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MORPHOLOGICAL DESCRIPTIONS OF LABORATORY REARED LARVAE AND POST-LARVAE OF THE AUSTRALIAN SHOVEL-NOSED LOBSTER *THENUS AUSTRALIENSIS* BURTON AND DAVIE, 2007 (DECAPODA, SCYLLARIDAE)

BY

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Running head: LARVAL DEVELOPMENT OF *THENUS AUSTRALIENSIS*

Abstract

Complete larval development from newly hatched larvae up to the juvenile stage was successfully achieved in the Australian shovel-nosed lobster *Thenus australiensis* under laboratory conditions. The larvae of this species passed through four phyllosoma Stages (each Stage has a single instar), and developed into the first juvenile stage via a post-larval, nisto stage. The shortest and mean durations from hatching to metamorphosis at a water temperature of 25 °C were 32 and 38 days, respectively. Morphologies of body and appendages for all four phyllosoma Stages and the nisto stage were described. The phyllosomas were fed exclusively on the jellyfish *Aurelia aurita* throughout their culture. Our results indicate that jellyfish may be a viable diet for *T. australiensis* phyllosoma in culture and may therefore be useful for commercial-scale lobster production.

INTRODUCTION

Lobsters in the genus *Thenus* Leach, 1815 belonging to the family Scyllaridae are commonly known as shovel-nosed lobsters, bay bugs, bay lobsters or reef bugs. Only a single species, *T. orientalis*, had been recognised in the genus *Thenus*, but this genus was revised by Burton & Davie (2007) and five species, *Thenus australiensis* Burton & Davie, 2007, *Thenus indicus* Leach, 1815, *Thenus orientalis* (Lund, 1793), *Thenus parindicus* Burton & Davie, 2007 and *Thenus unimaculatus* Burton & Davie, 2007 are currently valid. They are widely distributed along the tropical and subtropical coasts of the Indo-West Pacific regions (Burton & Davie, 2007) and have been exploited as commercially important seafood bycatch, particularly in Australia, India and Southeast Asian countries (Jones, 2007; Vijayakumaran & Radhakrishnan, 2011). Catches of shovel-nosed lobsters in Australia have ranged from 324 to 893 t in the last two and half decades (Zeller et al., 2014). In the Great Barrier Reef Marine Park (GBRMP), Queensland, where harvesting pressure is the greatest in Australia, about 300 t of *T. australiensis* and 100 to 200 t of *T. parindicus* are caught annually (Pears et al., 2012). The stock status of these lobsters in GBRMP has been assessed as sustainable on the basis of evidence of permanent biomass protection, retention of berried females, and reliance on minimum size restriction (Zeller et al., 2014). On the other hand, in Asian countries, there is a concern about the collapse of shovel-nosed lobster stocks due to overfishing (Radhakrishnan et al., 2007; Iamsuwansuk et al., 2012). The natural populations of the shovel-nosed lobsters have dramatically declined, for example in Mumbai, India, from 250 to 375 t in the 1980's to 2.2 t in 1994 (Radhakrishnan et al., 2005; Vijayakumaran & Radhakrishnan, 2011). To meet the increasing demand, resource management and aquaculture techniques for these lobsters are urgently required.

The life history of scyllarid lobsters is similar to palinurid lobsters. The larvae, called phyllosomas, hatch from eggs attached externally to the female abdomen. They develop through a series of instars. Scientists categorise the instars into groups according to

major changes in structure. These are called Stages. The Stages are indicated with a capital letter to indicate that they are artificial delineations in a continuous series of development. A nisto stage metamorphoses from the final Stage of larval development. The comparable stage in palinurid lobster development is a puerulus stage. Both the nisto and puerulus are post-larval stages. The nisto and/or puerulus stages are unique to these two crustacean groups. After the nisto or puerulus stage they moult into the first juvenile stage and grow through successive juvenile stages to become adult lobsters (Phillips & Sastry, 1980; Mikami & Kuballa, 2007).

In the genus *Thenus*, development from newly hatched phyllosoma to juvenile in culture was first described in *T. orientalis* and *Thenus* sp. obtained from Hervey Bay in Queensland and off Cairns, Australia, respectively (Mikami & Greenwood, 1997). However, *T. orientalis* is not regarded as occurring in Australia (Burton & Davie, 2007; Zeller et al., 2014). Mikami & Greenwood's *T. orientalis* and *Thenus* sp. may be either *T. australiensis* or *T. parindicus*. The larval development of these two species needs to be re-examined to avoid further confusion. Except for *Thenus* spp. in Australia, the only other larval development which has been described is *T. unimaculatus* caught on the coast of Chennai, India (Kizhakudan & Krishnamoorthi, 2014).

The aim of this study was to describe the entire process of larval development of the Australian shovel-nosed lobster, *T. australiensis*. Jellyfish were used as the only diet for the phyllosomas in this study as scyllarid phyllosomas have been observed associating with gelatinous zooplankton both in the wild (Shojima, 1963, 1973; Thomas, 1963; Herrnkind et al., 1976; Phillips & Sastry, 1980; Barnett et al., 1986; Ates et al., 2007) and in the laboratory (Wakabayashi et al., 2012a, b, 2016, Kizhakudan & Krishnamoorthi, 2014). In this paper, Mikami & Greenwood's *T. orientalis* and *Thenus* sp. is named as *Thenus* sp.1 and *Thenus* sp.2, respectively, to avoid confusion.

MATERIALS AND METHODS

Brood stock of *T. australiensis*

Thirteen individual ovigerous female lobsters were caught in Shark Bay, Western Australia by the Department of Fisheries in Western Australia (DoFWA) during November 2014. The lobsters were identified as *Thenus australiensis* Burton & Davie, 2007 based on dark brown spotting on the pereiopods (fig. 1). The female lobsters were shipped to the laboratory in the DoFWA, Hillarys, Western Australia on 24 November, 2014. Meanwhile, they were kept in a stone tank with running ocean water taken from the Hillarys marina. Five, two and then six of the female lobsters were transferred to the Curtin Aquatic Research Laboratory (CARL) in Curtin University, Bentley, Western Australia on 25 November, 2 and 10 December, 2014, respectively.

A recirculating tank system consisting of two polycarbonate tanks was designed for the incubation of these ovigerous lobsters. The upper tank was for the lobsters and the lower one was for filtration. The filtration tank was equipped with a UV steriliser (UV07-9W, Resun), a foam fractionation (SA-2011, Weipro) powered by a submersible aquarium pump (HQB-3500, Zenblue) and a biofilter consisting of bioballs, ceramic noodles and activated carbon pellets. At the beginning of the operation of this system, the upper and lower tanks were filled with 200 L and 100 L of water, respectively, which was taken from the Hillarys Laboratory in the DoFWA and stored in a water reservoir (30,000 L) in CARL. Once the system was started, the water overflowed from the upper tank to the lower tank. The cleaned and sterilized water was pumped back to the upper tank from the lower tank using a submersible aquarium pump (WH-8000, Weipro). A probiotic bacterial solution (e-Viro 3, Enviroplus) was used to reduce ammonia, nitrite and nitrate present in the water. The water temperature was controlled at 25 ºC using an aquarium heater (HA-200, Aquacare). This was to maintain it to the water temperature during late November in 2012 at a depth of 1.5 m in Shark Bay. This is where the ovigerous females were collected (SHARKFL1 in AIMS,

2013). This system was run for at least 24 h without animals prior to the introduction of the ovigerous lobsters.

Two or three individuals ovigerous lobsters were incubated in one recirculating tank system until the phyllosomas hatched. Salinity was monitored daily using a portable refractometer and controlled at 35 psu by adding freshwater to the lower tank once the salinity was over 36 psu. Light conditions in the laboratory were 14L:10D regimes, and the light intensity was approximately 5 μmol m^{-2} s^{-1} during the light phase. Each lobster was fed three times a week with a whole live mussel (*Mytilus galloprovincialis* Lamarck, 1819). A mesh case (10 cm × 14 cm × 6 cm, 200 μm in mesh size) was attached to the drain of the upper tank to prevent newly hatched phyllosomas from escaping into the drain. Phyllosomas used in this study hatched on 12, 18 and 24 December, 2014.

Jellyfish

Moon jellyfish *Aurelia aurita* (Linnaeus, 1758) sensu lato (Dawson & Jacobs, 2001) were used as the diet for phyllosomas. All jellyfish used in this study were collected at the Como Jetty on the Swan River, Como, Western Australia. Up to 10 individual jellyfish were kept in a 20 L plastic pail filled with ambient water (22–25 °C) and transported to CARL within 1 h of collection.

Jellyfish were kept in a 100 L polycarbonate tank with the same water cleaning system as that for the lobster tank. Water temperature was ambient (23–26 °C). Salinity was monitored and controlled at 35 psu. Jellyfish were used for phyllosoma feeding within seven days after collection. The jellyfish were not fed during holding.

Culture of phyllosomas and nistos

Individual culture

The tank for individual phyllosoma culture designed by Wakabayashi et al. (2016)

was used in this study with modifications. A grid sheet (59 cm × 29 cm) legged with four PVC pipes (20 cm in length) was placed into a glass tank (60 cm × 30.5 cm × 30.5 cm) filled with 50 L of ocean water. The tank was equipped with an external filter (uvf-1200, "Biopro"), and the pro-biotic bacterial solution e-Viro 3 was used. Water temperature was maintained at 25 ºC. Salinity was controlled at 35 psu. The tank was placed under a 14L:10D light regime, and the light intensity was approximately 5 μmol m^{-2} s^{-1} during the light phase.

A total of ten phyllosomas hatched on 18 December and another 10 phyllosomas on 24 December were selected. All were reared in this tank. They were kept individually in PVC pipes (4 cm in diameter and 8 cm in height) placed on the grid sheet. The pipe ends were covered by a plankton net (200 μm in mesh size) to prevent phyllosomas from escaping. The PVC pipes were exchanged daily with clean pipes before feeding, and were replaced with mesh cases (12 cm × 9 cm × 10 cm) once the phyllosomas reached Stage III. Throughout the culture phyllosomas were fed daily with two slices of fresh jellyfish sized twice as big as their carapace. Nistos were kept in mesh cases individually without feeding. Mortality and moulting of the phyllosoma and nisto were recorded daily.

Group culture

Approximately 500 phyllosomas hatched on 12 December were kept in a glass tank (60 cm × 30.5 cm × 30.5 cm). The tank was filled with 60 L of ocean water. An external filter was equipped for this tank to clean the water and to make vertical water currents (Wakabayashi et al., 2012b). The water and light regime for this tank were the same conditions as those for the individual culture tank. Fifty to 100 g of fresh sliced jellyfish was added daily to the tank as food for the phyllosomas. Debris was removed together with up to 5% of the water by siphon and then the same amount of fresh marine water was added once a week. Ten individual phyllosomas at Stage I, II and III, and nine individual phyllosomas at

159 Stage IV (the final stage) which survived more than one day after hatching or moulting, were
160 randomly selected and preserved in 70% ethanol after being rinsed with distilled water. Five
161 nistos were obtained from this group culture; four of them were preserved in 70% ethanol and
162 another was transferred to the tank for individual culture and kept in the mesh case without
163 feeding until it moulted into the juvenile stage. Mortality was not recorded in animals in
164 group culture.
165
166 Measurements of specimens
167 All preserved specimens of phyllosomas and nistos were photographed using a
168 digital camera (DS-Fi1, Nikon) mounted on a stereo-microscope (SMZ1500, Nikon). The
169 photographs were analysed to determine measurements of phyllosomas and nistos using an
170 image processing program Image J (Schneider et al., 2012). Body dimensions of
171 phyllosomas including total body length (TL), cephalic shield length (CL), cephalic shield
172 width (CW), thorax width (TW) and abdomen length (AL) were measured as defined by
173 Mikami & Greenwood (1997). TL of nistos was measured from the anterior margin of the
174 antenna to the posterior margin of the telson. The longest and widest parts of the nistos'
175 carapace was measured as carapace length (CL) and width (CW), respectively.
176
177 Drawing of specimens
178 The drawings of the body structure of each developmental Stage were made under a
179 stereo-microscope (Typ 308700, Wild Heerbrugg) with the aid of a drawing tube. The
180 specimens were immersed in 70% ethanol during the drawing to prevent them from drying
181 out. Then phyllosomas and nistos were dissected under the stereo-microscope and the
182 appendages prepared on glass slides were observed under a compound light microscope (CHB,
183 Olympus). Drawings of the appendages were also made with the aid of a drawing tube. A
184 fair copy of each drawing was made using a vector graphic editor (Adobe Illustrator, Adobe

systems). Materials examined in this study were deposited in the National Museum of Natural Science, Tsukuba (NSMT-Cr 24262–24271).

RESULTS

Survival and growth of *T. australiensis*

Phyllosomas were fed with jellyfish exclusively from Stage I to IV, and successfully metamorphosed into the nisto stage in both the individual and group cultures. The phyllosomas showed a common feeding behaviour by consuming all of the jellyfish regardless of the Stages of the phyllosoma.

In the individual culture, the number of phyllosomas at Stage I to IV moulting into the next stage were 9, 7, 2 and 1 in the first trial, and 4, 2, 1 and 0 in the second trial, respectively. The durations (mean ± SE) of phyllosomas at Stage I to III were 7.9 ± 0.6 (n = 13), 8.8 ± 1.1 (n = 9) and 8.7 ± 0.9 (n = 3), respectively, and the duration of a phyllosoma at Stage IV which successfully metamorphosed into the nisto stage was 17 days. This phyllosoma took 40 days to develop into the nisto stage from hatching (fig. 2).

In the group culture, the shortest duration of phyllosoma from hatching to metamorphosis was 32 days and those of phyllosomas at Stage I to IV was 5, 7, 8 and 11 days, respectively. The other two individual phyllosomas took 41 days to complete metamorphosis, that is, the mean duration of phyllosomas from hatching to metamorphosis was 38 days (n = 3). A nisto moulted into the first juvenile Stage 7 days after metamorphosis. However, the juvenile was not normal, showing twisted antenna and walking legs.

Descriptions of *T. australiensis* phyllosoma and nisto

Stage I Phyllosoma (fig. 3)

Body (fig. 3a) length 4.03 ± 0.20 mm (table I); cephalic shield length slightly smaller than width (CW/CL ranged from 1.02 to 1.22), and wider than thorax (CW/TW ranged from 1.42 to 1.91); eyestalk unsegmented. Antennule (fig. 3b) unsegmented; biramous; 3 sensory setae at terminal; 1 short spine at inner distal angle; 1 spine at terminal of inner process. Antenna (fig. 3b) unsegmented; uniramous; 1 spine with setae at terminal; one-third as long as antennule. Mandible asymmetrical, left (fig. 3c) and right (fig. 3d) bearing a row of 17–19 slender and 12–13 thick teeth at the middle of anterior part, respectively; molar and canine-like processes well-developed. First maxilla (fig. 3e) bilobed; 3 long serrated spines at terminal of basal endite; 2 long serrated setae at terminal of coxal endite. Second maxilla (fig. 3f) single segment; 2 small spines on anterior margin; 3 long plumose setae at terminal. First maxilliped absent. Second maxilliped (fig. 3f) 5-segmented; no exopod; 1 long and 2 short serrated setae at inner distal area of fourth segment. Third maxilliped (fig. 3a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; comb-like setae on distal segment. First to fourth pereiopods (fig. 3a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; 14–15, 14–16, and 13–16 pairs of setae on exopods of first, second and third pereiopods, respectively; exopod bud with 0-3 setae on fourth pereiopods (both right and left exopods of 5 specimens examined). Fifth pereiopod (fig. 3g) elongated bud without segmentation; parallel to abdomen; two-third as long as abdomen. Pleopod absent. Uropod (fig. 3g) rudimentary bud. Telson undifferentiated; 1 spine and 3 setae on each side of distal end of abdomen (fig. 3g). Gill bud absent.

Stage II Phyllosoma (fig. 4)

Body (fig. 4a) length 6.01 ± 0.26 mm (table I); cephalic shield length slightly smaller than width (CW/CL ranged from 1.04 to 1.13), and wider than thorax (CW/TW ranged from 1.52 to 1.77); eyestalk segmented. Antennule (fig. 4b) 2-segmented; 1 simple and 4 sensory setae at terminal, 1 short spine at inner distal angle, 4 groups of sensory setae at anterior

margin of distal segment, 1 simple seta at the outer side of third group; 1–2 short spines and 1 long seta at terminal of proximal segment. Antenna (fig. 4b) unsegmented; biramous; 1 spine and 1 plumose seta at terminal of inner process; 1 spine at terminal of outer process; half as long as antennule. Mandible asymmetrical, left (fig. 4c) and right (fig. 4d) bearing a row of 17–19 slender and 12–13thick teeth at the middle of anterior part, respectively; molar and canine-like processes well-developed. First maxilla (fig. 4e) bilobed; 3 long serrated spines at terminal of basal endite; 2 long serrated setae at terminal of coxal endite. Second maxilla (fig. 4f) single segment; paddle-shaped; 2 small spines on anterior margin; setae absent. First maxilliped (fig. 4f) rudimentary bud. Second maxilliped (fig. 4f) 5-segmented; no exopod; 1 long and 2 short serrated setae at inner distal area of fourth segment. Third maxilliped (fig. 4a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; comb-like setae on distal segment. First to fourth pereiopods (fig. 4a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; 17–18, 17–19, 14–17, and 7–11 pairs of setae on exopods, respectively (both right and left exopods of 5 specimens examined). Fifth pereiopod (fig. 4g) incompletely 2-segmented; one and half times as long as abdomen; 1 long and 1 short spines at terminal. Pleopod absent. Uropod (fig. 4g) incomplete bifurcation. Telson undifferentiated; 1 spine and 3 setae on each side of distal end of abdomen (fig. 4g). Gill bud absent.

Stage III Phyllosoma (fig. 5)

Body (fig. 5a) length 9.11 ± 0.69 mm (table I); Cephalic shield length slightly smaller than width (CW/CL ranged from 1.04 to 1.28), and wider than thorax (CW/TW ranged from 1.48 to 1.77); Eyestalk segmented. Antennule (fig. 5b) 4-segmented; 1 simple and 4 sensory setae at terminal, 1 short spine at inner distal angle, 8 groups of sensory setae at anterior margin of distal segment, 1 simple seta at the outer side of fifth and seventh group; 1–2 short spines and 1 long seta at terminal of third segment. Antenna (fig. 5b) incompletely

segmented; biramous and flattend; inner process with 1 spine and 1 plumose seta at terminal, 3 teeth at inner margin, 1 small spine on each tooth; 2 teeth at outer margin of outer process; half as long as antennule. Mandible asymmetrical, left (fig. 5c) and right (fig. 5d) bearing a row of 18–19 slender and 12–13 thick teeth, respectively; molar and canine-like processes well-developed. First maxilla (fig. 5e) bilobed; 3 long serrated spines at terminal of basal endite; 2 long serrated setae at terminal of coxal endite. Second maxilla (fig. 5f) single segment; incompletely trilobed; 2 small spines on anterior margin; setae absent. First maxilliped (fig. 5f) rudimentary bud. Second maxilliped (fig. 5f) 5-segmented; no exopod; 1 long and 2 short serrated setae at inner distal area of fourth segment. Third maxilliped (fig. 5a) 5-segmented; 1 ventral coxal spine with 1 accessory seta; comb-like setae on distal segment. First to fourth pereiopods (fig. 5a) 5-segmented; 1 ventral coxal spine with 1 accessory seta; 21–22, 20–22, 20–22, and 15–17 pairs of setae on exopods, respectively (both right and left exopods of 5 specimens examined). Fifth pereiopod (fig. 5g) 5-segmented; 1 ventral coxal spine with 1 accessory seta; exopod absent; twice as long as abdomen. Pleopod (fig. 5g) 4 pairs of rudimentary bud present. Uropod (fig. 5g) bifurcated; unsegmented; reaching posterior margin of telson; setae absent. Telson (fig. 5h) differentiated; 1 spine and 3 setae at lateral margin. Gill bud absent.

Stage IV Phyllosoma (fig. 6)

Body (fig. 6a) length 15.05 ± 1.16 mm (table I); cephalic shield length slightly smaller than width (CW/CL ranged from 1.01 to 1.18), and wider than thorax (CW/TW ranged from 1.34 to 1.69); eyestalk segmented. Antennule (fig. 6b, c) 4-segmented; 2 simple and 4 sensory setae at terminal, 1 short spine at inner distal angle, 10 groups of sensory setae at anterior margin of distal segment, 1 simple seta at the outer side of third, fifth, seventh and ninth group; 1 short spines, 2 long and 2 short setae at terminal of third segment. Antenna (fig. 6b) incompletely segmented; biramous; inner process with 1–2 spines and 1

plumose seta at terminal, 5–6 teeth at inner margin, 3 teeth on outer margin,1 small spine on each tooth; outer process with 4 teeth at outer margin; two-third as long as antennule. Mandible asymmetrical, left (fig. 6d) and right (fig. 6e) bearing a row of 19–21 slender and 12–13 thick teeth, respectively; molar and canine-like processes well-developed. First maxilla (fig. 6f) bilobed; 3 long serrated spines at terminal of basal endite; 2 long serrated setae at terminal of coxal endite. Second maxilla (fig. 6g) single segment; trilobed; 2 small spines on anterior margin; setae absent. First maxilliped (fig. 6g) bifurcated. Second maxilliped (fig. 6g) 5-segmented; exopod bud on second segment; 1 long and 2 short serrated setae at inner distal area of fourth segment. Third maxilliped (fig. 6a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; comb-like setae on distal segment, hook-like exopod bud on second segment. First to fourth pereiopods (fig. 6a) 5-segmented; 1 spine with 1 accessory seta at ventral on coxa; 22–25, 22–25, 20–24, and 20–21 pairs of setae on exopods, respectively. Fifth pereiopod (fig. 6h) 5-segmented; 1 ventral coxal spine with 1 accessory seta; exopod absent; twice as long as abdomen. Pleopod (fig. 6h) 4 pairs of rudimentary bud present. Uropod (fig. 6h) bifurcated; incompletely segmented; extending beyond the posterior margin of telson; setae absent. Telson (fig. 6i) differentiated; 1 spine and 3 simple setae at lateral margin. Gill bud (fig. 6j) present on dorsal side of coxal segments of third maxilliped and first to fifth pereiopods; 1 bilobed bud on coxa, 1 unilobed bud on the edge of thorax, and 1 unilobed bud on thorax at the basal area of third maxilliped and first pereiopod; 1 bilobed bud on coxa, 1 unilobed bud on the edge of thorax, and 2 unilobed buds on thorax at the basal area of second to fourth pereiopods; 1 unilobed bud on thorax at the basal area of fifth pereiopod; absent at the basal area of second maxilliped.

Nisto stage (fig. 7)

Body (fig. 7a) length 15.95 ± 0.56 mm (table I); small setae lined on the margin of carapace, abdominal somites, uropods and telson; carapace length smaller than width (CW/CL

ranged from 1.15 to 1.58); 2 processes on midpoint of carapace anterior margin; carapace lateral margin serrulate with 1 prominent and 1 moderate notches; eye placed in V-shaped orbits at antero-lateral angle of carapace; 1 longitudinal row of spines with small ridge on carapace at inner area of orbits. Antennule (fig. 7b) 4-segmented; 8 complete and 1 incomplete articulations on distal segment; 13 complete and 1 incomplete articulations on second segment; at least 6 groups of sensory setae present on anterior margin of distal segment. Antenna (fig. 7c, d) 6-segmented; second and third segments fused; 4 teeth on outer margin of fourth segment; 9–10 teeth on anterior to outer margin of distal segment. Mandible (fig. 7e) incompletely developed; 1 incisor process meshing between right and left asymmetrically; molar and canine-like processes lacking; finger-like plap without setae. Paragnath (fig. 7e) tubercular process. First maxilla (fig. 7f) bilobed; 5 robust and 2 short terminal spines on basal endite; 1 long and 4 short terminal spines on coxal endite. Second maxilla (fig. 7g) single segment; flattened, trilobed; hairy setae lined on outer margin of scaphognathite; no setae on basal and coxal endites. First maxilliped (fig. 7h) 2-segmented; flattened; distal segment bilobed, exopod bearing 5 small spines at terminal and 15 setae on outer margin, endopod bud without setae; epipod on proximal segment membranous, expanding posteriorly. Second maxilliped (fig. 7i) 4-segmented, proximal segment with further 4 incomplete segments; exopod with 2 segments on proximal segment; endopod slightly longer than exopod; distal end of exopod bearing 19–20 plumose setae; endopod with 3 small spicules at terminal of distal segment, 1 seta on outer margin of third and fourth segment, 1 spicule on inner distal angle of fourth segment; 1 bilobed gill bud on proximal segment and 1 unilobed gill bud on body surface at the base. Third maxilliped (fig. 7j) 5-segmented, distal and second segment with further 2 incomplete segments; exopod on second segment, 7–6 setae lined on outer margin, 2 setae at terminal, 1–2 setae on inner margin; outer margin and antero-dorsal margin of fourth segment bearing spinose setae densely; gill at the base completely clustered. Walking leg (fig. 7k) 5-segmented, 3

incomplete segments on the second segment; first to fourth with vestigial exopod on second segment; gill at the base completely clustered. Pleopod (fig. 7l, m) 4 pairs; biramous; setae absent. Uropod (fig. 7m) incompletely segmented; extending beyond posterior margin of telson.

DISCUSSION

Complete larval development from Stage I phyllosoma to juvenile was achieved in the Australian shovel-nosed lobster *T. australiensis*. The morphologies of the phyllosomas and nisto have not been described previously although the development from egg to juvenile in this species was achieved in 2004 by Roger Barnard (Rogers et al., 2010).

T. australiensis passed through four phyllosoma Stages before the metamorphosis into the nisto stage. Each Stage had a single instar, that is, the number of Stage and instar were equal in this species. *T. unimaculatus* also had four phyllosoma Stages but the phyllosomas at Stage I had two instars (Kizhakudan & Krishnamoorthi, 2014). Several differences in morphology between the two species of phyllosomas were also recognised: 5-segmented second maxillipeds in *T. australiensis*, but 4-segmented in *T. unimaculatus*; rudimentary buds of first maxillipeds appeared at the Stage II in *T. australiensis* but at the Stage III in *T. unimaculatus*; exopod buds on second and third maxillipeds at the final Stage appeared on the second segment in *T. australiensis*, but first segment in *T. unimaculatus*. The final Stage phyllosomas had four and three teeth on the outer margin of antennal outer process in *T. australiensis* and *T. unimaculatu*s, respectively. The numbers of pairs of setae on exopods were similar in the phyllosomas at Stages I, II and III between the two species but different in the final Stage phyllosomas: the maximum number of pairs of setae on the first, second, third and fourth pereiopods were 25, 25, 24 and 21 in *T. australiensis* but 29, 29, 29 and 24 in *T. unimaculatus*, respectively. On the other hand, there are little morphological difference at the nisto stage between *T. australiensis* and *T. unimaculatus*. These findings

366 may be useful as the diagnostic morphological characteristics for both identification of
367 species of wild-caught phyllosomas and evaluation of integrity of phyllosomas in culture.
368 Phyllosomas of *T. australiensis* had a single spine at the inner distal angle of
369 antennule, showing similarity to the phyllosomas of *Thenus* sp.1 described by Mikami &
370 Greenwood (1997). The average number of pairs of setae on the first to fourth pereiopods in
371 the final Stage phyllosomas of *T. australiensis* (23.6, 23.3, 22.7 and 20.3) was also similar to
372 those of *Thenus* sp.1 (25.2, 25.5, 24.8 and 20.4) but different from *Thenus* sp.2 (28.3, 28.8,
373 28.8 and 23.7). In contrast, the number of segments on the second maxillipeds was not
374 matched: 5-segmented in *T. australiensis* but 4-segmented in both *Thenus* sp.1 and *Thenus*
375 sp.2. Nistos of *T. australiensis* had pleopods without seate, but the nisto of *Thenus* sp.1 had
376 pleopods with three short setae on the exopod. Even though the majority of morphological
377 characteristics of *T. australiensis* phyllosomas are likely to be identical to those of Mikami &
378 Greenwood's *Thenus* sp.1 rather than *Thenus* sp.2, we could not conclude whether *Thenus*
379 sp.1 corresponded to *T. australiensis*. Observation of the larval development in another
380 species of Australian shovel-nosed lobster *T. parindicus* should be completed to solve this
381 problem.
382 Water temperature is one of the major environmental factors in the regulation of
383 growth and survival in crustacean larvae including phyllosomas (Hartnoll, 1982; Anger, 2001).
384 In palinurid lobsters such as the green rock lobster *Sagmariasus verreauxi* (H. Milne
385 Edwards, 1851) (Moss et al., 2001) and the Japanese spiny lobster *Panulirus japonicus* (von
386 Siebold, 1824) (Matsuda & Yamakawa, 1997), it is known that the duration of larval
387 development can be shortened as the water temperature increases, and then extended as the
388 water temperature increases more. Similar effects of water temperature on the survival rates
389 of phyllosomas have been reported in the western rock lobster *Panulirus cygnus* George, 1962
390 (Liddy et al., 2004). *T. australiensis* phyllosomas took 32–41 days from hatching to
391 metamorphosis in this study, longer than those of *T. unimaculatus* (26–30 days, Kizhakudan

& Krishnamoorthi, 2014), *Thenus* sp.1 and *Thenus* sp.2. (approximately 28 days, Mikami & Greenwood, 1997). The survival rates of *T. australiensis* phyllosomas from hatching to metamorphosis in this study (5% in individual culture, and 0.8% in group culture) were low compared with those of *T. unimaculatus* (22%, Kizhakudan & Krishnamoorthi, 2014) and *Thenus* sp.1 (80%, Mikami & Greenwood, 1997) but similar to those of *Thenus* sp.2 (5%, Mikami & Greenwood, 1997). The phyllosomas of *T. australiensis* were reared at 25 ºC but those of the other *Thenus* species were reared at higher than 25 ºC (25–27 ºC in *T. unimaculatus*, and 27 ± 0.5 ºC in *Thenus* sp.1 and *Thenus* sp.2), suggesting that the longer duration and lower survival in *T. australiensis* might have been caused by the water temperatures.

Post-larvae of palinurid and scyllarid lobsters are non-feeding (Mikami & Kuballa, 2007). The post-larvae show much simpler mouthparts (e.g. mandible and first maxilla) and foregut structure compared with those of phyllosomas and juveniles, being ineffective in manipulating food items (Nishida et al., 1990; Wolfe & Felgenhauer, 1991; Mikami & Takashima, 1993). We also observed that the nisto stage of *T. australiensis* moulted into the juvenile stage without feeding, and the appendages consisting of mouthparts of the nistos were simpler than those of phyllosomas in *T. australiensis*. Biochemical analyses has demonstrated that reserves are accumulated during the final phyllosoma Stage and are consumed during the post-larval stage in these lobsters (Lemmens, 1994; Jeffs et al., 1999). To develop an efficient juvenile production technique, quality and quantity of food items for the final Stage phyllosomas must satisfy the energy consumption of the nisto stage.

Marine bivalves which contain essential amino and fatty acids for crustaceans have been used as the main food items for phyllosoma culture in both palinurid and scyllarid lobsters (Kittaka, 2000). However, we may need an alternative food item to marine bivalves in order to reduce the labour of removing their shells, lower the chance of fouling the water due to leftover diets, and prevent competitive consumption of marine bivalves with humans.

In this study, the *T. australiensis* phyllosomas metamorphosed into the nisto stage when fed on jellyfish exclusively and a nisto successfully moulted into the juvenile stage. Previous laboratory experiments have also demonstrated that phyllosomas of the genus *Ibacus* Leach, 1815 (Scyllaridae) are capable of developing from hatching to metamorphosis when fed only on jellyfish (Wakabayashi et al., 2012b 2016). These results suggest that jellyfish may be a viable diet for phyllosomas of scyllarid lobsters in culture. Techniques for mass culture of several species of jellyfish such as moon jellyfish and sea nettles have already been established (Purcell et al., 2013), and the nutritional conditions of jellyfish can possibly be controlled by feeding of brine shrimp cultured in an enrichment procedure (Fukuda & Naganuma, 2001). Phyllosomas are capable of feeding on any part of a jellyfish body and eating it completely (Wakabayashi et al., 2012a). Also, jellyfish can be easily cut into pieces because of their gelatinous body. Considering these characteristics, jellyfish may be feasible as an alternative diet for in the lobster hatchery at least in scyllarids.

Large-scale production of *Thenus* spp. has been achieved by two private companies, "Australian Fresh Research and Development Corporation Pty Ltd" (Mikami & Kuballa, 2007) and "Lobster Harvest Ltd" (Rogers et al., 2010) in Australia. Lobsters in the genus *Thenus* are ideal species as aquaculture candidates because their larval duration is relatively short and growth from the first juvenile stage to a marketable size is also rapid compared with the other palinurid and scyllarid lobsters (Mikami & Kuballa, 2007; Rogers et al., 2010). However, commercial production of *Thenus* spp. has not been launched. Successful aquaculture of scyllarid lobsters including *Thenus* spp. relies mainly on increasing our understanding of the larval biology related to the life cycle, moulting, and nutritional needs of the lobsters (Mikami & Kuballa, 2007). We have described the definitive morphologies of the phyllosoma Stages and nisto stage in *T. australiensis*, which should be useful as a fundamental knowledge basis for further understanding of its feeding behaviour and to improve the techniques for *T. australiensis* aquaculture.

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REFERENCES

ANGER, K., 2001. The Biology of Decapod Crustacean Larvae, 1st edition: 1–417. (A.A. Balkema, Rotterdam).

ATES, R., D. J. LINDSAY & H. SEKIGUCHI, 2007. First record of an association between a phyllosoma larva and a Prayid siphonophore. Plankton Benthos Res., **2**: 67–69.

AUSTRALIAN INSTITUTE OF MARINE SCIENCE, 2013. Temperature Loggers. In: AIMS Data Catalogue. Available online at http://www.aims.gov.au/docs/data/data.html (accessed 25 November 2014).

BARNETT, B. M., R. F. HARTWICK & N. E. MILWARD, 1986. Description of the nisto stage of *Scyllarus demani* Holthuis, two unidentified *Scyllarus* species, and juvenile of *Scyllarus martensii* Pfeffer (Crustacea: Decapoda: Scyllaridae), reared in the laboratory; and behavioural observations of the nistos of *S. demani, S. martensii* and *Thenus orientalis* (Lund). Aust. Journ. mar. freshw. Res., **37**: 595–608.

BURTON, T. E. & P. J. E. DAVIE, 2007. A revision of the shovel-nosed lobsters of the genus *Thenus* (Crustacea: Decapoda: Scyllaridae), with descriptions of three new species.

Zootaxa**, 1429**: 1–38.

DAWSON, M. N. & D. K. JACOBS, 2001. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biol. Bull., **200**: 92–96.

FUKUDA, Y. & T. NAGANUMA, 2001. Potential dietary effects on the fatty acid composition of the common jellyfish *Aurelia aurita*. Mar. Biol., **138**: 1029–1035.

HARTNOLL, R. G., 1982. Growth. In: L. G. Abele (ed), The Biology of Crustacea, **2**: 111–196. (Academic Press, New York).

HERRNKIND, W., J. HALUSKY & P. KANCIRUK, 1976. A further note on phyllosoma larvae associated with medusae. Bull. mar. Sci., **26**: 110–112.

IAMSUWANSUK, A., J. DENDUANGBORIPANT & P. J. F. DAVIE, 2012. Molecular and morphological investigations of shovel-nosed lobsters *Thenus* spp. (Crustacea: Decapoda: Scyllaridae) in Thailand. Zool. Stud., **51**: 108–117.

JEFFS, A. G., M. E. Willmott, & R. M. G. Wells, 1999. The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. Comp. Biochem. Phys. A, **123**: 351–357.

JONES, C. M., 2007. Biology and fishery of the bay lobster, *Thenus* spp. In: K. L. Lavalli & E. Spanier (eds.), The Biology and Fisheries of the Slipper Lobster. Crustacean Issues, **17**: 325–358. (CRC Press, Boca Raton).

KITTAKA, J., 2000. Culture of larval spiny lobsters. In: B. F. Phillips & J. Kittaka (eds.), Spiny Lobsters: Fisheries and Culture: 508–532. (Fishing News Books, Oxford).

KIZHAKUDAN, J. K. & S. KRISHNAMOORTHI, 2014. Complete larval development of *Thenus unimaculatus* Burton & Davie, 2007 (Decapoda, Scyllaridae). Crustaceana, **87**: 570–584.

LEMMENS, J. W. T. J., 1994. Biochemical evidence for absence of feeding in puerulus larvae of the Western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae). Mar. Biol., **118**: 383–391.

LIDDY, G. C., B. F. PHILLIPS & G. B. MAGUIRE, 2004. Effects of temperature and food density on the survival and growth of early stage phyllosoma of the western rock lobster, *Panulirus cygnus*. Aquaculture, **242**: 207–215.

MATSUDA, H. & T. YAMAKAWA, 1997. Effects of temperature on growth of the Japanese spiny lobster, *Panulirus japonicas* (V. Siebold) phyllosomas under laboratory conditions. Mar. freshw. Res., **48**: 791–796.

MIKAMI, S. & F. TAKASHIMA, 1993. Development of the proventriculus in larvae of the slipper lobsters, *Ibacus ciliatus* (Decapoda: Scyllaridae). Aquaculture, **116**: 199–217.

MIKAMI, S. & J. G. GREENWOOD, 1997. Complete development and comparative morphology of larval *Thenus orientalis* and *Thenus* sp. (Decapoda: Scyllaridae) reared in the laboratory. Journ. Crust. Biol., **17**: 289–308.

MIKAMI, S. & A. V. KUBALLA, 2007. Factors important in larval and postlarval molting, growth, and rearing. In: K. L. Lavalli & E. Spanier. (eds.), The Biology and Fisheries of the Slipper Lobster. Crustacean Issues, **17**: 91–110. (CRC Press, Boca Raton).

MOSS, G. A., L. J. TONG & S. E. ALLEN, 2001. Effect of temperature and food ration on the growth and survival of early and mid-stage phyllosomas of the spiny lobster *Jasus verreauxi*. Mar. freshw. Res., **52**: 1459–1464.

NISHIDA, S., B. D. QUIGLEY, J. D. BOOTH, T. NEMOTO & J. KITTAKA, 1990. Comparative morphology of the mouthparts and foregut of the final-stage phyllosoma, puerulus, and postpuerulus of the rock lobster *Jasus edwardsii* (Decapoda: Palinuridae). Journ. Crust. Biol., **10**: 293–305.

PEARS, R. J., A. K. MORISON, E. J. JEBREEN, M. C. DUNNING, C. R. PITCHER, A. J. COURTNEY, B. HOULDEN & I. P. JACOBSEN, 2012. Ecological Risk Assessment of the East Coast Otter Trawl Fishery in the Great Barrier Reef Marine Park, Data Report: 1–200. (Great Barrier Reef Marine Park Authority, Townsville).

PHILLIPS, B. F. & A. N. SASTRY, 1980. Larval ecology. In: B. F. Phillips & J. S. Cobb.

(eds.), The Biology and Management of Lobsters, **2**: 11–57. (Academic Press, New York).

PURCELL, J. E., E. J. BAXTER & V. L. FUENTES, 2013. Jellyfish as products and problems of aquaculture. In: G. Allan & G. Burnell (eds.), Advances in aquaculture hatchery technology: 404–430. (Woodhead Publishing, Cambridge).

RADHAKRISHNAN, E. V., V. D. DESHMUKH, M. K. MANISSERI, M. RAJAMANI, J. K. KIZHAKUDAN & R. THANGARAJA, 2005. Status of the major lobster fisheries in India. New Zealand Journ. mar. freshw. Res., **39**: 723–732.

RADHAKRISHNAN, E. V., M. K. MANISSERI & V. D. DESHMUKH, 2007. Biology and fishery of the slipper lobster *Thenus orientalis*, in India. In: K. L. Lavalli & E. Spanier (eds.), The Biology and Fisheries of the Slipper Lobster. Crustacean Issues, **17**: 309–324. (CRC Press, Boca Raton).

ROGERS, P. P., R. BARNARD, & M. JOHNSTON, 2010. Lobster aquaculture a commercial reality: A review. Journ. mar. biol. Assoc. India, **52**: 327–335.

SCHNEIDER, C. A., W. S. RASBAND & K. W. ELICEIRI, 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods, **9**: 671–675.

SHOJIMA, Y., 1963. Scyllarid phyllosomas' habit of accompanying the jelly-fish (preliminary report). Bull. Jpn. Soc. Sci. Fish., **29**: 349–353.

SHOJIMA, Y., 1973. [The phyllosoma larvae of Palinura in the East China Sea and adjacent waters. I. *Ibacus novemdentatus*.] Bull. Seikai Reg. Fish. Res. Lab., **43**: 105–115. [in Japanese, with English abstract].

THOMAS, L. R., 1963. Phyllosoma larvae associated with medusae. *Nature*, **198**: 208.

VIJAYAKUMARAN, M. & E. V. RADHAKRISHNAN, 2011. Slipper lobsters. In: R. K. Fotedar & B. F. Phillips (eds.), Recent Advances and New Species in Aquaculture: 85–114. (Wiley-Blackwell, Oxford).

WAKABAYASHI, K., R. SATO, A. HIRAI, H. ISHII, T. AKIBA & Y. TANAKA, 2012a.

548 Predation by the phyllosoma larva of *Ibacus novemdentatus* on various kinds of
549 venomous jellyfish. Biol. Bull., **222**: 1–5.
550 WAKABAYASHI, K., R. SATO, H. ISHII, T. AKIBA, Y. NOGATA & Y. TANAKA, 2012b.
551 Culture of phyllosomas of *Ibacus novemdentatus* (Decapoda: Scyllaridae) in a closed
552 recirculating system using jellyfish as food. Aquaculture, **330–333**: 162–166.
553 WAKABAYASHI, K., S. NAGAI & Y. TANAKA, 2016. The complete larval development of
554 *Ibacus ciliatus* from hatching to the nisto and juvenile stages using jellyfish as the sole
555 diet. Aquaculture, **450**: 102–107.
556 WOLFE, S. H. & B. E. FELGENHAUER, 1991. Mouthparts and foregut ontogeny in larval,
557 postlarval, and juvenile spiny lobster, *Panulirus argus* Latreille (Decapoda, Palinuridae).
558 Zool. Scr., **20**: 57–75.
559 ZELLER, B., M. KANGAS & J. LARCOMBE, 2014. Moreton Bay Bug *Thenus australiensis*,
560 *T. parindicus*. In: M. Flood et al. (eds.), Status of Key Australian Fish Stocks 2014:
561 191–199. (Fisheries Research and Development Corporation, Canberra).

562 Figure captions

563 Fig.1. *Thenus australiensis* Burton & Davie, 2007, adult female used in this study. A,
564 dorsal; B, ventral. The photos were taken after moulting following hatching. Scale bar: 5
565 cm.

566

567 Fig.2. Survivorships of phyllosomas of *Thenus australiensis* Burton & Davie, 2007 in the first
568 (black) and second (gray) trials of individual culture. Arrows indicate the fastest
569 development of phyllosoma reaching the Stage II, II, IV and the nisto stage (N).

570

571 Fig.3. *Thenus australiensis* Burton & Davie, 2007, Stage I phyllosoma. A, body, ventral; B,
572 right antennule and antenna, ventral; C, left mandible, dorsal; D, right mandible, dorsal; E,
573 right first maxilla, dorsal; F, second maxillae and second maxillipeds, ventral; G, fifth
574 pereiopods and abdomen, ventral. Abbreviations: ata (antenna); atu (antennule); be (basal
575 endite); ce (coxal endite). Scale bars: 2 mm (A); 500 μm (B, F, G); 200 μm (E); 100 μm (C,
576 D).

577

578 Fig.4. *Thenus australiensis* Burton & Davie, 2007, Stage II phyllosoma. A, body, ventral;
579 B, right antennule and antenna, ventral; C, left mandible, dorsal; D, right mandible, dorsal; E,
580 left first maxilla, ventral; F, left second maxilla, rudimentary lump of first maxilliped and
581 second maxilliped, ventral; G, abdomen and right fifth pereiopod, ventral. Abbreviations:
582 ata (antenna); atu (antennule); be (basal endite); ce (coxal endite); fmp (first maxilliped).
583 Scale bars: 2 mm (A); 500 μm (B, F, G); 200 μm (E); 100 μm (C, D).

584

585 Fig.5. *Thenus australiensis* Burton & Davie, 2007, Stage III phyllosoma. A, body, ventral;
586 B, right antennule and antenna, ventral; C, left mandible, dorsal; D, right mandible, dorsal; E,
587 right first maxilla, ventral; F, right second maxilla, rudimentary bud of first maxilliped and

second maxilliped, ventral; G, abdomen and right fifth pereiopod, ventral; H, telson, dorsal. Abbreviations: ata (antenna); atu (antennule); be (basal endite); ce (coxal endite). Scale bars: 3 mm (A); 500 µm (B, F, G, H); 250 µm (E); 100µm (C, D).

Fig.6. *Thenus australiensis* Burton & Davie, 2007, Stage IV (final stage) phyllosoma. A, body, ventral; B, right antennule and antenna, ventral; C, distal tips of left antennules, ventral; D, left mandible, dorsal; E, right mandible, dorsal; F, right first maxilla, ventral; G, right second maxilla, first maxilliped and second maxilliped, ventral; H, abdomen and right fifth pereiopod, ventral; I, telson, dorsal; J, gill buds arrangement, dorsal. Abbreviations: ata (antenna); atu (antennule); be (basal endite); ce (coxal endite); fp (fifth pereiopod); gb (gill bud); tmp (third maxilliped). Scale bars: 3 mm (A); 1 mm (H, J); 500 µm (B, G, I); 250 µm (C, F); 100 µm (D, E).

Fig.7. *Thenus australiensis* Burton & Davie, 2007, nisto. A, body, dorsal; B, right antennule (setae on the tips of third and distal segment omitted), dorsal; C, right antenna, dorsal; D, proximate area of left antenna, ventral; E, mouthpart, ventral; F, right first maxilla, ventral; G, right second maxilla, postero-ventral; H, left first maxilliped, postero-ventral; I, left second maxilliped, ventral; J, left third maxilliped, ventral; K, sternum and left walking legs, ventral; L, left second pleopod, dorsal; M, uropods and telson, ventral. Abbreviations: be (basal endite); ce (coxal endite); cp (carapace); en (endopod); ep (epipod); ex (exopod); mb (mandible); pg (paragnath); pl (pleopod); sc (scaphognathite). Scale bars: 5 mm (A); 1mm (K, M); 500 µm (B, C, D, E, G, H, I, J); 250 µm (F, L).

Figure 1

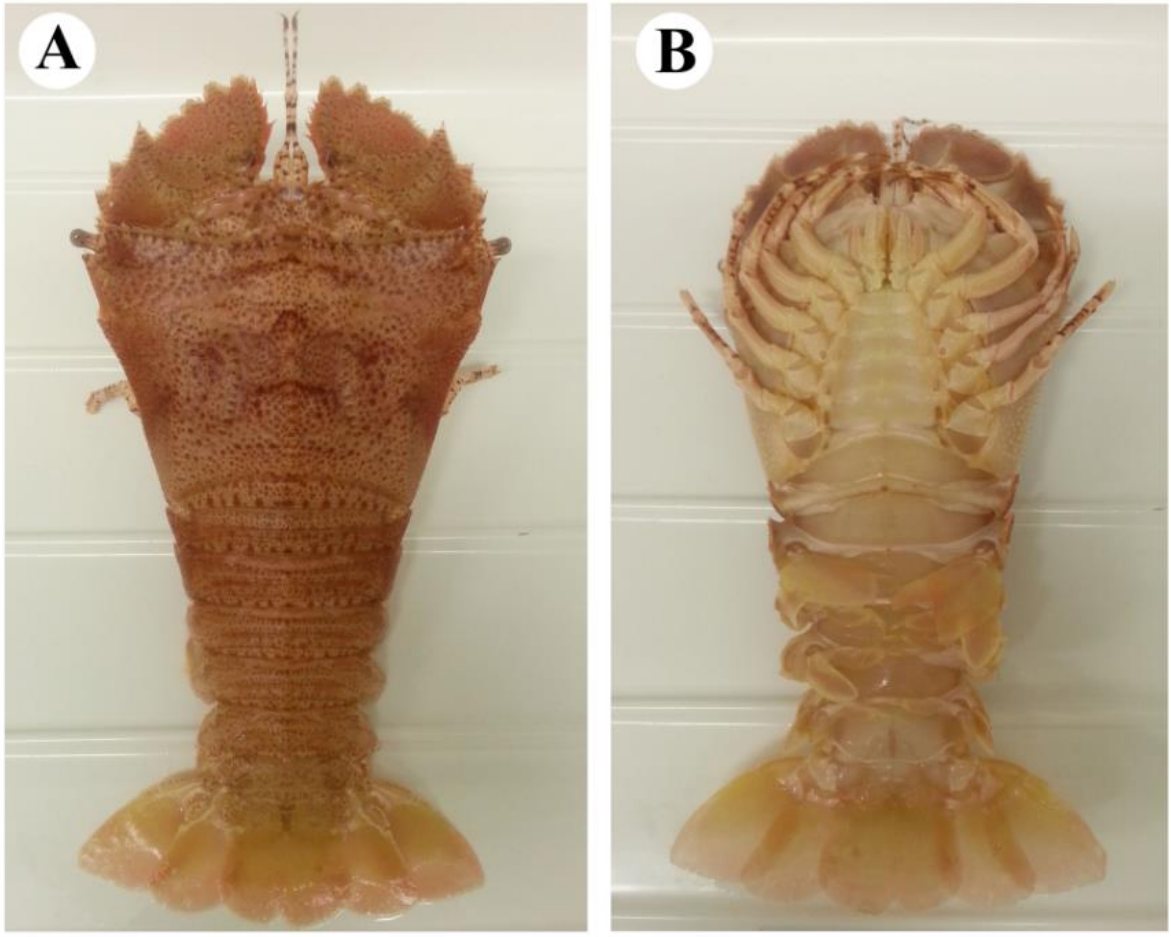

Figure 2

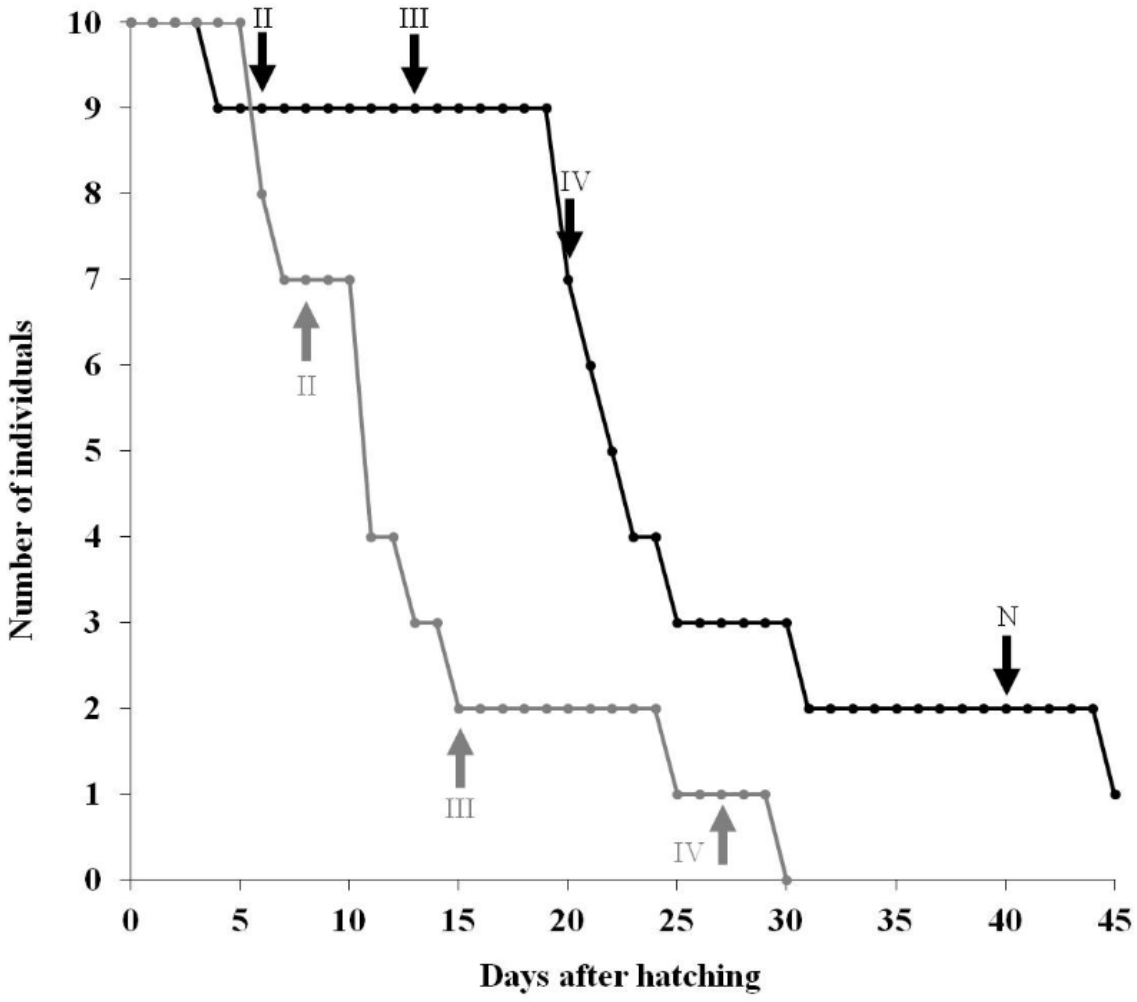
Number of individuals
Days after hatching
II
III
IV
N
II
III
IV
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Figure 3

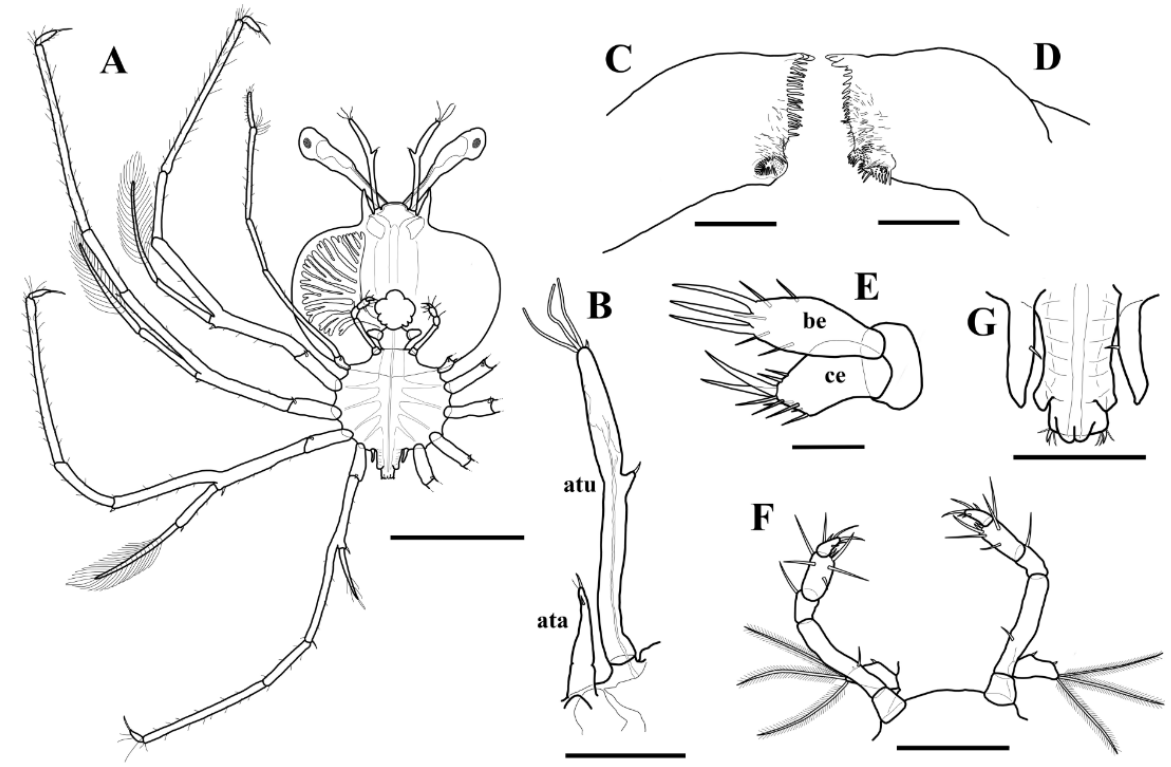

Figure 4

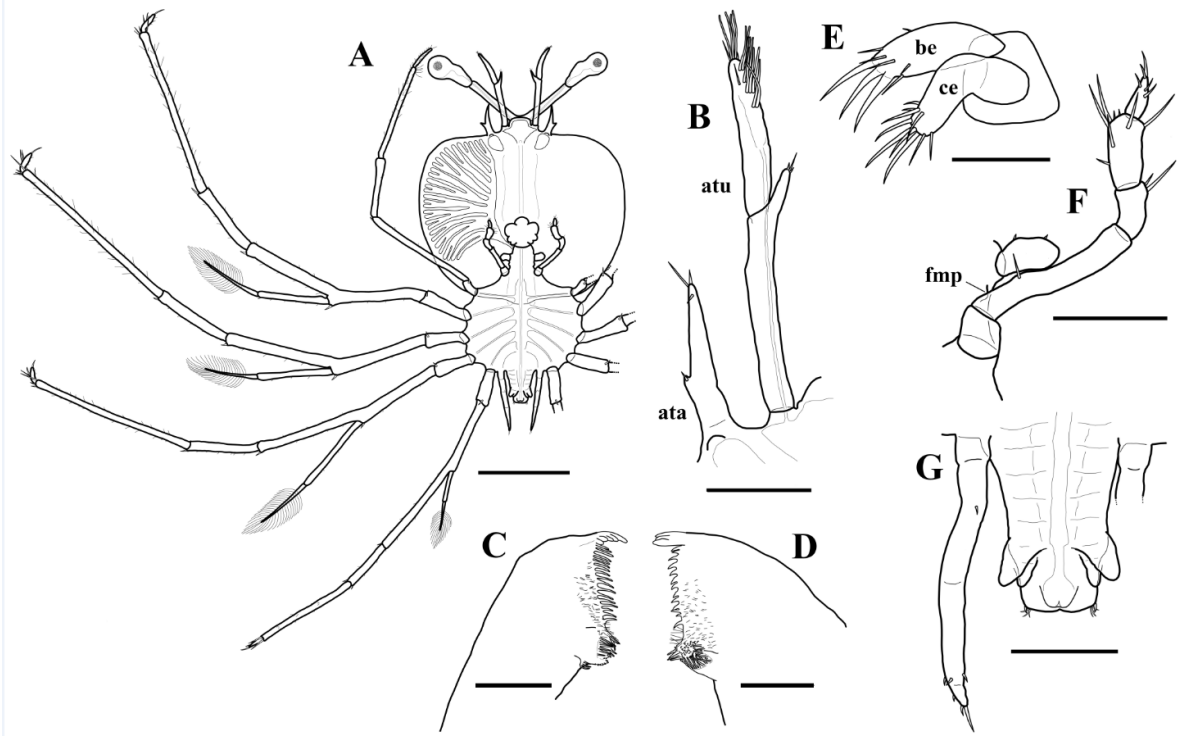

Figure 5

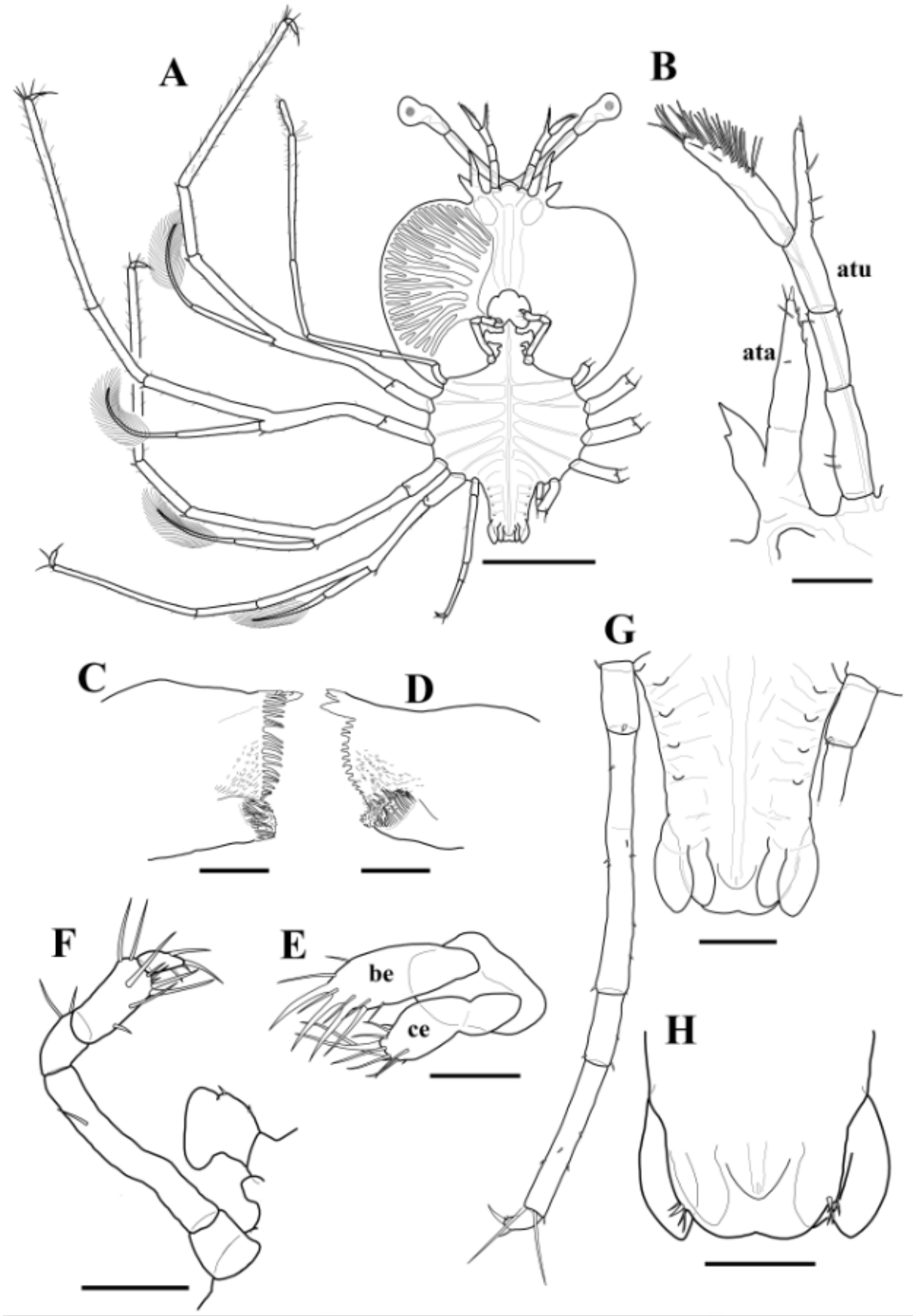

Figure 6

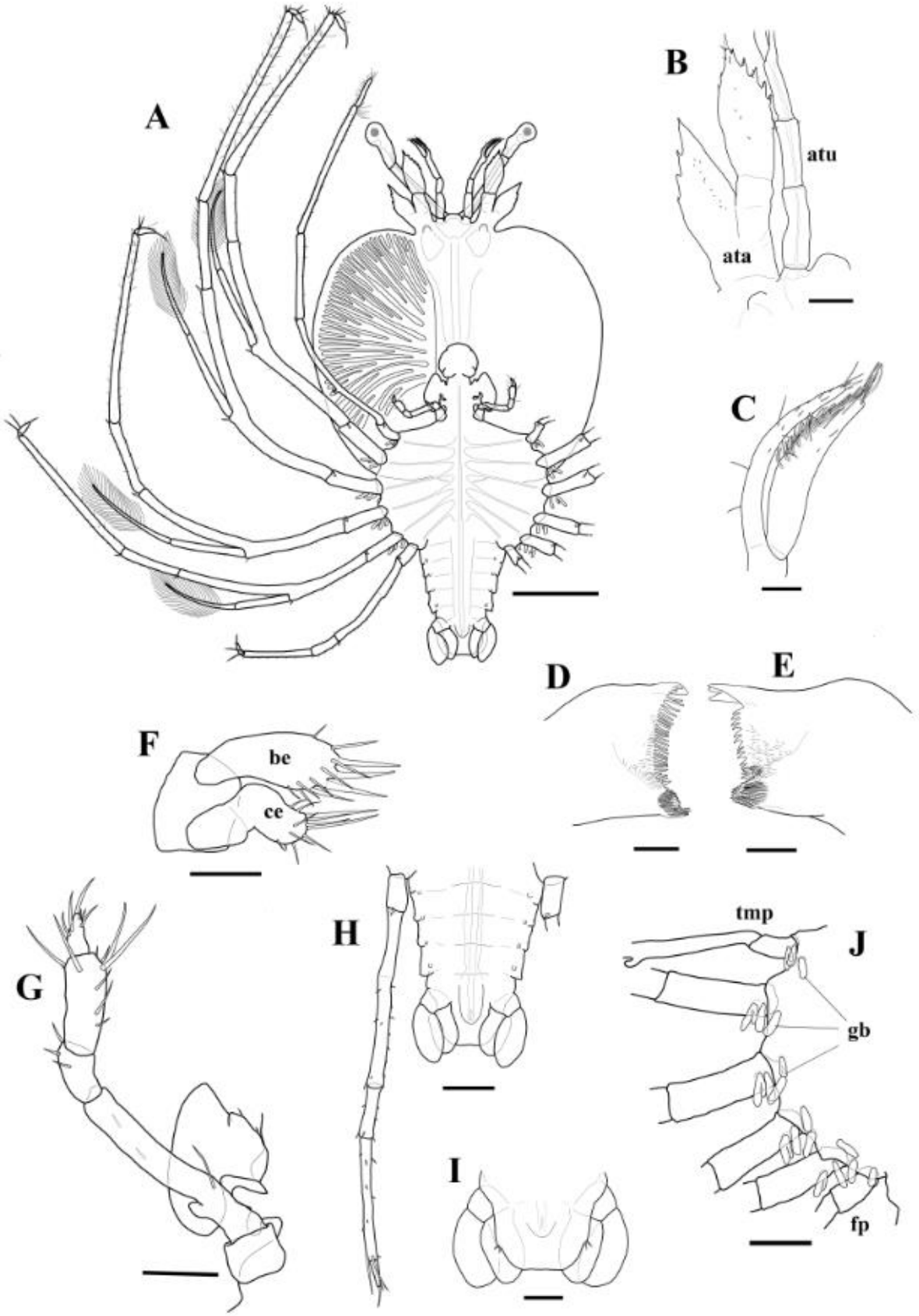

Figure 7

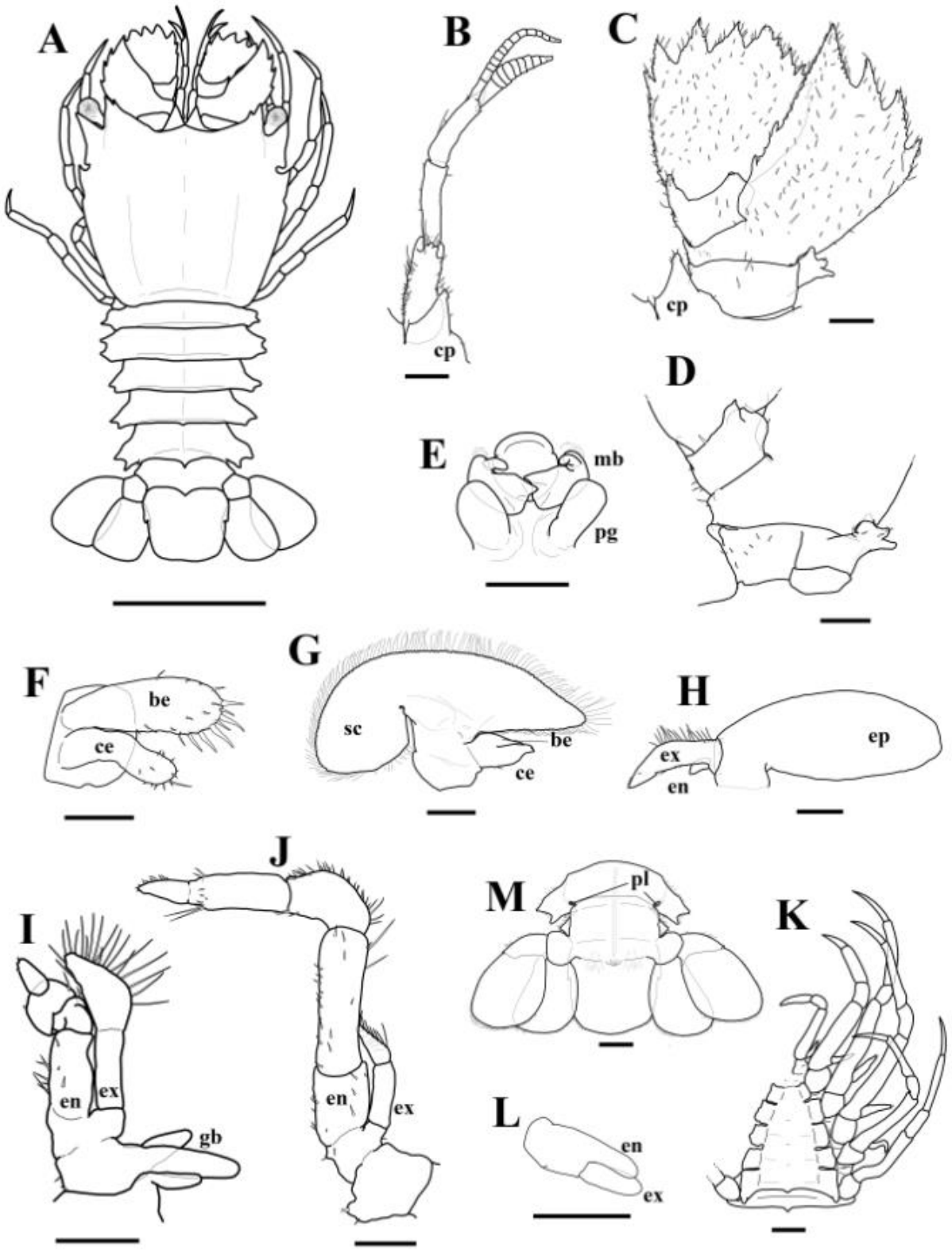
A
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TABLE I

Body dimensions (mm) of phyllosomas and nisto of *Thenus australiensis* Burton & Davie in group culture.

Measurement		Phyllosoma				Nisto
		St I (n = 10)	St II (n = 10)	St III (n = 10)	St IV (n = 9)	(n = 4)
BL	mean ± SD	4.03 ± 0.20	6.01 ± 0.26	9.11 ± 0.69	15.05 ± 1.16	15.95 ± 0.56
	max.	4.26	6.32	10.25	16.31	16.39
	min.	3.56	5.49	8.40	12.78	15.19
CL	mean ± SD	2.51 ± 0.17	3.97 ± 0.20	5.68 ± 0.47	8.93 ± 0.88	5.05 ± 0.39
	max.	2.68	4.26	6.47	9.74	5.57
	min.	2.13	3.68	5.08	7.06	4.72
CW	mean ± SD	2.84 ± 0.28	4.33 ± 0.18	6.65 ± 0.50	10.06 ± 1.20	6.68 ± 0.62
	max.	3.10	4.58	7.53	11.26	7.55
	min.	2.20	4.07	5.89	7.96	6.14
TW	mean ± SD	1.65 ± 0.08	2.64 ± 0.09	4.10 ± 0.31	6.37 ± 0.51	-
	max.	1.72	2.75	4.53	6.98	-
	min.	1.46	2.50	3.68	5.44	-
AL	mean ± SD	0.50 ± 0.04	0.73 ± 0.05	1.56 ± 0.13	3.84 ± 0.31	-
	max.	0.54	0.79	1.76	4.20	-
	min.	0.43	0.63	1.38	3.30	-

Numbers of individuals examined are shown in parentheses. AL: Abdomen length, BL: Body length, CL: Cephalic sheild length, CW: Cephalic sheild width, St: Stage, TW: total length