Redescription of the larval stages of *Lysmata seticaudata* (Risso, 1816) (Crustacea, Decapoda, Hippolytidae) reared under laboratory conditions

**INTRODUCTION**

Fransen (Fransen, 1991) listed six species of the genus *Lysmata* Risso, 1816 occurring in the North Eastern Atlantic and the Mediterranean Sea: *L. grabhami* (Gordon, 1935), *L. intermedia* (Kingsley, 1878), *L. nilita* Dohrn and Holthuis, 1950, *L. olavoi* Fransen, 1991, *L. seticaudata* (Risso, 1816) and *L. uncinornis* Holthuis and Maurin, 1952. However, Udekem d’Acoz (Udekem d’Acoz, 2000) showed that the record of *L. intermedia* was actually based on the description of some large specimens of *L. seticaudata*, therefore reducing the number of species present in these regions to five. The Mediterranean cleaner shrimp (*L. seticaudata*) is the most common of all these species and has been recorded from the Western part of the English Channel to the Atlantic coast of Morocco, the Azores, Madeira and Canary Islands and the Mediterranean Sea (Udekem d’Acoz, 1999).

Caroli (Caroli, 1918) described the larval stages of the genus *Lysmata* and found that Chun’s *Miersia clavigera* was actually ‘il stadio misidiforme’ of *L. seticaudata*. Although assuming the possible existence of nine larval stages, Caroli was only able to describe in his work eight of those stages. While the first five larval stages were described from larvae hatched and reared in the laboratory, the remaining stages were collected from the plankton in the Bay of Naples. Kurian (Kurian, 1956) observed eight larval stages collected from plankton in the Adriatic Sea that he identified as *L. seticaudata*. The same author speculated the possible existence of nine larval stages, since the third zoeal stage was missing in his samples. Bourdillon-Casanova (Bourdillon-Casanova, 1960) was able to sample from the plankton in the Gulf of Marseille the complete larval series of what she thought to be *L. seticaudata*. Nevertheless, she noticed the existence of some morphological differences between these larvae and those described by Caroli and Kurian. For several years, *L. seticaudata* was assumed to be the only *Lysmata* species present in the Mediterranean Sea. With the description of the closely related species *L. nilita* by Dohrn and Holthuis (Dohrn and Holthuis, 1950), Bourdillon-Casanova recognized that the existing studies would not allow the clear diagnosis of the larvae of these two species. According to Barnich (Barnich, 1996), a definitive identification of the larvae from this genus in plankton samples will only be possible if both species are reared in the laboratory. The need of such study is further increased with the recent record of *L. olavoi* in the Mediterranean Sea (Koukouras and Dounas, 2000), raising to three the number of species of *Lysmata* known for this area.

The knowledge of decapod complete larval development is also of vital importance in the study of phylogenetic relationships (Pohle and Marques, 2000), subspecies differentiation from various geographical areas (Cuesta and Schubart, 1998) and in the understanding of the species ecology (Harms, 1992). This knowledge is also significant in the evaluation of the rearing potential for commercial purposes of decapods (Provenzano, 1985).
In recent years, several decapod species have become highly popular in the marine aquarium trade industry (Fletcher et al., 1995). Among them, the genus *Lysmata* has received special attention, mainly due to its high market prices [e.g. (Fletcher et al., 1995; Zhang et al., 1998a, b)]. However, the inaccuracy of the few existing larval descriptions for the genus, and the lack of knowledge on the larval morphology and development of the majority of *Lysmata* species, are among the bottlenecks impairing the commercial production of these highly priced shrimp.

The purpose of the present work is to describe the complete larval development of *L. seticaudata* according to modern standards and to compare it with previous *L. seticaudata* descriptions and with those of other species within the genus.

**METHOD**

Ovigerous *L. seticaudata* were collected during May 2001 using baited traps at Cape Raso, 30 km west of Lisbon (Portugal), and transported to the nearby laboratory (Laboratório Marítimo da Guia). The females were kept in darkness until hatching in a 180 L tank connected to a larval collector, at a salinity of 35 and a temperature of about 22 ± 1°C with moderate aeration. The most active larvae (the ones displaying pronounced positive phototactic responses) were selected and stocked at a density of about 18 larvae L$^{-1}$ in a 200 L cylindrico-conical recirculating tank (Calado et al., 2003). Sea water was filtered, salinity was maintained at 35 ± 1 and temperature was kept at 22 ± 1°C by a heating/cooling system. The tank was illuminated from above with fluorescent light, with an intensity of 18.5 μmol m$^{-2}$ s$^{-1}$ at the water surface and a photoperiod of 14 h light: 10 h dark. Although the first larval stage is able to moult to the second stage without exogenous feeding (personal observations), all larval stages were fed daily on *Artemia franciscana* (Kellogg, 1906) metanauplii, enriched in Algamac 2000 (Bio Marine) at a density of 5000 metanauplii L$^{-1}$. Ten randomly selected larvae were sampled daily and staged to determine stage duration. The sampled larvae were fixed in 4% formaldehyde.

Drawings and measurements were made with the aid of a *camera lucida* on a binocular Nikon Wild M8. Setal observations and drawings were made using a Zeiss microscope with *camera lucida*. The preparation of slides with appendages was made with Faure’s liquid (Reyne, 1949). Larval description followed the method proposed by Clark et al. (Clark et al., 1998) and setal terminology is according to Ingle (Ingle, 1992) and Garm and Høeg (Garm and Høeg, 2000). The long aesthetascas on the antennules and the long plumose setae on the distal exopod segments are drawn truncated and setules from setae were omitted from drawings when necessary. Measurements taken were distance between tip of rostrum and posterior end of telson (TL), and carapace length from tip of rostrum to posterior margin of carapace (CL). The spent females and complete larval series have been deposited in the Instituto Nacional de Investigação Agrária e das Pescas (IPIMAR) in Lisbon, Portugal (number IPIMAR/H/Ls/06/2002).

**RESULTS**

Nine zoeal and one megalopal stages were recognized. The first larval stage is completely described, while only the main differences of following larval stages are described in detail.

**First zoea (Figure 1)**

Dimension: TL = 3.09–3.24 mm; CL = 0.98–1.03 mm. Carapace (Figure 1a, a1): rostrum slender and pointed, not reaching end of antennular peduncle, eyes compound and sessile; 1 pterigostomial spine, 6 denticles along ventral margin. Antennule (Figure 1b): peduncle unsegmented, bears terminally 1 long plumose seta, and short outer flagellum with 1 plumodenticulate seta and 4 aesthetascas. Antenna (Figure 1c): protopod unsegmented; endopod 1 simple; exopod 3-segmented, bearing 2, 2, 4 plumose setae; basis bilobed with 4 plumose setae each; endopod unsegmented bearing 3 + 2 + 1 + 3 setae; scaphognathite with 5 marginal plumose setae. Mandible (Figure 1d): asymmetrical, palp absent, armature of incisor and molars processes as illustrated. Maxillule (Figure 1e): coxa with 5 strong pappose setae and 2 simple setae, basis with 3 strong serrate setae and 2 simple setae; endopod with 2 strong subterminal setae and 3 strong terminal. Maxilla (Figure 1f): coxa bilobed with 8 + 4 plumose setae, basis bilobed with 4 plumose setae each; endopod unsegmented bearing 3 + 2 + 1 + 3 setae; scaphognathite with 5 marginal plumose setae. First maxilliped (Figure 1g): coxa with 5 plumose setae; basis with 12 plumose setae; endopod 4-segmented with 3, 1, 2, 3 setae; exopod unsegmented, bearing 1 shorter seta subapically on lateral margin and 3 long plumose setae terminally. Second maxilliped (Figure 1h): basis with 2 + 2 plumose setae; endopod 4-segmented with 3, 1, 2, 1 simple plus 5 setae terminally (3 serrate, 1 plumodenticulate and 1 simple); exopod 5-segmented, bearing 2, 2, 4 plumose setae. Third maxilliped (Figure 1i): basis with 3 pappose setae; endopod 4-segmented, with 2 + 1, 0, 2 + 4, 3 pappose setae; exopod 4-segmented, bearing 2, 2, 2, 4 plumose setae.
First pereiopod (Figure 1j): biramous bud.
Second to fourth pereiopods: absent.
Fifth pereiopod (Figure 1k): uniramous bud.
Abdomen (Figure 1l): 5 somites; 2 small dorso-lateral spines on posterior margin of 5th somite.
Pleopods: absent.
Uropod: absent.
Telson (Figure 1m): triangular, broader posteriorly; indented medially with 7 + 7 setae (inner 5 plumose, outer 2 plumose on proximal axis only); minute spines between and around setae.

Second zoea (Figure 2a–g)
Dimension: TL = 3.12–3.22 mm; CL = 0.94–0.96 mm.
Carapace (Figure 2a): eyes stalked with long peduncle; with 1 pair of supraorbital, 1 pair of antennal and 1 pair of pterigostomial spines and 6 denticles on ventral margin.
Antennule (Figure 2b): peduncle 2-segmented, first segment with 4 pappose setae distally, distal segment bears terminally 1 pappose + 1 long plumose setae; flagellum with 4 aesthetascs and 2 plumodenticulate setae.

Antenna (Figure 2c): protopod unsegmented; endopod small conical shaped; scaphocerite 4-segmented, 3 short segments distally, with 13 plumose setae on inner side and 1 plumose seta and 1 simple very small seta on outer side, plus a simple small seta on apex.

Mandible: unchanged.

Maxillule (Figure 2d): coxa with 5 pappose and 2 simple setae; basal endite with 7 strong cuspidate setae; endopod with 2 subterminal and 3 terminal plumodenticulate setae.

Maxilla: scaphognathite with 8 marginal plumose setae; otherwise unchanged.

First maxilliped (Figure 2e): basis with 5 + 11 setae; endopod 4-segmented with 3, 1, 2, 3 setae; exopod bearing 1 shorter seta on outer lateral margin and 4 long plumose setae terminally.
Second maxilliped: unchanged.
Third maxilliped: unchanged.
First pereiopod (Figure 2f): biramous; basis with 1 simple seta; endopod 4-segmented, with 2 + 1, 0, 4, 3 (2 serrate and 1 simple) setae; exopod 4-segmented with 2, 2, 4 plumose setae.
Second to fourth pereiopods: absent.
Fifth pereiopod (Figure 2g): developed, uniramous. Basis bears 1 seta; ischium with 1 simple seta; merus with a small spine-like process; carpus without any seta; propodus flattened and paddle-like enlarged with margins serrated (7 and 9 teeth on each side respectively), bearing 2 setae distally and 1 seta on lateral margin; dactylus small with 2 terminal setae.
Abdomen (Figure 2a): unchanged.
Pleopods: absent.
Uropod: absent.
Telson: 8 + 8 plumose setae, the outer ones on proximal axis only.

Third zoea (Figure 2h–n)
Dimension: TL = 3.15–3.23 mm; CL = 0.96–1.04 mm.
Carapace: unchanged besides size.
Antennule (Figure 2h): peduncle 2-segmented, with 3 small plumose setae proximally, 1 small seta in a more distal position, and 4 distally; distal segment bearing 5 simple setae; inner flagellum bearing a long plumose seta; outer flagellum with 3 aesthetascs and 2 plumodenticulate setae.
Antenna (Figure 2i): scaphocerite 3-segmented, with 13 plumose setae on inner margin, on outer margin 1 strong spine and 1 plumose seta, 1 simple small seta on apex. Otherwise unchanged.
Mandible: unchanged.
Maxillule: unchanged.
Maxilla (Figure 2j): unchanged.
First maxilliped (Figure 2k): endopod 4-segmented with 3, 1, 2, 1 + 3 setae. Otherwise unchanged.
Second maxilliped: basis with 2 + 2 setae; endopod 4-segmented with 3, 1, 2, 1 + 5 setae respectively. Otherwise unchanged.
Third maxilliped (Figure 2k): endopod 4-segmented, with 2 + 1, 1, 2 + 4, 3 pappose setae. Otherwise unchanged.
First pereiopod (Figure 2l): endopod 4-segmented, with 2 + 1, 1 or 2, 2 + 2, 3 setae. Otherwise unchanged.
Second pereiopod (Figure 2m): biramous bud.
Third and fourth pereiopods: absent.
Fifth pereiopod: merus 1 simple seta; carpus with 1 + 2 simple setae; propodus flattened and paddle-like with margins serrated (10 and 12 teeth on each side respectively) bearing 2 setae distally and 1 seta on lateral margin. Otherwise unchanged.
Abdomen: absence of the dorso-lateral spines on posterior margin of 5th somite; abdominal somite 6 separated from telson.
Pleopods: absent.
Uropod (Figure 2n): biramous; exopod well developed reaching the end of telson, with 14 plumose setae; endopod small with 2 plumose setae apically.
Telson (Figure 2n): unchanged.

Fourth zoea (Figure 3)
Dimension: TL = 3.50–3.54 mm; CL = 1.04–1.08 mm.
Carapace (Figure 3a, a1): one spine in front of the dorsal organ; pterigostomial spine followed by 3 denticles on ventral margin. Otherwise unchanged.
Antennule (Figure 3b): peduncle 2-segmented, proximal segment with 3 + 3 + 3 plumose setae, distal segment with 1 small plumose seta; inner flagellum bearing a long plumose and 1 small simple setae; outer flagellum unchanged.
Antenna (Figure 3c): scaphocerite unsegmented; inner margin with 16–17 plumose setae, being the 2nd one a simple seta; outer margin terminates in a spine. Otherwise unchanged.
Mandible: unchanged.
Maxillule (Figure 3d): coxa with 8 setae; endopod with 2 plumodenticulate and 1 small simple setae proximally, and 3 plumodenticulate setae apically. Otherwise unchanged.
Maxilla: coxa with 9 + 4 setae; basis with 4 + 4 setae; scaphognathite with 10–11 plumose setae. Otherwise unchanged.
First maxilliped (Figure 3e): unchanged.
Second maxilliped (Figure 3f): unchanged.
Third maxilliped: exopod 4-segmented with 2 + 2, 2, 2, 4 plumose setae. Otherwise unchanged.
First pereiopod: basis with 1 seta; endopod longer than exopod, 4-segmented, with 2 + 1, 2, 2 + 4, 3 setae; exopod 5-segmented with 2, 2, 2, 2, 4 plumose setae.
Second pereiopod (Figure 3g): basis with 1 seta; endopod 4-segmented with 2 + 1, 0, 4, 3 setae; exopod 3-segmented with 2, 2, 4 plumose setae.
Third and fourth pereiopods: absent.
Fifth pereiopod: merus with 1 simple seta, and a small spine-like process; carpus with 3 simple setae, and a spine-like process; propodus paddle-like with margins serrated (14 and 15 teeth on each side respectively) and bearing 4 setae. Otherwise unchanged.
Abdomen (Figure 3a): unchanged.
Pleopods: absent.
Uropod (Figure 3h): endopod with 10 plumose setae, between the 1st outer seta and the second a small row of microtrichia; exopod longer than telson, with 17 sparsely
plumose setae distributed on the inner and bottom margins, outer margin with 1 spine on apex.

Telson (Figure 3h): almost rectangular shaped; 1 pair of lateral spines, on the posterior end bears 6 pairs of plumose setae and 1 pair of outer spines.

**Fifth zoea (Figure 4a–g)**

Dimension: TL = 3.65–3.77 mm; CL = 1.12–1.19 mm.

Carapace: pterigostomial spine followed by 2 denticles on ventral margin. Otherwise unchanged.

Antennule (Figure 4a): peduncle 2-segmented; proximal segment with 7 small plumose setae on stylocerite and 1 + 1 + 2 + 3 plumose setae along the segment; distal segment with 4 plumose setae; inner flagellum with 1 plumose and 2 simple setae; outer flagellum 2-segmented bearing 3 aesthetasc, 1 plumose and 1 simple setae on distal segment.

Antenna: protopodal process pointed; scaphocerite bears 17–18 plumose setae, outer margin terminates in a spine.
Mandible (Figure 4b): armature of incisor and molar processes as illustrated.
Maxillule: basis with 8 cuspidate setae. Otherwise unchanged.
Maxilla (Figure 4c): unchanged.
First maxilliped: basis with 3 + 2 + 12 setae. Otherwise unchanged.
Second maxilliped (Figure 4d): unchanged.
Third maxilliped: basis with 3 setae; endopod 4-segmented, with 2 + 1, 1, 1 + 1 + 2 + 4, 3 apical pappose setae; exopod 5-segmented with 2, 2, 2, 2, 4 plumose setae.

First pereiopod: endopod unchanged; exopod 5-segmented with 2 + 2, 2, 2, 2, 4 plumose setae.
Second pereiopod: endopod 4-segmented with 2 + 1, 2, 4, 3 setae; exopod 5-segmented with 2, 2, 2, 2, 4 plumose setae.
Third pereiopod (Figure 4e): biramous bud.
Fourth pereiopod (Figure 4f): biramous bud.
Fifth pereiopod (Figure 4g): propodus margins serrated with 15 and 16 teeth on each side respectively and bearing 8 setae. Otherwise unchanged.
Abdomen: unchanged.
Pleopods: absent.

Fig. 4. *Lysmata seticaudata*. Fifth zoea: (a) antennule; (b) mandibles; (c) maxilla; (d) second maxilliped; (e) third pereiopod; (f) fourth pereiopod; (g) propodus of fifth pereiopod. Sixth zoea: (h) lateral view; (i) antenna; (j) maxillule; (k) third maxilliped; (l) third pereiopod; (m) fourth pereiopod; (n) telson and uropod. Scale bars: 100 μm (a–g, i–j); 1000 μm (h, k–m).
Uropod: longer than telson, endopod with 4 simple setae on the proximal outer margin, and 15 sparsely plumose setae on the other margin; exopod with 1 simple seta on outer margin, 20 sparsely plumose setae on inner and bottom margins and 1 spine on apex.

**Telson:** margins laterally parallel, slightly narrower posteriorly.

**Sixth zoea (Figure 4h–n)**

**Dimension:** TL = 4.41–4.52 mm; CL = 1.40–1.45 mm.

**Carapace (Figure 4h):** ventral margin of carapace with 1–2 denticles. Otherwise unchanged.

**Antennule:** peduncle 2-segmented; proximal segment with 7 small plumose setae on stylocerite, 5 plumose setae on inner margin, 2 on outer margin and 3 distally; distal segment with 4 plumose setae; inner flagellum 2-segmented, distal segment with 1 plumose and 2 simple setae. Otherwise unchanged.

**Antenna (Figure 4i):** protopodal process bigger than the previous stage; scaphocerite with 20 plumose setae.

**Mandibles:** unchanged.

**Maxillule (Figure 4j):** coxa with 5 plumodenticulate and 4 simple setae; basis with 9 strong cuspidate setae. Otherwise unchanged.

**Maxilla:** scaphognathite with 12 plumose setae. Otherwise unchanged.

**First maxilliped:** basis with 3 + 2 + 13 setae. Otherwise unchanged.

**Second maxilliped:** unchanged.

**Third maxilliped (Figure 4k):** basis with 3 setae; endopod 4-segmented, with 2 + 1, 1 + 1 + 1 + 2 + 4, 3 apical pappose setae; exopod 5-segmented with 2 + 2, 2, 2, 2, 4 plumose setae.

**First pereiopod (Figure 4l):** basis with 1 seta; endopod 4-segmented, with 2 + 2, 3, 1 + 2 + 4, 3 setae; exopod 4-segmented with 2, 2, 2, 4 plumose setae.

**Second pereiopod:** basis with 1 seta; endopod 4-segmented with 2 + 2, 3, 4, 3 setae; exopod 6-segmented with 2, 2, 2, 2, 2, 4 plumose setae.

**Third pereiopod (Figure 4m):** basis with 1 seta; endopod 4-segmented, with 2 + 1, 3, 1 + 2 + 4, 3 setae; exopod 4-segmented with 2, 2, 2, 4 plumose setae.

**Fourth pereiopod (Figure 4n):** basis with 1 seta; endopod 4-segmented, with 2 + 1, 0, 4, 3 setae; exopod no segmented with 4 plumose setae. Two in ten individuals presented this pair of pereiopods with a biramous bud and a developed normal one.

**Fifth pereiopod:** carpus with 4 simple setae and a spine-like process; propodus margins serrated with 16 and 17 teeth and bearing 8 setae; dactylus small with 3 setae. Otherwise unchanged.

**Abdomen:** unchanged.

**Pleon:** present as small buttons.

**Uropod (Figure 4n):** endopod with 4 simple and 20 sparsely plumose setae; exopod with 4 simple and 23 sparsely plumose setae; otherwise unchanged.

**Telson (Figure 4n):** tapering towards posterior end bears terminally 6 + 6 setae of which the inner 4 pairs are plumose, with 2 pairs of simple setae laterally.

**Seventh zoea (Figure 5)**

**Dimension:** TL = 4.47–4.79 mm; CL = 1.40–1.56 mm.

**Carapace:** ventral margin of carapace without denticles. Otherwise unchanged.

**Antennule (Figure 5a):** peduncle 2-segmented; proximal segment with 8 small plumose setae on stylocerite, 7 plumose setae on inner margin, 3 on outer margin and 3 distally; distal segment with 5 plumose setae; inner flagellum 6-segmented with 0, 0, 1, 2, 1, 1 (plumose) + 2 simple setae; outer flagellum 5-segmented with 2 aesthetascs in 2nd segment, 4 aesthetascs in 3rd, 1 simple seta in 4th and 1 plumose and 2 simple small setae in terminal segment.

**Antenna (Figure 5b):** scaphocerite bears 22 plumose setae; flagellum longer and more slender, 2-segmented, with 2 small simple setae on the distal segment.

**Mandibles:** unchanged.

**Maxillule:** unchanged.

**Maxilla (Figure 5c):** basis with 5 + 5 setae; scaphognathite with 18 plumose setae. Otherwise unchanged.

**First maxilliped:** basis with 3 + 2 + 14 setae. Otherwise unchanged.

**Second maxilliped:** unchanged.

**Third maxilliped:** basis with 3 setae; endopod 4-segmented with 2 + 1, 1 + 1 + 1 + 2 + 4, 3 apical pappose setae; exopod 5-segmented with 2 + 2, 2, 2, 2, 4 plumose setae.

**First pereiopod (Figure 5d):** basis with 1 seta; endopod 4-segmented, with 1, 2 + 1, 3, 1 + 2 + 4, 3 setae; exopod 7-segmented with 2 + 2, 2, 2, 2, 2, 4 plumose setae.

**Second pereiopod:** basis with 1 seta; endopod 4-segmented with 2 + 1, 2 + 3, 4, 3 setae; exopod 7-segmented with 2, 2, 2, 2, 2, 2, 4 plumose setae.

**Third pereiopod (Figure 5e):** basis with 1 seta; endopod 4-segmented, with 2 + 1, 3, 1 + 2 + 4, 3 setae; exopod 7-segmented with 2 + 2, 2, 2, 2, 4 plumose setae.

**Fourth pereiopod (Figure 5f):** basis with 1 seta; endopod 4-segmented with 2 + 1, 0, 4, 3 setae; exopod no segmented with 4 plumose setae.

**Fifth pereiopod (Figure 5g):** propodus with 13 setae and margins serrated with 23–24 and 20 teeth. Otherwise unchanged.

**Abdomen (Figure 5h):** unchanged.

**Pleon:** biramous buds.
Uropod: endopod with 5 simple and 23–24 plumose setae; exopod with 5 simple and 26–27 plumose setae; otherwise unchanged.

Telson (Figure 5i): unchanged.

Eighth zoea (Figure 6a–k)

Dimension: TL = 5.76–6.00 mm; CL = 1.60–1.76 mm.

Carapace (Figure 6a): small spine developed on rostrum. Otherwise unchanged.

Antennule: peduncle 2-segmented; proximal segment with 9 small plumose setae on stylocerite, 9 plumose setae on inner margin, 5 on outer margin and 3 distally; distal segment with 6 plumose setae; inner flagellum 9-segmented with 1 small simple seta in the 2nd, 5th, 7th and 8th segments, and 1 plumose and 2 simple setae in the 9th segment; outer flagellum 7-segmented with 1 simple seta and 2 aesthetascs in the 2nd, 4 aesthetascs in the 3rd, 1 simple seta in the 4th, 2 simple setae in 6th and 1 plumose and 2 simple small setae in 7th segment.

Antenna (Figure 6b): scaphocerite with 23–24 plumose setae; flagellum 8-segmented longer than scaphocerite, with 2 smaller segments proximally, 3rd segment the longer one, with 3 setae, 5 short segments distally, 8th segment with 4 simple setae.

Mandibles: unchanged.

Maxillule: unchanged.
Maxilla: scaphognathite with 21–22 plumose setae. Otherwise unchanged.

First maxilliped: unchanged.

Second maxilliped (Figure 6c): basis with 3 + 2 setae. Otherwise unchanged.

Third maxilliped: endopod 4-segmented, with 2 + 1, 10 + 4, 5 setae. Otherwise unchanged.

First pereiopod: basis with 1 seta; endopod 4-segmented, with 2 + 1, 3, 4 + 4, 7 setae; exopod 9-segmented with 2, 2, 2, 2, 2, 2, 2, 2, 4 plumose setae.

Second pereiopod (Figure 6d): basis with 1 seta; endopod 4-segmented, with 2 + 1, 1 + 3 + 3, 4, 5 setae; exopod 8-segmented with 2, 2, 2, 2, 2, 2, 4 plumose setae.

Third pereiopod: basis with 1 seta; endopod 4-segmented, with 2 + 1, 3, 8 + 4, 5 setae; exopod 7-segmented with 2, 2, 2, 2, 2, 2, 4 plumose setae.

Fourth pereiopod (Figure 6e): basis with 1 seta; endopod 4-segmented, with 2 + 1, 1 + 3, 7 + 4, 4 setae; exopod 4-segmented with 2, 2, 4 plumose setae.
Fifth pereiopod (Figure 6f): carpus with 6 simple setae, and a spine-like process; propodus with 18–19 setae and, 25 and 28 teeth on each margin; dactylus with 5 setae apically. Otherwise unchanged.

Abdomen (Figure 6a): unchanged.

Pleopods (Figure 6g–k): endopod bud-like with 2 simple apical setae; exopod rudimentary.

Uropod: endopod with 6 simple setae on outer margin, microtricha and 26–27 sparsely plumose setae; exopod with 8 simple setae on outer margin, 30–31 sparsely plumose setae on inner and bottom margins and, 2 simple setae dorsally.

Telson: posterior end bears terminally 5 + 5 setae, laterally with 2 + 2 simple setae.

**Ninth zoea (Figure 6l–q)**

**Dimension:** TL = 6.40–6.80 mm; CL = 2.00–2.24 mm.

Carapace (Figure 6l1–6l2): one or two small spines on rostrum.

Antennule (Figure 6m): peduncle 2-segmented, proximal segment with 10 small plumose setae on stylocerite, 9 plumose setae on inner margin, 5 on outer margin and 3 distally; distal segment with 6 plumose setae; inner flagellum composed of 17 segments, each with 1–4 setae on distal margin, arranged as figured, except for the distal segment with 3 simple and 1 plumose setae; outer flagellum composed of 16 segments, each with 0–4 setae on distal margin, arranged as figured, except for the 1st, 2nd, 3rd and 4th segment with 3, 3 + 3, 3 + 3 and 5 aesthetascs respectively, the distal segment with 3 simple and 1 plumose setae.

Antenna: flagellum composed of 22 segments, with 1 setae on 8th and on 19th, 2 setae on 5th, 7th, 9th, 16th, 17th, and on 18th, 3 setae on 3rd and on 12th, 6 setae on the 20th and on 21st, 7 setae on the last segment, being the remaining segments without setae on distal margin; scaphocerite with 28–29 plumose setae.

Mandibles (Figure 6n): armature of incisor and molar processes as illustrated.

Maxillule: coxa with 12 setae; basis with 13–14 strong setae; endopod with 2 strong plumodonticulate and 1 simple setae, and 3 strong plumodonticulate setae.

Maxilla (Figure 6o): coxa with 15 setae; basis with 8 + 8 setae; endopod unsegmented with 3, 2, 1, 3 setae; scaphognathite with 32–33 plumose setae.

First maxilliped (Figure 6p): basis with 3 + 2 + 17–18 setae; endopod 4-segmented with 3, 2, 2, 1 + 3 setae; exopod with 4 long plumose setae terminally and 1 shorter seta subterminally on lateral margin.

Second maxilliped: basis with 3 + 2 setae; endopod 4-segmented with 3, 1, 4, 7–8 setae respectively; exopod 4-segmented with 2, 2, 2, 2, 4 long setae.

Third maxilliped (Figure 6p): basis with 3 setae; endopod 4-segmented, with 8, 4, 21–22, 5 setae; exopod 8-segmented with 2, 2, 2, 2, 2, 2, 4 plumose setae.

First pereiopod (Figure 6q): basis with 3 setae; endopod 4-segmented, with 5–6, 5, 21–22, 14–15 setae, with internal distal margin of propodus produced forward to about one third of dactylus; otherwise unchanged.

Second pereiopod: basis with 1 seta; endopod 4-segmented, with 2 + 1, 15–16, 12, 12 setae; exopod 11-segmented with 2 setae on each, except for the distal one with 4 plumose setae.

Third pereiopod: basis with 3 setae; endopod 4-segmented, with 10, 8–9, 35–36, 11–12 setae; exopod 9-segmented with 2 setae on each, except for the distal one with 4 plumose setae.

Fourth pereiopod: basis with 2 setae; endopod 4-segmented, with 8, 9, 29–30, 9 setae; exopod 7-segmented with 2, 2, 2, 2, 2, 4 plumose setae.

Fifth pereiopod: basis, ischium and merus unchanged; carpus with 6 simple setae, and a spine-like process; propodus bearing 18–19 setae, 28 spines laterally towards dactylus on one side, 25 on the other side; dactylus with 5 setae apically.

Abdomen: unchanged.

Pleopods (Figure 6r–s): endopods with 13, 16, 19, 16, 12 spines; exopods with 6, 9, 10, 5, 3 spines; small appendix interna present from second to fifth endopod of pleopods.

Uropod: endopod with 7–8 simple setae proximally on outer margin and 34–35 sparsely plumose setae; exopod with 17–18 simple setae on outer margin, 37–38 sparsely plumose setae on inner and bottom margin and 3 simple setae dorsally and 1 spine on apex.

Telson: rather triangular, narrower distally than proximally. Otherwise unchanged.

**Megalopa (Figures 7–8)**

**Dimension:** TL = 6.24–6.80 mm; CL = 2.32–2.56 mm.

Carapace (Figure 7a): smooth; without supra-orbital spines, with antennal and pterigostomial spines; rostrum narrow, shorter than the antennular peduncle, with 5 dorsal teeth; 1 ventral tooth close to the rostrum apex.

Antennule (Figure 7b): peduncle 3-segmented, stylocerite with 6 setae, proximal segment with 6 plumose setae on inner margin, 4 setae on outer margin, 6 plumose setae and 2 spines on distal margin; 2nd segment with 1 seta on outer margin, 3 plumose setae and 2 spines on distal margin; 3rd segment with 1 plumose setae on outer margin, 8 plumose setae and 2 spines on distal margin; outer flagellum composed of 38–44 segments, with 3 aesthetascs on the 2nd, 3 + 3 on 3rd–5th, and 4 on the 6th segments; inner flagellum with 52–57 segments.
Antenna (Figure 7c): scaphocerite with 32–33 plumose setae; flagellum composed of 90–92 segments, 3rd segment being the longer.

Mandibles (Figure 7d): palp absent; armature of incisor and molar processes as illustrated.

Maxillule (Figure 7e): coxa with 15 setae; basis with 21–23 setae; endopod unilobed, with 2 simple setae on distal margin.

Maxilla (Figure 7f): coxa with 9–10 setae, basis bilobed, with 11–13 and 12 simple setae, respectively; endopod with one subterminal and one terminal seta; scaphognathite with 42–43 plumose setae.

First maxilliped (Figure 7g): coxal with 4 setae; basis with 21–24 setae; endopod with 3 feeble segments, with 3, 3, 3 setae; exopod with 7–10 plumose setae on proximolateral margin and 3 lateral and 4 terminal setae on peduncle distal margin.

Second maxilliped (Figure 7h): basis with 12–13 setae; endopod 4-segmented with 2, 1, 10–12, 32–36 setae, respectively; exopod 4-segmented with 2, 2, 2, 4 setae.

Third maxilliped (Figure 7i): basis with 6–7 setae; endopod 3-segmented, proximal segment with 30–31 setae and 1 spine, median segment with 23–24 setae and distal segment with 110–115 setae distributed in 8 rows, as...
figured, and 5 large conical teeth; exopod unsegmented without setae.

First pereiopod (Figure 8a, 8a1, 8a2): all segments well differentiated and setose as figured; propodus with a stout distal spine and dactylus with one tooth, forming a chela; exopod reduced and unsegmented.

Second pereiopod (Figure 8b, 8b1): all segments well differentiated and setose as figured; carpus with developing segments visible beneath exoskeleton; propodus forming the chela with 2 stout teeth.

Third to fifth pereiopods (Figure 8c–e): all segments well differentiated and setose as figured, propodus not chelate. Third and fourth pereiopods with exopod reduced and unsegmented.

Abdomen (Figure 7a): 5 somites and a rectangular telson; each somite with well developed pleopods.

Pleopods (Figure 8f–h): well developed, biramous, endopod with 3 setae on 1st pleopod and 15–18 sparsely setae on 2nd to 5th pleopods; exopod with 15–17 setae on 1st pleopod and 19–21 sparsely setae on 2nd to 5th pleopods; epipodite on 2nd to 5th pleopods with 3–5 cincinilli.

Uropod: endopod with 39–43 plumose and 7–8 simple setae marginally and 11–14 setae dorsally; exopod with
3 spines, 68–71 plumose setae marginally and 35–37 simple setae sub-marginally.

The first zoal stage collected by Kurian (Kurian, 1956) from plankton samples differs greatly from the present work, particularly on the development of the antennule and pereiopods and in the size of the early larval stages. The first zoal stage collected by Kurian is larger than the first and second zoal stages of the present work, while the fourth stage recorded by us is larger than those described by Kurian. The first zoal stage collected by Kurian already displays the two first pereiopods segmented, while on the present study the 2nd pereiopod of the first larval stage is absent. The segmentation and setation of the antennule and scaphocerite of early larval stages illustrated by Kurian also differs from those recorded in the present study (e.g. zoal I scaphocerite is 6-segmented). Such differences seem to indicate that Kurian was dealing with a collected larval series that cannot be allocated to L. seticaudata. The larvae assigned to L. seticaudata by Bourdillon-Casanova (Bourdillon-Casanova, 1960) also display considerable differences with the present ones. The most striking difference of the larvae described by Bourdillon-Casanova is the presence of one to three additional dorsal spines in the 5th abdominal somite of early zoal stages. The sequence of pereiopod development recorded by Bourdillon-Casanova also shows significant differences (e.g. the 4th zoal stage has all the pereiopods present and functional with the exception of the 4th, which appears as a biramous bud). Due to all these differences, we are forced to conclude that the larval series described by Bourdillon-Casanova cannot be assigned to L. seticaudata.

The differences recorded between the larvae described in the present study and those of Kurian and Bourdillon-Casanova seem to indicate that these authors may have collected in their plankton samples the larval stages of L. nilia and/or L. olavi. Additionally, since some Lysmata species are known to occur at considerable depth (e.g. L. stenolepis was recorded by Crosnier and Forest (Crosnier and Forest, 1973) in the Cape Verde Islands at 150–275 m; L. olavi was recorded by Fransen (Fransen, 1991) in the Azores at 360 m), the occurrence of unrecorded species in the studied area should not be overlooked.

The complete larval series currently available for comparison is that of L. wurdemanni (Gibbes, 1850) reared in the laboratory by Kurata (Kurata, 1970) and L. ensirostris (Kemp, 1914) cultured by Pillai (Pillai, 1974). Additionally, the early zoal stages of L. anchistus Chace, 1972 and L. ambienensis (De Man, 1888) are known from larvae hatched from the egg (see Knowlton and Alavi (Knowlton and Alavi, 1995) and Wunsch (Wunsch, 1996), respectively). Table I summarizes and compares some morphological differences of the zoal stages of these species with L. seticaudata larvae. The early larval stages of L. vittata (Stimpson, 1860) described by Pillai (Pillai, 1966) are not considered for comparison since they do not display the morphological characters typically attributed to Lysmata species. Gurney (Gurney, 1937) assigned with reservation the larvae of species RS I and RS II to L. multiscisa (Nobili, 1904) and L. tristiseta (Heller, 1861), respectively. However, since these larvae were collected from the plankton and a positive diagnosis of the species is not possible, they will not be used for comparison.

As it can be seen in Table I, newly hatched L. seticaudata larvae are larger in size when compared with the other species. Although, when larvae reach the fifth zoal stage, L. wurdemanni, L. ensirostris and L. anchistus are similar in size to L. seticaudata. When they reach the last zoal stages, L. ambienensis and L. ensirostris larvae are much larger in size than those of L. seticaudata and L. wurdemanni, probably a consequence of mark-time molting (see (Gore, 1985)). The first zoal stage of L. seticaudata differs from all other known first larval stages in the genus in the early development of pereiopods 1 and 5. In L. seticaudata the 5th pereiopod is functional in the second zoal stage, while only in the fourth stage is the 5th pereiopod functional for all other Lysmata species for which the larval sequence is known, with the exception of L. anchistus presenting the 5th pereiopod functional in the fifth larval stage. On the sixth zoal stage all pereiopods are functional in L. seticaudata and L. ensirostris larvae, while this only occurs in the seventh and eight zoal
stages of *L. amboinensis* and *L. wurdemanni*, respectively. Pleopod development also occurs in an earlier stage in *L. seticaudata* (sixth zoeal stage) than in the other members of the genus. Despite the observed differences, larval appendage development, namely of pereiopods, does not seem to be precocious in *L. seticaudata*. In *L. wurdemanni* each pereiopod bud only becomes functional after two more larval stages. In *L. amboinensis*, *L. ensirostris* and *L. seticaudata*, the bud of a pereiopod appears in one stage and becomes functional in the next. All *Lysmata* larvae described, with the exception of *L. anchisteus*, present a pair of dorso-lateral spines on the 5th abdominal somite that disappears in the third stage in *L. seticaudata* and *L. amboinensis* and in the fifth and sixth larval stages for *L. ensirostris* and *L. wurdemanni*, respectively. Additionally, the first five zoeas in the larval series of *L. amboinensis* and *L. seticaudata* present marginal denticles on the carapace ventral margin, whereas *L. ensirostris* and *L. wurdemanni* present these same denticles on the first four and six zoeal stages, respectively.

Like other *Lysmata* species whose larvae have already been cultured from the egg, *L. seticaudata*'s last larval stage presents the propodus of the 5th pereiopod expanded, while only *L. amboinensis* larvae differ from other species on having the propodus of the 3rd, 4th and 5th pereiopod pairs expanded.

Similar to the majority of other known larval stages of *Lysmata* species, *L. seticaudata* larvae do not display any spine on the eyestalk. So far, this morphological character has only been recorded in *L. ensirostris* larvae, which display a single spine on the eyestalk.

Even with the present work, only 3 of the 26 species in the genus *Lysmata* have their complete larval series known from laboratory studies. Therefore, further studies are needed in order to establish the general pattern of larval development in the genus. Notwithstanding, the complete

<table>
<thead>
<tr>
<th>Morphological feature</th>
<th><em>L. amboinensis</em>&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>L. anchisteus</em>&lt;sup&gt;b&lt;/sup&gt;</th>
<th><em>L. ensirostris</em>&lt;sup&gt;c&lt;/sup&gt;</th>
<th><em>L. seticaudata</em>&lt;sup&gt;d&lt;/sup&gt;</th>
<th><em>L. wurdemanni</em>&lt;sup&gt;e&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZI, total length (mm)</td>
<td>2.7–2.8</td>
<td>2.2–2.3</td>
<td>1.89–2.23</td>
<td>3.09–3.24</td>
<td>2.7</td>
</tr>
<tr>
<td>ZV, total length (mm)</td>
<td>ND</td>
<td>3.3–3.6</td>
<td>3.68</td>
<td>3.65–3.77</td>
<td>3.8</td>
</tr>
<tr>
<td>Last zoea, total length (mm)</td>
<td>?; 21.8</td>
<td>ND</td>
<td>ZIX: 11.39</td>
<td>ZIX: 6.40–6.80</td>
<td>ZIX: ± 6.0</td>
</tr>
<tr>
<td>Carapace, marginal denticles</td>
<td>Present, not described</td>
<td>Present (ZI–ZIV), not described</td>
<td>Present (ZI–ZIV), not described</td>
<td>Present (ZI–ZIV), not described</td>
<td></td>
</tr>
<tr>
<td>Rostral spines on last stage</td>
<td>≥5</td>
<td>ND</td>
<td>9</td>
<td>1–2</td>
<td>3</td>
</tr>
<tr>
<td>Eyestalk spine</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Antenna, scaphocerite no segments</td>
<td>ZI:5; ZII:4; ZIII:3</td>
<td>ZI:5; ZII:5; ZIII:4; ZIV:3</td>
<td>ZI:3</td>
<td>ZII:3</td>
<td>ZIII:3</td>
</tr>
<tr>
<td>Antennal endopod as long as scale</td>
<td>ND</td>
<td>ND</td>
<td>ZVIII</td>
<td>ZVII</td>
<td>ZX</td>
</tr>
<tr>
<td>1st pereiopod: bud, functional</td>
<td>ZII, ZIII</td>
<td>ZII, ZIV</td>
<td>ZII, ZIII</td>
<td>ZII, ZIII</td>
<td>ZII, ZIII</td>
</tr>
<tr>
<td>2nd pereiopod: bud, functional</td>
<td>ZIV, ZV</td>
<td>ZV, ?</td>
<td>ZIII, ZIV</td>
<td>ZIII, ZIV</td>
<td>ZIV–ZVI</td>
</tr>
<tr>
<td>3rd pereiopod: bud, functional</td>
<td>ZV, ZVI</td>
<td>?,?</td>
<td>ZIV, ZV</td>
<td>ZV, ZVI</td>
<td>ZV, ZVII</td>
</tr>
<tr>
<td>4th pereiopod: bud, functional</td>
<td>ZVI, ZVII</td>
<td>ND</td>
<td>ZV, ZVI</td>
<td>ZV, ZVI</td>
<td>ZVI, ZVIII</td>
</tr>
<tr>
<td>5th pereiopod: bud, functional</td>
<td>ZIII, ZIV</td>
<td>ZIV, ZV</td>
<td>ZIII, ZIV</td>
<td>ZII, ZIV</td>
<td>ZII, ZIV</td>
</tr>
<tr>
<td>Last stage pereiopods with expanded propodus</td>
<td>P3–P5</td>
<td>ND</td>
<td>P5</td>
<td>P5</td>
<td>P5</td>
</tr>
<tr>
<td>5th abdominal somite, dorso-lateral spines</td>
<td>ZI–ZII</td>
<td>ND</td>
<td>ZI–ZIV</td>
<td>ZI–ZII</td>
<td>ZI–ZV</td>
</tr>
<tr>
<td>Pleopod buds</td>
<td>≥ZVII</td>
<td>ZIX ?, ZIX</td>
<td>ZVII</td>
<td>ZVI</td>
<td>ZIX</td>
</tr>
</tbody>
</table>

ND, not described; *a*Wunsch, 1996; *b*Knowlton and Alavi, 1995; *c*Pillai, 1974; *d*Present study; *e*Kurata, 1970.
diagnosis of all forms of the composite larval genus *Eretmomaris* and the understanding of the taxonomic significance of intriguing morphological features such as the paddle-shaped pereiopods’ propodus in a distinct genus such as *Lysmata* (Gurney, 1937, 1942), *Cardion* (Lebour, 1930) and the unidentified larval forms *Eretmomaris dolichops* and *Eretmomaris* × (Gurney and Lebour, 1941) are still a way off being accomplished.

**ACKNOWLEDGEMENTS**

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