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

(Crustacea, Decapoda)

Hannes Geiselbrecht \& Roland R. Melzer


#### Abstract

Geiselbrecht, H. \& Melzer, R. R. 2010. Mandibles of zoea I larvae of nine decapod species: a scanning EM analysis (Crustacea, Decapoda). Spixiana 33(1): 27-47.

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.

Hannes Geiselbrecht and Roland R. Melzer, Zoologische Staatssammlung, Münchhausenstr. 21, 81247 München, Germany; e-mail: melzer@zsm.mwn.de


## Introduction

Inspired by the classical works of Lebour $(1928,1943)$, Aikawa (1937), Gurney (1939, 1942), and BourdillonCasanova (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. amethystheus 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 Staatsammlung 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 ( $70 \%, 80 \%, 90 \%, 10 \mathrm{~min}$ 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 $100 \mu \mathrm{~m}$, 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 A20080767769; 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); Pisidialongicornis: 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 $20 \mu \mathrm{~m}$ ). C. Lateral view of zoea I of Periclimenes amethysteus (bar 0.25 mm ). D. Ventral view of dissected zoea I of Periclimenes amethysteus (bar $20 \mu \mathrm{~m}$ ). Abbreviations: AN, antenna; AU, antennule; E, eye; LAB, labrum; MN1, left mandible; MNr, right mandible; PG, paragnaths.

## Results

## Description of the mandibles

## 1. Palaemon elegans (Rathke, 1837) <br> (Figs 1A,B, 2)

Basic form: slender, a bent tube flattened anteriorposteriorly 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 anteriorposteriorly 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 $10 \mu \mathrm{~m}$ ). B. Inner view of right mandible (bar $10 \mu \mathrm{~m}$ ). C. Anterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $10 \mu \mathrm{~m}$ ). E. Dorsal view of left mandible (bar $10 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). Abbreviations: Arrowheads, 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 $10 \mu \mathrm{~m}$ ). B. Anterior view of right mandible (bar $10 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $10 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $10 \mu \mathrm{~m}$ ). E. Dorso-median view of left mandible (bar $10 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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 $100 \mu \mathrm{~m}$ ). C. Lateral view of zoea I of Pisidia longicornis (bar 0.5 mm ). D. Ventral view of dissected zoea I of Pisidia longicornis (bar $20 \mu \mathrm{~m}$ ). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MN1, 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 $10 \mu \mathrm{~m}$ ). B. Dorso-median view of right mandible (bar $20 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $10 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Ventro-median view of left mandible (bar $20 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $10 \mu \mathrm{~m}$ ). 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 $20 \mu \mathrm{~m}$ ). B. Ventro-median view of right mandible (bar $20 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Dorso-median view of left mandible (bar $10 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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 tubero$s a($ bar $20 \mu \mathrm{~m}$ ). C. Lateral view of zoea I of Liocarcinus pusillus (bar 0.2 mm ). D. Ventral view of dissected zoea I of Liocarcinus pusillus (bar $20 \mu \mathrm{~m}$ ). 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 $20 \mu \mathrm{~m}$ ). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MN1, left mandible; MNr, right mandible; PG, paragnaths; 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 $20 \mu \mathrm{~m}$ ). B. Ventral view of right mandible (bar $20 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Inner view on molar process of left mandible (bar $20 \mu \mathrm{~m}$ ). F. Anterior view of left mandible (bar $30 \mu \mathrm{~m}$ ). Abbreviations: A, anterior; D, dorsal; IP, incisor process; MOP, molar process; P, posterior; tu, tuberculettes; V, ventral.

## 5. Ebalia tuberosa (Pennant, 1777) <br> (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 welldefined, 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 $20 \mu \mathrm{~m}$ ). B. Posterio-median view of right mandible (bar $10 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $10 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Anterio-median view of left mandible (bar $20 \mu \mathrm{~m}$ ). F. Anterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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. Posterio-median view of right mandible (bar $20 \mu \mathrm{~m}$ ). B. Inner view of molar process of right mandible (bar $10 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Ventral view of left mandible (bar $20 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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 $20 \mu \mathrm{~m}$ ). 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 $20 \mu \mathrm{~m}$ ). Abbreviations: AN, antenna; AU, antennules; E, eye; LAB, labrum; MN1, 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 $20 \mu \mathrm{~m}$ ). B. Inner view on molar process of right mandible (bar $20 \mu \mathrm{~m}$ ). C. Anterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $10 \mu \mathrm{~m}$ ). E. Inner view on molar process of left mandible (bar $20 \mu \mathrm{~m}$ ). F. Posterior view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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 $20 \mu \mathrm{~m}$ ). B. Inner view on molar process of right mandible (bar $20 \mu \mathrm{~m}$ ). C. Posterior view of right mandible (bar $20 \mu \mathrm{~m}$ ). D. Inner view of left mandible (bar $20 \mu \mathrm{~m}$ ). E. Inner view on molar process of left mandible (bar $10 \mu \mathrm{~m}$ ). F. Posterio-median view of left mandible (bar $20 \mu \mathrm{~m}$ ). 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: $\mathbf{1}$, left; MN, mandible; pc, process; p, pore; $\mathbf{r}$, right; $\mathbf{s}$, seta; $\mathbf{s p}$, spine; ssp, small spine; st, setule; tu, tuberculette; vn, varying number).

| Families | Pala | monidae | Porce | lanidae | Leucosiidae | Portunidae | Pilumnidae | Xant | idae |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Genera | Palaemon | Periclimenes |  | cellana | Ebalia | Liocarcinus | Pilumnus | Xar |  |
| Species | P. elegans | P. amethysteus | P. longicornis | P. platycheles | E. tuberosa | L. pusillus | P. hirtellus | X. pilipes | X. poressa |
| basic form | slender | slender | slender/oval | slender/oval | massive | massive | massive | massive | massive |
| MN r |  |  |  |  |  |  |  |  |  |
| Incisor pc |  |  |  |  |  |  |  |  |  |
| sp on ventral margin | 3 | 3 | 1 | 1 | $10-11+\mathrm{vn}$ of tu | 6-8 | 9-10 | 5 | 5 |
| sp submarginal | 1 | 1 | 1+3(4) | 3 | 0 | 0 | 0 | 0 | 0 |
| sp on posterior margin | 0 | 0 | 2 | 2 | 4-6 | 3-5 | 4(3-5) | 3 pc | 3 pc |
| pores | 1 | 0 | ? | 1-2 | 0 | 0 | 0 | 0 | 0 |
| 'lacinia mobilis' | present | present | 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) | 4-6 |
| sp submarginal | 9-11 | 3 | vn of ssp | vn of ssp | 1 | 1-2 | 2-3 | 1(2) | 1-2 |
| sp on posterior margin | 0 | 0 | 13(12) | 7-9+1+4(3)+3-4 | 0 | 1 | 1 | 1 | 1 |
| pores | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| MN 1 |  |  |  |  |  |  |  |  |  |
| Incisor pc |  |  |  |  |  |  |  |  |  |
| sp on ventral margin | 5 | 4 | 1 | 1 | $9-12+\mathrm{vn}$ of tu | $1 \mathrm{pc}+7-8 \mathrm{ssp}$ | 9-12 | $2 \mathrm{pc}+1-3 \mathrm{ssp}$ | 2pc |
| sp submarginal | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| sp on posterior margin | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 pc | 1 pc |
| pores | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 |
| 'lacinia mobilis' | present | present | 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 |
| sp submarginal | 6-8 | 2(3) | vn of ssp | vn of ssp | 1(2) | 2-3 | 2-3 | 2 | 1 |
| sp on posterior margin | 0 | 0 | 6 | $\mathrm{pc}(3-4)+4-5$ | 0 | 3 | 2-3 | 4 | 3-4(+2) |
| pores | 1 | 0 | 3 | 2 | 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, devaluate 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 Dendrobrachiata - 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; Ahyong \& 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 \& Fielder 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.

## Acknowledgements

We thank Stefan Friedrich (München) for expert technical assistance. Special thanks go to Roland Meyer (München) for collecting, raising and conservating many of the studied zoeae. This study was partly supported by the Sea Life Center München.

## References

Abele, L. G. \& Felgenhauer, B. E. 1986. Phylogenetic and phenetic relationships among the lower Decapoda. Journal of Crustacean Biology 6: 385-400.

Ahyong, S. T. \& O'Meally, D. 2004. Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. The Raffles Bulletin of Zoology 52: 673-693.
Aikawa, H. 1937. Further notes on brachyuran larva. Records of Oceanographic Works in Japan 9: 87-162.
Barnich, R. 1996. The larvae of the Crustacea Decapoda (excl. Brachyura) in the plankton of the French Mediterranean coast (identification keys and systematic review). 198 pp., Göttingen (Cuvillier).
Bolanos, J., Rivero, W.,Hernández, J., Magán, I., Hernández, G., Cuesta, J. A. \& Felder, D. L. 2005. Abbreviated larval development of the pea crab Orthotheres barbatus (Decapoda: Brachyura: Pinnotheridae) described from laboratory-reared material, with notes on larval characters of the Pinnotheridae. Journal of Crustacean Research 25: 500-506.
Bookhout, C. G. \& Costlow, Jr., J. D. 1974. Larval development of Portunus spinicarpus reared in the laboratory. Bulletin of Marine Research 24: 20-51.

-     - \& - - 1977. Larval development of Callinectes similis reared in the laboratory. Bulletin of Marine Research 27: 704-728.
Bourdillon-Casanova, L. 1950. Le méroplancton du Golfe de Marseille. Les larves de Crustacés Décapodes. Recueil des Travaux de la Station Marine d'Endoume, Marseille 30: 1-286.
Casanova, B., Jong, L. \& Moreau, X. 2002. Carapace and mandibles ontogeny in the Dendrobranchiata (Decapoda), Euphausiacea, and Mysidacea (Crustacea): a phylogenetic interest. Canadian Journal of Zoology 80: 296-306.
Christiansen, M. E. 1973. The complete larval development of Hyas araneus (Linnaeus) and Hyas coarctatus (Decapoda, Brachyura, Majidae) reared in the laboratory. Norwegian Journal of Zoology 21: 63-89.
Chu, K. H., Tsang, L. M., Ma, K. Y., Chan T. Y. \& Ng, P. K. L. 2009. Decapod phylogeny: What can proteincoding genes tell us? Pp. 89-99 in: Martin, J. W., Crandall, K. A. \& Felder, D. L. (eds). Decapod crustacean phylogenetics. Crustacean Issues 18. Baton Raton, FL (CRC Press).
Clark, P. F. 1984. A comparative study of zoeal morphology in the genus Liocarcinus (Crustacea: Brachyura: Portunidae). Zoological Journal of the Linnean Society of London 82: 273-290.
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 of London 74: 133-146.
Dixon, C. J., Ahyong. S. T. \& Schram, F. R. 2003. A new hypothesis of decapod phylogeny. Crustaceana 76: 935-975.
Dos Santos, A., Calado, R., Bartilotti, C. \& Narciso, L. 2004. The larval development of the partner shrimp Periclimenes sagittifer (Norman, 1861) (Decapoda: Caridea: Palaemonidae: Pontoniinae) described from laboratory-reared material, with a note on chemical settlement cues. Helgoland Marine Research 58: 129-139.

Dupré, E., Flores, L. \& Palma, S. 2008. Larval development of the rock shrimp Rhynchocinetes typus Milne Edwards, 1937 (Decapoda, Caridea) reared in the laboratory. Revista Chilena de Historia Natural 81: 155-170.
Factor, J. R. 1978. Morphology of the mouthparts of larval lobsters, Homarus americanus (Decapoda: Nephropidae), with special emphasis on their setae. Biological Bulletin 154: 383-408.

-     - 1989. Development of the feeding apparatus in decapod crustaceans. Pp. 173-184 in: Felgenhauer, B. E. (ed.). Functional morphology of feeding and grooming in crustaceans. Crustacean Issues 6. Rotterdam (A. A. Balkema).
Fincham, A. A. 1977. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia) 1. Laboratory methods and review of Palaemon (Paleander) elegans Rathke, 1837. Bulletin of the Natural History Museum. Zoology Series 32: 1-28.
Fransen, C. H. J. M. \& De Grave, S. 2009. Evolution and radiation of shrimp-like decapods: An overview. Crustacean Issues 18: 245-259.
Geiselbrecht, H. \& Melzer, R. R. 2009. Morphology of the first zoeal stage of the partner shrimp Periclimenes amethysteus Risso, 1827 (Decapoda: Caridea: Palaemonidae: Pontoniinae) studied with the scanning EM. Zootaxa 2140: 45-55.
Ghory, F. S., Siddiqui, F. A. \& Kazmi, Q. B. 2005. The complete larval development including juvenile stage of Microprostema validum Stimpson, 1860 (Crustacea: Decapoda: Spongicolidae), reared under laboratory conditions. Pakistan Journal of Marine Sciences 14: 33-64.
González-Gordillo, J. I., Cuesta, J. A. \& Rodrìguez, A. 1996. Studies on the larval development of northeastern Atlantic and Mediterranean Porcellanidae (Decapoda, Anomura). I - Redescription of the larval stages of Porcellana platycheles (Pennant, 1777) reared under laboratory conditions. Helgoländer Meeresuntersuchungen 50: 517-531.
Greenwood, J. G. \& Fielder, D. R. 1979. The zoeal stages and megalopa of Portunus rubromarginatus (Lanchester) (Decapoda: Portunidae), reared in laboratory. Journal of Plankton Research 1: 191-205.
Gurney, R. 1939. Bibliography of the larvae of decapod Crustacea. The Ray Society 125: ii-vii, 1-125.
-     - 1942. Larvae of decapod Crustacea. The Ray Society 129: 1-306.
Haynes, E. 1977. Description of larvae of a hippolytid shrimp, Lebbeus groenlandicus, reared in situ in Kachemak Bay, Alaska. Fishery Bulletin 76: 457-465.
Higa, T., Fujita, Y. \& Shokita, S. 2005. Complete larval development of a scyllarine lobster Galaearctus kitanoviriosus (Harada, 1962) (Decapoda: Scyllaridae: Scyllarinae), reared under laboratory conditions. Crustacean Research 34: 1-26.
Ingle, R. W. 1983. A comparative study of the larval development of Monodaeus couchi (Couch), Xantho incisus Leach and Pilumnus hirtellus (Linnaeus) (Crustacea: Bachyura: Xanthidae). Journal of Natural History 17: 951-978.
-     - 1992. Larval stages of Northeastern Atlantic crabs. An illustrated key. 388 pp., London (Chapman and Hall).
Johnston, M., Johnston, D. \& Knott, B. 2008. Ontogenetic changes in the structure and function of the mouthparts and foregut of early and late stage Panulirus ornatus (Fabricus, 1798) phyllosoma (Decapoda: Palinuridae). Journal of Crustacean Biology 28: 46-56.
Konishi, K. 1989. Larval development of the mud shrimp Upogebia (Upogebia) major (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families. Bulletin of National Research Institute of Aquaculture 15: 1-17.
-     - 2007. Morphological notes on the mouthparts of decapod crustacean larvae, with emphasis on palinurid phyllosomas. Bulletin of the Fisheries Research Agency 20: 73-75.
-     - \& Kim, J. N. 2000. The first zoeal stage of sand shrimp Crangon amurensis Brashnikov, 1907, with a discussion of the larval characters of the Crangonidae (Crustacea, Decapoda, Caridea). Bulletin of National Research Institute of Aquaculture 30: 1-12.
Kraus, H. 2006. Larvalmorphologie der Porcellanidae (Crustacea: Decapoda: Anomura). 108 pp., PhD thesis, Justus-Liebig-Univ. Gießen.
Kurian, C. V. 1956. Larvae of decapod Crustacea from the Adriatic Sea. Acta Adriatica 6: 1-108.
Le Roux, A. 1966. Le développement larvaire de Porcellana longicornis Pennant (Crustacé, Décapode, Anomoure, Galatheide). Cahiers de Biologie Marine 7: 69-78.
Lebour, M. V. 1928. Studies of the Plymouth Brachyura. II. The Larval Stages of Ebalia and Pinnotheres. Journal of the Marine Biological Association of the UK 15: 109-122.
-     - 1943. The larvae of the genus Porcellana (Crustacea, Decapoda) and related forms. Journal of the Marine Biological Association of the UK 25: 721-737.
Li, H. Y. \& Hong, S. Y. 2004. Larval development of Crangon uritai (Decapoda: Crangonidae) reared in the laboratory. Journal of Crustacean Biology 24: 576-591.
Lumasag, G. J., Quinitio, E. T., Aguilar, R. O., Baldevarona, R. B. \& Saclauso, C. A. 2007. Ontogeny of feeding apparatus and foregut of mud crab Scylla serrata Forsskal larvae. Aquaculture Research 38: 1500-1511.
Maas, A. \& Waloszek, D. 2001. Larval development of Euphausia superba Dana, 1852 and a phylogenetic analysis of the Euphausiacea. Hydrobiologia 448: 143-169.
Martin, J. W. \& Goy, J. W. 2004. The first larval stage of Microprostema semilaeve (Von Martens, 1872) (Crustacea: Decapoda: Stenopodidea) obtained in the laboratory. Gulf and Caribbean Research 16: 19-25.
Mc Iver, S. B. 1975. Structure of cuticular mechanorezeptors of Arthropods. Annual Review of Entomology 20: 381-397.

Meyer, R. \& Melzer, R. R. 2004. Scanning EM diagnosis of marine Decapoda larvae: A comparison of preparation techniques. Crustaceana 77: 883-886.

-     - , Friedrich, S. \& Melzer, R. R. 2004. Xantho poressa (Herbst, 1780) and Xantho pilipes A. MilneEdwards, 1867 Larvae (Brachyura, Xanthidae): Scanning EM diagnosis of zoea I from the Adriatic Sea. Crustaceana 77: 997-1005.
-     - , Wehrtmann, I. S. \& Melzer, R. R. 2006. Morphology of the first zoeal stage of Portunus acuminatus Stimpson, 1871 (Decapoda: Portunidae: Portuninae) reared in the laboratory. Scientia Marina 70: 261-270.
Minagawa, M. \& Takashima, F. 1994. Developmental changes in larval mouthparts and foregut in the red frog crab, Ranina ranina (Decapoda, Raninidae). Aquaculture 126: 61-71.
Paula, J. \& Dos Santos, A. 2000. Larval and early postlarval stages of the crab, Xantho pilipes A. MilneEdwards, 1867 (Crustacea, Decapoda, Xanthidae) reared under laboratory conditions. Invertebrate Reproduction \& Development 38: 253-264.
Porter, M. L., Pérez-Losada, M. \& Crandall, K. A. 2005. Model-based multi locus estimation of decapod phylogeny and divergence times. Molecular Phylogenetics and Evolution 37: 355-369.
Rice, A. L. 1979. A plea for improved standards in descriptions of crab zoeae. Crustaceana 37: 214-218.
-     - 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Transactions of the Zoological Society of London 35: 271-424.
-     - \& Ingle, R. W. 1978. The larval development of the portunid crab Macropipus pusillus (Leach) reared in the laboratory. Bulletin of the Natural History Museum. Zoology Series 33: 287-296.
Richter, S. \& Kornicker, L. S. 2006. The mandibles of a halocyprid ostracode (Halocypridina: Halocypridae) - A new record of mandibular gnathal edges with a "lacinia mobilis". Journal of Crustacean Biology 26: 113-118.
-     - , Edgecombe, G. D. \& Wilson, G. D. F. 2002. The lacinia mobilis and similar structures - a valuable character in arthropod phylogenetics. Zoologischer Anzeiger 241: 339-361.
Robertson, P. B. 1968. The complete larval development of the sand lobster, Scyllarus americanus (Smith), (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from plankton. Bulletin of Marine Science 18: 294-342.

Rodríguez, A. \& Martin, J. W. 1997. Larval development of the crab Xantho poressa (Decapoda, Xanthidae) reared in the laboratory. Journal of Crustacean Biology 17: 98-110.
Ronquillo, J. D. \& Saisho, T. 1995. Developmental stages of Trachypenaeus curvirostris (Stimpson, 1860) (Decapoda, Penaeidae) reared in the laboratory. Crustaceana 68: 833-863.

-     - , - - \& McKinley, R. S. 2006. Early developmental stages of the green tiger prawn, Penaeus semisulcatus de Haan (Crustacea, Decapoda, Penaeidae). Hydrobiologia 560: 175-196.
Salman, D. S. 1982a. Larval development of the crab Pilumnus hirtellus (L.) reared in the laboratory (Decapoda, Brachyura, Xanthidae). Crustaceana 42: 113-126.
-     - 1982b. Observations on the larvae of North European crabs of the genus Ebalia (Brachyura, Leucosiidae). Crustaceana 42: 256-269.
Scholtz, G. \& Richter, S. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca) Zoological Journal of the Linnean Society 113: 289-328.
Schram, F. R. \& Dixon, C. J. 2004. Decapod phylogeny: addition of fossil evidence to a robust morphological cladistic data set. Bulletin of the Mizunami Fossil Museum 31: 1-19.
Thatje, S., Bacardit, R., Romero, M. C., Tapella, F. \& Lovrich, G. A. 2001. Description and key to the zoeal stages of the Campylonotidae (Decapoda, Caridea) from the Magellan Region. Journal of Crustacean Biology 21: 492-505.
Tsang, L. M., Maa, K. Y., Ahyong, S. T., Chan T. Y. \& Chu, K. H. 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: Origin and evolution of the Reptantia. Molecular Phylogenetics and Evolution 48: 359-368.
Wear, R. G. 1976. Studies on the larval development of Metanephros challengeri (Balss, 1914) (Decapoda, Nephropidae). Crustaceana 30: 113-122.
Weigmann-Haass, R. 1977. Die Calyptotis- und FurciliaStadien von Euphausia hanseni (Crustacea: Euphausiacea). Helgoländer Wissenschaftliche Meeresuntersuchungen 29: 315-327.

