Article

Redescription of the early larval stages of the pandalid shrimp *Chlorotocus crassicornis* (Decapoda: Caridea: Pandalidae)

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Abstract

The first four larval stages of the pandalid shrimp *Chlorotocus crassicornis* (A. Costa, 1871) are described and illustrated from laboratory-reared material obtained from ovigerous females collected in the southwestern Spain and south Taiwan. The second to fourth larval stages of this species are reported for the first time to science. Detailed examination of the first larval stages reveals that previous description misidentified some key larval characters which have prevented its identification in plankton samples. It is found that the zoeal morphology of *Chlorotocus* is not very different from other pandalid larvae, and in fact closely resembles *Plesionika* and *Heterocarpus*.

Key words: *Chlorotocus crassicornis*, Pandalidae, zoea, taxonomy, larval morphology

Introduction

Pandalidae Haworth, 1825 is one of the most diverse caridean families, accounting around 189 recognized species (De Grave & Fransen 2011). Worldwide distributed and inhabiting shallow and deep waters below 4000 m depth, they occupy an intermediate trophic position in both benthic and pelagic food webs. This group includes many species of high economic value (Holthuis 1980) that has motivated an intense research effort to understand their biology and fishing feasibilities, for example *Pandalus borealis* Krøyer, 1838 in the North Atlantic (Bergström 2000). However, there are still significant lack of knowledge on the phylogeny and larval morphology of pandalids. Li *et al.*'s (2011) molecular analysis based on five nuclear genes supports the monophyly of pandalid family, but more investigations are needed to understand its phylogeny and biogeographical relationships amongst the different genera (Matzen da Silva *et al.* 2012). Regarding the larval morphology, there is only information on 9 out the 23 currently accepted genera of this family (i.e. *Pandalina* Calman, 1899*, Pandalus* Leach, 1814*, Pandalopsis* Bate, 1888*, Dichelopandalus* Caullery, 1896*, Stylopandalus* Coutiére, 1905*, Plesionika* Bate, 1888*, Heterocarpus* A. Milne-Edwards, 1881*, Chlorotocela* Balss, 1914 and *Chlorotocus* A. Milne-Edwards, 1882). Moreover, some of the available larval descriptions are based on plankton collected samples with doubtful identities and/or do not follow the current standards of larval morphology proposed by Clark *et al.* (1998).

Currently, the genus *Chlorotocus* includes two species, *C. crassicornis* (A. Costa, 1871) and *C. novaezealandiae* (Borradaile, 1916). The only larval description for this genus was provided by Heegaard (1969) and is based on the first zoeal stage of *C. crassicornis* obtained in laboratory conditions from ovigerous females. According to this description, zoea I of *C. crassicornis* can be distinguished from other first stages of caridean larvae (at least from European waters) by the presence of six abdominal somites and segmented antennal scales (dos Santos & González-Gordillo 2004). Nevertheless, more developed zoeal stages of this species was not known.

Consequently, the very limited knowledge on the larval features of the genus *Chlorotocus* impedes detailed comparisons of the larval pattern of this genus with other carideans.

The present work succeeded in rearing the first four zoeal stages of *C. crassicornis* hatched under laboratory conditions from ovigerous females. The morphology of the first zoeal stage of the different genera in the family Pandalidae is reviewed and their distinguishing characters are discussed.

Materials and methods

The larvae used for the morphological descriptions were obtained from ovigerous shrimps collected by benthic trawling (100–250 m depth) off south-west Spain (36º35.23'N, 6º34,21'W) and off south Taiwan (22º12.35'N, 120º33.36'E). The specimens were maintained in a 2-l beaker containing well-aerated filtered natural seawater until hatching. No food was added. The first culture experience was performed during November of 2008 in the University of Cádiz, Spain, where after hatching; actively swimming larvae were transferred to 5-l glass bottles with aeration at constant temperature (22 ºC) and were fed freshly hatched nauplii of *Artemia* spp. The second larval rearing was conducted using the aquaculture facilities of the National Museum of Marine Biology and Aquarium, Taiwan, during October of 2014. This time the temperature was fixed to 26ºC and the larvae were fed with rotifers. In both laboratory cultures, the water was changed daily, and larvae were checked for evidence of molting and mortality. Each time the water was renewed, 3–4 larvae were preserved in 4% formaldehyde.

For the analysis of the larval morphology, appendages were dissected under an OLYMPUS SZX12 stereomicroscope using entomological needles. Drawings and measurements were taken using an OLYMPUS BX50 compound microscope equipped with a *camera lucida*. Larval descriptions and setal counts follow the method proposed by Clark *et al.* (1998), and the setal terminology used by Landeira *et al.* (2009a) for the descriptions of pandalid larvae. All figures and descriptions were based on observations of at least 5 specimens belonging to each larval stage. The long plumose natatory setae were drawn truncated and setules from setae were omitted from drawings whenever necessary. Cephalothorax length (CL) was measured from the postorbital margin to the posteromedian end of the cephalothorax. Voucher specimens were deposited in the "Museo de la Naturaleza y el Hombre of Santa Cruz de Tenerife" (catalogue number DL/000735) and in the National Taiwan Ocean University (catalogue number NTOUM01869).

Using the SPSS system for Windows v.12.0, the parametric statistical method Student's t-test was used to evaluate size (CL) differences among Atlantic and Taiwanese larvae for zoea I and zoea II stages.

Results

In the first culture experiment at Spain, the female shrimp released larvae 48 h after its collection. The culture was stopped the third day when a mass death was observed. At this moment some remaining larvae in zoea II stage were collected for morphological analysis. The culture in Taiwan had more success, with larval rearing lasted for 6 days and obtaining four zoeal stages. The t-test revealed that the Atlantic zoea I and zoea II were significant larger than the Taiwanese larvae at the level P <0.001. Nevertheless, there is no notable difference in their morphology.

Morphological description

First Zoea (Fig.1a–j); NE Atlantic: CL = 0.56 ± 0.01 mm (n = 10); Taiwan: CL = 0.47 ± 0.02 mm (n = 10).

Cephalothorax (Figs. 1a, a', b). Flattened; anterior and posterior dorsomedian tubercles present; rostrum smooth, slender, pointed downward and slightly shorter than antennular peduncle length; 1 pterygostomian spine, 3 spines along anteroventral margin; compound and sessile eyes.

Antennule (Fig. 1c). Peduncle unsegmented, slender, bearing 1 small tubercle; endopod as long plumose seta; exopod unsegmented with 1 short plumose seta, 1 spatulate setae and 3 aesthetascs distally.

Antenna (Fig. 1d). Peduncle unsegmented, with 1 spiniform seta distally; endopod unsegmented, with 1 slender spiniform seta and 1 long plumose seta; exopod broad and distally 6-segmented with 11 marginal plumose setae, 1 simple distolateral seta.

Mandible. Palp absent; incisor process with *lacinia mobilis* and strong armature; molar process with small denticles.

Maxillule (Fig. 1f). Coxal endite with 1 simple seta, 5 plumodenticulate setae, 1 plumose seta and microtrichias; basial endite with 2 plumodenticulate cuspidate setae, 2 plumodenticulate setae, 1 simple seta and microtrichias; endopod unsegmented with 6 setae forming 3 subgroups: basal group with 1 simple, 1 sparsely and 1 sparsely hardly plumose setae; following group with 1 sparsely and 1 sparsely hardly plumose setae; distal group with 1 slender sparsely seta. Exopod absent.

Maxilla (Fig. 1e). Coxal endite bilobed with 9 plumose setae and 1 sparsely, 1 laterally plumose plus 2 plumose setae; basial endite bilobed with 3 sparsely plus 1 laterally plumose setae in each; endopod unsegmented and tetralobed, first lobe with 2 sparsely plus 1 sparsely hardly plumose setae, second lobe with 1 sparsely and 1 sparsely hardly plumose setae, third lobe with 1 sparsely hardly plumose seta, fourth lobe with 2 sparsely hardly plumose plus 1 sparsely setae and microtrichias; exopod with 5 long plumose marginal setae and microtrichias.

First maxilliped (Fig. 1g). Coxa with 1 plumose, 1 sparsely hardly plumose, and 1 sparsely plus 1 sparsely hardly plumose setae; basis with 12 setae forming 4 groups (one group with 2 sparsely hardly plumose plus 1 sparsely setae, three groups with 3 sparsely plumose setae); endopod not extending beyond middle of exopod, 4-segmented, with 3,1,2 sparsely plumose setae and with 1 simple plus 3 serrulate setae. Exopod unsegmented bearing 1 subterminal plus 3 terminal plumose natatory setae.

Second maxilliped (Fig. 1h). Coxa without seta; basis with 1+3+3 sparsely plumose setae; endopod 4-segmented with 3 sparsely plumose setae, 1 sparsely plumose seta, 1 sparsely plumose plus 1 serrulate setae, and in the distal segment with 1 simple plus 4 serrulate setae; exopod unsegmented with 2 subterminal plus 3 terminal plumose natatory setae.

Third maxilliped (Fig. 1i). Coxa without seta; basis with 1+1+2 sparsely plumose setae; endopod 4-segmented, as long as exopod and with 2 sparsely plumose setae and 1 small tubercle,1 sparsely plumose seta, 2 serrulate setae and 1 simple plus 3 serrulate setae; exopod unsegmented with 2 subterminal plus 3 terminal plumose natatory setae.

Pereiopods. Absent.

Abdomen (Figs. 1a, j). Five somites without spines or setae. Anteroventral margin of pleura of the first somite slightly bent outward.

Pleopods. Absent.

Uropods. Absent.

Telson (Fig. 1j). Triangular, broad posteriorly, with 7+7 setae (inner 5 plumoserrulate, outer 2 laterally plumose setae). A row of spinules on the distal margin and around the base of setae.

Second Zoea (Figs. 2a–j); NE Atlantic: CL = 0.76 ± 0.03 mm (n = 10); Taiwan: CL = 0.57 ± 0.02 mm (n = 10).

Cephalothorax (Figs. 2a, b). Eyes stalked, funnel-shape type; rostrum shorter, as long as frontal lobe; with 1 pair of supraorbital spines, 1 pair of pterygostomial spines followed by 3 spines along anteroventral margin.

Antennule (Fig. 2c). Peduncle unsegmented with 2 small tubercles; endopod and exopod unchanged.

Antenna (Fig. 2d). Unchanged.

Mandible. Unchanged.

Maxillule (Fig. 2f). Unchanged.

Maxilla (Fig. 2e). Unchanged.

First maxilliped (Fig. 2g). Exopod unsegmented bearing 1 subterminal plus 4 terminal plumose natatory setae; other unchanged.

Second maxilliped (Fig. 2h). Coxa and basis without changes; endopod 5-segmented with 11 setae (3,1,0,2,1+4); exopod unsegmented with 2 subterminal plus 4 terminal plumose natatory setae.

Third maxilliped (Fig. 2i). Coxa and basis unchanged; endopod 5-segmented with 2,1,0,2,1+3 setae; exopod with 2 subterminal plus 4 terminal plumose natatory setae.

Pereiopods. Absent.

Abdomen. Unchanged.

Pleopods. Absent.

Uropods. Absent.

Telson (Fig. 2j). Triangular, with 8+8 setae (inner 6 plumoserrulate, outer 2 laterally plumose setae).

Third Zoea (Figs. 3 a–k); NE Atlantic: no larvae available; Taiwan: CL = 0.614 ± 0.04 mm (n = 5).

Cephalothorax (Figs. 3a, b). Rostrum shorter but still longer than frontal lobe; other unchanged.

Antennule (Fig. 3c). Biramous. Peduncle 2-segmented: proximal segment with 1 medial plumose seta plus 4 terminal plumose setae (1 long and 3 short); distal segment with 4 plumose setae (2 long and 2 short) plus other 4 plumose setae distributed over the margin of a small process. Endopod bud with a long plumose seta. Exopod with 1 plumose seta plus 4 aesthetascs plus 1 spiniform seta.

Antenna (Fig. 3d). Peduncle unchanged. Endopod unsegmented with 1 spiniform plus 1 simple setae. Exopod 4-segmented with 11 marginal plumose setae and 1 simple seta on apex.

Mandible (Fig. 3e). Unchanged.

Maxillule (Fig. 3f). Coxal endite unchanged; basial endite with 4 plumodenticulate cuspidate setae plus 3 sparsely plumose setae; endopod unchanged.

Maxilla (Fig. 3g). Coxal endite bilobed, with 10 plumose setae, and 1 sparsely, 1 laterally plumose plus 2 plumose setae; basial endite unchanged; endopod unchanged; exopod with 7 long plumose setae and microtrichias.
First maxilliped (Fig. 3h). Unchanged.

Second maxilliped (Fig. 3i). Coxa and basis unchanged; endopod 5-segmented with 12 setae arranged as 3,1,0,2,1+5; exopod unsegmented with 1+2 subterminal plus 4 terminal plumose natatory setae.

Third maxilliped (Fig. 3j). Coxal and basis unchanged; endopod 5-segmented, longer than exopod, with 2,1,1,1+3,1+3 setae; exopod with 2+2 subterminal plus 4 terminal plumose natatory setae.

Pereiopods. First pereiopod (Fig. 3k) as biramous bud; other absent.

Pleopods. Absent.

Abdomen (Fig. 3l). Sixth somite differentiated from telson; otherwise unchanged.

Uropods (Fig. 3l). Biramous, shorter than telson length; endopod rudimentary with 2 plumose setae; exopod well developed with 6 plumose setae.

Telson (Fig. 3l). With 8+8 plumose setae, the outermost pair of setae with a subterminal position.

Forth Zoea (Figs. 4a–l); NE Atlantic: no larvae available; Taiwan: CL = 0.72 ± 0.06 mm (n = 5).

Cephalothorax (Figs. 4a, b, b'). Rostrum smooth, other unchanged.

Antennule (Fig. 4c). Biramous. Peduncle 3-segmented: basal segment with 1 proximal plumose seta, 1 strong spiniform seta and 1 plumose seta plus 1 long and 3 short plumose setae in the distal edge; medial segment with 1 long plumose seta and 4 plumose setae plus 1 long plumose seta; distal segment with 6+5 plumose setae arranged in 2 groups; endopod bud with a long plumose seta; exopod with 2 plumose setae plus 3 aesthetascs.

Antenna (Fig. 4d). Endopod shorter than previous stages with 1 spiniform seta; exopod unsegmented with 12 plumose setae on the inner margin plus 1 plumose seta on the outer margin; other unchanged.

Mandible (Fig. 4e). Unchanged.

Maxillule (Fig. 4f). Coxal endite with 4 plumodenticulate plus 4 sparsely plumose setae; basial endite unchanged; endopod unchanged.

Maxilla (Fig. 4g). Coxal endite unchanged; basial endite bilobed with 5 sparsely plumose setae in each; endopod unchanged; exopod with 8 long plumose setae and microtrichias.

First maxilliped (Fig. 4h). Coxa with 5 plumose setae. Other unchanged.

Second maxilliped (Fig. 4i). Exopod unsegmented with 2+2 subterminal plus 4 terminal plumose natatory setae. Other unchanged.

Third maxilliped (Fig. 4j). Endopod 5-segmented with 2,1,1 sparsely plumose setae,1+4 serrulate setae, and 1 simple + 3 serrulate setae; exopod as long as endopod with 1+2+2+4 plumose natatory setae.

First pereiopod (Fig. 4k). Coxa without seta; basis with 1+1 sparsely plumose setae; endopod 5-segmented with 2,1,2 sparsely plumose setae, 2 serrulate setae, 1 simple plus 1 serrulate plus 1 sparsely plumose setae; exopod unsegmented, as long as endopod, with 2 subterminal and 4 terminal plumose natatory setae.

Second pereiopod (Fig. 4l). Biramous bud.

Third pereiopod. Absent.

Abdomen (Fig. 4m, m'). Presence of anal spine. Other unchanged.

Pleopods. Absent.

Uropods (Fig. 4m). Protopod without seta; endopod well developed with 9 plumose setae; exopod with 10 terminal and 3 subterminal plumose setae plus 1 simple seta on the outer apex.

Telson (Fig. 4m). Almost rectangular shaped; 1 pair of lateral simple setae, on the posterior margin with 5 pairs of plumoserrulate setae plus 2 pairs of outer simple setae.
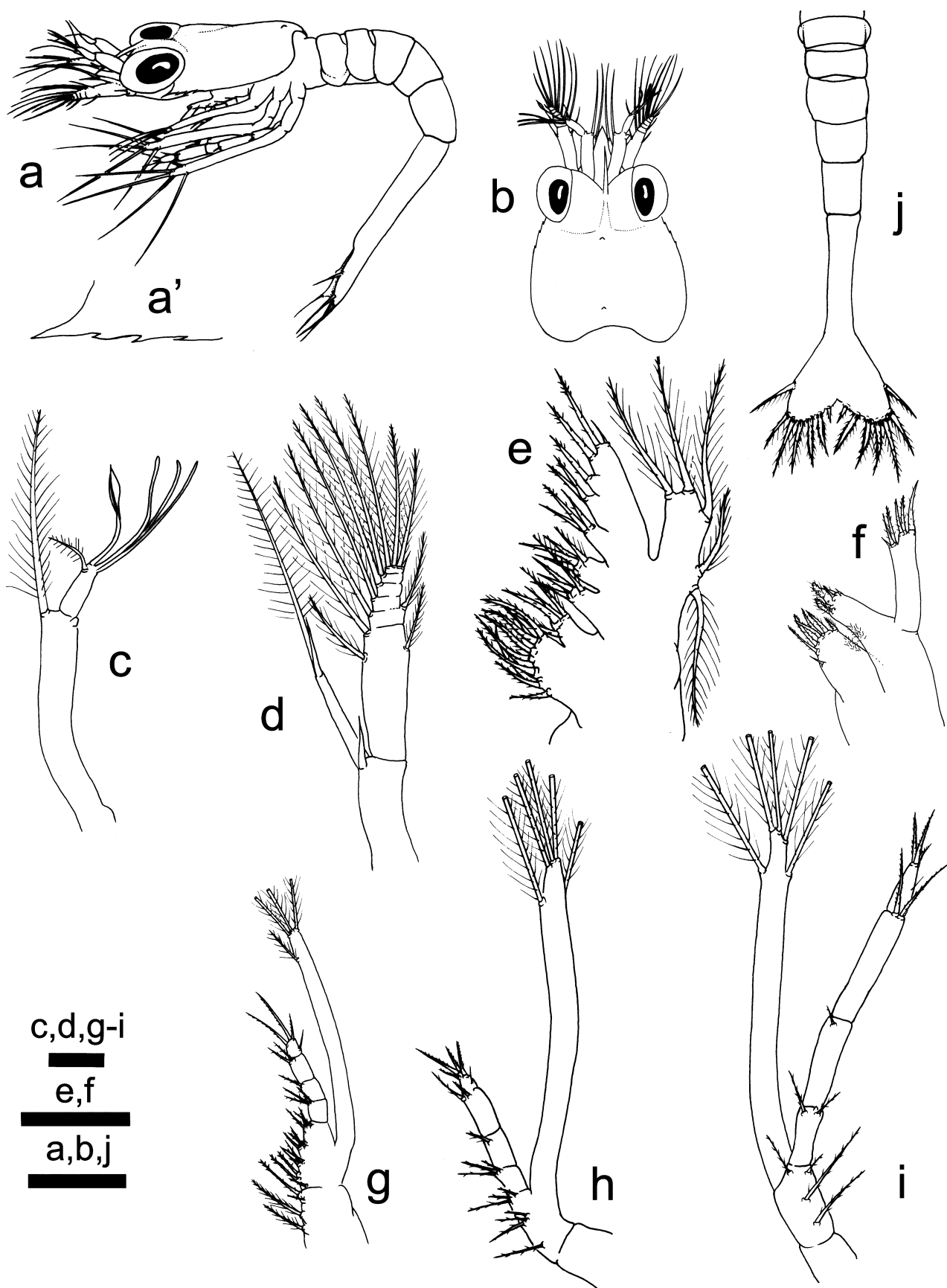
FIGURE 1. *Chlorotocus crassicornis* (A. Costa, 1871). Zoea I, **a** lateral view, whole larva, **a'** detail of anteroventral spines of cephalothorax; **b** dorsal view of cephalothorax; **c** antennule; **d** antenna; **e** maxilla; **f** maxillule; **g** first maxilliped; **h** second maxilliped; **i** third maxilliped; **j** abdomen dorsal view. Scale bars: a,b,j = 500 μm; c–i = 100 μm.
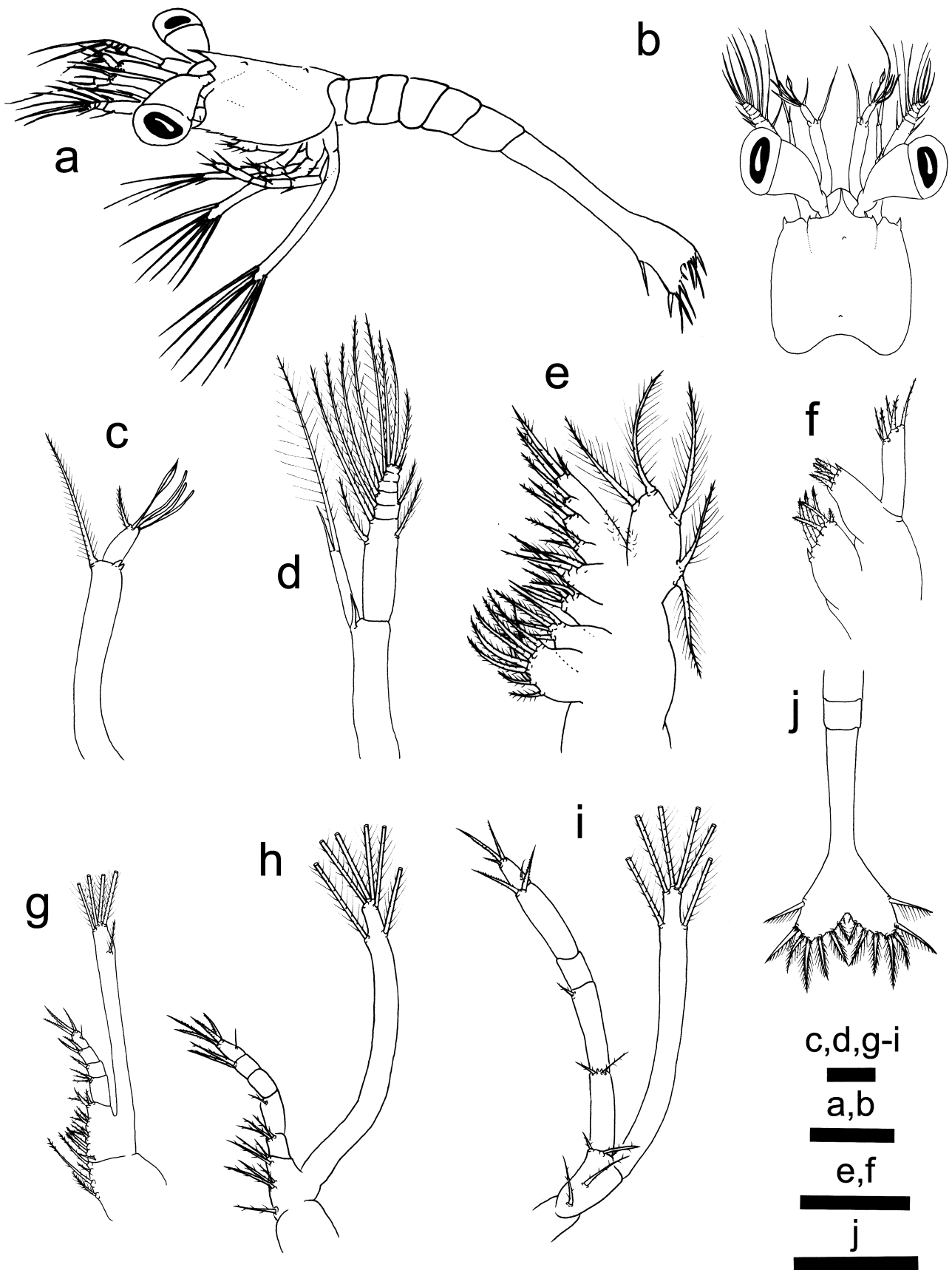
FIGURE 2. *Chlorotocus crassicornis* (A. Costa, 1871). Zoea II, **a** lateral view, whole larva; **b** dorsal view of cephalothorax; **c** antennule; **d** antenna; **e** maxilla; **f** maxillule; **g** first maxilliped; **h** second maxilliped; **i** third maxilliped; **j** telson dorsal view. Scale bars: a,b,j = 500 μm; c–i = 100 μm.
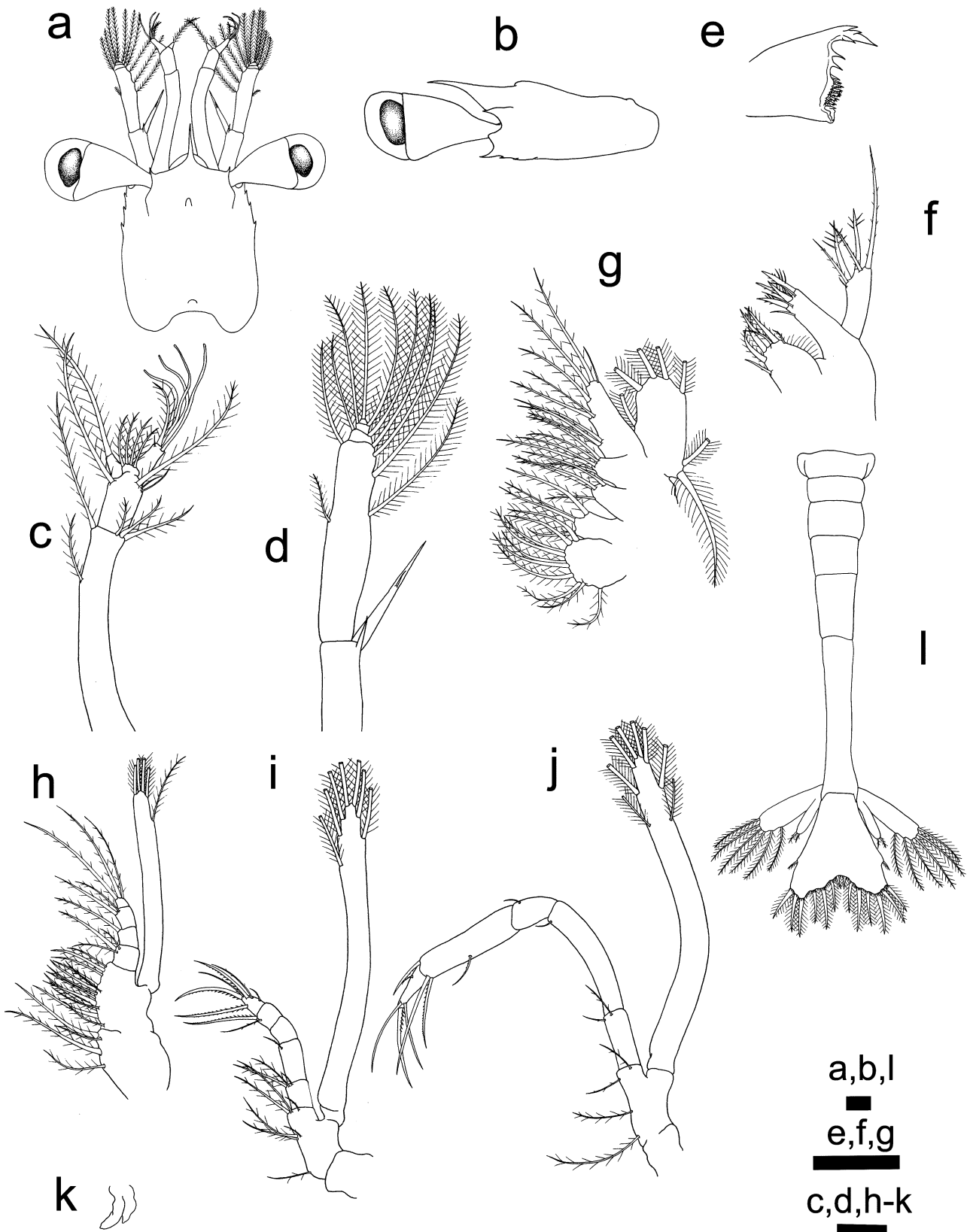
FIGURE 3. *Chlorotocus crassicornis* (A. Costa, 1871). Zoea III, **a** dorsal view of cephalothorax; **b** lateral view of cephalothorax; **c** antennule; **d** antenna; **e** mandible; **f** maxillule; **g** maxilla; **h** first maxilliped; **i** second maxilliped; **j** third maxilliped; **k** first pereiopod; **l** abdomen dorsal view. Scale bars: a,b,l = 500 μm; c–k = 100 μm.
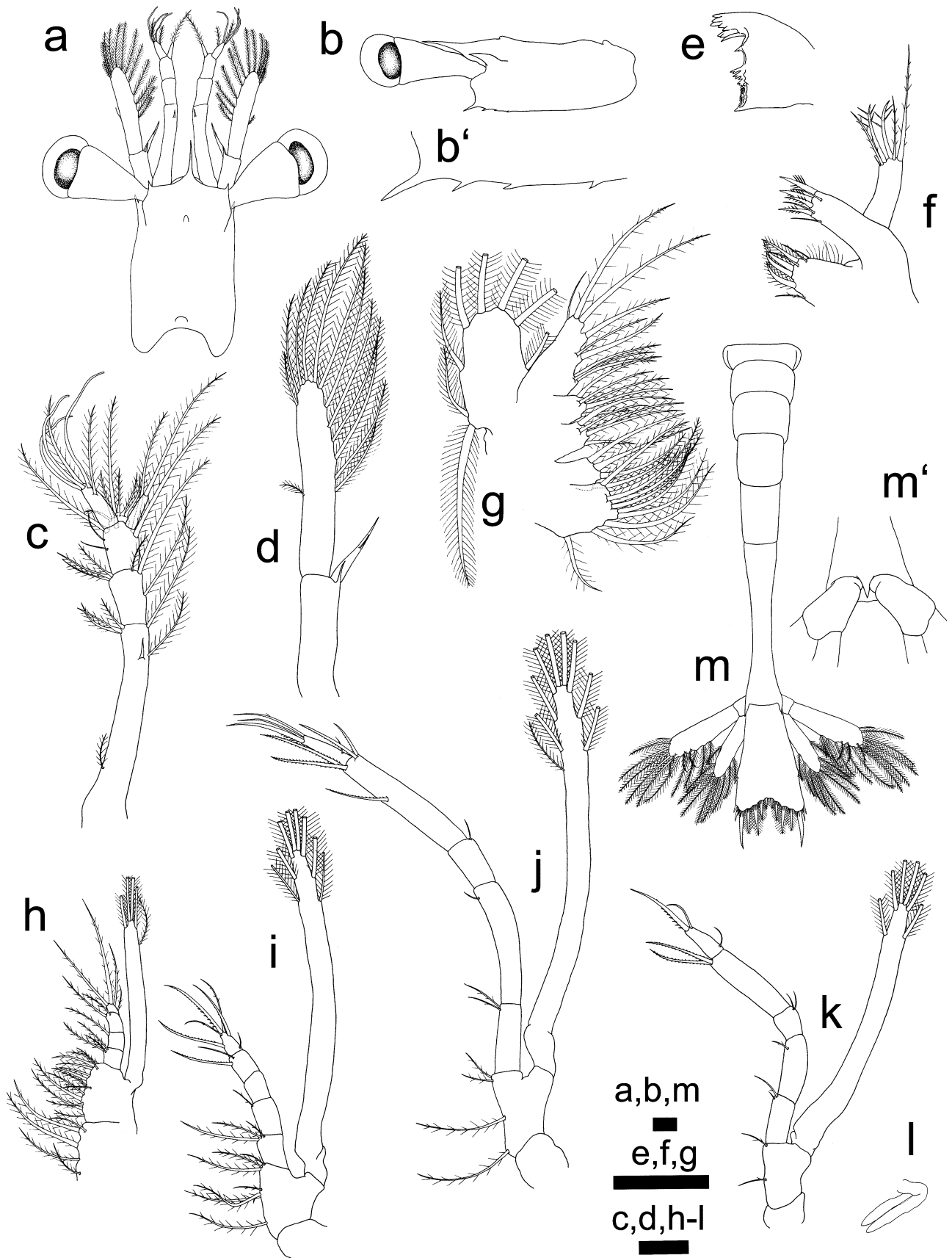
FIGURE 4. *Chlorotocus crassicornis* (A. Costa, 1871). Zoea IV, **a** dorsal view of cephalothorax; **b** lateral view of cephalothorax; **b'** detail of anteroventral spines of cephalothorax; **c** antennule; **d** antenna; **e** mandible; **f** maxillule; **g** maxilla; **h** first maxilliped; **i** second maxilliped; **j** third maxilliped; **k** first pereiopod; **l** second perieopod; **m** abdomen dorsal view; **m'** ventral view of anal spine. Scale bars: a,b,m = 500 µm; c–l = 100 µm.

Discussion

Knowledge of larval development and morphology can provide important insights to understand the phylogenetic relationships amongst decapod crustaceans (Pohle & Marques 2000; Cuesta *et al.* 2010). However, it requires accurate descriptions following current standards and extensive information about the morphology of closed taxa. Although the family Pandalidae has been studied in this sense, there are still many genera with the larval morphology completely unknown. Nevertheless, available information suggests that pandalid zoea can be identified with the following characters: eye peduncle narrowed at base, antennular peduncles strongly concave with bases of antennules separated by more than width of one of them, well developed rostrum in zoea I, supraorbital spines present, and cephalothorax with two dorsal protuberances (Thatje & Bacardit 2000; Landeira *et al.* 2010).

The description of *C. crassicornis* larvae by Heegaard (1969a) agreed with the family characters, but it showed exceptional features that are not present in other pandalid genera. These exceptional features were the presence of two small lateral processes on the first abdominal somite and separation sixth abdominal somite since zoea I. Heegaard (1969a) described the lateral processes like hooks at each side of the somite but these features are not observed in our larvae from Spain and Taiwan. Heegaard (1969a) hypothesized that the function of this lateral process seemed to prevent the cephalotorax from sliding backwards and to lift it a little free of the thorax so that the gills are not crushed. Moreover, this lateral process could provide an open space between the cephalotorax and thorax for the respiratory water in and out the gills. Heegaard (1969a) also mentioned the presence of such structure in the description of Amphionides larvae, reporting the presence of similar processes not only in Amphionides but also in *Solenocera* Lucas, 1849 and *Penaeus* Fabricius, 1798 larvae. In that study Heegaard (1969b, see Figs. 11, 13) described and illustrated the process, explaining that the cuticle of the dorsolateral surface of the first abdominal segment continues as a collar under which the posterior border of the carapace can become inserted and fixed. This is exactly what we observed in our specimens, but it is not like "hooks" nor an exceptional feature since it can be observed in many caridean larvae including other pandalid larvae. It is true that this lateral expansion of the pleura, or the "Heegaard's process", is often overlooked in larval descriptions, probably due to it is slightly hidden under the cephalotorax. In any case, this expansion is unimportant as a diagnostic character to distinguish *C. crassicornis* larvae from other closely related taxa.

Regarding the separation of the sixth abdominal somite since zoea I stage, Heegaard (1969a) considered this morphological character as an abbreviated development feature. This ontogenetic feature is also present in other members of the family with abbreviated development such as *Pandalopsis* and in the species groups of *Pandalus hypsinotus* Brandt 1851 and *Pandalus platyceros* Brandt 1851 (Lee *et al.* 2007). However, our specimens from Spain and Taiwan both did not show this key character. All zoea I and zoea II specimens showed only five abdominal somites. The separation of the sixth somite always occurred in the third zoeal stage, following the typical larval development pattern of most caridean shrimps (dos Santos & González-Gordillo 2004). It is highly likely that Heegaard (1969a) mistakenly interpreted the zoea I morphology by placing the specimens over microscope slides and covered them with a cover slip during observation. This procedure straightens the body of the larvae (which is normally curved, convex) but often resulted in forming wrinkles at the thinner connecting region between the telson and the fifth abdominal somite, generating a false impression of a sixth abdominal somite.

The morphology and setation patterns of the first two zoeal stages of *C. crassicornis* from two geographically very far apart regions in the Atlantic (Spain) and western Pacific (Taiwan) did not show any significant variation. However, morphometrically the zoeae I and II from the Atlantic are larger than those from Taiwan. Size plasticity is a relatively well documented feature in marine invertebrate larvae and seems to be related to temperature (Anger 2001). For example, Marco-Herrero *et al.* (2012) observed size differences between the larvae of *Macropodia rostrata* (Linnaeus, 1761) from UK and Spain, and linked this to a latitudinal gradient of temperature. In our case the warmer temperature regime of Taiwan waters could explain the smaller size of the larvae obtained there. It may need to point out that the size and number of larval stages in pandalid larvae appear also related to the latitudinal distribution of the species, and hence may be controlled by temperature. For example, *Pandalus* and *Pandalopsis* species distributed in higher and colder latitudes produce larger larvae with a more abbreviated development mode than temperate-tropical species like *Plesionika*, *Heterocarpus*, *Stylopandalus* and *Chlorotocus* (Lebour 1940; Lee *et al.* 2007; Landeira *et al.* 2009a, b; Landeira *et al.* 2010; Jiang *et al.* 2014).

Our observations suggest that the development mode of *Chlorotocus crassicornis* resembles those of *Atlantopandalus* Komai, 1999, *Austropandalus* Holthuis, 1952, *Heterocarpus*, *Plesionika*, *Pandalina*, *Dichelopandalus* and *Stylopandalus*, that undergo a normal or extended larval development but not abbreviated. Their early zoeae all have the following characters: mandible without palp, antennal exopod segmented, sixth abdominal somite appeared in zoea III, first pereiopod functional in zoea III or zoea IV (Lebour 1940; Pike & Williamson 1964; Thatje & Bacardit 2000; Landeira *et al.* 2009b; Landeira *et al.* 2010; Jiang *et al.* 2014). The larval descriptions for *Atlantopandalus propinqvus* (Sars 1870), *Pandalina brevirostris* (Rathke 1843), *Dichelopandalus bonnieri* Caullery 1896 and *Stylopandalus richardii* (Coutière 1905) were reported in more than half century ago (Lebour 1940; Pike & Williamson 1964). Although re-descriptions of the larvae of these taxa in modern standards are desirable to understand the setation pattern of their appendages, the available information appears to be enough in determining the distinctive larval characters of these genera. For example, *Dichelopandalus* and *Atlantopandalus* are the only members of the family with a pair of dorsolateral spines at the fifth abdominal somite (Pike & Williamson 1964). The length of the distal spine of the antennal endopod seems to be diagnostic since in *Austropandalus* (Thatje & Bacardit 2000), *Atlantopandalus* (to be confirmed) and *Dichelopandalus* (Pike & Williamson 1964) this spine reaches as far as the tip of the antennal exopod, whereas this spine is smaller in the other genera. Moreover, *Austropandalus* is unique in bearing one exopodal plumose seta in the maxillule (Thatje & Bacardit 2000). The rostrum length has been proposed as a key character in the family (dos Santos & González-Gordillo 2004) but it should be used with caution, because its length tends to decrease significantly as the larvae develop. Generally, *Chlorotocus* (present study), *Heterocarpus* (Landeira *et al.* 2010; Jiang *et al.* 2014), *Plesionika* (Landeira *et al.* 2009a, b) and *Dichelopandalus* (Lebour 1940; Pike & Williamson 1964) have longer rostrum, whereas *Stylopandalus* and specially *Pandalina* have shorter rostrum (Lebour 1940). Dos Santos and González-Gordillo (2004) proposed that the presence of "funnel-shaped eyes" from zoea II can be used to differentiate the larvae of *Plesionika* species from other pandalid larvae. However, in a recent series of our studies, we not only have confirmed this feature in *Plesionika* larvae (Landeira *et al.* 2009a, b) but also found the presence of funnel-shaped eyes in *Heterocarpus* (Landeira *et al.* 2010; Jiang *et al.* 2014) and *Chlorotocus* larvae (present study). Such a funnel-shaped eye may also be present in *Stylopandalus* and *Chlorotocella* but there are doubts on their larval descriptions since their descriptions were based on plankton samples (Gurney 1937; Lebour 1940). For example, Lebour (1940: fig. 8a) clearly illustrated the presence of elongated eyes in the fifth zoeal stage of larvae assigned to *Stylopandalus richardi*. Although the rostrum shape of the decapodid stages described in Lebour (1940) showed that these decapodids are indeed *Stylopandalus richardi*, the exact identities of the earlier larval stages in the same work cannot be certain. Regarding *Chlorotocella*, Gurney (1937) assigned some larvae found in the Red Sea as *Chlorotocella gracilis* Balss 1914. These larvae had very elongated eyes (funnel-shape) and some very distinctive characters such as rostrum small, hump in the third abdominal segment (*Acanthephyra*-like) with a mid-dorsal posterior carina, sixth abdominal somite with one posterior dorsal spine in zoea III.

The present study reveals strong larval affinities amongst *Chlorotocus*, *Heterocarpus* and *Plesionika*, with their larvae almost indistinguishable. Nevertheless, *Chlorotocus crassicornis* and *H. ensifer* A. Milne-Edwards, 1881 show one anal spine from zoea IV, while this spine is absent in *Plesionika*. *Heterocarpus* and *Plesionika* are the most speciose genera of the family, and at present only few of them (namely *Heterocarpus abulbus* Yang, Chan & Chu, 2010, *H. ensifer*, *H. hayashii* Crosnier, 1988, *H. sibogae* De Man, 1917, *Plesionika edwardsii* (Brandt, 1851) and *P. narval* (Fabricius, 1787)) with their larvae (all incomplete) known. Knowledge on the larval development of more panadalid species may contribute to a better understanding on the phylogenetic relationships of these shrimps.

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