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Relevant role of the labrum associated with the mandibles in the *Lophogaster typicus* digestive function

L. De Jong*, X. Moreau, R.-M. Barthélémy and J.-P. Casanova

EA Biodiversité no. 2202, Laboratoire de Biologie Animale (Plancton), case 18, Université de Provence, 3 place Victor Hugo, 13331 Marseille cedex 3, France. *Corresponding author, e-mail: bioplank@up.univ-mrs.fr

This study was aimed at understanding the diet and the digestive function of the deep-living Lophogastrida species *Lophogaster typicus* (Mysidacea: Lophogastrida). Scanning electron microscopy (SEM) investigations have revealed that the mandibles exhibit typical features of a carnivorous diet, i.e. large and sharp incisor process and small molar one with only few scales. The analysis of gut contents confirms morphological data as crustacean remains have been recognized. However, the presence of a large quantity of unidentifiable soft particulate matter also indicates a saprophagous tendency. The external asymmetrical edge of the labrum consists of a small grinding area. The entire external face of the labrum exhibits numerous pores, which are related with glandular units. These units are organized into acini of two to four large cells. Two types of acini have been observed, i.e. with dark or clear cells. According to ultrastructural and cytochemical data, labral secretions are believed to be mucopolysaccharidic (for clear acini) and enzymatic components (for dark acini), and are therefore involved both in coating and in digesting the food. Moreover, presence of neuronal endings and endocrine cells, both associated with glandular units, and comparison between glandular units in starved and fed animals suggest a controlled release of the secretions. Therefore, the labrum plays a crucial role in the digestive function of the lophogastrid crustacean *L. typicus*, as it involves both mechanical and chemical breakdown of the food.

INTRODUCTION

Species of the genus *Lophogaster* are known to have a very different foregut from that observed in other Lophogastrida (De Jong, 1996; De Jong & Casanova, B., 1997; De Jong & Casanova, J.-P., 1997; De Jong-Moreau & Casanova, J.-P., 2001). Indeed, these species exhibit a foregut with a large alimentary pouch occupying half the length of the cephalothorax and an intestine that does not allow the passage of coarse particles (De Jong-Moreau et al., 2000). As most of the species of the genus, *Lophogaster typicus* M. Sars, 1857 is benthic (Fage, 1942; Tattersall & Tattersall, 1951; Mauchline, 1980; Casanova, J.-P., 1993, 1996a, 1997). Its feeding habits remain unknown. In Mysidacea, it is acknowledged that the peri-oral structures are directly involved in feeding and their detailed morphology, observed with scanning electron microscope (SEM), is considered as one of the best indicators of the food preference of the species (Webb & Wooldridge, 1989; De Jong-Moreau et al., 2001).

In the present study, the mandibles, the labrum and the foregut contents of *L. typicus* have been studied for a better understanding of the functional morphology of the digestive system of this Lophogastrida. Moreover, ultrastructural data of the labral glands, for the first time described in Mysidacea, allowed us to propose an interpretation on the role of the labrum in digestive function and enlarge the investigations on the foregut, the midgut and the hepatopancreas in this species.

MATERIALS AND METHODS

Ten specimens of *Lophogaster typicus* were collected off Gibraltar (35°45′0N 05°17′0W, 17 June 1984, 280–300 m). The animals were preserved in 70% ethanol solution. They were dissected under a stereomicroscope. Mandibles and labrum were critical point-dried, sputter coated with gold and examined with an SEM (JEOL JSM 35 CF) or ESEM (Philips XL 30). Three foreguts were opened and their contents observed by SEM. The gut contents of the other seven specimens were removed carefully and stained with chlorazol black in 50% ethanol solution at 40°C before their observation with a light microscope.

For semi-thin and thin sections, four specimens were collected off Marseille (43°08′07N 5°15′5E, 30 October 1997, 100 m, during the night). They were utilized in feeding experiments in order to study the labral glands. First, they were starved for four days. Three of them were then fed for 1 h with large amounts of TetraMin® and *Artemia* sp. The four specimens were then fixed in 0.2 M sodium cacodylate buffer (pH 7.3) containing 2% glutaraldehyde, 1% paraformaldehyde, 30% filtered seawater, at 4°C (osmolarity 1200 mOsM). The labrum of each specimen was then dissected, washed in 0.2 M cacodylate buffer, postfixed in buffered 1% osmium tetroxide (Arnaud et al., 1978) and embedded in Epon. Semi-thin sections were then stained with 50% Unna blue for light microscopy. For ultrastructural observations, thin sections were stained with uranyl acetate followed by lead citrate (Reynolds, 1963) before examination in a Zeiss EM 912 electron microscope (IBDM, Luminy, Marseille) at an accelerating voltage of 80 kV. Other thin sections were used for the PATAg cytochemical test (Thiéry & Rambourg, 1974) in view to detect polysaccharides in glandular secretions. For this purpose, the sections were mounted on gold grids and treated as follows: oxidation in 1% periodic acid solution for 25 min, incubation in

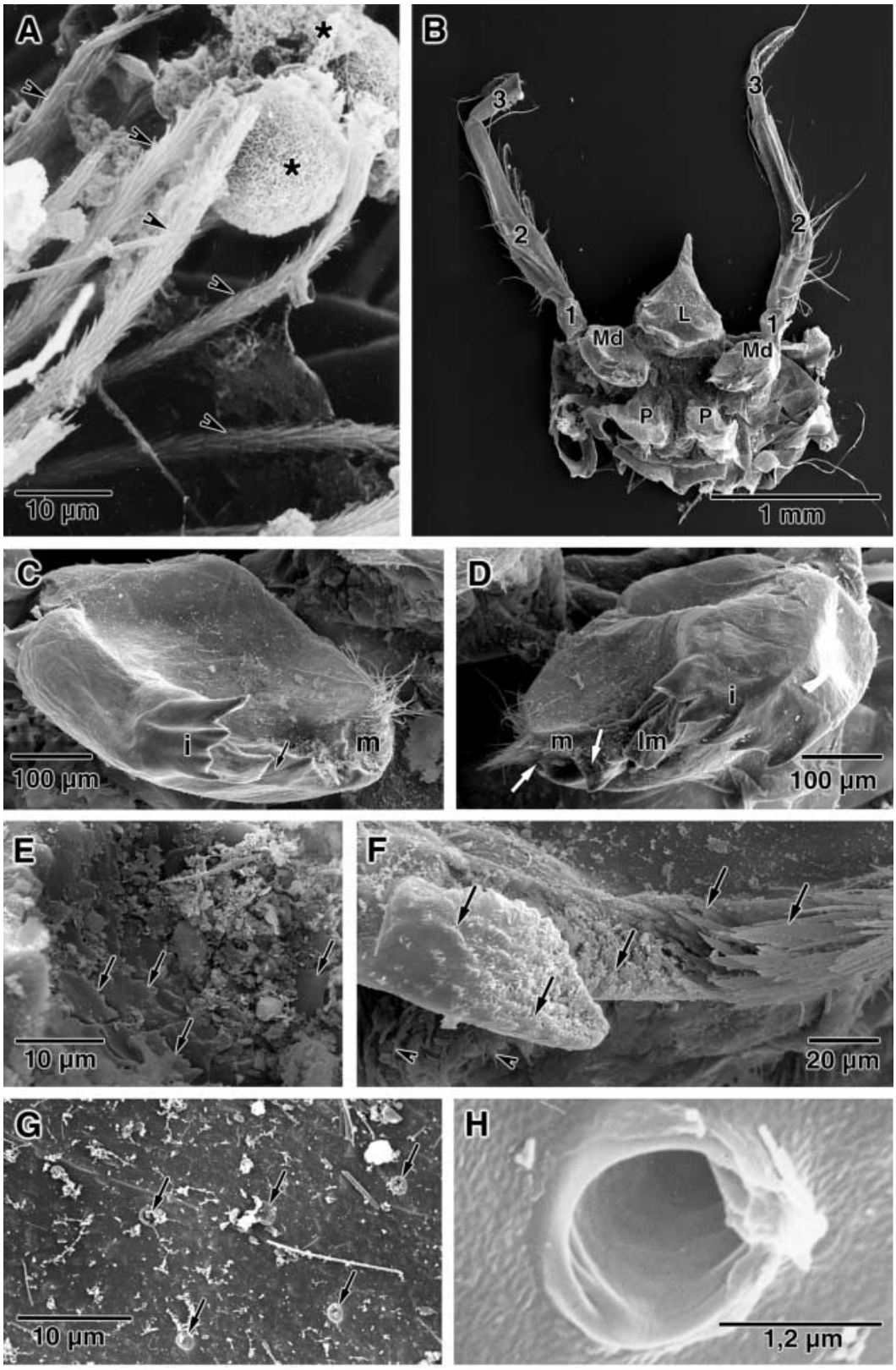

Figure 1. Scanning electron micrographs of the foregut content (A) and of the mandibles and labrum of *Lophogaster typicus* (B–H). (A) Note the presence of unidentifiable material (asterisks) between the setae (arrowheads) of the foregut; (B) general external view of the labrum (L), mandibles (Md) and paragnaths (P). Note the well-developed 3-segmented palps of the mandibles (1–3); (C, D) right and left mandibles. Note the huge incisor process (i) compared to the reduced molar one (m). The molar process of the left mandible is split into two areas (D, white arrows). The left mandible exhibits a large *lacinia mobilis* (lm) that fits with an unarticulated bicuspid structure of the right mandible (C, black arrow); (E) enlargement of the right molar process showing few blunted scale-like spines (arrows); (F) posterior asymmetrical edge of the labrum. Its right side forms a hooked lamella provided with short spines delimiting a small grinding area (arrows). All the spines of the labrum posterior edge are directed anteriorly (arrows). A few small setae, directed towards the mouth, are observable on the inner face of the labrum (arrowheads); (G) enlargement of the external face of the labrum showing numerous pores (arrows); (H) detail of a labral pore.

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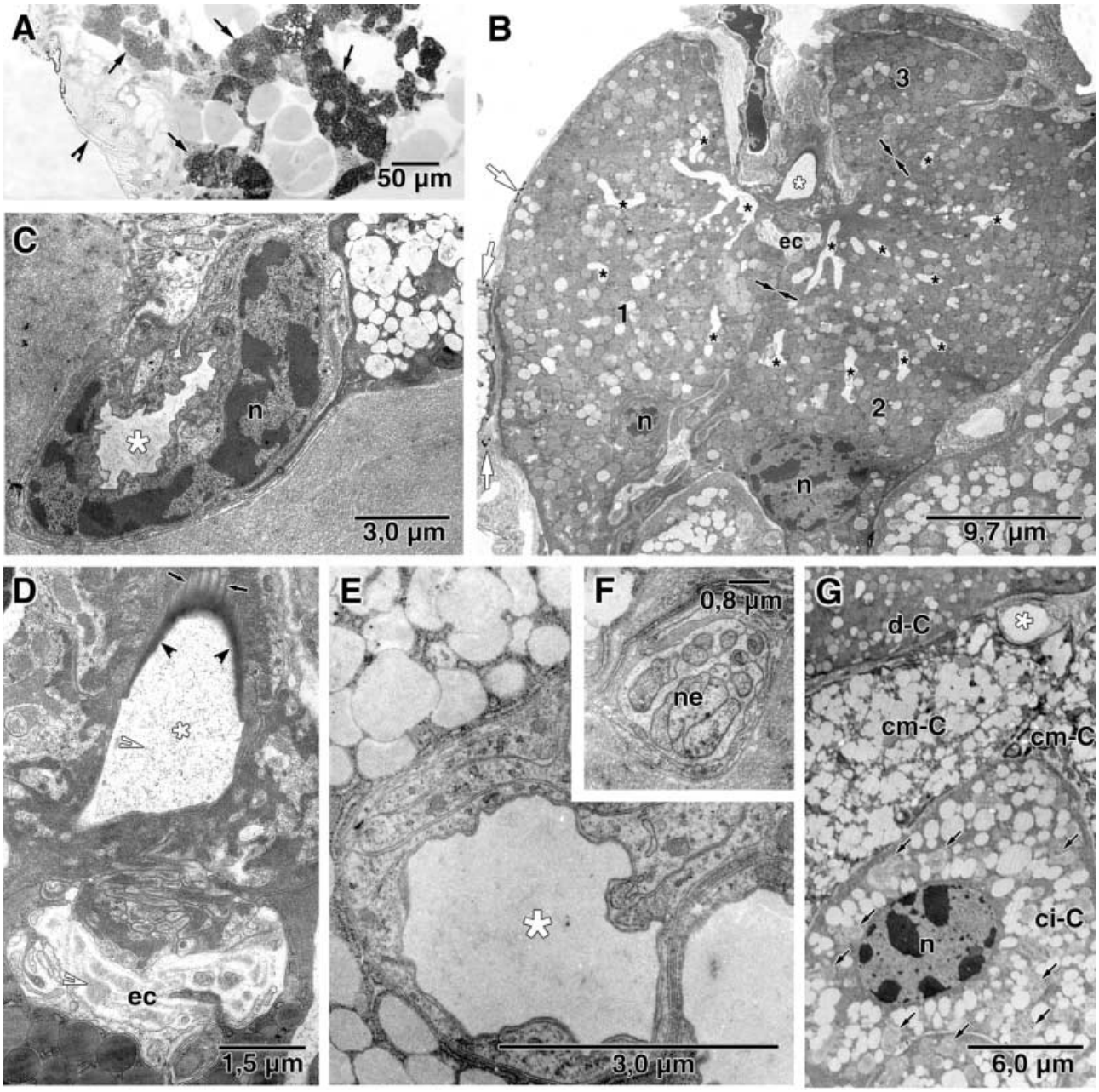

Figure 2. Structure and ultrastructure of the labral glandular units of *Lophogaster typicus*. (A) Photomicrograph of a semi-thin frontal section of the left half of the labrum. The arrowhead indicates the posterior edge of the labrum and arrows show the glandular units. (B–G) Transmission electron micrographs of sections through the glandular units; (B) longitudinal section through a dark acinus displaying three large cells (1, 2, 3) obtained from a fed animal. Opposing black arrows indicate the plasma membranes of two adjacent cells. Note the abundance of granules, the deep plasma membrane invaginations (black asterisks) leading to an excretory chamber (ec) and the duct of the acinus (white asterisk). White arrows indicate dense granules of endocrine-like cells which are closely associated with the glandular unit; (C) transverse section through a duct. Note the oblong curved nucleus (n) of the canalar cell; (D) enlargement of the excretory chamber and the duct of the acinus of (B) micrograph. Secretion products are present in the excretory chamber and in the collector duct (white arrowheads). Note the cuticularized distal part of the duct (black arrowheads) and the parallel microtubules lining the duct (arrows); (E) transverse section through empty ducts obtained from a starved animal; (F) nervous fibers (ne) in the connective tissue surrounding the acini; (G) section through the two different types of glandular units. Note the presence of clear immature cells in secretion synthesis phase (ci-C) and clear mature cells (cm-C) in which the granules are fused. Arrows indicate numerous Golgi bodies in clear immature cells. d-C indicates dark cell; ec, excretory chamber; n, nucleus; white asterisk, duct.

0.2% TCH (thiocarbohydrazide, Serva) in a 20% acetic acid solution for 6 min to 72 h and final treatment with 1% silver proteinate in distilled water for 20–30 min. In control sections, the periodic acid was substituted by 10% H_2O_2.

RESULTS

Observations of the foregut contents

In light microscopy, the foregut contents always consist of a mash where only a few small hard parts, i.e. some

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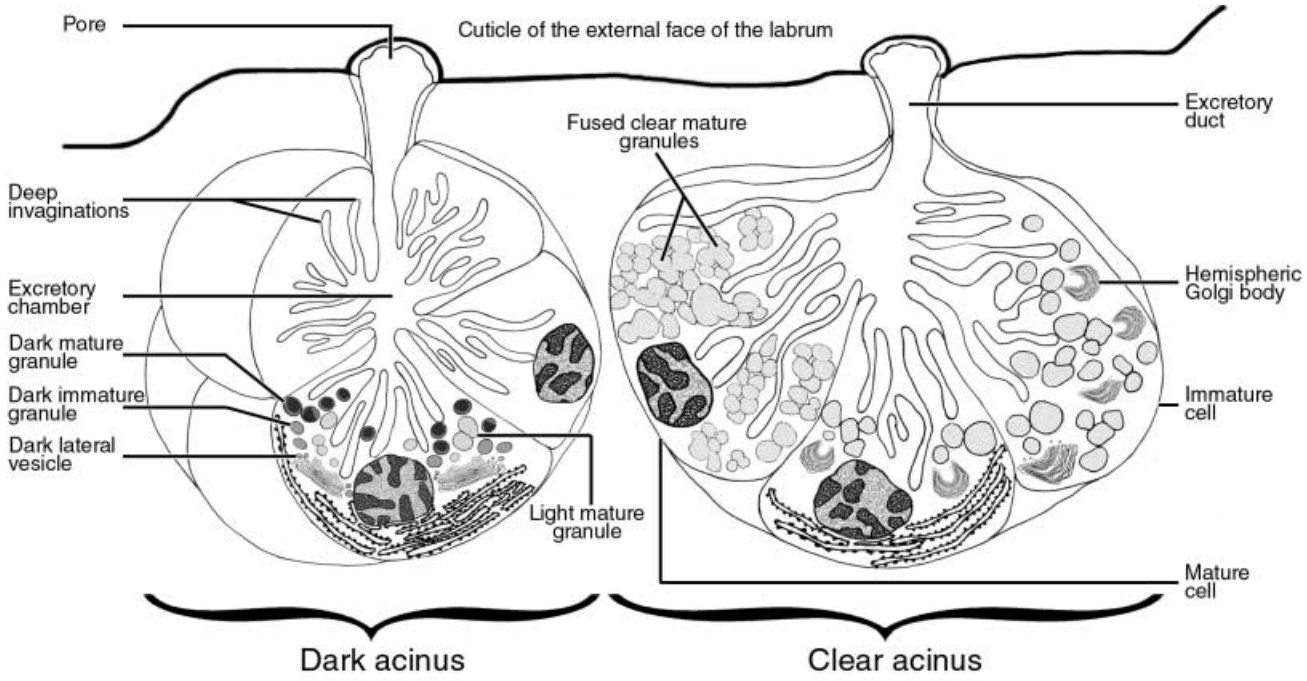

Figure 3. Schematic drawing of two glandular units showing their implantation in the labrum.

remains of crustacean cuticle such as setae and copepod mandibles, are recognizable after staining with chlorazol black. Sand particles have also been observed. Observations by SEM also reveal the presence of soft unidentifiable materials throughout the foregut (Figure 1A).

SEM observations of the mandibles and labrum (Figure 1B–H)

Mandibles are strongly asymmetrical (Figure 1B–D). A *lacinia mobilis*, inserted at the basis of the incisor process, is only present on the left mandible (Figure 1D). This well developed *lacinia mobilis* looks like a second smaller incisor process and fits into an unarticulated bicuspid structure of the right mandible (Figure 1C). The incisor process is extremely developed, particularly for the left mandible where it exhibits five sharp cusps instead of four in the right one (Figure 1C,D). The molar process is very reduced. It is split into two small areas in the left mandible (Figure 1D). An enlargement of the molar process shows few blunted scale-like spines (Figure 1E).

The labrum is asymmetrical to fit with the mandibles (Figure 1B); its right posterior edge forms a hooked lamella provided with some spines delimiting a small grinding area (Figure 1F). All the spines are directed anteriorly at the opposite of the mouth. Enlargements of the labrum show many pores on its external face (Figure 1G, H). The inner face of the labrum exhibits few small setae directed towards the mouth (Figure 1F).

Mandibles and labrum are covered with soft unidentifiable materials (Figure 1C–G) similar to that found in the foregut.

Structure and ultrastructure of the labral glandular units (Figures 2–6)

The labral glandular units occupy a large part of the labrum (Figure 2A). Each unit consists of numerous acini with two to four large cells in sections (Figures 2B & 3). The glandular cells, enlarged in their basal part containing the nucleus, display abundant secretory granules occupying the whole of the cytoplasm (Figure 2B). The apical plasma membrane of these cells forms deep invaginations which converge on the acinus lumen corresponding to an excretory chamber (Figures 2B & 3). Each acinus is related to a large short excretory duct (Figures 2B & 3) leading to the outside via a pore located on the external face of the labrum (Figure 3). These ducts consist of only one canalar cell with generally an oblong and curved nucleus (Figure 2C) and with parallel microtubules, equidistant the one from another, in the cuticularized distal part of the ducts (Figure 2D). Secretion materials in the ducts are only observed in fed animals (Figure 2D,E). Many nerves have been observed in the connective tissue surrounding the acini (Figure 2F). These latter consist of either dark or clear cells (Figures 2G & 3).

Dark cells exhibit both dark and light granules of variable density according to their state of maturation (Figure 4A,B). These cells display highly developed rough endoplasmic reticulum (rer) arranged in parallel cisternae and numerous Golgi bodies of more than 15 saccules (Figure 4A). Saccules of the cis-Golgi network are filled with dense material and produce dark lateral vesicles close to dark granules (Figure 4A). The last saccules of the trans-Golgi network produce light vesicles at the origin of the light granules (Figure 4A). Thus, both types of granules seem to arise from the same Golgi bodies. To confirm this hypothesis, thin sections of animals only fixed in 1% glutaraldehyde were incubated with Au-HPA (Helix pomatia agglutinin, 10 nm) lectin (in pH 7.4 PBS buffer (1:40) added to 0.5% albumin and 0.05% Tween 20 for 60 min). Labelling was observed in the light granules and in the trans-saccules of the Golgi network, while dark granules were not labelled (Figure 4C–E). As the

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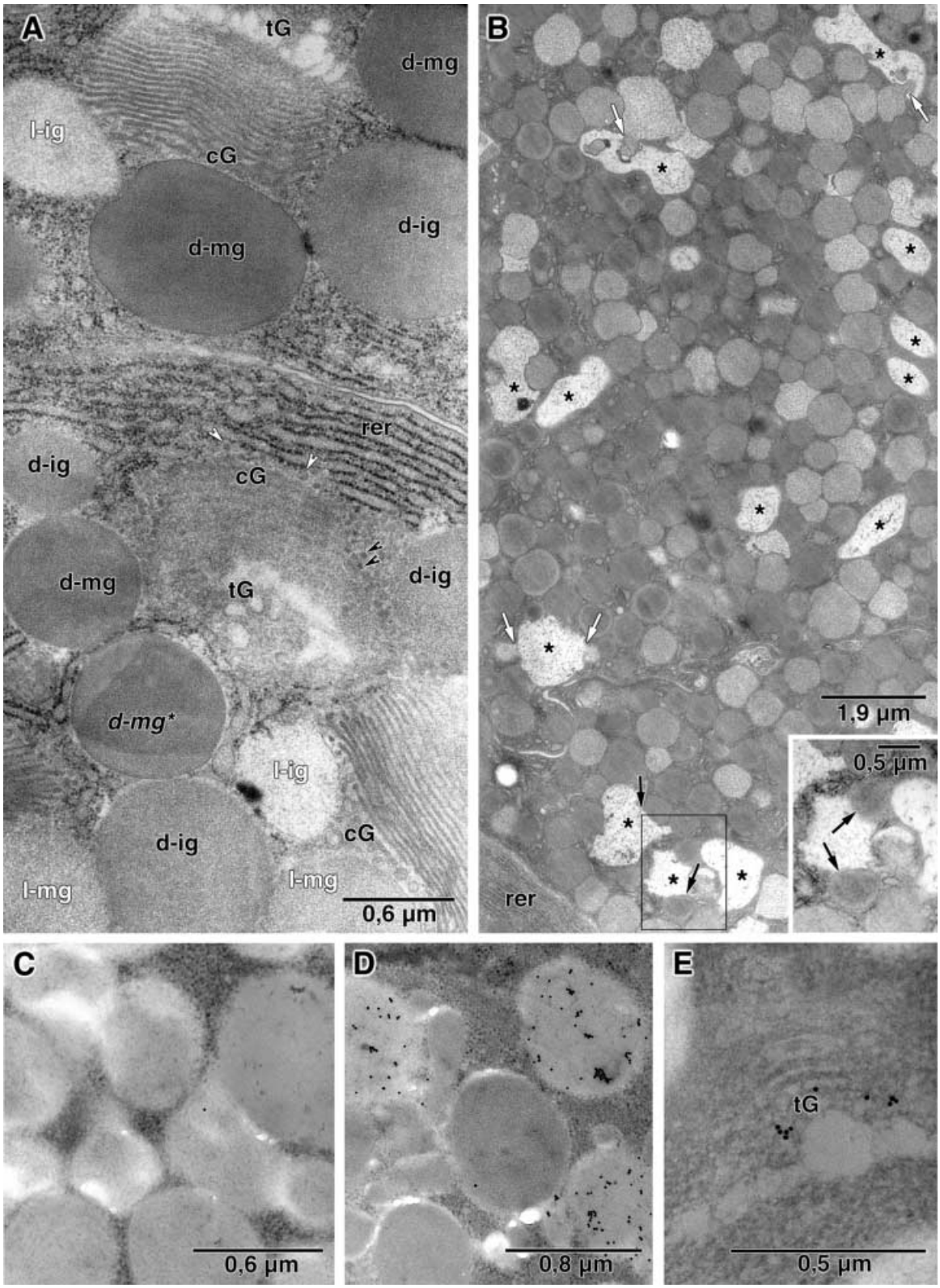

Figure 4. Transmission electron micrographs of sections through a dark glandular unit of a fed *Lophogaster typicus*. (A) Details of Golgi bodies. Note the dark transition vesicles (white arrowheads) between the rough endoplasmic reticulum (rer) and the cis-Golgi network (cG). Saccules of the cis-Golgi network are filled with dense material and produce dark lateral vesicles (black arrowheads) from which dark immature granules (d-ig) seem to arise. Note the production of light vesicles from the trans-Golgi network (tG) which are probably at the origin of light immature granules (l-ig). The density of light (l-mg) and dark (d-mg) granules increases with their maturity. Dark mature granules often exhibit a dual structure (*d-mg**); (B) exocyted products at the level of the plasma membrane invaginations (asterisks). White and black arrows indicate exocytosis of light and dark mature granules respectively. Note the exocytosis of a dark granule exhibiting a dual structure (insert corresponding to the encircled area). (C–E) Transmission electron micrographs of the dark-cells of *L. typicus* after incubation with gold-labelled HPA. (C) Control. Specificity of lectin binding was tested by addition of 0.5 M N-acetylgalactosamine. Note the labelling only in the light granules (D) and in the saccules of the trans-Golgi (tG) network (E).

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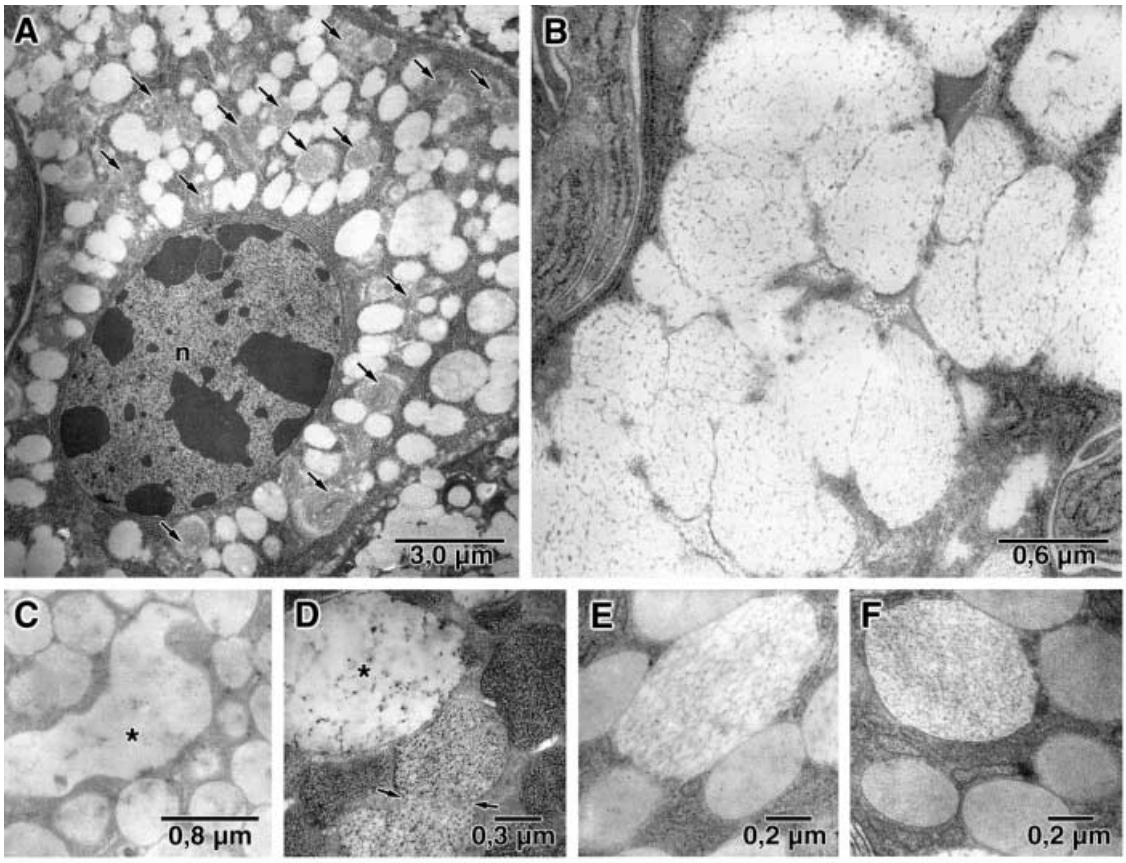

Figure 5. (A & B) Transmission electron micrographs of sections through the clear glandular units of *Lophogaster typicus*. (A) Clear cell in secretion synthesis phase. Arrows indicate the numerous Golgi bodies. Note the abundance of clear immature granules; (B) clear mature granules fused together to form large areas of secretion products. Note the heterogeneous content of these granules. (C–F) Transmission electron micrographs of labral glandular cells of *L. typicus* after the PATAg cytochemical test. Control (C) and PATAg test (D) after 40 min incubation in TCH in clear cells. Note the strong reactivity of the light granules and that of the material inside a plasma membrane invagination (asterisk). Arrows indicate a fusion between two granules. Control (E) and PATAg test (F) after 72 h incubation in TCH in dark cells. Note the slight reactivity of the granules. n, nucleus.

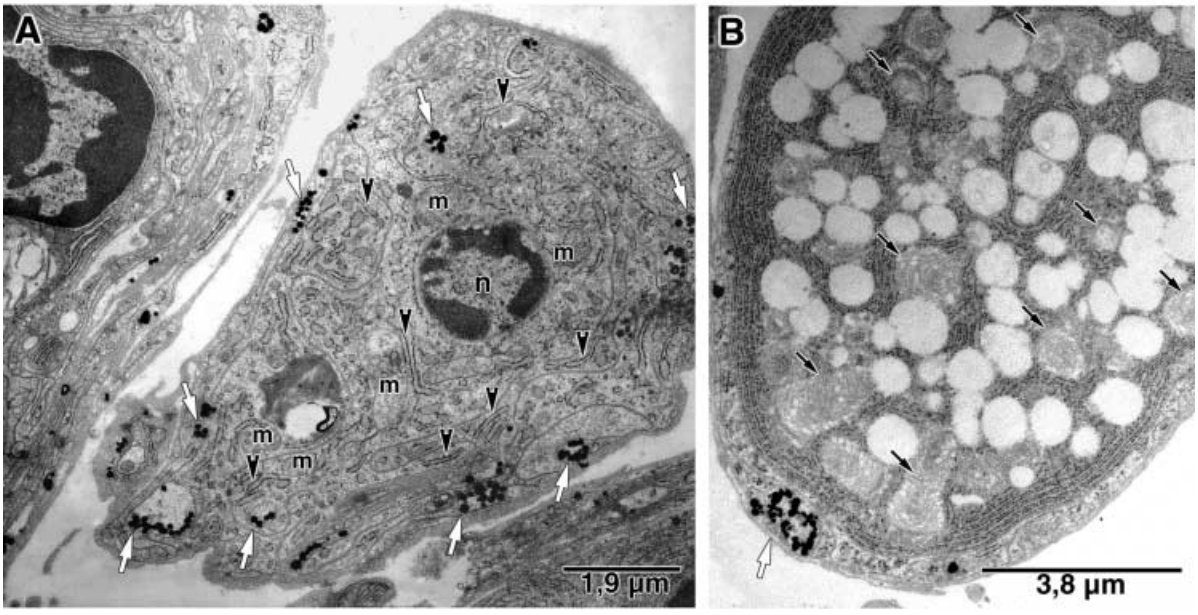

Figure 6. (A) Transmission electron micrograph of a section through the endocrine-like cells in the labrum of *Lophogaster typicus*; (B) note an extension of an endocrine-like cell closely associated with a clear glandular cell. Black arrows indicate the numerous Golgi bodies of the glandular cell and the white arrow shows dense granules of the endocrine-like cell. Arrowheads, rough endoplasmic reticulum; m, mitochondria; white arrows, dense granules.

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Au-HPA lectin shows specificity for the N-acetylgalactosamine (GalNAc) glycoconjugate, the labelling indicates that this glycoconjugate is added in the last trans-saccules of the Golgi bodies. These data validate the above hypothesis and confirm ultrastructural observations, i.e. the dark granules arise from the lateral vesicles, while the light ones arise from the trans-saccules of the Golgi network. No exocytosis figures have been observed in the labrum of the starved animal. Whereas, in fed animals, some exocytosis figures are present at the level of the plasma membrane invaginations, which correspond to the sites of secretion release (Figure 4B). Exocytosis involves mature light granules and dark granules with a dual structure (Figure 4B). So, the presence of a dual structure in the dark granules reflects their ultimate stage of maturation.

Clear cells exhibit only clear heterogeneous granules (Figures 2G & 5A,B). In immature cells, many hemispheric Golgi bodies are present. Their saccules are numerous (generally more than 15) and filled with clear material. Both the lateral Golgi vesicles and those of the trans-Golgi network are also filled with clear material. Clear mature granules fuse together (Figure 5B) to form large areas that occupy almost all the cytoplasm of clear mature cells (Figures 2G & 3).

In clear acini, the PATAg cytochemical test gives a strong positive reaction that already occurs after 40 min incubation in TCH, which indicates an abundance of polysaccharides very sensitive to periodic acid (Figure 5C,D). This reaction is located in the matrix of the clear granules and is more intense in the granules themselves than in large areas of fused granules. Content of the sites of secretion release may also exhibit a positive reaction (Figure 5D). On the other hand, in dark acini, both the light and dark granules appear to be PATAg-negative after 40 min and slightly reactive after 72 h incubation in TCH (Figure 5E,F).

Numerous cells are closely associated with the glandular labral cells (Figures 2B & 6). These cells display ultrastructural features of 'endocrine cells': sparsely distributed rer, numerous mitochondria, small Golgi complexes and, small and dense secretory granules (50–300 nm in diameter) located in interdigitating cell extensions (Figure 6A).

DISCUSSION AND CONCLUSIONS

The only previous investigations on the mandibles of *Lophogaster typicus* were carried out by Manton (1928), which, however, do not permit recognition of the shape of these masticatory peri-oral structures (Dahl & Hessler, 1982). As revealed by SEM observations, the general shape of the mandibles of *L. typicus* shows similarities with that of *Gnathophausia* species (Dahl & Hessler, 1982; Casanova, J.-P., 1996b) and their topography seems to be a feature of the lophogastrids (De Jong-Moreau, 1998). Despite strong similarities in their topographic organization, the mandibles of *L. typicus* exhibit a very reduced molar process compared with that of *Gnathophausia* species. In the latter, the molar process forms a grater of strong sharp spines that are joined together to form rows of parallel lamellae. Conversely, in *L. typicus*, it is only constituted of a few blunted scale-like spines. Now, the structure of the molar process in mysids and euphausiids determines the food preferences of a species (De Jong-Moreau et al., 2001). In *L. typicus*, both the size and the structure of the molar process indicates a carnivorous feeding habit, which is also attested by the efficient huge incisor process. This diet seems to be emphasized by the foregut content analysis, which reveals the presence of small crustacean cuticle remains. Moreover, SEM observations of soft unidentifiable materials in the foreguts and between the mouthparts seem also to indicate a saprophagous diet. This is in agreement with the ecology of this species. Indeed, *L. typicus* is a bottom species living in muddy habitat (Mauchline, 1980) and may be incapable of filter feeding (Manton, 1928).

Like in *Gnathophausia* species, the posterior edge of *L. typicus* labrum forms a hooked lamella. This area is provided with some spines forming a small grinding surface. However, this grinding surface is smaller than that of *Gnathophausia childressi* Casanova, 1996. As in other carnivorous and saprophagous mysid species, the inner face of the labrum exhibits a few setae (De Jong-Moreau, 1998).

The main finding of this study is the presence of numerous excretory pores on the external face of the labrum related to numerous labral glandular units. To our knowledge, these observations have never been reported before in Malacostraca. The location of these glandular pores could be explained as follows: (i) the food is dispatched towards the mouth via the thoracic appendages; (ii) the food is bitten by the mandibular incisor process and the grinding area of the labrum; (iii) part of the food gets over the labrum where it is maintained against the excretory pores by the mandibular palps; (iv) the mandibular palps pouch the food between the mandibles; (v) the food is squeezed against the reduced molar process before reaching the mouth. In this hypothesis, the external face of the labrum and the mandibular palps delimit an area where the food is prepared by the secretions before ingestion. The ornamentation of the posterior edge of the labrum is consistent with this hypothesis. Indeed, the spines are all directed toward the opposite direction as the mouth and then could guide and retain the food against the external face of the labrum. In the Copepoda Crustacea, excretory labral pores (2–5) have also been described, but occur at the inner face, except for a few primitive calanoid species in which they have been observed on the external face (Houache, 1997). In *Lophogaster typicus*, the abundance of excretory pores is probably related to the particular digestive physiology of this species. As previously reported (De Jong, 1996; De Jong et al., 2000), the intestine only serves to remove solute molecules for absorption and coarse particles retained in the foregut must be eliminated by regurgitation. It is possible that part of this regurgitated material could be once again guided towards the external face of the labrum and after ingested again. Thus, the abundance of labral excretory pores could be explained by the regurgitation-ingestion cycles.

In *L. typicus*, the labral glandular units are organized in small acini. Similarities are observed with the salivary glands of insects where the units are also organized in acini. Labral glandular units are also observed in Crustacea other than Malacostraca, e.g. in Copepoda (Gharagozlou-Van Ginneken, 1977; Defaye et al., 1985; Arnaud et al., 1988a,b; Nishida & Ohtsuka, 1996),

Cladocera (Zaffagnini & Zeni, 1987), Branchiopoda (Zeni & Stagni, 2000) and Cephalocarida (Elofsson et al., 1992), but they are all glands of unicellular type.

In *L. typicus*, the apical part of each labral glandular cell made deep invaginations in which secretions are discharged using a merocrine mode. These invaginations meet in the acinus lumen which is functionally an excretory chamber. The secretions are released in the plasma membrane invaginations and accumulated in the excretory chamber. Then, they converge to a single pore located on the external labral face via an excretory duct.

The structural organization suggests that the secretions are not continuously released. This hypothesis is supported by the following observations: (i) numerous active Golgi bodies are only present in immature cells, while mature ones exhibit storage of mature granules; (ii) exocytosis figures have only been observed in fed animals; (iii) the excretory chambers are full of secretions only in fed animals; (iv) the acini are surrounded by connective tissue in which neuronal endings have been observed; (v) a regular arrangement of cytoskeleton microtubules lines the excretory ducts. Therefore, the secretions, first stored in numerous secretory granules, are then released by exocytosis, probably after a neuronal or hormonal stimulus. Such a controlled release of the secretions ensures that the secretory flow is evenly distributed when the food is present. In Branchiopoda too, the presence of nerve fibres in contact with the labral glands suggests that the nervous system can intervene in the regulation of the secretory activity (Zeni & Zaffagnini, 1988, 1992). Likewise, a comparison with results obtained in ixodid ticks supports this hypothesis: (i) nerves are closely associated with the ducts and terminate in synapses on cells near the lumen of the acini (Fawcett et al., 1986); (ii) the secretions of the salivary gland fluid are under neuronal control (Sauer et al., 1995). It has been reported that dopamine is the neurotransmitter which regulates the fluid secretion (Sauer et al., 2000). Furthermore, the dilatation of the ducts is induced by a dopamine-mediated stimulation of nitric oxide that modulates the network of actin cytoskeleton (Lamoreaux et al., 2000). Our above-mentioned structural and ultrastructural observations suggest that the labral glandular units of *L. typicus* offer a secretory functional control which is similar to that described in ixodid ticks. However, further experiments, as immunolocalization of dopamine or other neurotransmitters, will be helpful to confirm this hypothesis.

Both ultrastructural and cytochemical results provide interesting information on both the composition and the putative role of the labral secretions in *L. typicus*. In clear acini, the appearance of the granules, containing heterogeneous material, and the high number of Golgi bodies, comprising numerous saccules, suggest the synthesis of mucopolysaccharides. The strong positive PATAg reaction of these clear granules that occurs after 40 min incubation of TCH, indicates the abundant presence of polysaccharides that are very sensitive to periodic acid. Furthermore, in dark cells, the abundance of rer, often arranged in parallel cisternae as in zymogen cells, indicates a high production of proteins. In these acini, the slight positive PATAg reaction of the granules after 72 h incubation in TCH supports the hypothesis of a glycoproteinic composition. Both the ultrastructural data and the Au-HPA lectin test confirm that Golgi bodies of these dark cells produce two types of granules, i.e. light granules arising from the trans-Golgi saccules, and dark ones arising from the lateral vesicles. Both granules exhibit different stages of maturation. Furthermore, the dark mature granules show a dual structure resulting from a segregation of the inside material. Such a dual structure has also been observed in mature granules of the shell glands of calanoid copepods (Barthélémy et al., 2001). In *L. typicus*, the production of mucopolysaccharides could serve for agglutination of the soft food particles, while that of glycoprotein digestive enzymes could be involved in the initial phase of digestion. These results are consistent with the ultrastructural data on the hepatopancreas of this species, since F-cells, implicated in enzyme secretions, have not been found in this digestive organ (De Jong-Moreau et al., 2000). Moreover, the hepatopancreas displays numerous absorptive B-cells that could take up the small molecules formed during the initial phase of digestion, which begins on the labrum and ends in the foregut.

The role of the endocrine-like cells that are closely related to the glandular labral ones is unknown. In Arthropoda, endocrine cells, also called paraneurones (Webster et al., 2000), play a major role in the regulation of numerous functions, e.g. stimulation of hindgut activity (Schoofs et al., 1994, 1997; Nässel, 1999), stimulation of Malpighian tubule secretion in insects (reviewed by Coast, 1998), stimulation of the extrinsic stomach muscle contraction, and modulation of the pyloric rhythm prior to ecdysis in the shore crab *Carcinus maenas* (Webster et al., 2000). Moreover, in ixodid ticks, there is some evidence that growth and development of the salivary glands might be controlled by factor(s) released into hemolymph (Coons & Kaufman, 1988). In *L. typicus*, further investigations are needed to elucidate the functions in which these cells are implicated.

In conclusion, it is obvious that the labrum plays a crucial role in the digestive function of the lophogastrid crustacean *L. typicus*. It is involved in both the mechanical, with the help of the mandibles, and the chemical breakdown of food. This chemical role of the labrum is, to our knowledge, unknown in other Malacostraca. Therefore, this investigation is of a relevant interest for a better understanding of the digestive function in many crustaceans, especially in species in which digestive enzymatic secretory cells in the hepatopancreas have not yet been found.

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REFERENCES

Arnaud, J., Brunet, M. & Mazza, J., 1978. Studies on the midgut of *Centropages typicus* (copepod, calanoid). I. Structural and ultrastructural data. *Cell and Tissue Research*, **187**, 333–353.

Arnaud, J., Brunet, M. & Mazza, J., 1988a. Labral glands in *Centropages typicus* (Copepoda, Calanoida). I. Sites of synthesis. *Journal of Morphology*, **197**, 21–32.

Arnaud, J., Brunet, M. & Mazza, J., 1988b. Labral glands in *Centropages typicus* (Copepoda, Calanoida). II. Sites of secretory release. *Journal of Morphology*, **197**, 209–219.

Barthélémy, R.-M., Cuoc, C., Caubit, X. & Brunet, M., 2001. The shell glands in some calanoid copepods (Crustacea). *Canadian Journal of Zoology*, **79**, 1490–1502.

Casanova, J.-P., 1993. Crustacea Mysidacea: les mysidacés Lophogastrida et Mysida (Petalophthalmidae) de la région néo-calédonienne. In *Résultats des campagnes MUSORSTOM*, vol. 10 (ed. A. Crosnier), pp. 33–53. *Mémoires du Muséum National d'Histoire Naturelle*, **156**.

Casanova, J.-P., 1996a. Crustacea Mysidacea: les lophogastridés d'Indonésie, de Nouvelle-Calédonie et des îles Wallis et Futuna. In *Résultats des campagnes MUSORSTOM*, vol. 15 (ed. A. Crosnier), pp. 125–146. *Mémoires de Muséum National d'Histoire Naturelle*, **168**.

Casanova, J.-P., 1996b. *Gnathophausia childressi*, new species, a mysid from deep near-bottom waters off California, with remarks on the mouthparts of the genus *Gnathophausia*. *Journal of Crustacean Biology*, **16**, 192–200.

Casanova, J.-P., 1997. Les mysidacés Lophogastrida (Crustacea) du canal de Mozambique (côte de Madagascar). *Zoosystema*, **19**, 91–109.

Coast, G.M., 1998. The regulation of primary urine production in insects. In *Recent advances in arthropod endocrinology* (ed. G.M. Coast and S.G. Webster), pp. 189–209. Cambridge: Cambridge University Press. [Society for Experimental Biology, Seminar Series, no. 65.]

Coons, L.B. & Kaufman, W.R., 1988. Evidence that developmental changes in type III acini in the tick *Amblyomma hebraeum* (Acari: Ixodidae) are initiated by a hemolymph-borne factor. *Experimental and Applied Acarology*, **4**, 117–139.

Dahl, E. & Hessler, R.R., 1982. The crustacean *lacinia mobilis*: a reconsideration of its origin, function and phylogenetic implications. *Zoological Journal of the Linnean Society*, **74**, 133–146.

Defaye, D., Such, J. & Dussart, B., 1985. The alimentary canal of a freshwater Copepoda, *Macrocyclops albidus*, and some other Cyclopoida. *Acta Zoologica*, **66**, 119–129.

De Jong, L., 1996. Functional morphology of the foregut of *Lophogaster typicus* and *L. spinosus* (Crustacea, Mysidacea, Lophogastrida). *Cahiers de Biologie Marine*, **37**, 341–347.

De Jong, L. & Casanova, B., 1997. Comparative morphology of the foregut of three *Eucopia* species (Crustacea, Mysidacea, Lophogastrida). *Journal of Natural History*, **31**, 389–402.

De Jong, L. & Casanova, J.-P., 1997. Comparative morphology of the foregut of four *Gnathophausia* species (Crustacea, Mysidacea, Lophogastrida). Relationships with other related taxa. *Journal of Natural History*, **31**, 1029–1040.

De Jong-Moreau, L., 1998. *L'appareil digestif des mysidacés: structure, ultrastructure, morphologie fonctionnelle et intérêt phylétique*. Thèse d'Université, Université d'Aix-Marseille I, France.

De Jong-Moreau, L., Brunet, M., Casanova, J.-P. & Mazza, J., 2000. Comparative structure and ultrastructure of the midgut and hepatopancreas of five species of Mysidacea (Crustacea): functional implications. *Canadian Journal of Zoology*, **78**, 822–834.

De Jong-Moreau, L., Casanova, B. & Casanova, J.-P., 2001. Detailed comparative morphology of the peri-oral structures of the Mysidacea and Euphausiacea (Crustacea): an indication for the food preference. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 235–241.

De Jong-Moreau, L. & Casanova, J.-P., 2001. The foreguts of the primitive families of the Mysida (Crustacea, Peracarida): a transitional link between those of the Lophogastrida (Crustacea, Mysidacea) and the most evolved Mysida. *Acta Zoologica*, **82**, 137–147.

Elofsson, R., Hessler, R.R. & Hessler, A.Y., 1992. Digestive system of the cephalocarid *Hutchinsoniella macracantha*. *Journal of Crustacean Biology*, **12**, 571–591.

Fage, L., 1942. Mysidacea. Lophogastrida. II. *Dana Reports*, **23**, 1–67.

Fawcett, D.W., Binnington, K.C. & Voight, W.R., 1986. The cell biology of the ixodid tick salivary gland. In *Morphology, physiology and behavioral biology of ticks* (ed. J.R. Saeuer and J.A. Hair), pp. 22–45. Chichester: Ellis Horwood.

Gharagozlou-Van Ginneken, I.D., 1977. Contribution à l'étude infrastructurale des glandes labrales de quelques harpacticoïdes (Crustacés, Copépodes). *Archives de Biologie*, **88**, 79–100.

Houache, N., 1997. *Tube digestif, labre et glandes labrales des copépodes calanoides et cyclopoides*. Thèse d'Université, Université d'Aix-Marseille III, France.

Lamoreaux, W.J., Needham, G.R. & Coons, L.B., 2000. Evidence that dilation of isolated salivary ducts from the tick *Dermacentor variabilis* (Say) is mediated by nitric oxide. *Journal of Insect Physiology*, **46**, 959–964.

Manton, S.M., 1928. On some points in the anatomy and habits of the lophogastrid Crustacea. *Transactions of the Royal Society of Edinburgh*, **56**, 103–119.

Mauchline, J., 1980. The biology of mysids and euphausiids. Chapter 4: vertical distribution and migration. In *Advances in Marine Biology*, vol. 18 (ed. J.H.S. Blaxter et al.), pp. 66–80. London: Academic Press.

Nässel, D.R., 1999. Tachykinin-related peptides in invertebrates: a review. *Peptides*, **20**, 141–158.

Nishida, S. & Ohtsuka, S., 1996. Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Calanoida: Heterorhabdidae), with special reference to the mandibular tooth and labral glands. *Marine Biology*, **126**, 619–632.

Reynolds, E.S., 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *Journal of Cell Biology*, **17**, 208–212.

Sauer, J.R., Essenberg, R.C. & Bowman, A.S., 2000. Salivary glands in ixodid ticks: control and mechanism of secretion. *Journal of Insect Physiology*, **46**, 1069–1078.

Sauer, J.R., McSwain, J.L., Bowman, A.S. & Essenberg, R.C., 1995. Tick salivary gland physiology. *Annual Review of Entomology*, **40**, 245–267.

Schoofs, L., Holman, G.M., Nachman, R.J., Hayes, T.K. & De Loof, A., 1994. Structure, function and distribution of insect myotropic peptides. In *Perspectives in comparative endocrinology* (ed. K.G. Davey et al.), pp. 155–165. Ottawa, Canada: National Research Council of Canada.

Schoofs, L., Veelaert, D., Vanden Broeck, J. & De Loof, A., 1997. Peptides in the locusts, *Locusta migratoria* and *Schistocerca gregaria*. *Peptides*, **18**, 145–156.

Tattersall, W.M. & Tattersall, O.S., 1951. *British Mysidacea*, pp. 1–460. London: The Ray Society.

Thiéry, J.-P. & Rambourg, A., 1974. Cytochimie des polysaccharides. *Journal de Microscopie (Paris)*, **21**, 225–232.

Webb, P. & Wooldridge, T.H., 1989. Diet elucidation: supplementary inferences from mysid feeding appendage morphology. *South African Journal of Zoology*, **24**, 106–109.

Webster, S.G., Dircksen, H. & Chung, J.S., 2000. Endocrine cells in the gut of the shore crab *Carcinus maenas* immunoreactive to crustacean hyperglycaemic hormone and its precursor-related peptide. *Cell and Tissue Research*, **300**, 193–205.

Zaffagnini, F. & Zeni, C., 1987. Ultrastructural investigations on the labral glands of *Daphnia obtusa* (Crustacea, Cladocera). *Journal of Morphology*, **193**, 23–33.

Zeni, C. & Stagni, A., 2000. Ducts of the labral glands of *Leptestheria dahalacensis* (Crustacea: Branchiopoda: Spinicaudata). *Journal of Morphology*, **246**, 68–84.

Zeni, C. & Zaffagnini, F., 1988. Occurrence of innervation in labral glands of *Daphnia obtusa* (Crustacea, Cladocera). *Journal of Morphology*, **198**, 43–48.

Zeni, C. & Zaffagnini, F., 1992. Labral glands of *Leptestheria dahalacensis* (Branchiopoda: Spinicaudata): an ultrastructural study. *Journal of Crustacean Biology*, **12**, 661–676.

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