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Mandibles of zoea I larvae of nine decapod species: a scanning EM analysis

(Crustacea, Decapoda)

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The morphology of the mandibles of nine decapod first stage zoeae belonging to the Caridea, Anomura and Brachyura is surveyed with the scanning EM and characters are compared with respect to their suitability for larval descriptions and reconstructions of phylogeny. Taxon-specific sets of characters include the basic form of the mandibles, the form and orientation of the incisor and molar processes, and the shape, number and arrangement of the appendages (e.g., teeth and denticles) inserted on their surface. It is demonstrated that closely related species exhibit well corresponding features while more distantly related do not. An evolutionary trend from a slender mandible as found in Caridea to a massive and rotund mandible as found in Brachyura is suggested. On the mandibles of *Palaemon elegans* and *Periclimenes amethysteus* a 'lacinia mobilis' is present, exhibiting features relevant for the discussion about putative homology of movable appendages on the gnathal edge of the Peracarida, Euphausiacea, and Decapoda.

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Introduction

Inspired by the classical works of Lebour (1928, 1943), Aikawa (1937), Gurney (1939, 1942), and Bourdillon-Casanova (1950), generally accepted standards for descriptions of decapod larvae have been established during recent decades with respect to drawings as well as textual presentation of the observed features (Christiansen 1973; Rice 1979, 1980; Ingle 1983, 1992). This method can be complemented using the resolving power of the scanning EM to get insights into tiny structures and describe the steric arrangement of analysed body parts (e.g., Greenwood & Fielder 1979; Dahl & Hessler 1982; Ingle 1992; Minagawa & Takashima 1994; Casanova et al. 2002; Konishi 2007; Lumasag et al. 2007; Johnston et al. 2008). Using dissection techniques that allow exposition of different parts of the body and its appendages in the desired views, we recently produced zoea descriptions according to the above-mentioned standards at SEM

resolution (Meyer & Melzer 2004; Meyer et al. 2004, 2006; Geiselbrecht & Melzer 2009).

Compared to other mouthparts, the mandibles, i.e. the main masticating organs in early zoeae, were somewhat neglected in the past. Though early descriptions were given, e.g. in Gurney (1942), in many zoea descriptions they are either not resolved in detail or omitted due to their minuteness, shape and way of insertion on the head. Therefore, detailed light microscopic analyses are currently available only for a limited number of species (e.g., Bookhout & Costlow 1974; Wear 1976; Haynes 1977; Konishi 1989; Martin & Goy 2004; Dos Santos et al. 2004; Bolanos et al. 2005; see also below) and depict the mandibles for methodological reasons in kind of side views that in fact show many details, but hardly illustrate their three dimensional arrangement. Furthermore, only a few zoea mandibles were analysed using the SEM in adequate view (Greenwood & Fielder 1979; Minagawa & Takashima 1994; Meyer et al. 2006; Lumasag

et al. 2007), while many SEM analyses suffer from the mandible's somewhat cryptic placement.

However, such analyses are needed, since the structure of the mandible in crustaceans, and arthropods in general, were shown to be relevant not only for species diagnoses, but also for comparative studies and reconstructions of their phylogeny, for which the lacinia mobilis, a movable appendage of the gnathal edge, is only one example (e.g., Dahl & Hessler 1982; Richter et al. 2002).

Since the knowledge of mandible structure in decapod zoeae is unsatisfactory with respect to these questions at the moment, we used our dissection technique to undertake a scanning EM survey of the larval mandibles of nine representative decapods with the aim to contribute to a future SEM atlas of zoea mandibles. The species used for this study were selected because of their availability and quality of the applied fixation procedure rather than making an attempt to span the whole taxonomic spectrum. Our study encompasses two Caridea (*Palaemon elegans* (Rathke, 1837) and *Periclimenes amethysteus* (Risso, 1827)), two Anomura (*Pisidia longicornis* (Linnaeus, 1767), and *Porcellana platycheles* (Pennant, 1777)) and five Brachyura (*Ebalia tuberosa* (Pennant, 1777), *Liocarcinus pusillus* (Leach, 1815), *Pilumnus hirtellus* (Linnaeus, 1761), *Xantho pilipes* (A. Milne-Edwards, 1867), and *Xantho hydrophilus* (Herbst, 1780)).

Standard light microscopical descriptions of the zoeas can be found in Fincham (1977) (*P. elegans*), Kurian (1956), Bourdillon-Casanova (1950), Barnich (1996) (*Periclimenes* sp.), Lebour (1943), Le Roux (1966) (*P. longicornis*), González-Gordillo (1996) (*P. platycheles*), Lebour (1928), Salman (1982b), Ingle (1992) (*E. tuberosa*), Rice & Ingle (1978), Clark (1984) (*L. pusillus*), Salman (1982a), Ingle (1983) (*P. hirtellus*), Paula and Dos Santos (2000) (*X. pilipes*) and Rodríguez and Martin (1997) (*X. poressa*). Some of these studies provide a gross description of the mandibles and the presence of molar and incisor processes, and some omit their analysis completely. In Ingle (1992), a SEM picture of *E. tuberosa* is depicted, showing its reticulated outer surface. A recent SEM description of the first zoea of *P. amethysteus* is found in Geiselbrecht & Melzer (2009), and a review on the zoea mandible's morphology and the morphogenetic changes they undergo during development is found, e.g., in Factor (1989).

Among our zoeas, are both closely related species "pairs" as well as examples of only distantly related taxa, and hence our expectation was that we can detect species-specific features as well as gain a first insight into the variability of mandibular structures on the SEM level.

Material and methods

For this study an existing collection of decapod larvae stored at the Zoologische Staatssammlung München (ZSM) was used. From this collection 9 species of 6 different families and 7 different genera were chosen. The larvae had been fixed after Meyer & Melzer (2004), and were stored in 70 % ethanol. Specimens were dissected using thin tungsten wires. Left and right mandibles were isolated and kept separately in small glass vials containing 70 % ethanol. In the subsequent procedure it was not possible not to lose some of the dissected mandibles; hence around 20 left and 20 right mandibles of every studied species were prepared.

For SEM preparation whole zoeae and dissected mandibles were dehydrated in a graded acetone series (70 %, 80 %, 90 %, 10 min each, plus 3 times 100 %, 20 min each), and then critical-point-dried in a Baltec CPD 030. Because dimensions of mandibles were mostly less than 100 µm, specimen-containers with smaller pore-dimension were used. Dried specimens were mounted on SEM stubs with self adhesive carbon stickers and sputtered with gold on a Polaron E 5100. Mandibles were studied with a LEO 1430VP SEM at 15 kV. Every specimen was scanned from different views, and the number of teeth, denticles, spines, setae and pores was counted and compared. The number of studied mandibles ranged between 1 and 16 (in *Pilumnus hirtellus*, only one of the dissected left mandibles was left after the procedure).

The SEM preparations are deposited at the ZSM under the following registration numbers: *Palaemon elegans*: ZSM A20080755-757; *Periclimenes amethysteus*: ZSM A20080793, -794 and -797; *Pisidia longicornis*: ZSM A20080774-779; *Porcellana platycheles*: ZSM A20080767-769; *Ebalia tuberosa*: ZSM A20080771-773; *Liocarcinus pusillus*: ZSM A20080759-761; *Pilumnus hirtellus*: ZSM A20080780-782; *Xantho pilipes*: ZSM A20080763-766 and *X. poressa*: ZSM A20080777-779.

Registration numbers of the lots with larvae and the corresponding ovigerous females are as follows: *Palaemon elegans*: ZSM A20080754 (Saline, Rovinj, Croatia); *Periclimenes amethysteus*: ZSM A20080785 (Cross Bay, Rovinj, Croatia); *Pisidia longicornis*: ZSM A20071633 (Roscoff, Bretagne, France); *Porcellana platycheles*: material expended (Kap Savudria, Croatia); *Ebalia tuberosa*: ZSM A20080770 (Roscoff, Bretagne, France); *Liocarcinus pusillus*: ZSM A20080758 (Roscoff, Bretagne, France); *Pilumnus hirtellus*: ZSM A20035541 (Bangnole, Rovinj, Croatia); *Xantho pilipes*: ZSM A20080762 (Saline, Rovinj, Croatia); *X. hydrophilus*: ZSM A20035543 (Saline, Rovinj, Croatia).

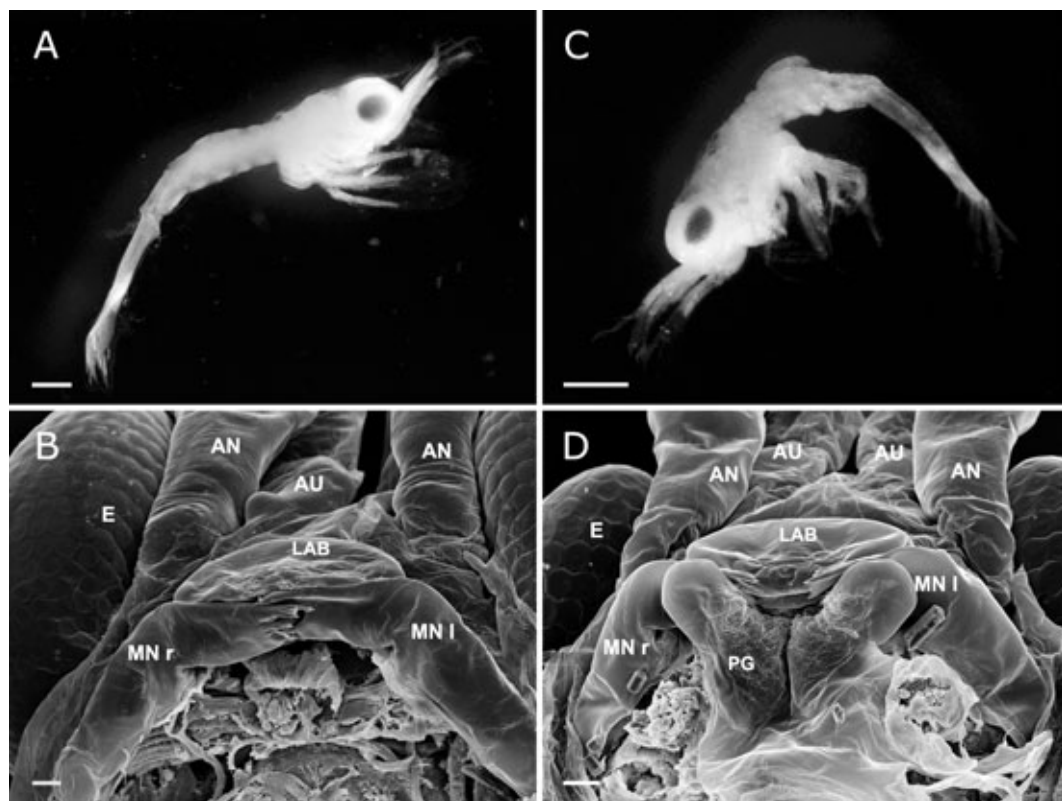


Fig. 1. A. Lateral view of zoea I of *Palaemon elegans* (bar 0.25 mm). B. Ventral view of dissected zoea I of *Palaemon elegans* (bar 20 µm). C. Lateral view of zoea I of *Periclimenes amethysteus* (bar 0.25 mm). D. Ventral view of dissected zoea I of *Periclimenes amethysteus* (bar 20 µm). Abbreviations: AN, antenna; AU, antennule; E, eye; LAB, labrum; MNl, left mandible; MNr, right mandible; PG, paragnaths.

Results

Description of the mandibles

1. *Palaemon elegans* (Rathke, 1837) (Figs 1A,B, 2)

Basic form: slender, a bent tube flattened anterior-posteriorly to its distal end. Outer surface unstructured, molar and incisor process fairly well developed. Incisor process ventral. Molar process dorsal to incisor process. Molar and incisor processes slender, with identical median orientations.

Right mandible (Fig. 2A-C): Incisor process a ventral marginal protrusion of fork-like shape formed of 3 acute spines. Median spine smaller than the outer ones. 1 submarginal spine and nearby a 'lacinia mobilis' of spine-like shape, with articulation on a basal ring and a pore at the base (Fig. 2A). Molar and incisor process nearly merge into each other. Molar process slender, with a group of 9-11

submarginal small spines, 1 blunt tuberculette on the anterior edge (Fig. 2B), and on the dorsal margin a row of 3 small spines.

Left mandible (Fig. 2D-F): Molar and incisor process well-defined. Incisor process a ventral process with 5 spines in a row and a serrated 'lacinia mobilis', articulated on a basal ring and a pore at the base (Fig. 2E), arranged in a U-shaped form. Molar process a group of small spines on a slender, slightly raised base. Group of spines arranged in a row of 4 small marginal spines on the dorsal margin and 6-8 small submarginal spines. A single pore at the base of the penultimate spine with respect to the median margin of the molar base.

2. *Periclimenes amethysteus* (Risso, 1827) (Figs 1C,D, 3)

Basic form: slender, a bent tube flattened anterior-posteriorly to its distal end. Outer surface unstructured, molar and incisor process fairly well devel-

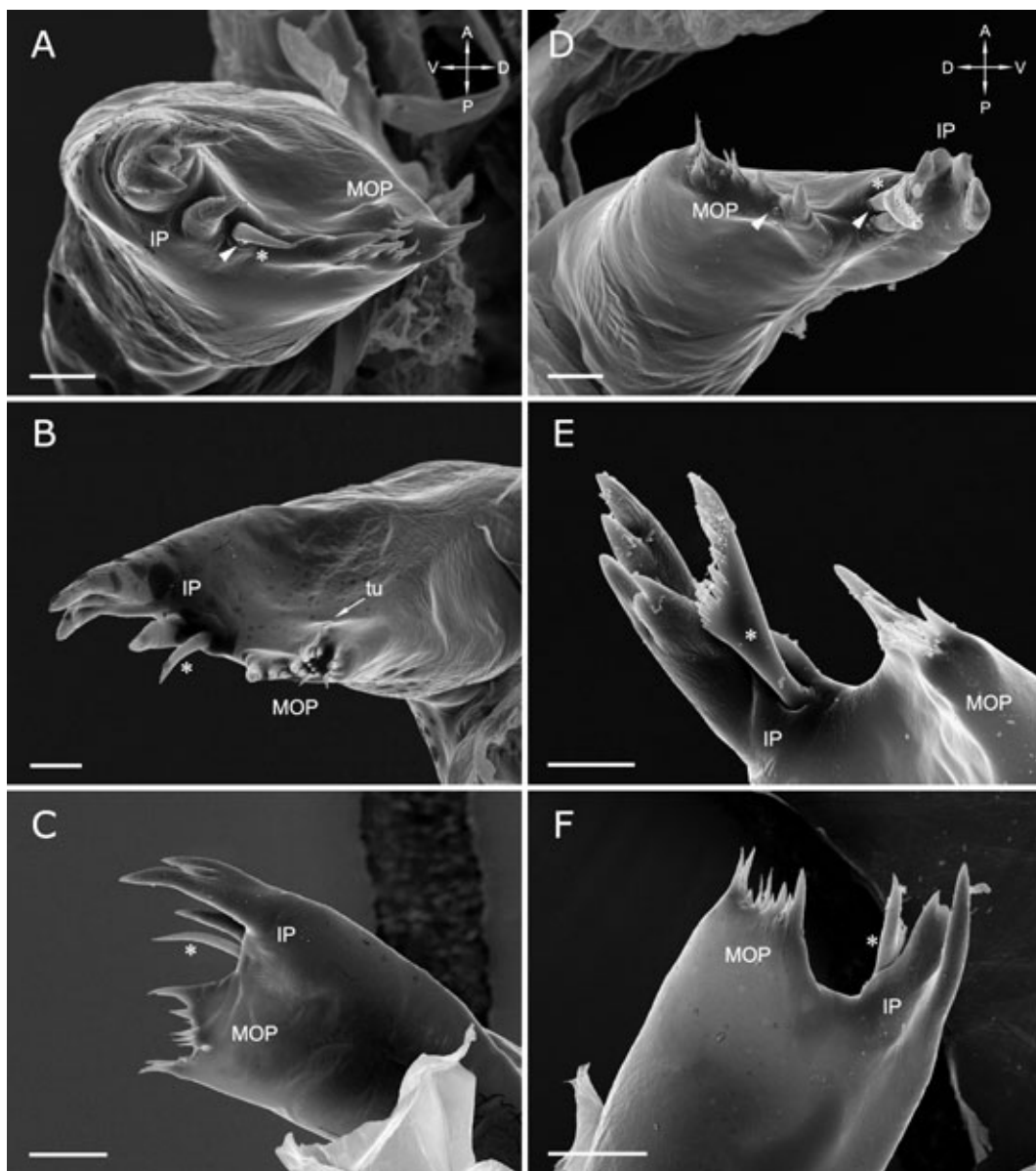


Fig. 2. *Palaemon elegans*, zoea I mandibles. **A.** Inner view of right mandible (bar 10 μ m). **B.** Inner view of right mandible (bar 10 μ m). **C.** Anterior view of right mandible (bar 20 μ m). **D.** Inner view of left mandible (bar 10 μ m). **E.** Dorsal view of left mandible (bar 10 μ m). **F.** Posterior view of left mandible (bar 20 μ m). Abbreviations: **Arrow-heads**, pores; **Asterisk**, 'lacinia mobilis'; **IP**, incisor process; **MOP**, molar process; **tu**, tuberculette.

oped. Incisor process ventral. Molar process dorsal to incisor process. Molar and incisor processes slender, with identical median orientation.

Right mandible (Fig. 3A-C): Molar and incisor process nearly merge into each other. Incisor process a ventral, marginal protrusion of fork-like shape

formed of 3 acute spines of about the same size, 1 submarginal spine and a serrated 'lacinia mobilis' with articulation on a basal ring and a pore at the base nearby. Molar process slender, with a group of 8 marginal small spines with no distinct arrangement on the dorsal margin, and a row of 3 submarginal

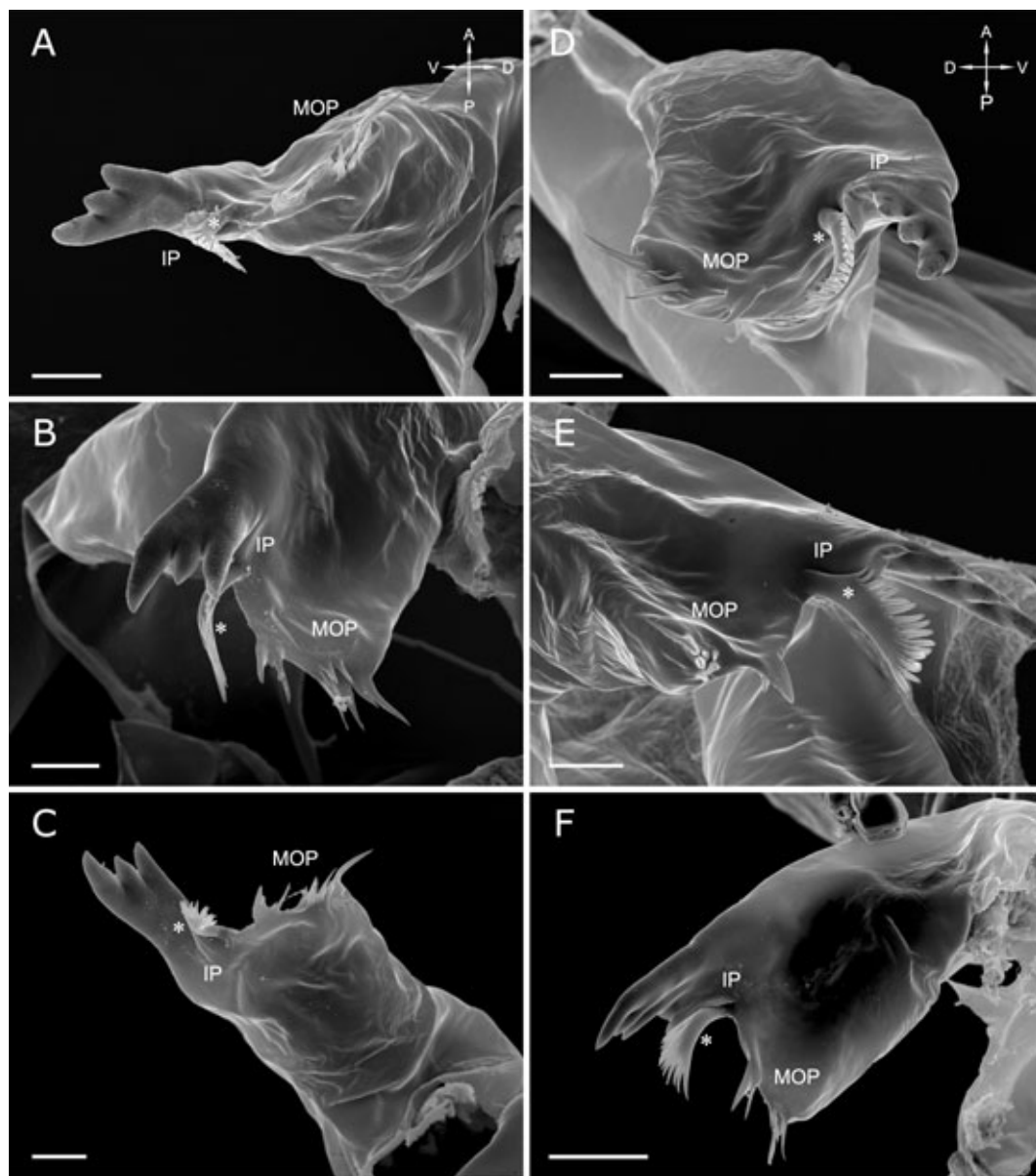


Fig. 3. *Periclimenes amethysteus*, zoea I mandibles. **A.** Inner view of right mandible (bar 10 μ m). **B.** Anterior view of right mandible (bar 10 μ m). **C.** Posterior view of right mandible (bar 10 μ m). **D.** Inner view of left mandible (bar 10 μ m). **E.** Dorso-median view of left mandible (bar 10 μ m). **F.** Posterior view of left mandible (bar 20 μ m). Abbreviations: **Asterisk**, 'lacinia mobilis'; **IP**, incisor process; **MOP**, molar process.

small spines on a common base. Of these, the median spine smaller than the other two.

Left mandible (Fig. 3D-F): Incisor process a ventral marginal protrusion armed with a row of 4 acute spines and a serrated 'lacinia mobilis' with

articulation on a basal ring and a pore at the base nearby located submarginally. Molar process slender, with a group of 6 (7) marginal small spines with no distinct arrangement on the dorsal margin, and 2 (3) small submarginal spines on a common base.

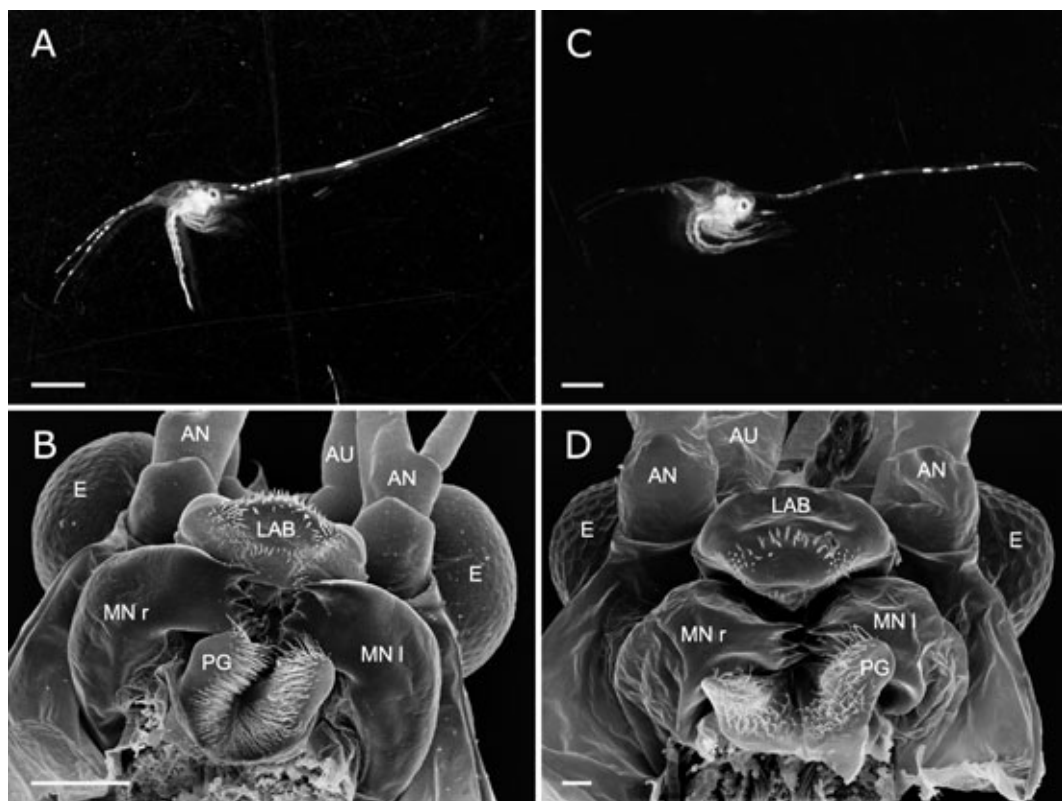


Fig. 4. A. Lateral view of zoea I of *Porcellana platycheles* (bar 0.5 mm). B. Ventral view of dissected zoea I of *Porcellana platycheles* (bar 100 µm). C. Lateral view of zoea I of *Pisidia longicornis* (bar 0.5 mm). D. Ventral view of dissected zoea I of *Pisidia longicornis* (bar 20 µm). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MNI, left mandible; MNr, right mandible; PG, paragnaths.

3. *Pisidia longicornis* (Linnaeus, 1767) (Figs 4C,D, 5)

Basic form: A rotund bent oval tube. Molar and incisor process with identical median orientations. Incisor process ventral. Molar process dorsal to incisor process. Cross-sectional shape of insides drop-shaped. Several setules on anterior and posterior surface and on the dorsal margin of the molar process.

Right mandible (Fig. 5A-C): Ventral margin of incisor process slender, armed with 1 acute spine. Process getting broader medially, armed with 2 upright rows of spines. First spines in both rows on the posterior margin, followed in the first row by 1 submarginal spine, and in the second row by 3(4) submarginal spines. Very small spines or tuberculettes randomly distributed between them. Molar process of staircase shape with 2 steps. Posterior margin armed with a row of 13(12) marginal spines. A varying number of small spines on the

step ridges. Several setules merge with the posterior row of spines on the dorsal margin of the molar process (Fig. 5A). A small pore on the ridge of both steps (Fig. 5A).

Left mandible (Fig. 5D-F): Ventral margin of incisor process slender, armed with 1 acute marginal spine and a pair of 2 submarginal spines. Molar process of staircase shape with 3 steps. A varying number of small spines on the step ridges. A row of 6 marginal small spines on the posterior margin of the third step merging with several setules on the dorsal margin (Fig. 5D). A small pore on the ridge of every step (Fig. 5D).

4. *Porcellana platycheles* (Pennant, 1777) (Figs 4A,B, 6)

Basic form: A rotund bent oval tube. Molar and incisor process with identical median orientations. Incisor process ventral. Molar process dorsal to incisor process. Cross-sectional shape of insides

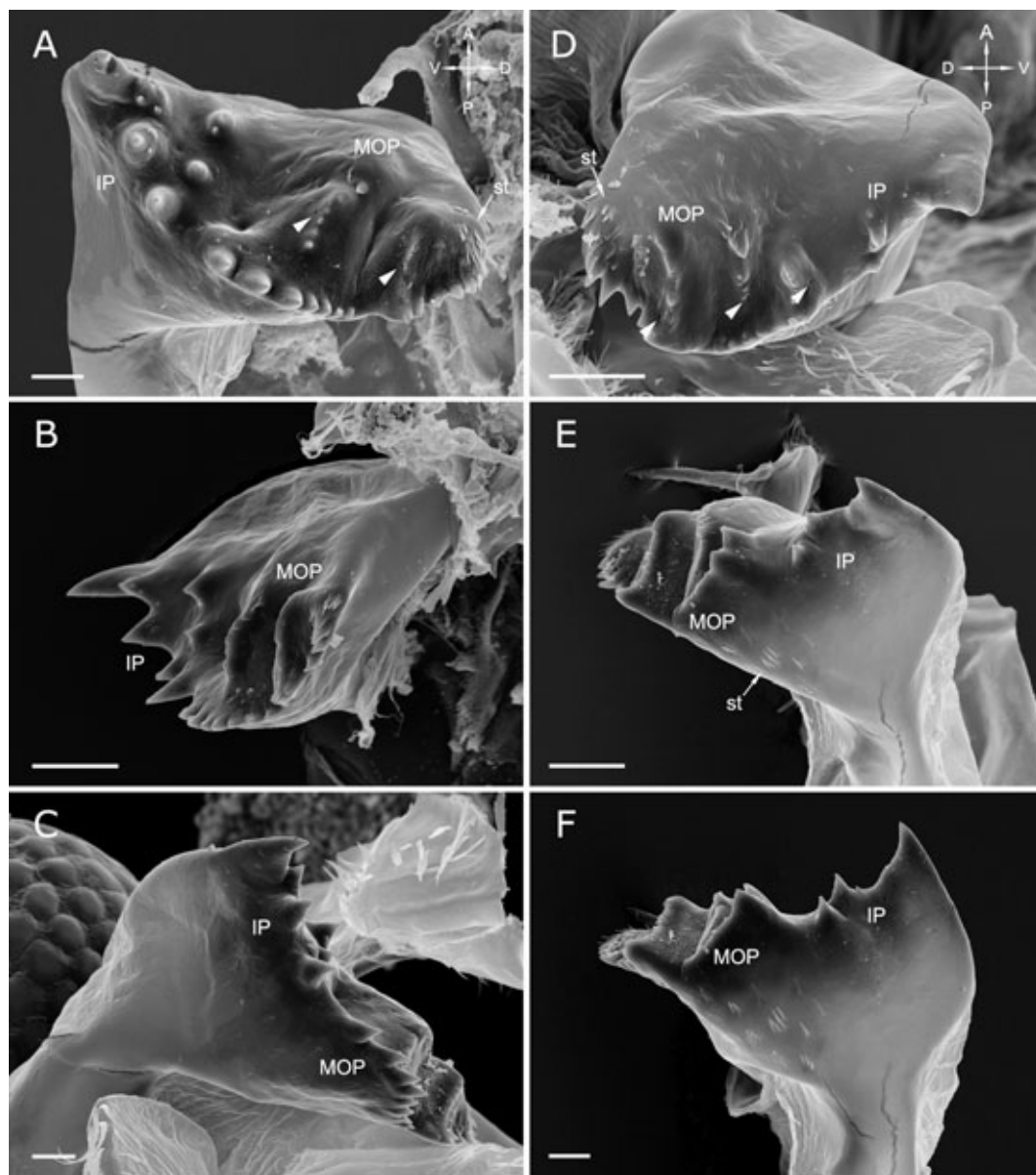


Fig. 5. *Pisidia longicornis*, zoea-I-mandibles. **A.** Inner view of right mandible (bar 10 μ m). **B.** Dorso-median view of right mandible (bar 20 μ m). **C.** Posterior view of right mandible (bar 20 μ m). **D.** Inner view of left mandible (bar 20 μ m). **E.** Ventro-median view of left mandible (bar 20 μ m). **F.** Posterior view of left mandible (bar 10 μ m). Abbreviations: **Arrowheads**, pores; **IP**, incisor process; **MOP**, molar process; **st**, setules.

drop-shaped. Several setules on anterior and posterior surface and on the dorsal margin of the molar process.

Right mandible (Fig. 6A-C): Ventral margin of incisor process slender, armed with 1 acute spine. Process getting broader medially, armed with 2

upright rows of spines. First spines in both rows on the posterior margin, followed in the first row by 1 submarginal spine, and in the second row by 2, seldom 3 submarginal spines. Very small spines or tuberculettes randomly distributed between the spines of the first row (Fig. 6A). 2 pores located medi-

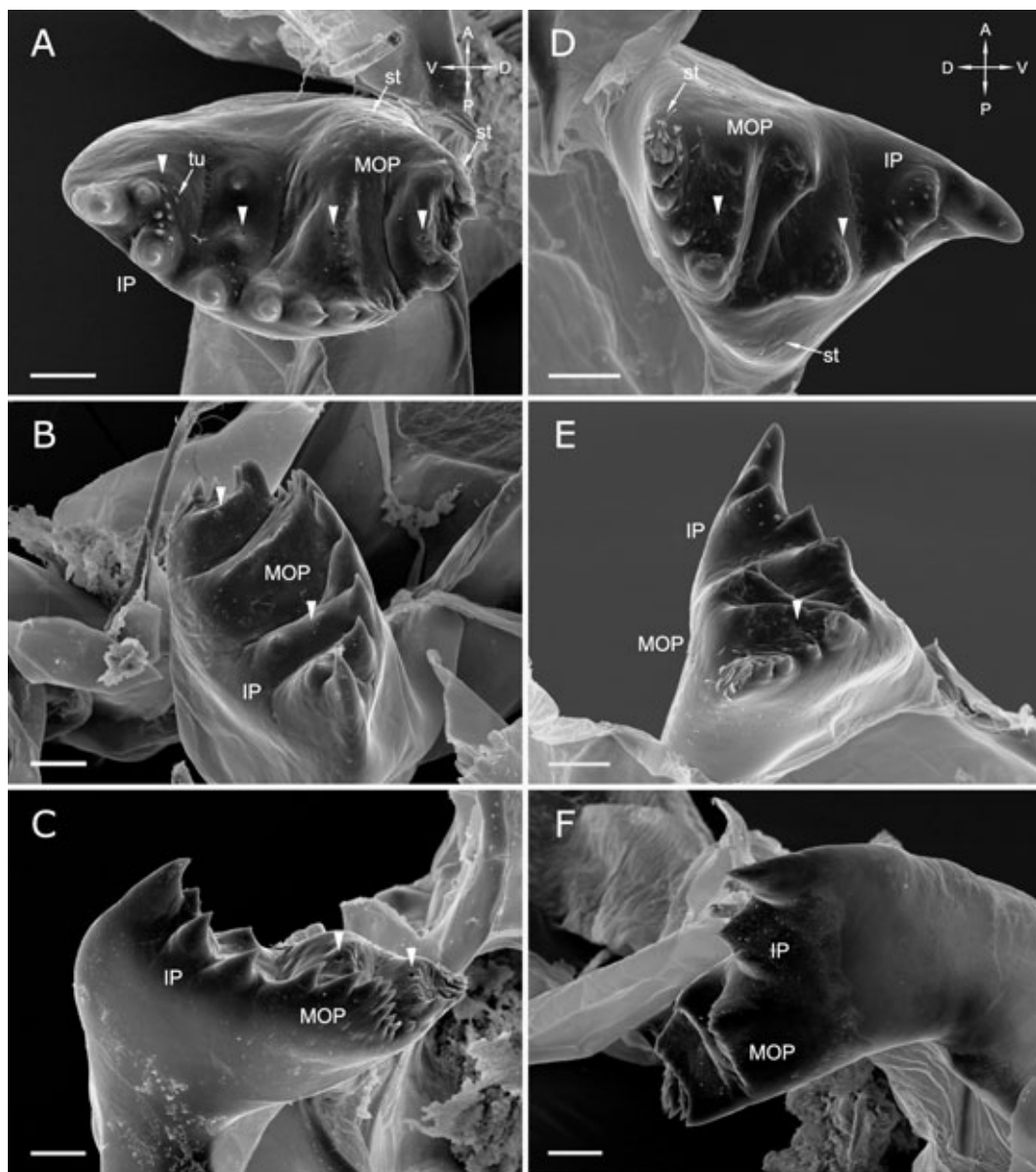


Fig. 6. *Porcellana platycheles*, zoea I mandibles. **A.** Inner view of right mandible (bar 20 μ m). **B.** Ventro-medial view of right mandible (bar 20 μ m). **C.** Posterior view of right mandible (bar 20 μ m). **D.** Inner view of left mandible (bar 20 μ m). **E.** Dorso-medial view of left mandible (bar 10 μ m). **F.** Posterior view of left mandible (bar 20 μ m). Abbreviations: **Arrowheads**, pores; **IP**, incisor process; **MOP**, molar process; **st**, setules; **tu**, tuberculettes.

ally on the incisor process (Fig. 6A,B). Molar process of staircase shape with 2 steps. Posterior margin of first step armed with a row of 7-9 marginal spines. Posterior margin of second step armed with a row of appendages composed of a single small marginal spine, a small marginal process with 4 (3) very small

spines and 3-4 small marginal spines, passing until the dorsal margin of the molar process. A varying number of small spines on the step ridges. Several setules merge with the posterior row of spines on the dorsal margin. A small pore medially on the ridge of both steps.

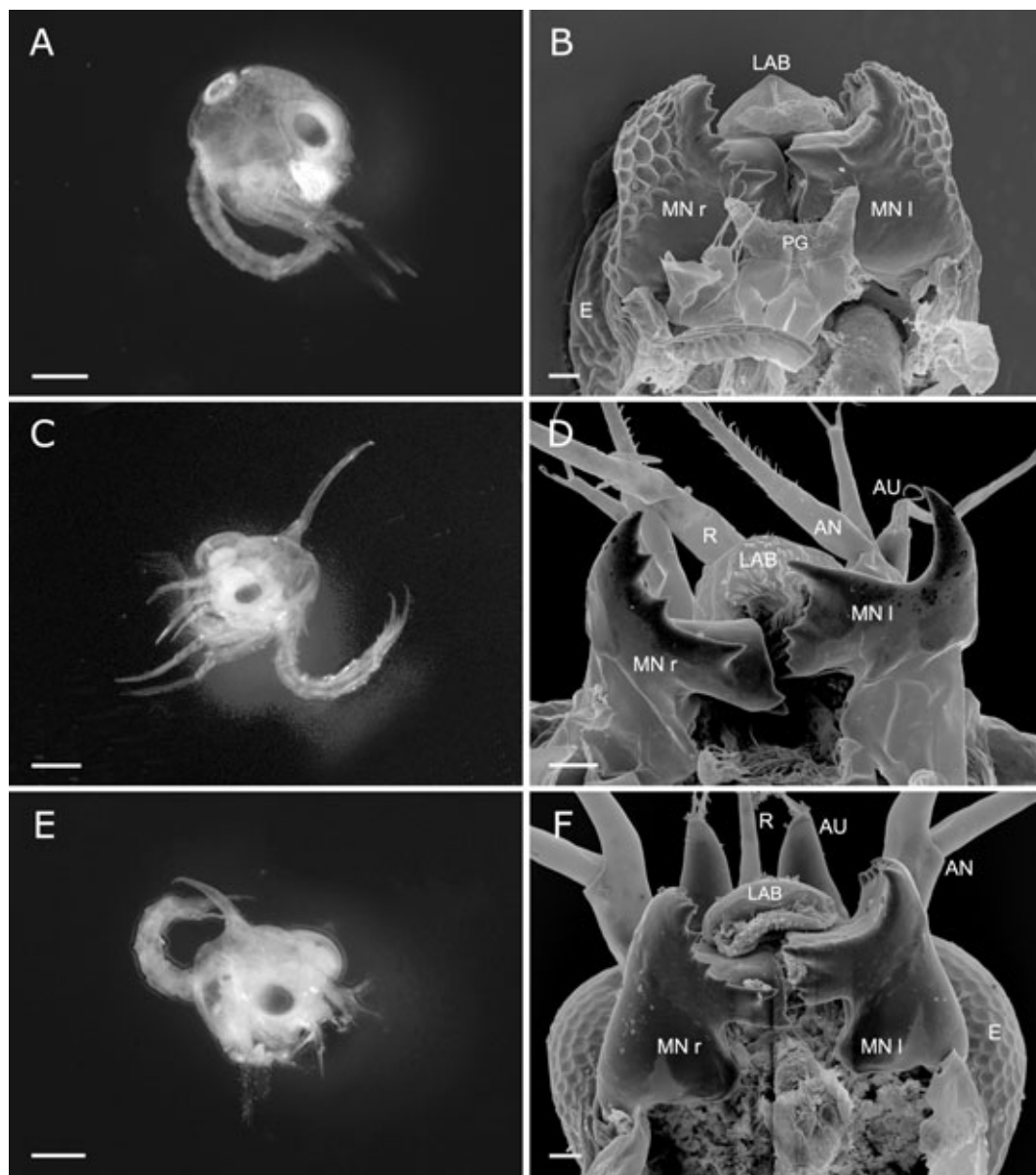


Fig. 7. A. Lateral view of zoea I of *Ebalia tuberosa* (bar 0.2 mm). B. Ventral view of dissected zoea I of *Ebalia tuberosa* (bar 0.2 mm). C. Lateral view of zoea I of *Liocarcinus pusillus* (bar 0.2 mm). D. Ventral view of dissected zoea I of *Liocarcinus pusillus* (bar 20 µm). E. Dorso-lateral view of zoea I of *Pilumnus hirtellus* (bar 0.2 mm). F. Ventral view of dissected zoea I of *Pilumnus hirtellus* (bar 20 µm). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MN l, left mandible; MN r, right mandible; PG, paragnath; R, rostrum.

Left mandible (Fig. 6D-F): Outer margin of incisor process slender, armed with 1 acute marginal spine and a pair of 2 submarginal spines. Molar process of staircase shape with 3 steps. A varying number of small spines on the step ridges. Posterior

margin of the third step armed with a small process with 2-4 small spines, and a marginal row of 4-5 spines merging with several setules on the dorsal margin (Fig. 6D). A pore on the first and the third step (Fig. 6D,E).

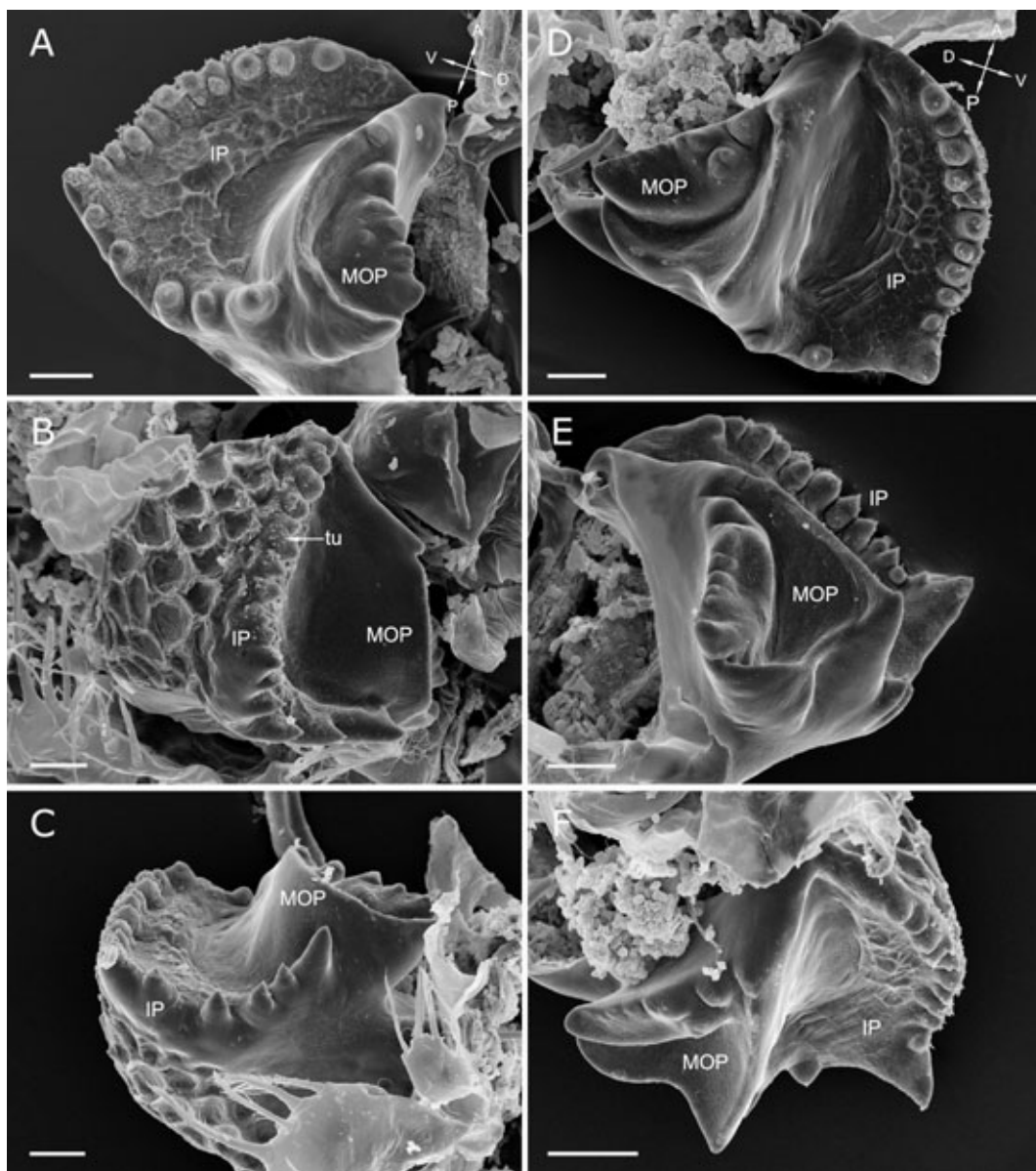


Fig. 8. *Ebalia tuberosa*, zoea I mandibles. **A.** Inner view of right mandible (bar 20 μ m). **B.** Ventral view of right mandible (bar 20 μ m). **C.** Posterior view of right mandible (bar 20 μ m). **D.** Inner view of left mandible (bar 20 μ m). **E.** Inner view on molar process of left mandible (bar 20 μ m). **F.** Anterior view of left mandible (bar 30 μ m). Abbreviations: **A**, anterior; **D**, dorsal; **IP**, incisor process; **MOP**, molar process; **P**, posterior; **tu**, tuberculettes; **V**, ventral.

5. *Ebalia tuberosa* (Pennant, 1777) (Figs 7A,B, 8)

Basic form: compact, massive, broad and rotund. Outer surface structured by honeycomb-shaped cuticular outgrowths. Incisor process ventral. Molar process dorsal to incisor process, chewing surface

oriented medially. Molar and incisor processes well-defined, spread in an oblique angle.

Right mandible (Fig. 8A-C): Ventral margin of incisor process armed with 10-11 marginal spines and a varying number of intermediate tuberculettes (Fig. 8B). 1 acute spine on the intersection between

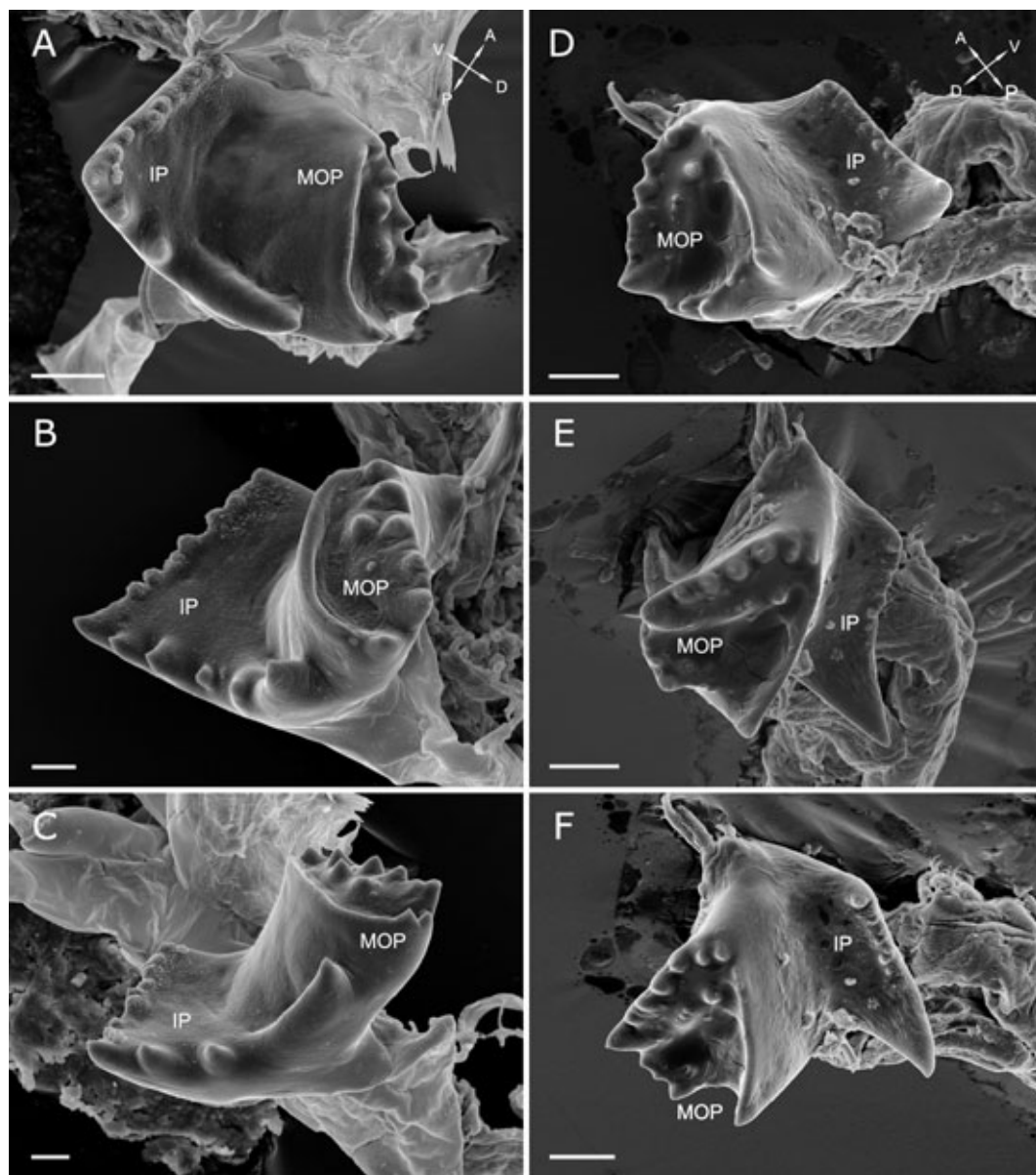


Fig. 9. *Liocarcinus pusillus*, zoea I mandibles. **A.** Inner view of right mandible (bar 20 μ m). **B.** Postero-median view of right mandible (bar 10 μ m). **C.** Posterior view of right mandible (bar 10 μ m). **D.** Inner view of left mandible (bar 20 μ m). **E.** Antero-median view of left mandible (bar 20 μ m). **F.** Anterior view of left mandible (bar 20 μ m). Abbreviations: A, anterior; D, dorsal; IP, incisor process; MOP, molar process; P, posterior; V, ventral.

ventral and posterior margin. Posterior margin armed with 4-6 marginal acute spines. Inner surface of incisor process structured by cuticular outgrowths. Chewing surface of molar process broad and triangular, pervaded by a clearly visible fluting; the inner margin of a curved ridge-like shape. Dorsal

margin armed with a row of 5(6) marginal spines and occasionally 1 submarginal spine.

Left mandible (Fig. 8D-F): Ventral margin of incisor process armed with a single row of 9-12 small marginal spines and a varying number of intermediate tuberculettes. 1 acute spine on the

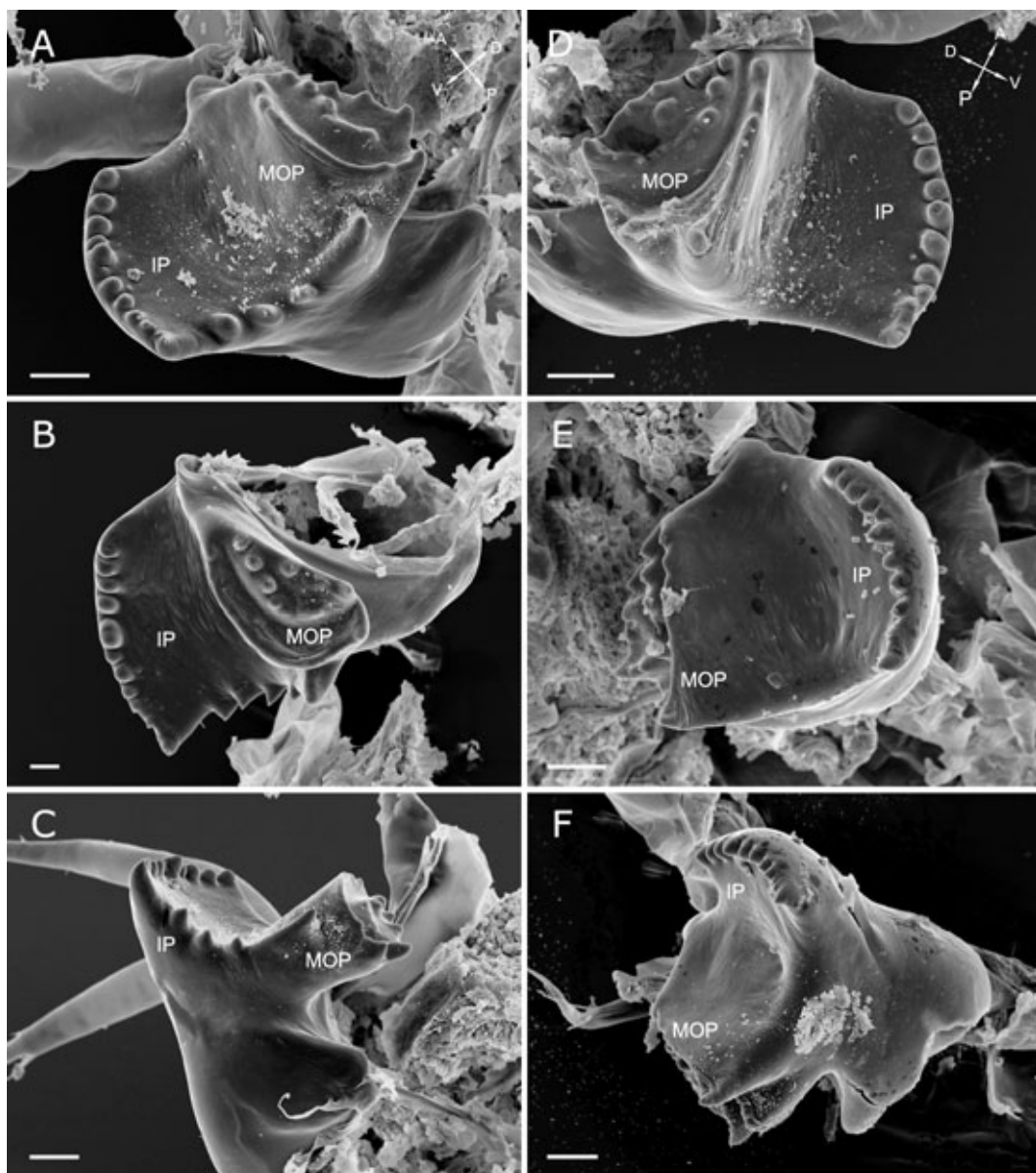


Fig. 10. *Pilumnus hirtellus*, zoea I mandibles. **A.** Postero-median view of right mandible (bar 20 µm). **B.** Inner view of molar process of right mandible (bar 10 µm). **C.** Posterior view of right mandible (bar 20 µm). **D.** Inner view of left mandible (bar 20 µm). **E.** Ventral view of left mandible (bar 20 µm). **F.** Posterior view of left mandible (bar 20 µm). Abbreviations: A, anterior; D, dorsal; IP, incisor process; MOP, molar process; P, posterior; V, ventral.

intersection between ventral and posterior margin. Posterior margin armed with 2 marginal acute spines. Molar process a broad structure, chewing surface triangular, the inner margin of a ridge-like shape which continues on posterior margin. Dorsal margin armed with a row of 6-7 marginal spines and 1 (2) submarginal spines.

6. *Liocarcinus pusillus* (Leach, 1815) (Figs 7C,D, 9)

Basic form: massive, broad and of rotund L-block shape. Outer surface unstructured. Incisor process ventral. Molar process dorsal to incisor process, chewing surface oriented medially. Molar and inci-

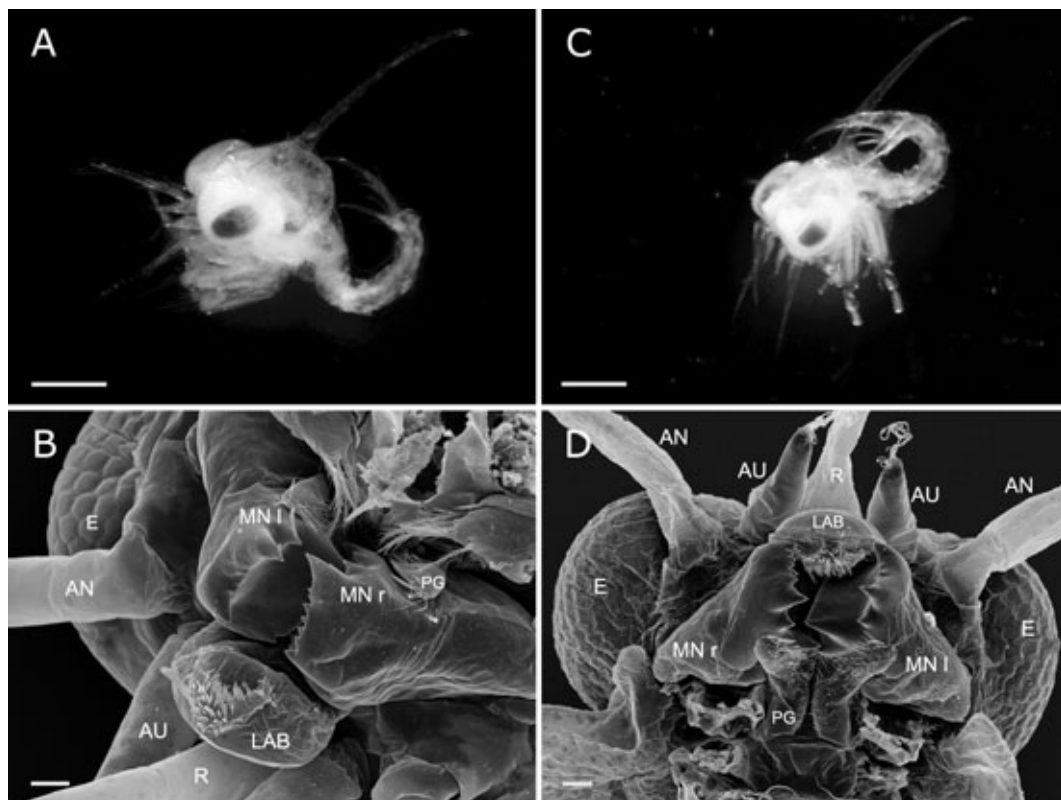


Fig. 11. A. Lateral view of zoea I of *Xantho pilipes* (bar 0.25 mm). B. Ventral view of dissected zoea I of *Xantho pilipes* (bar 20 µm). C. Dorso-lateral view of zoea I of *Xantho poressa* (bar 0.25 mm). D. Ventral view of dissected zoea I of *Xantho poressa* (bar 20 µm). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MNl, left mandible; MNr, right mandible; PG, paragnaths; R, rostrum.

sor processes well-defined, spread in an oblique angle.

Right mandible (Fig. 9A-C): Ventral margin of incisor process armed with a single row of 6-8 small marginal spines. 1 acute spine on the intersection between ventral and posterior margin. Posterior margin armed with 3-5 marginal acute spines. Molar process a broad structure, the inner margin of a curved ridge-like shape, flanked anterior by 1, posterior by 1 (2) small spines. A row of 4-5 marginal spines on the dorsal margin, and 1-2 submarginal spines.

Left mandible (Fig. 9D-F): Incisor process formed of 1 big acute protrusion and 7-8 small marginal spines on the ventral margin. Chewing surface of molar process broad and triangular, inner margin of a straight ridge-like shape flanked by 2 small spines. Dorsal margin armed with 6 marginal and 2-3 submarginal spines arranged in two rows. A row of 3 marginal spines on the posterior margin.

7. *Pilumnus hirtellus* (Linnaeus, 1761)

(Figs 7 E,F, 10)

Basic form: massive, broad and of rotund L-block shape. Outer surface unstructured. Incisor process ventral. Molar process dorsal to incisor process, chewing surface oriented medial. Molar and incisor processes well-defined, spread in an oblique angle.

Right mandible (Fig. 10A-C): Ventral margin of incisor process armed with a single row of 9-10 small marginal spines. 1 acute spine on the intersection between ventral and posterior margin. Posterior margin armed with 4(3-5) marginal acute spines. Molar process a broad structure, the inner margin of a curved ridge-like shape, flanked by 2 small spines. Dorsal margin with 4(5) marginal and 2-4 submarginal spines arranged in two rows.

Left mandible (Fig. 10D-F): Ventral margin of incisor process armed with a single row of 9-12 small marginal spines. Posterior margin unarmed. Chew-

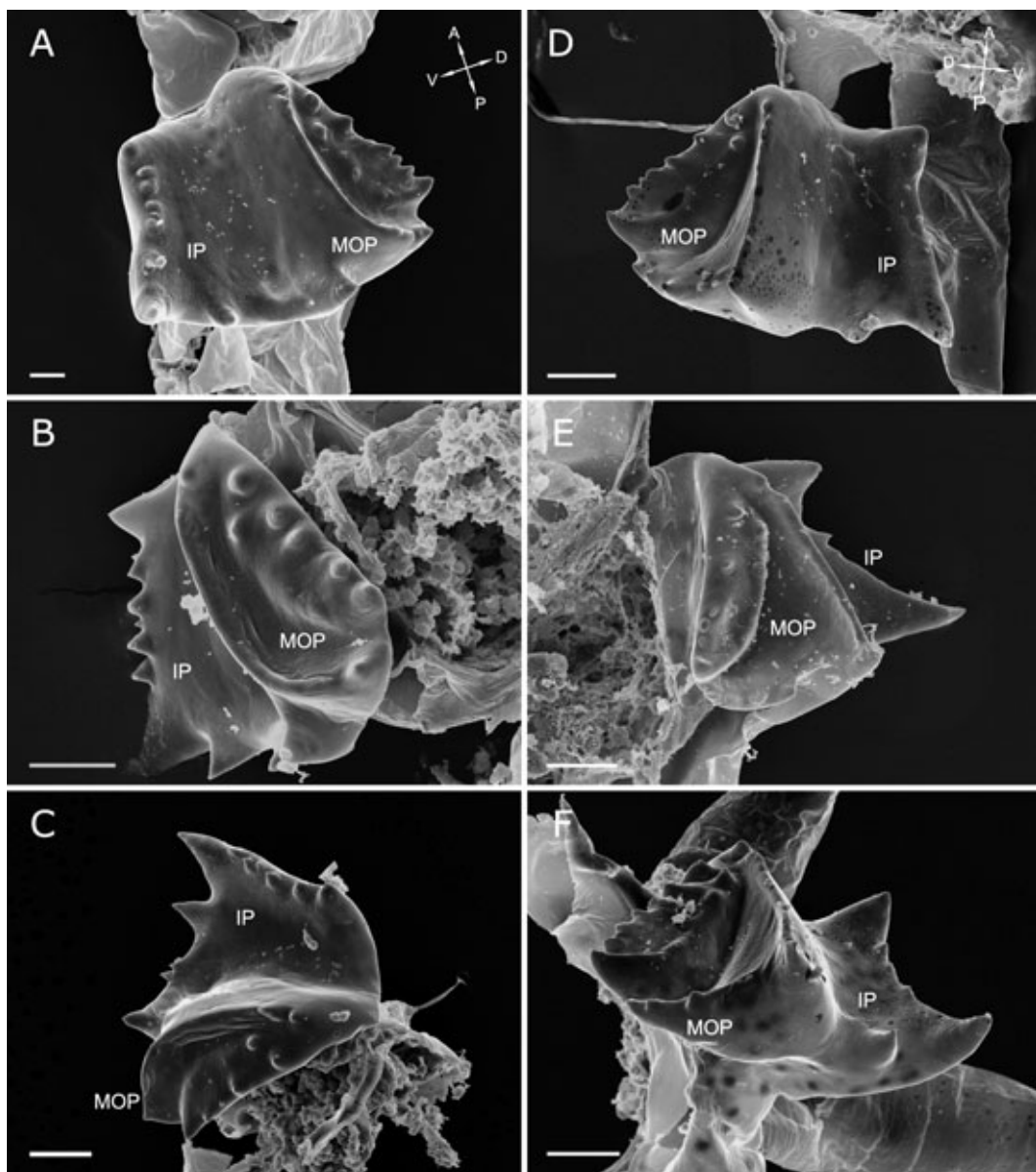


Fig. 12. *Xantho pilipes*, zoea I mandibles. **A.** Inner view of right mandible (bar 20 µm). **B.** Inner view on molar process of right mandible (bar 20 µm). **C.** Anterior view of right mandible (bar 20 µm). **D.** Inner view of left mandible (bar 10 µm). **E.** Inner view on molar process of left mandible (bar 20 µm). **F.** Posterior view of left mandible (bar 20 µm). Abbreviations: **A**, anterior; **D**, dorsal; **IP**, incisor process; **MOP**, molar process; **P**, posterior; **V**, ventral.

ing surface of molar process broad and triangular, inner margin of a straight ridge-like shape anteriorly flanked by 1 small spine, posteriorly flanked by 2 (1) small spines. Dorsal margin armed with 4-5 marginal

and 2-3 submarginal spines arranged in two rows. A row of 2-3 marginal spines on the posterior margin.

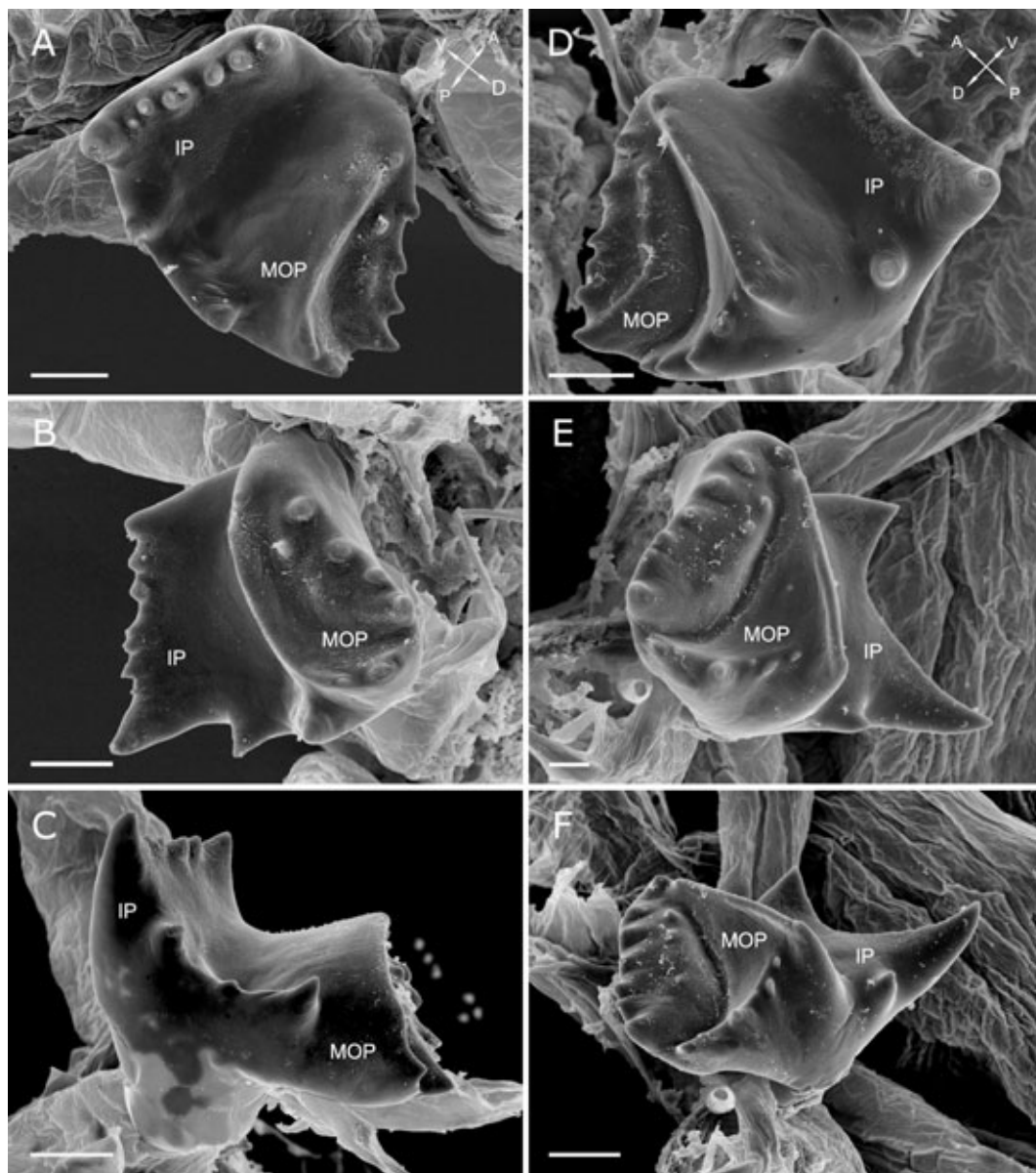


Fig. 13. *Xantho poressa*, zoea I mandibles. A. Inner view of right mandible (bar 20 μ m). B. Inner view on molar process of right mandible (bar 20 μ m). C. Posterior view of right mandible (bar 20 μ m). D. Inner view of left mandible (bar 20 μ m). E. Inner view on molar process of left mandible (bar 10 μ m). F. Postero-median view of left mandible (bar 20 μ m). Abbreviations: A, anterior; D, dorsal; IP, incisor process; MOP, molar process; P, posterior; V, ventral.

8. *Xantho pilipes* (A. Milne-Edwards, 1867)
(Figs 11A,B, 12)

Basic form: massive, broad and of rotund L-block shape. Outer surface unstructured. Incisor process ventral. Molar process dorsal to incisor process,

chewing surface oriented medially. Molar and incisor processes well-defined, spread in an oblique angle.

Right mandible (Fig. 12A-C): Ventral margin of incisor process armed with a single row of 5 small

marginal spines. An acute marginal process on the intersection between ventral and posterior margin and 3 acute processes located on the posterior margin. Molar process a broad structure, the inner margin of a curved ridge-like shape, flanked by 2 small spines. Dorsal margin with 5(6) marginal and 1(2) submarginal spines arranged in two rows.

Left mandible (Fig. 12D-F): Incisor process formed of 2 acute ventral processes, 1-3 little marginal spines between them and 1 acute posterior process. Chewing surface of molar process broad and triangular, pervaded by a clearly visible fluting, inner margin of a straight ridge-like shape flanked by 2 small spines. Dorsal margin armed with 6 marginal and 2 submarginal spines arranged in two rows. A row of 4 marginal spines on the posterior margin.

9. *Xantho hydrophilus* (Herbst, 1780) (Figs 11C,D, 13)

Basic form: massive, broad and of rotund L-block shape. Outer surface unstructured. Incisor process ventral. Molar process dorsal to incisor process, chewing surface oriented medially. Molar and incisor processes well-defined, spread in an oblique angle.

Right mandible (Fig. 13A-C): Ventral margin of incisor process armed with a single row of 5 small marginal spines. An acute marginal process on the intersection between ventral and posterior margin and 3 acute processes, located on the posterior margin. Molar process a broad structure, the inner margin of a curved ridge-like shape flanked by 2 small spines. Dorsal margin with 4-6 marginal and 1-2 submarginal spines arranged in two rows.

Left mandible (Fig. 13D-F): Incisor process armed with 2 acute ventral processes and 1 acute posterior process. Molar process broad and triangular, pervaded by a clearly visible fluting, inner margin a straight ridge-like shape flanked by 2 small spines. Dorsal margin armed with a row of 6 marginal spines and 1 submarginal spine. A row of 3-4(+2) spines on the posterior margin.

Discussion

General features

The first zoeae of all studied species do not possess mandibular palps. This corresponds to Ingle's (1992) notion that these, in most taxa, appear as an unsegmented bud in the terminal stage zoea, but not earlier during their development (see, however, Factor 1978). Furthermore, dissimilarity of right and left mandibles in decapods (Ingle 1992) is also sup-

ported by our study. In addition, all zoea mandibles examined have in common that they are composed of a lateral and a gnathal lobe, whereas the gnathal lobe always has an incisor and a molar process. It has been suggested that this is a basic feature of first stage zoeas (Factor 1989; see also Abele & Felgenhauer (1986) for adult structures).

On the gnathal edges of the mandibles various forms of appendages were found, e.g. acute spines, small denticles and tuberculettes mainly arming the outer margins. According to Ingle (1992) these are non-articular outgrowths of the cuticle. Surprisingly, however, we also found protrusions with a defined articulation on a basal ring and a distinct pore at the base, either in the form of the 'lacinia mobilis' or of small, spine-like appendages. Even single pores located somewhere on the mandible's surface without exhibiting other cuticular specialisations were found. These pores might partly represent gland pores. However, many of them strongly remind of ecdysial pores, i.e. structures normally connected to setae or other sensillar types (e.g., McIver 1975). In particular, the 'lacinia mobilis' of *P. elegans* and *P. amethysteus* with its basal articulation and ecdysial pore resembles a specialised seta or trichoid sensillum of either simple or serrated form as found in numerous arthropods.

Are there taxon-specific sets of characters?

In principle, functional constraints might have produced numerous divergent and convergent morphological adaptations to food preferences in the different taxa. However, the survey of our results given in Table 1 suggests that the above mentioned question deserves an affirmative answer. The distribution of characters indicates that a significant phylogenetic signal is present on the mandibles. Very closely related species show a high degree of correspondence, with the few differences thus being valuable species-specific or diagnostic features, and more distantly related taxa representing different decapod main lineages exhibit less corresponding sets of characters.

When examining the closely related species "pairs" *P. longicornis*/*P. platycheles* and *X. pilipes*/*X. hydrophilus*, it is difficult to find differential features (Table 1). Both porcellanids have the same basic mandible form, both have several setules on the anterior and posterior surface of the mandibles and on the dorsal margin of the molar processes, and both have the same number of spines on corresponding positions. The same applies to the two species of *Xantho* studied here. They have 3 acute processes on the posterior margin of the incisor process of the right mandible and 1 acute process

Table 1. Morphological differences among mandibles of zoea I larvae of selected representatives of families, genera and species of Decapoda. Abbreviations: **l**, left; **MN**, mandible; **pc**, process; **p**, pore; **r**, right; **s**, seta; **sp**, spine; **ssp**, small spine; **st**, setule; **tu**, tuberculette; **vn**, varying number).

Families		Palaemonidae		Porcellanidae		Leucosiidae		Portunidae		Pilumnidae		Xanthidae	
Genera		<i>Palaemon</i>	<i>Periclimenes</i>	<i>Porcellana</i>		<i>Ebalia</i>	<i>Liocarcinus</i>	<i>Liocarcinus</i>	<i>Pilumnus</i>	<i>Pilumnus</i>	<i>Pilumnus</i>	<i>Xantho</i>	<i>Xantho</i>
Species		<i>P. elegans</i>	<i>P. amathysteus</i>	<i>P. longicornis</i>	<i>P. platycheles</i>	<i>E. tuberosa</i>	<i>L. pusillus</i>	<i>L. pusillus</i>	<i>P. hirtellus</i>	<i>P. hirtellus</i>	<i>P. hirtellus</i>	<i>X. pilipes</i>	<i>X. pilipes</i>
basic form		slender	slender	slender/oval	slender/oval	massive	massive	massive	massive	massive	massive	massive	massive
MN r													
Incisor pc													
sp on ventral margin		3	3	1	1	10-11 +vn of tu	6-8	9-10	5	5	5	5	5
sp submarginal		1	1	1+3(4)	3	0	0	0	0	0	0	0	0
sp on posterior margin		0	0	2	2	4-6	3-5	4(3-5)	3pc	3pc	3pc	3pc	3pc
pores		1	0	?	1-2	0	0	0	0	0	0	0	0
'lacinia mobilis'		present	present	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Molar pc													
sp on dorsal margin		3	8	0+st	0+st	5(6)	4-5	4(5)	5(6)	5(6)	5(6)	5(6)	5(6)
sp submarginal		9-11	3	vn of ssp	vn of ssp	1	1-2	2-3	1(2)	1(2)	1(2)	1(2)	1(2)
sp on posterior margin		0	0	13(12)	7-9+1+4(3)+3-4	0	1	1	1	1	1	1	1
pores		0	0	2	2	0	0	0	0	0	0	0	0
MN l													
Incisor pc													
sp on ventral margin		5	4	1	1	9-12+vn of tu	1pc+7-8ssp	9-12	2pc+1-3ssp	2pc	2pc	2pc	2pc
sp submarginal		0	0	2	2	0	0	0	0	0	0	0	0
sp on posterior margin		0	0	0	0	2	0	0	1pc	1pc	1pc	1pc	1pc
pores		1	0	?	0	0	0	0	0	0	0	0	0
'lacinia mobilis'		present	present	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Molar pc													
sp on dorsal margin		4	6(7)	st	st	6-7	6	4-5	6	6	6	6	6
sp submarginal		6-8	2(3)	vn of ssp	vn of ssp	1(2)	2-3	2-3	2	2	2	2	2
sp on posterior margin		0	0	6	pc(3-4)+4-5	0	3	2-3	4	4	4	4	4
pores		1	0	3	2	0	0	0	0	0	0	0	0

on the left mandible, as well as the same number of spines on the ventral margin of the incisor process of the right mandible and on the dorsal margin of the molar process of the left mandible.

Conversely, *P. elegans* and *P. amethysteus*, two representatives of the Palaemonidae belonging to more distant genera, exhibit a different arrangement of mandible appendages in that the number of spines on the dorsal margin and that of the submarginal spines on the molar process of the left mandible varies distinctly. Furthermore, the five brachyurans belonging to different families studied here show marked differences, e.g. in the numbers of spines on the ventral margin of the incisor processes.

The most pronounced differences become clear when the representatives of the three decapod main lineages covered in this study are compared, i.e. the carideans, anomurans and brachyurans. Most obvious is the different basic form of the mandibles, i.e. slender in the carideans, slender/oval in the anomurans, and massive in the brachyurans, suggesting an evolutionary trend from slender to massive mandible forms. In addition, almost every group of spines and other processes on according mandible sections show differences, i.e. their number differs or some types of spines are absent in one group, like the spines on the posterior margin of the right mandible's incisor process that are absent in the studied carideans, present in small quantities in the anomurans, and distinct in the brachyurans.

The 'lacinia mobilis'

Of particular interest is the presence of a 'lacinia mobilis' on the mandibles of the two studied caridean zoeas, *P. elegans* and *P. amethysteus*. For *P. elegans*, the presence of a 'lacinia' was mentioned by Fincham (1977), and for some other carideans it was also reported (Haynes 1977; Dahl & Hessler 1982; Konishi and Kim 2000; Thatje et al. 2001; Li & Hong 2004; Yang 2005; Dupré et al. 2008) or a similar structure was depicted without using the term 'lacinia' (Dos Santos et al. 2004; Calado et al. 2004). In our zoeas, a 'lacinia mobilis' is located on the base of the incisor process of both, the left and the right mandible. Furthermore, in *P. elegans*, the 'lacinia' on the right mandible is spine-like, and that on the left mandible is serrated, and hence they are dissimilar. In *P. amethysteus*, a 'lacinia mobilis' in the form of a serrated seta is found on both mandibles.

Why could this be important? Various arthropods possess a movable, articulated protrusion on the mandible's gnathal edge, often referred to as lacinia mobilis. This observation led to hypotheses about their homology or non-homology (reviewed in Dahl & Hessler 1982; Richter et al. 2004; Richter &

Kornicker 2006). Among Crustacea, it was found at the base of the incisor process in adult Peracarida as well as in larval Euphausiacea and Caridea (review: Richter et al 2002; Euphausiacea: Weigmann-Haass 1977, Maas & Waloszek 2001; Caridea: see above).

Richter et al. (2002) propose that the 'lacinia mobiles' of the euphausicean and decapod larvae are rather not homologous to the 'true' lacinia mobilis of the Peracarida, because (1) the only structural similarities are their motility and their location on the mandible's gnathal edge, (2) they are found only on one mandible, (3) there have not been found two different kinds of a lacinia mobilis on the left and the right mandible, and (4) they are only present in the larvae. This corresponds to the observation that in other caridean larvae a 'lacinia mobilis' has been demonstrated on one mandible only (Dahl & Hessler 1982, Konishi and Kim 2000, Dupré et al. 2008), and this is the reason why we have put caridean 'lacinias' in inverted commas in this paper.

Our findings, however, devalue two of the above mentioned arguments (caridean 'lacinia mobiles' can be present on both mandibles, and be dissimilar). Therefore, the hypotheses about homology of these structures should be reassessed. At least, caridean zoeas might represent an ancestral character state compared to the derived adult mandible without lacinia, and more structural features of these appendages might be found in the future that link the crustacean lacinias more closely to each other.

Perspectives

In most published trees the Dendrobranchiata – rather than Caridea – are the first sidebranch of the decapod stem lineage, and the Caridea follow as the second one (e.g., Scholtz & Richter 1995; Schram and Dixon 2004; Ah Yong & O'Meally 2004; Porter et al 2005; Tsang et al. 2008; Chu et al. 2009; Fransen & De Grave 2009 and many others). Hence, how is the situation in Dendrobranchiata? In many descriptions of protozoeas of Penaeoidea and related taxa, the same problem as in Caridea occurs, viz., the resolution of mandible details is not sufficient. However, there are some reports on 'lacinia mobilis'-like appendages also in this taxon. For example, Ronquillo & Seicho (1995) and Ronquillo et al. (2006), in their detailed analysis of larval development of *Trachypenaeus curvirostris* and *Penaeus semisulcatus*, respectively, found serrated setae on the incisors that look similar to the 'lacinia mobiles' described in the present study, without, however, using the term 'lacinia'. A structure of the larval mandible close to the one described here for *Palaemon* and *Periclimenes* (slender, with 'lacinia') might therefore represent a plesiomorph

condition in Dendrobranchiata and Caridea, while the one found in Anomura (slender/oval, without 'lacinia') and Brachyura (massive, without 'lacinia') indicate apomorph sets of characters derived from the ancestral forms.

A survey of available mandible drawings in light microscopic zoea descriptions gives this notion some support: In anomurans other than those studied here, a similar slender to oval mandible seems to be present, e.g. in *Megalobrachium mortenseni*, *Pisidia brasiliensis* and *Petrolisthes ortmanni* (Kraus 2006), and massive mandibles have been demonstrated for different brachyurans, e.g. *Callinectes similis* (Bookhout & Costlow 1977), *Orotheres barbatus* (Balanos et al. 2005), and species of *Portunus* (Bookhout & Costlow 1974; Greenwood & Felder 1979, Meyer et al. 2006).

What about zoea mandibles in decapod main lineages not covered by the present study? In Astacidea (Waer 1976; Factor 1978) and Achelata (Robertson 1968; Higa et al. 2005), drawings suggest a rather flattened, slender mandible shape, while for Thalassinids, mandibles of intermediate form have been depicted (e.g., Konishi 1989). This might correspond well with the above mentioned evolutionary trend. However, at the moment difficult to compare are zoeal mandibles described for Stenopodidea such as species of *Microprosthema*, which seem to be relatively slender and flattened, but show no indication of a 'lacinia' (Martin & Goy 2004; Ghory et al. 2005).

Furthermore the few species studied in detail until present reminds us of looking at these ideas with care. We don't see them as more than tendencies that may reveal their significance only after a wide set of representatives of all decapod main lineages are analysed using the SEM. However, with the structure of decapod zoea mandibles a previously underestimated and phylogenetically important signal seems to be available.

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