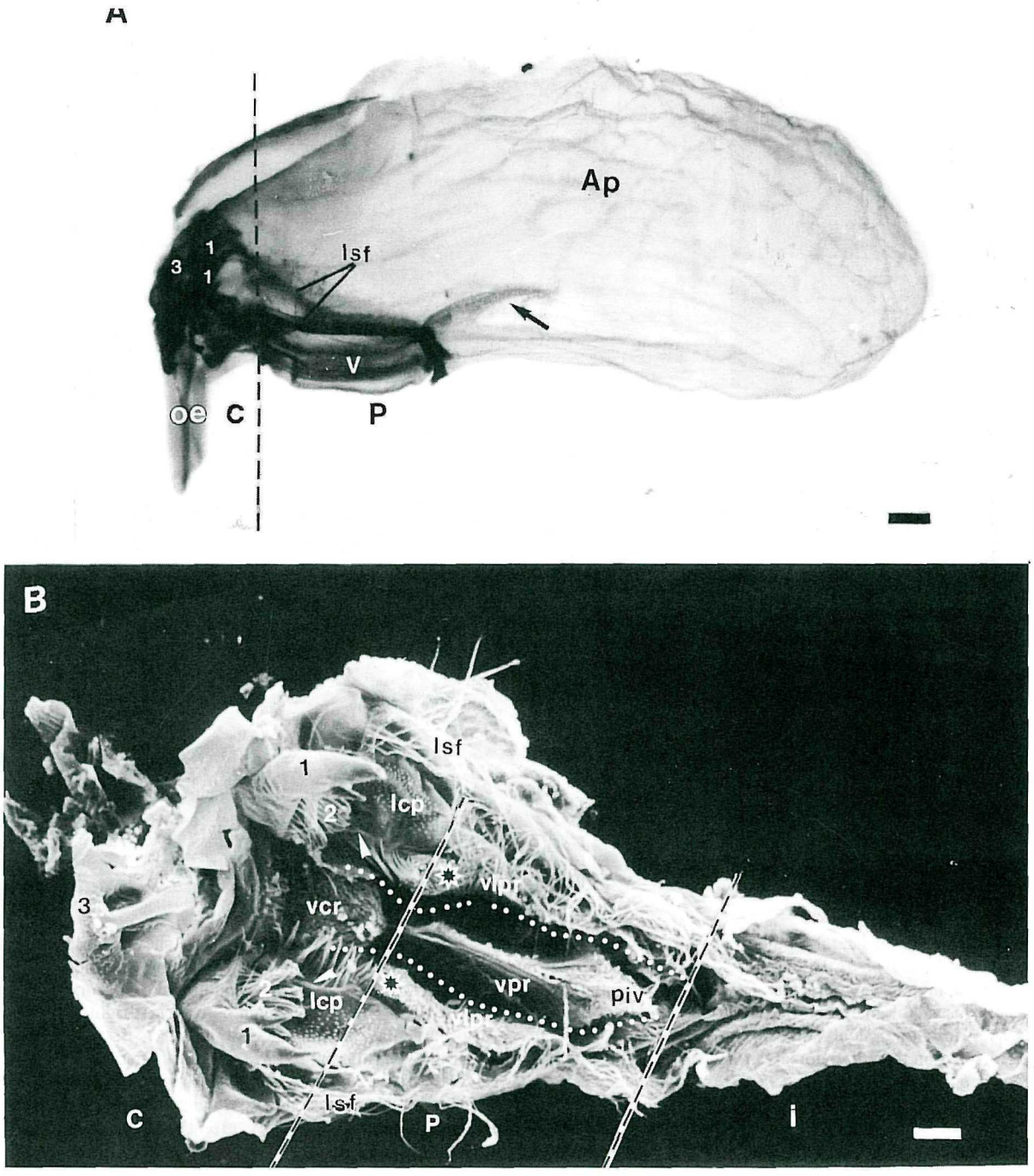

Figure 1. Foregut of *Lophogaster*: A, micrograph of the foregut of *L. typicus* in lateral view; B, SEM micrograph of the foregut of *L. spinosus* in dorsal view with the dorsal alimentary pouch removed. Ap: alimentary pouch, arrow: pyloric valves, arrow-heads: ventrolateral cardiac ridges, dotted lines: filter channels, C: cardiac part, i: intestinal part, lcp: lateral cardiac plates, lsf: lateral setose fold, oe: vertical oesophagus, P: pyloric part, piv: pyloro-intestinal valve, stars: cardio-pyloric valves, V: ventral pyloric chamber, vcr: ventral cardiac ridge, vlpr: ventrolateral pyloric ridges, vpr: ventral pyloric ridge, 1: first lateral teeth, 2: small lateral setose folds (corresponding to the second lateral teeth of other Lophogastrida), 3: anterodorsal cardiac tooth. Scale bars: (A, B) 100 µm.

Figure 1. Stomodeum de *Lophogaster*. A, micrographie du stomodeum de *L. typicus* en vue latérale. B, micrographie de microscopie électronique à balayage de *L. spinosus*, en vue dorsale, après avoir retiré la poche alimentaire dorsale. Ap : poche alimentaire, flèche : valves pyloriques, têtes de flèches : crêtes cardiaques ventro-latérales, lignes en pointillé : canaux de filtration, C : partie cardiaque, i : partie intestinale, lcp : plaques cardiaques latérales, lsf : replis latéraux sétigères, œ : œsophage vertical, P : partie pylorique, piv : valvule pyloro-intestinale, étoiles : valvules cardio-pyloriques, V : chambre pylorique ventrale, vcr : crête cardiaque ventrale, vlpr : crêtes pyloriques ventro-latérales, vpr : crête pylorique ventrale, 1 : premières dents latérales, 2 : petits replis latéraux sétigères (correspondant aux secondes dents latérales des autres Lophogastrida), 3 : dent cardiaque antéro-dorsale. Échelles = 100 µm.

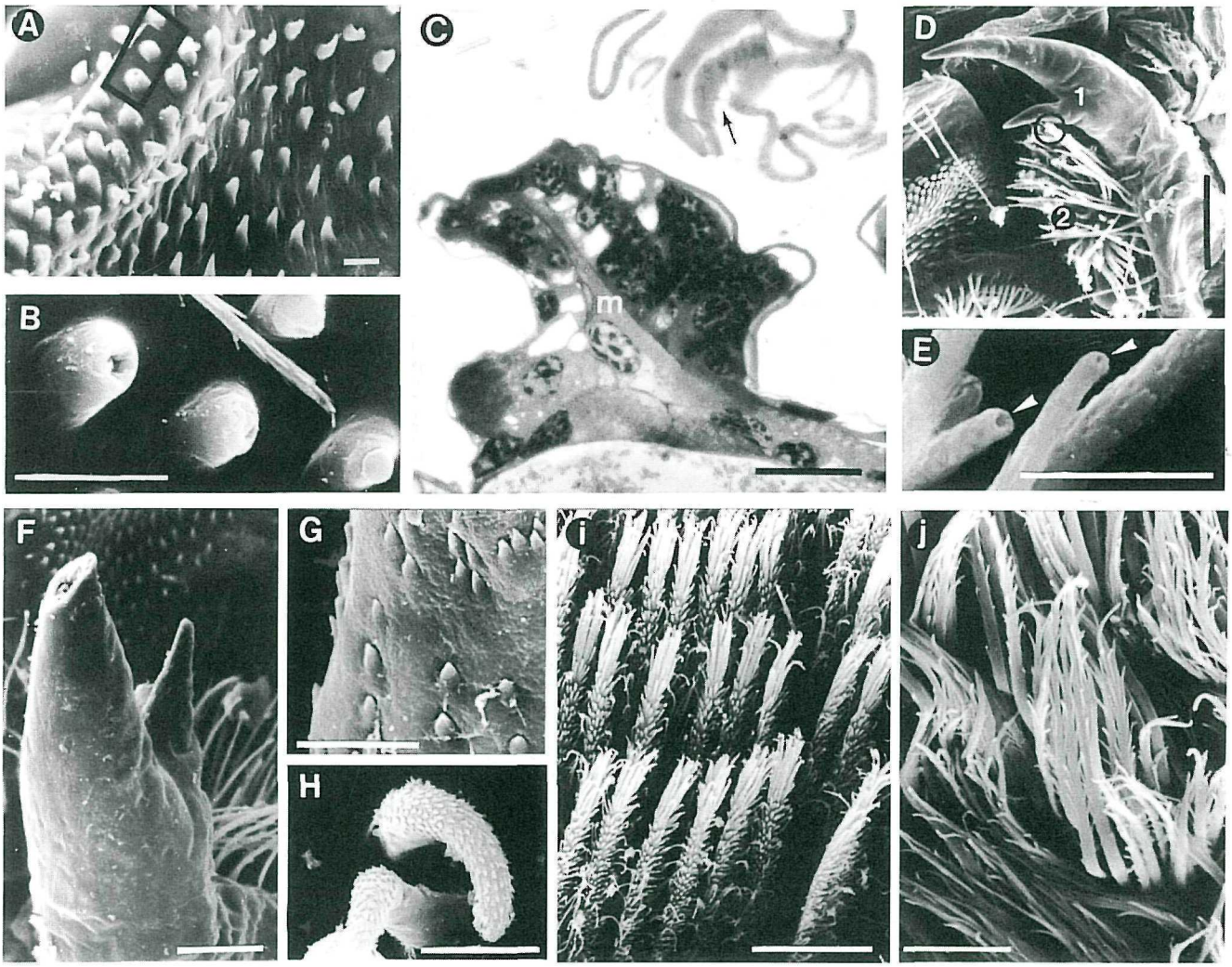

Figure 2. A, spines on lateral cardiac plates in *L. spinosus*. B, details of the spines boxed in figure 2A, showing apical apertures (= pores ?). C, D, E, *L. typicus*. C, Cross-section through the right mandible-like lateral cardiac tooth, arrow: coarse particles within the alimentary pouch, m: internal muscle. D, left first lateral tooth (1) and small lateral setose fold (2) corresponding to the second lateral tooth in other Lophogastrida. E, detail of one of the first lateral tooth, circled in figure 2D, arrowheads: apical pore. F, first right lateral tooth of *L. spinosus* showing apical aperture. G, H, I, *L. typicus*. G, ornamentation of the tip of the first lateral tooth. H, serrulated spine on the anterodorsal cardiac tooth. I, three rows of setae of the ventrolateral pyloric ridge. J, flattened serrulated setae of the ventrolateral pyloric ridge of *L. spinosus*. Scale bars: A, B, E, G, H, I: 10 µm, C: 25 µm, D, 100 µm, F, 50 µm, J: 5 µm.

Figure 2. A, Épines sur les plaques cardiaques latérales de *L. spinosus*. B, détail des épines encadrées dans la figure 2A, montrant un pore apical. C, D, E, *L. typicus*. C, coupe transversale de la dent cardiaque latérale droite, flèche : grosses particules dans la poche alimentaire, m : muscle interne. D, première dent latérale gauche (1) et petit repli latéral sétigère (2), correspondant à la seconde dent latérale des autres Lophogastrida. E, détail des soies des premières dents latérales, marquées d'un cercle dans la figure 2D, têtes de flèche : pores apicaux. F, première dent latérale droite de *L. spinosus* montrant l'ouverture apicale. G, H, I, *L. typicus*. G, ornementation du sommet de la première dent latérale. H, épine de la dent cardiaque antéro-dorsale. I, trois rangs de soies de la crête pylorique ventro-latérale. J, soies aplaties de la crête pylorique ventro-latérale de *L. spinosus*. Échelles = A, B, E, G, H, I : 10 µm. C : 25 µm, D : 100 µm, F : 50 µm, J : 5 µm.

(Fig. 2J), while in *L. typicus* (Fig. 2I) they are different and similar to those found in both *Eucopia* and *Gnathophausia*. The ventral filtration system of the stomach is separated from the dorsal region by a pair of simple lateral folds ornamented with very long setae (Figs. 1A, 1B). As said above, the dorsal region is a large alimentary pouch (Fig. 1A), containing coarse particles (Fig. 2C), which are broken down by the anterior gastric mill of the cardiac chamber. Owing to this pouch, the junction between the stomach and the intestine takes place at the level of the

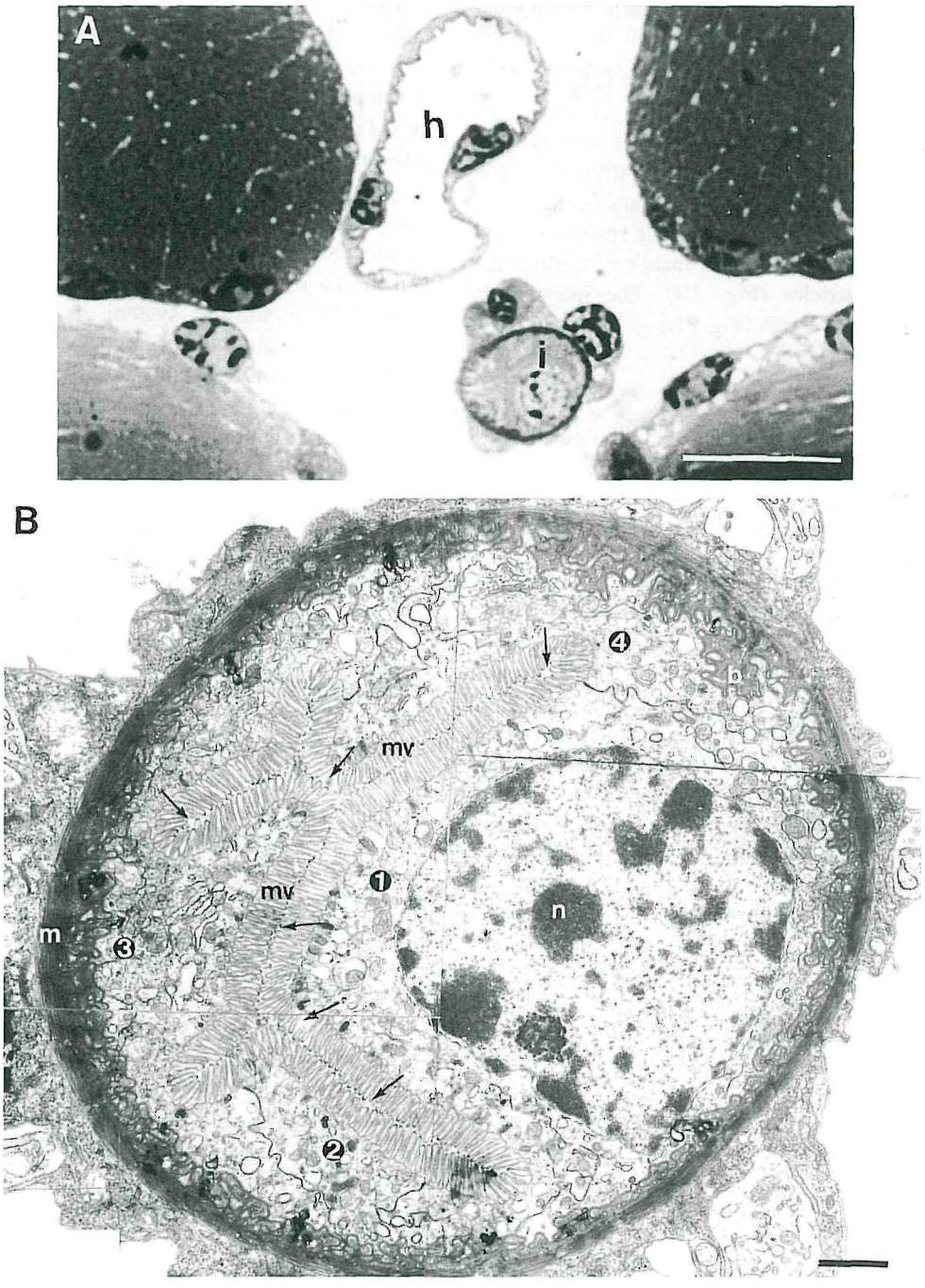

Figure 3. A, B. cross section of the intestine of a juvenile specimen of *L. typicus* after the junction with the foregut. A, semi-thin section: note the small size of the intestine (the lumen is not visible), h: heart, i: intestine. B, thin section of the intestine observed electron microscopically: note the small size of the lumen (arrows). The intestine is constituted by only four cells (1, 2, 3, 4), b: basal lamina, m: circular muscles, n: nucleus, mv: microvilli. Scale bars: A: 25 µm, B: 1,5 µm.

Figure 3. A, B. Coupes transversales de l'intestin d'un spécimen juvénile de *L. typicus,* au niveau postérieur à la jonction avec le stomodeum. A, coupe semi-fine : notez que l'intestin est étroit (la lumière n'est pas visible). h : cœur, i : intestin. B, coupe ultrafine de l'intestin, à lumière (flèches) très étroite, ne comptant que quatre cellules (1 à 4). b : lame basale, m : muscles circulaires, n : noyau, mv : microvillosités. Échelles : A = 25 µm, B = 1,5 µm.

ventral pyloric chamber (Fig. 1B). The pyloric valves enter into the intestine, but there is here no real funnel region similar to that which exists in *Eucopia* and *Gnathophausia*.

Intestine

The lumen of the intestine is not visible in semi-thin transverse section at the stomach junction (Fig. 3A). The intestine wall only comprises a small number of cells, about four to five in transverse section in juvenile specimens, and the small size of the lumen can probably not allow the passage of coarse particles (Fig. 3B). The intestine is surrounded by circular muscles (Fig. 3B).

Discussion

The present study demonstrates that the main features of the foregut in *Lophogaster* are remarkably uniform since the sole difference between the two species is the type of spines of the ventrolateral pyloric ridges. It appears that the morphology of the stomach is not related to the ecology of the species, (benthic or pelagic life), as it would be expected. Indeed, it has been demonstrated in recent studies on Euphausiacea (Suh, 1990) and Decapoda (Icely & Nott, 1992), that the morphology of the digestive system depends primarily on the phylogenetic history of the species, even if other factors such as dietary differences may modify the anatomy of the foregut. The present study confirms the first part of this hypothesis as well as the previous investigations on *Eucopia* (De Jong & Casanova, 1997a) and *Gnathophausia* (De Jong & Casanova, 1997b).

Common features of the foregut of *Eucopia* and *Gnathophausia* are also found in *Lophogaster* and are certainly typical features of the Lophogastrida. Among them, the vertical oesophagus, the elongated shape of the stomach and the functionally separated regions of the stomach are noticeable. Moreover, the gastric mill is situated at the beginning of the cardiac chamber, while it is located at the limit between the cardiac and the pyloric chambers in the Euphausiacea (Suh & Nemoto, 1988), the Decapoda (Icely & Nott, 1992) and the Mysida (Nath & Pillai, 1973; Friesen *et al.*, 1986; Storch, 1989; Metillo & Ritz, 1994), except *Spelaeomysis longipes* (Nath & Pillai, 1971). The gastric mill comprises at least a pair of lateral teeth. The second pair of lateral teeth is often reduced to a setose fold. The anterodorsal cardiac tooth is present in all the genera studied, even if it is reduced to a simple fold in *Eucopia unguiculata* and *E. australis*.

In these Lophogastrida, the pyloric chamber is always longer than the cardiac chamber and the ventral pyloric chamber is not isolated beneath the rest of the stomach, contrary to species of the sub-order Mysida. The most important structure of the pyloric region is the ventral pyloric ridge, which bears numerous rows of plumose setae, instead of two or three in the Mysida (Gelderd, 1909).

However, the morphology of the foregut of the genus *Lophogaster* differs from *Gnathophausia* and *Eucopia*: 1) in the absence of the oesophageal cardiac valve, 2) in the development of the ventrolateral cardiac ridges into wide lateral plates, 3) in the first pair of lateral teeth looking like internal mandibles, 4) in the presence of a wide alimentary pouch and, as a consequence, the absence of a funnel region and the junction of the intestine with the ventral pyloric chamber and not with the dorsal pyloric chamber as in other genera. To our knowledge, the alimentary pouch, which constitutes a storage system, is original among the crustaceans having a caridoid facies, e. g. Mysidacea, Euphausiacea and Decapoda.

The morphology of this foregut implies that ingested food is stored within the alimentary pouch and crushed by the gastric mill. Sand has been found within the alimentary pouch and it probably helps in grinding. As in other crustaceans, a chemical breakdown of ingested material by digestive enzymes is likely. Fine and soluble particles are separated from coarse material by the ventral filter systems and transported for further treatment in the midgut. Since in *Lophogaster* the junction between the stomach and the intestine takes place at the ventral pyloric chamber level, only filtered material reach the intestine. Contrary to other Mysidacea (Friesen *et al.*, 1986), coarse undigested material probably cannot be transferred to the intestine, and this is probably correlated with the reduced size of its lumen. Coarse undigested material stored in the alimentary pouch might be evacuated through the oesophagus, which might also explain the absence of an oesophageal cardiac valve.

It still remains unclear if most of the pores observed in the stomach are real pores or just the result of a damage during mastication. Further investigations are needed to resolve this problem. However, the setae of the strong lateral teeth exhibit a real apical pore. In *Eucopia sculpticauda* spines with an apical pore have also been found on the first pair of lateral teeth (De Jong & Casanova, 1997a). To our knowledge, apertures or pores through the cuticle of the stomach or its outgrowths have never been observed in other Malacostraca. The presence of these pores suggests that the cardiac chamber may possess its own enzymatic system within the underlying epithelium. This supports the suggestion made by Arnould and Jeuniaux (1982) of a secretory enzymatic system specific to the foregut for several species of *Pagurus* (Decapoda).

Conclusion

The morphology of the foregut of the two species of *Lophogaster* studied is very similar and differs from the other genera of the same sub-order, *Gnathophausia* and *Eucopia*, especially in its peculiar adaptation for food storage. However, common features are characteristic of the

sub-order Lophogastrida. The intestine is also unique in its small diameter. Its function seems to be different from that of other Mysidacea, since it could probably not allow the transport of coarse particles.

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