1 MORPHOLOGICAL DESCRIPTIONS OF LABORATORY REARED LARVAE AND

2 POST-LARVAE OF THE AUSTRALIAN SHOVEL-NOSED LOBSTER *THENUS*

3 *AUSTRALIENSIS* BURTON AND DAVIE, 2007 (DECAPODA, SCYLLARIDAE)

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5 BY

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16

18   Abstract

19   Complete larval development from newly hatched larvae up to the juvenile stage was

20   successfully achieved in the Australian shovel-nosed lobster *Thenus australiensis* under

21   laboratory conditions.   The larvae of this species passed through four phyllosoma Stages

22   (each Stage has a single instar), and developed into the first juvenile stage via a post-larval,

23   nisto stage. The shortest and mean durations from hatching to metamorphosis at a water

24   temperature of 25 °C were 32 and 38 days, respectively.   Morphologies of body and

25   appendages for all four phyllosoma Stages and the nisto stage were described. The

26   phyllosomas were fed exclusively on the jellyfish *Aurelia aurita* throughout their culture. Our

27   results indicate that jellyfish may be a viable diet for *T. australiensis* phyllosoma in culture

28   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*

83   Thirteen individual ovigerous female lobsters were caught in Shark Bay, Western

84 Australia by the Department of Fisheries in Western Australia (DoFWA) during November

85 2014. The lobsters were identified as *Thenus australiensis* Burton & Davie, 2007 based on

86 dark brown spotting on the pereiopods (fig. 1). The female lobsters were shipped to the

87 laboratory in the DoFWA, Hillarys, Western Australia on 24 November, 2014. Meanwhile,

88 they were kept in a stone tank with running ocean water taken from the Hillarys marina.

89 Five, two and then six of the female lobsters were transferred to the Curtin Aquatic Research

90 Laboratory (CARL) in Curtin University, Bentley, Western Australia on 25 November, 2 and

91 10 December, 2014, respectively.

92   A recirculating tank system consisting of two polycarbonate tanks was designed for

93 the incubation of these ovigerous lobsters. The upper tank was for the lobsters and the lower

94 one was for filtration. The filtration tank was equipped with a UV steriliser (UV07-9W,

95 Resun), a foam fractionation (SA-2011, Weipro) powered by a submersible aquarium pump

96 (HQB-3500, Zenblue) and a biofilter consisting of bioballs, ceramic noodles and activated

97 carbon pellets. At the beginning of the operation of this system, the upper and lower tanks

98 were filled with 200 L and 100 L of water, respectively, which was taken from the Hillarys

99 Laboratory in the DoFWA and stored in a water reservoir (30,000 L) in CARL. Once the

100 system was started, the water overflowed from the upper tank to the lower tank. The cleaned

101 and sterilized water was pumped back to the upper tank from the lower tank using a

102 submersible aquarium pump (WH-8000, Weipro). A probiotic bacterial solution (e-Viro 3,

103 Enviroplus) was used to reduce ammonia, nitrite and nitrate present in the water. The water

104 temperature was controlled at 25 ºC using an aquarium heater (HA-200, Aquacare). This

105 was to maintain it to the water temperature during late November in 2012 at a depth of 1.5 m

106 in Shark Bay. This is where the ovigerous females were collected (SHARKFL1 in AIMS,

107 2013).   This system was run for at least 24 h without animals prior to the introduction of the

108 ovigerous lobsters.

109   Two or three individuals ovigerous lobsters were incubated in one recirculating tank

110 system until the phyllosomas hatched.   Salinity was monitored daily using a portable

111 refractometer and controlled at 35 psu by adding freshwater to the lower tank once the salinity

112 was over 36 psu.   Light conditions in the laboratory were 14L:10D regimes, and the light

113 intensity was approximately 5 μmol m^{-2} s^{-1} during the light phase.   Each lobster was fed

114 three times a week with a whole live mussel (*Mytilus galloprovincialis* Lamarck, 1819).   A

115 mesh case (10 cm $\times$ 14 cm $\times$ 6 cm, 200 μm in mesh size) was attached to the drain of the

116 upper tank to prevent newly hatched phyllosomas from escaping into the drain.   Phyllosomas

117 used in this study hatched on 12, 18 and 24 December, 2014.

118

119   Jellyfish

120   Moon jellyfish *Aurelia aurita* (Linnaeus, 1758) sensu lato (Dawson & Jacobs, 2001)

121 were used as the diet for phyllosomas.   All jellyfish used in this study were collected at the

122 Como Jetty on the Swan River, Como, Western Australia. Up to 10 individual jellyfish were

123 kept in a 20 L plastic pail filled with ambient water (22–25 °C) and transported to CARL

124 within 1 h of collection.

125   Jellyfish were kept in a 100 L polycarbonate tank with the same water cleaning

126 system as that for the lobster tank.   Water temperature was ambient (23–26 °C).   Salinity

127 was monitored and controlled at 35 psu.   Jellyfish were used for phyllosoma feeding within

128 seven days after collection.   The jellyfish were not fed during holding.

129

130   Culture of phyllosomas and nistos

131 Individual culture

132   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 ℃. Salinity was controlled at 35 psu. The tank was placed under a 14L:10D light regime, and the light intensity was approximately 5 $\mu mol\ m^{-2}\ s^{-1}$ 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

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

187

188 RESULTS

189 Survival and growth of *T. australiensis*

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

194 In the individual culture, the number of phyllosomas at Stage I to IV moulting into
195 the next stage were 9, 7, 2 and 1 in the first trial, and 4, 2, 1 and 0 in the second trial,
196 respectively. The durations (mean $\pm$ SE) of phyllosomas at Stage I to III were 7.9 $\pm$ 0.6 (n =
197 13), 8.8 $\pm$ 1.1 (n = 9) and 8.7 $\pm$ 0.9 (n = 3), respectively, and the duration of a phyllosoma at
198 Stage IV which successfully metamorphosed into the nisto stage was 17 days. This
199 phyllosoma took 40 days to develop into the nisto stage from hatching (fig. 2).

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

207

208 Descriptions of *T. australiensis* phyllosoma and nisto

209 Stage I Phyllosoma (fig. 3)

210   Body (fig. 3a) length 4.03 ± 0.20 mm (table I); cephalic shield length slightly smaller

211   than width (CW/CL ranged from 1.02 to 1.22), and wider than thorax (CW/TW ranged from

212   1.42 to 1.91); eyestalk unsegmented. Antennule (fig. 3b) unsegmented; biramous; 3 sensory

213   setae at terminal; 1 short spine at inner distal angle; 1 spine at terminal of inner process.

214   Antenna (fig. 3b) unsegmented; uniramous; 1 spine with setae at terminal; one-third as long

215   as antennule.   Mandible asymmetrical, left (fig. 3c) and right (fig. 3d) bearing a row of

216   17–19 slender and 12–13 thick teeth at the middle of anterior part, respectively; molar and

217   canine-like processes well-developed.   First maxilla (fig. 3e) bilobed; 3 long serrated spines

218   at terminal of basal endite; 2 long serrated setae at terminal of coxal endite.   Second maxilla

219   (fig. 3f) single segment; 2 small spines on anterior margin; 3 long plumose setae at terminal.

220   First maxilliped absent.   Second maxilliped (fig. 3f) 5-segmented; no exopod; 1 long and 2

221   short serrated setae at inner distal area of fourth segment.   Third maxilliped (fig. 3a)

222   5-segmented; 1 spine with 1 accessory seta at ventral on coxa; comb-like setae on distal

223   segment.   First to fourth pereiopods (fig. 3a) 5-segmented; 1 spine with 1 accessory seta at

224   ventral on coxa; 14–15, 14–16, and 13–16 pairs of setae on exopods of first, second and third

225   pereiopods, respectively; exopod bud with 0-3 setae on fourth pereiopods (both right and left

226   exopods of 5 specimens examined).   Fifth pereiopod (fig. 3g) elongated bud without

227   segmentation; parallel to abdomen; two-third as long as abdomen.   Pleopod absent.

228   Uropod (fig. 3g) rudimentary bud.   Telson undifferentiated; 1 spine and 3 setae on each side

229   of distal end of abdomen (fig. 3g).   Gill bud absent.

230

231   Stage II Phyllosoma (fig. 4)

232   Body (fig. 4a) length 6.01 ± 0.26 mm (table I); cephalic shield length slightly smaller

233   than width (CW/CL ranged from 1.04 to 1.13), and wider than thorax (CW/TW ranged from

234   1.52 to 1.77); eyestalk segmented.   Antennule (fig. 4b) 2-segmented; 1 simple and 4 sensory

235   setae at terminal, 1 short spine at inner distal angle, 4 groups of sensory setae at anterior

236 margin of distal segment, 1 simple seta at the outer side of third group; 1–2 short spines and 1

237 long seta at terminal of proximal segment.   Antenna (fig. 4b) unsegmented; biramous; 1

238 spine and 1 plumose seta at terminal of inner process; 1 spine at terminal of outer process;

239 half as long as antennule.   Mandible asymmetrical, left (fig. 4c) and right (fig. 4d) bearing a

240 row of 17–19 slender and 12–13thick teeth at the middle of anterior part, respectively; molar

241 and canine-like processes well-developed.   First maxilla (fig. 4e) bilobed; 3 long serrated

242 spines at terminal of basal endite; 2 long serrated setae at terminal of coxal endite.   Second

243 maxilla (fig. 4f) single segment; paddle-shaped; 2 small spines on anterior margin; setae

244 absent.   First maxilliped (fig. 4f) rudimentary bud.   Second maxilliped (fig. 4f)

245 5-segmented; no exopod; 1 long and 2 short serrated setae at inner distal area of fourth

246 segment.   Third maxilliped (fig. 4a) 5-segmented; 1 spine with 1 accessory seta at ventral on

247 coxa; comb-like setae on distal segment.   First to fourth pereiopods (fig. 4a) 5-segmented; 1

248 spine with 1 accessory seta at ventral on coxa; 17–18, 17–19, 14–17, and 7–11 pairs of setae

249 on exopods, respectively (both right and left exopods of 5 specimens examined).   Fifth

250 pereiopod (fig. 4g) incompletely 2-segmented; one and half times as long as abdomen; 1 long

251 and 1 short spines at terminal.   Pleopod absent.   Uropod (fig. 4g) incomplete bifurcation.

252 Telson undifferentiated; 1 spine and 3 setae on each side of distal end of abdomen (fig. 4g).

253 Gill bud absent.

254

255 Stage III Phyllosoma (fig. 5)

256   Body (fig. 5a) length 9.11 ± 0.69 mm (table I); Cephalic shield length slightly

257 smaller than width (CW/CL ranged from 1.04 to 1.28), and wider than thorax (CW/TW

258 ranged from 1.48 to 1.77); Eyestalk segmented.   Antennule (fig. 5b) 4-segmented; 1 simple

259 and 4 sensory setae at terminal, 1 short spine at inner distal angle, 8 groups of sensory setae at

260 anterior margin of distal segment, 1 simple seta at the outer side of fifth and seventh group;

261 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

340 incomplete segments on the second segment; first to fourth with vestigial exopod on second

341 segment; gill at the base completely clustered.   Pleopod (fig. 7l, m) 4 pairs; biramous; setae

342 absent.   Uropod (fig. 7m) incompletely segmented; extending beyond posterior margin of

343 telson.

344

345   DISCUSSION

346   Complete larval development from Stage I phyllosoma to juvenile was achieved in

347 the Australian shovel-nosed lobster *T. australiensis*. The morphologies of the phyllosomas and

348 nisto have not been described previously although the development from egg to juvenile in

349 this species was achieved in 2004 by Roger Barnard (Rogers et al., 2010).

350   *T. australiensis* passed through four phyllosoma Stages before the metamorphosis

351 into the nisto stage.   Each Stage had a single instar, that is, the number of Stage and instar

352 were equal in this species.   *T. unimaculatus* also had four phyllosoma Stages but the

353 phyllosomas at Stage I had two instars (Kizhakudan & Krishnamoorthi, 2014).   Several

354 differences in morphology between the two species of phyllosomas were also recognised:

355 5-segmented second maxillipeds in *T. australiensis*, but 4-segmented in *T. unimaculatus*;

356 rudimentary buds of first maxillipeds appeared at the Stage II in *T. australiensis* but at the

357 Stage III in *T. unimaculatus*; exopod buds on second and third maxillipeds at the final Stage

358 appeared on the second segment in *T. australiensis*, but first segment in *T. unimaculatus*.

359 The final Stage phyllosomas had four and three teeth on the outer margin of antennal outer

360 process in *T. australiensis* and *T. unimaculatu*s, respectively.   The numbers of pairs of setae

361 on exopods were similar in the phyllosomas at Stages I, II and III between the two species but

362 different in the final Stage phyllosomas: the maximum number of pairs of setae on the first,

363 second, third and fourth pereiopods were 25, 25, 24 and 21 in *T. australiensis* but 29, 29, 29

364 and 24 in *T. unimaculatus*, respectively.   On the other hand, there are little morphological

365 difference at the nisto stage between *T. australiensis* and *T. unimaculatus*.   These findings

15

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

16

392   & Krishnamoorthi, 2014), *Thenus* sp.1 and *Thenus* sp.2. (approximately 28 days, Mikami &

393   Greenwood, 1997). The survival rates of *T. australiensis* phyllosomas from hatching to

394   metamorphosis in this study (5% in individual culture, and 0.8% in group culture) were low

395   compared with those of *T. unimaculatus* (22%, Kizhakudan & Krishnamoorthi, 2014) and

396   *Thenus* sp.1 (80%, Mikami & Greenwood, 1997) but similar to those of *Thenus* sp.2 (5%,

397   Mikami & Greenwood, 1997). The phyllosomas of *T. australiensis* were reared at 25 ℃ but

398   those of the other *Thenus* species were reared at higher than 25 ℃ (25–27 ℃ in *T.*

399   *unimaculatus*, and 27 ± 0.5 ℃ in *Thenus* sp.1 and *Thenus* sp.2), suggesting that the longer

400   duration and lower survival in *T. australiensis* might have been caused by the water

401   temperatures.

402   Post-larvae of palinurid and scyllarid lobsters are non-feeding (Mikami & Kuballa,

403   2007). The post-larvae show much simpler mouthparts (e.g. mandible and first maxilla) and

404   foregut structure compared with those of phyllosomas and juveniles, being ineffective in

405   manipulating food items (Nishida et al., 1990; Wolfe & Felgenhauer, 1991; Mikami &

406   Takashima, 1993). We also observed that the nisto stage of *T. australiensis* moulted into the

407   juvenile stage without feeding, and the appendages consisting of mouthparts of the nistos

408   were simpler than those of phyllosomas in *T. australiensis*. Biochemical analyses has

409   demonstrated that reserves are accumulated during the final phyllosoma Stage and are

410   consumed during the post-larval stage in these lobsters (Lemmens, 1994; Jeffs et al., 1999).

411   To develop an efficient juvenile production technique, quality and quantity of food items for

412   the final Stage phyllosomas must satisfy the energy consumption of the nisto stage.

413   Marine bivalves which contain essential amino and fatty acids for crustaceans have

414   been used as the main food items for phyllosoma culture in both palinurid and scyllarid

415   lobsters (Kittaka, 2000). However, we may need an alternative food item to marine bivalves

416   in order to reduce the labour of removing their shells, lower the chance of fouling the water

417   due to leftover diets, and prevent competitive consumption of marine bivalves with humans.

418   In this study, the *T. australiensis* phyllosomas metamorphosed into the nisto stage when fed

419   on jellyfish exclusively and a nisto successfully moulted into the juvenile stage.   Previous

420   laboratory experiments have also demonstrated that phyllosomas of the genus *Ibacus* Leach,

421   1815 (Scyllaridae) are capable of developing from hatching to metamorphosis when fed only

422   on jellyfish (Wakabayashi et al., 2012b 2016).   These results suggest that jellyfish may be a

423   viable diet for phyllosomas of scyllarid lobsters in culture.   Techniques for mass culture of

424   several species of jellyfish such as moon jellyfish and sea nettles have already been

425   established (Purcell et al., 2013), and the nutritional conditions of jellyfish can possibly be

426   controlled by feeding of brine shrimp cultured in an enrichment procedure (Fukuda &

427   Naganuma, 2001).   Phyllosomas are capable of feeding on any part of a jellyfish body and

428   eating it completely (Wakabayashi et al., 2012a).   Also, jellyfish can be easily cut into pieces

429   because of their gelatinous body.   Considering these characteristics, jellyfish may be feasible

430   as an alternative diet for in the lobster hatchery at least in scyllarids.

431   Large-scale production of *Thenus* spp. has been achieved by two private companies,

432   "Australian Fresh Research and Development Corporation Pty Ltd" (Mikami & Kuballa,

433   2007) and "Lobster Harvest Ltd" (Rogers et al., 2010) in Australia.   Lobsters in the genus

434   *Thenus* are ideal species as aquaculture candidates because their larval duration is relatively

435   short and growth from the first juvenile stage to a marketable size is also rapid compared with

436   the other palinurid and scyllarid lobsters (Mikami & Kuballa, 2007; Rogers et al., 2010).

437   However, commercial production of *Thenus* spp. has not been launched.   Successful

438   aquaculture of scyllarid lobsters including *Thenus* spp. relies mainly on increasing our

439   understanding of the larval biology related to the life cycle, moulting, and nutritional needs of

440   the lobsters (Mikami & Kuballa, 2007).   We have described the definitive morphologies of

441   the phyllosoma Stages and nisto stage in *T. australiensis*, which should be useful as a

442   fundamental knowledge basis for further understanding of its feeding behaviour and to

443   improve the techniques for *T. australiensis* aquaculture.

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

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

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

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

Fig.5. *Thenus australiensis* Burton & Davie, 2007, Stage III phyllosoma.   A, body, ventral; B, right antennule and antenna, ventral; C, left mandible, dorsal; D, right mandible, dorsal; E, 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).
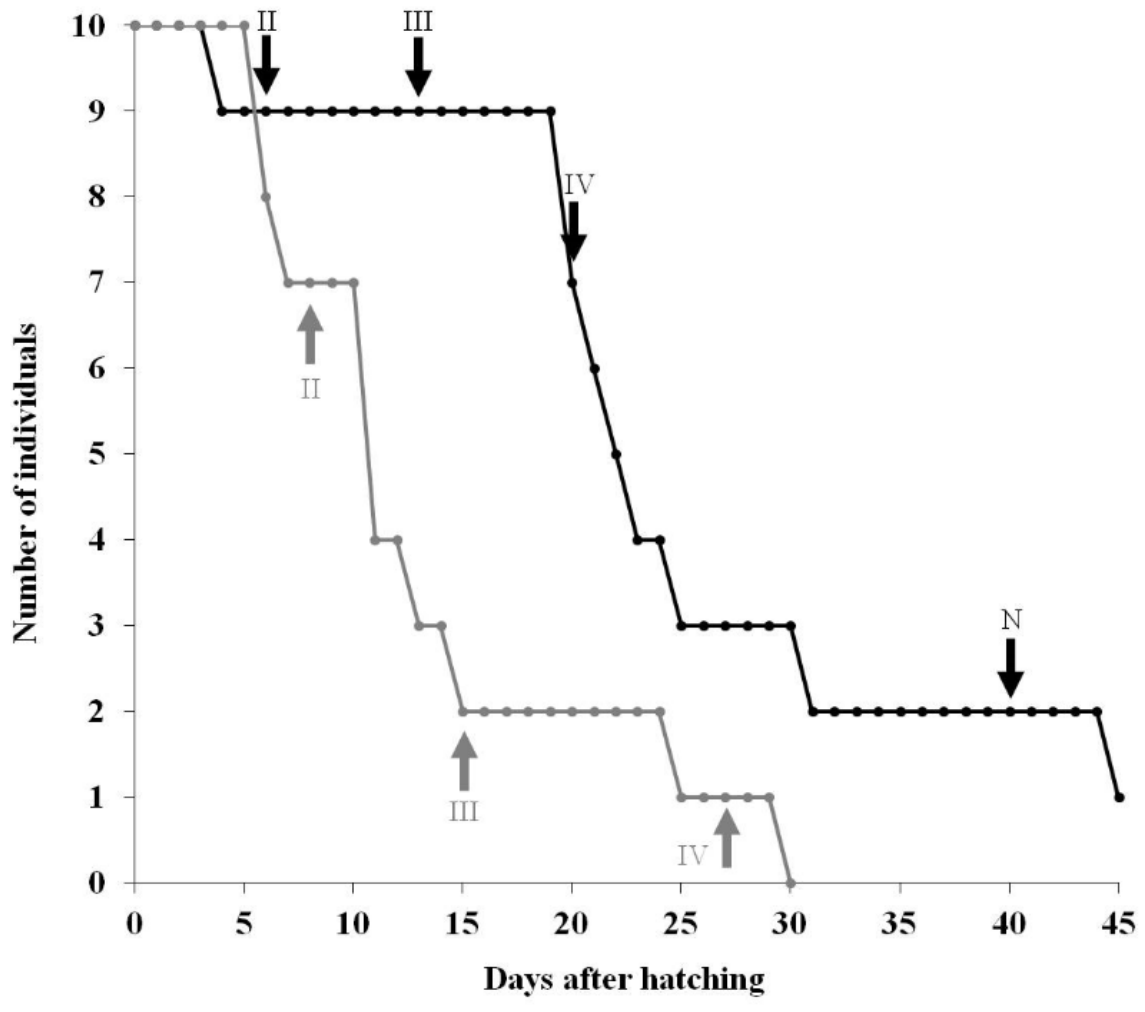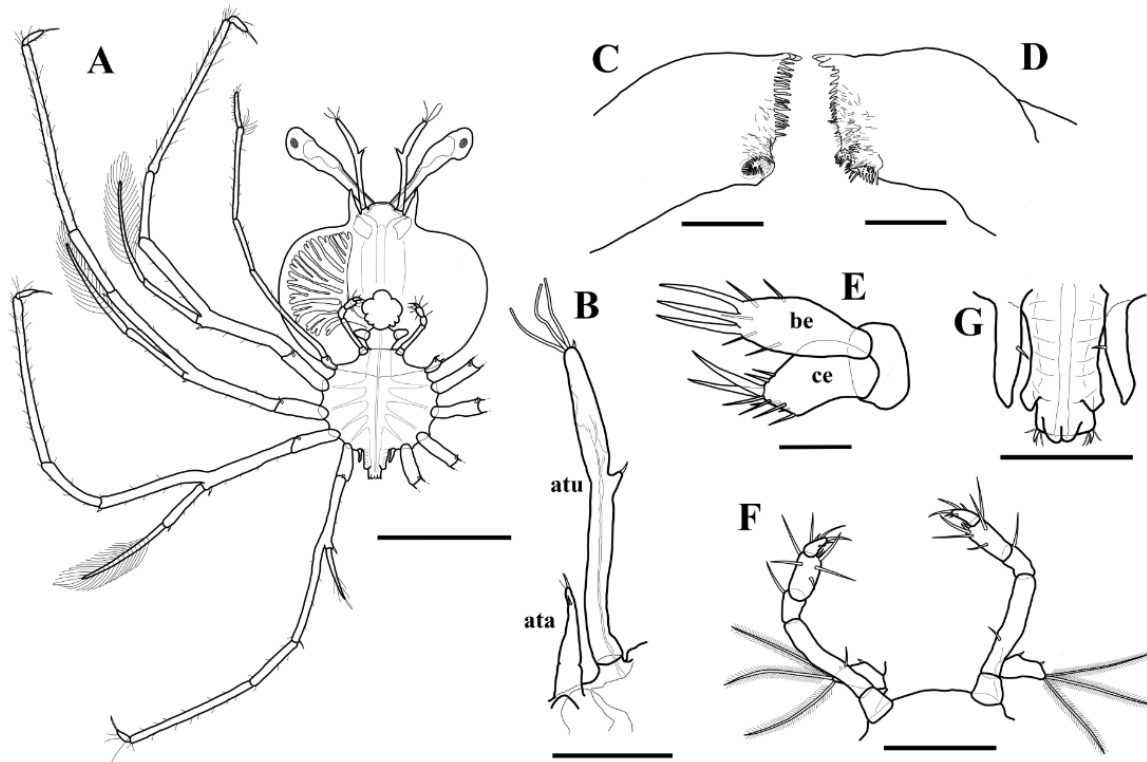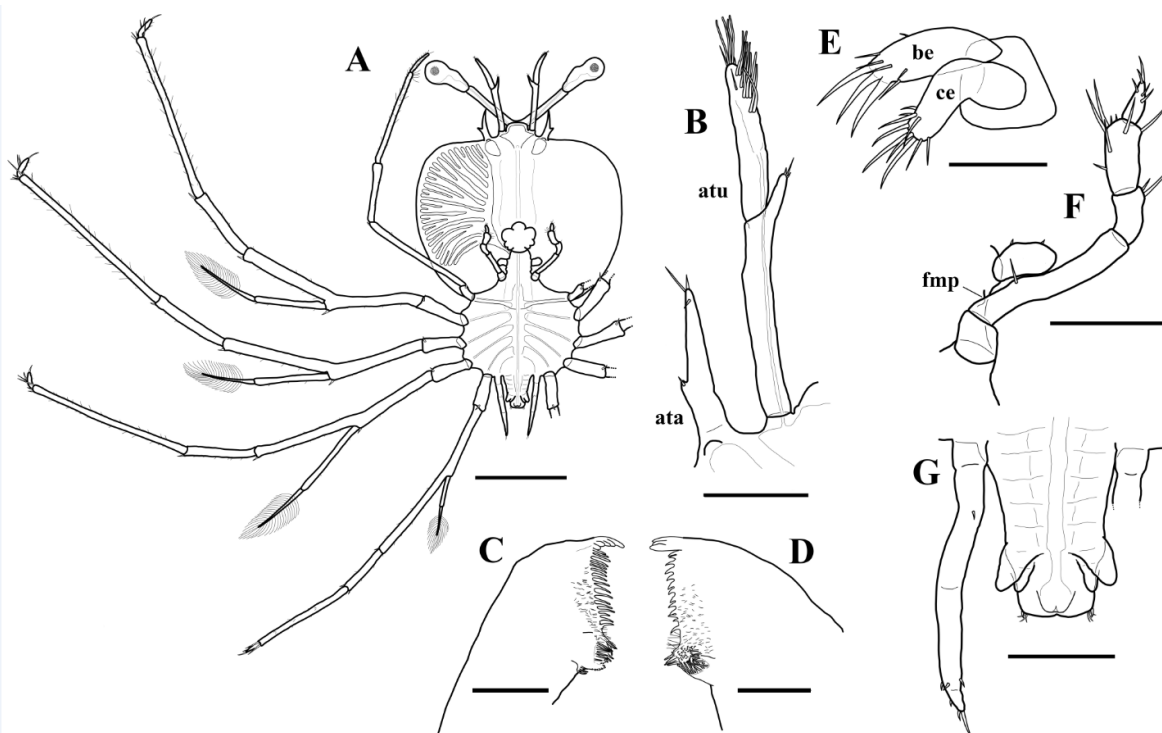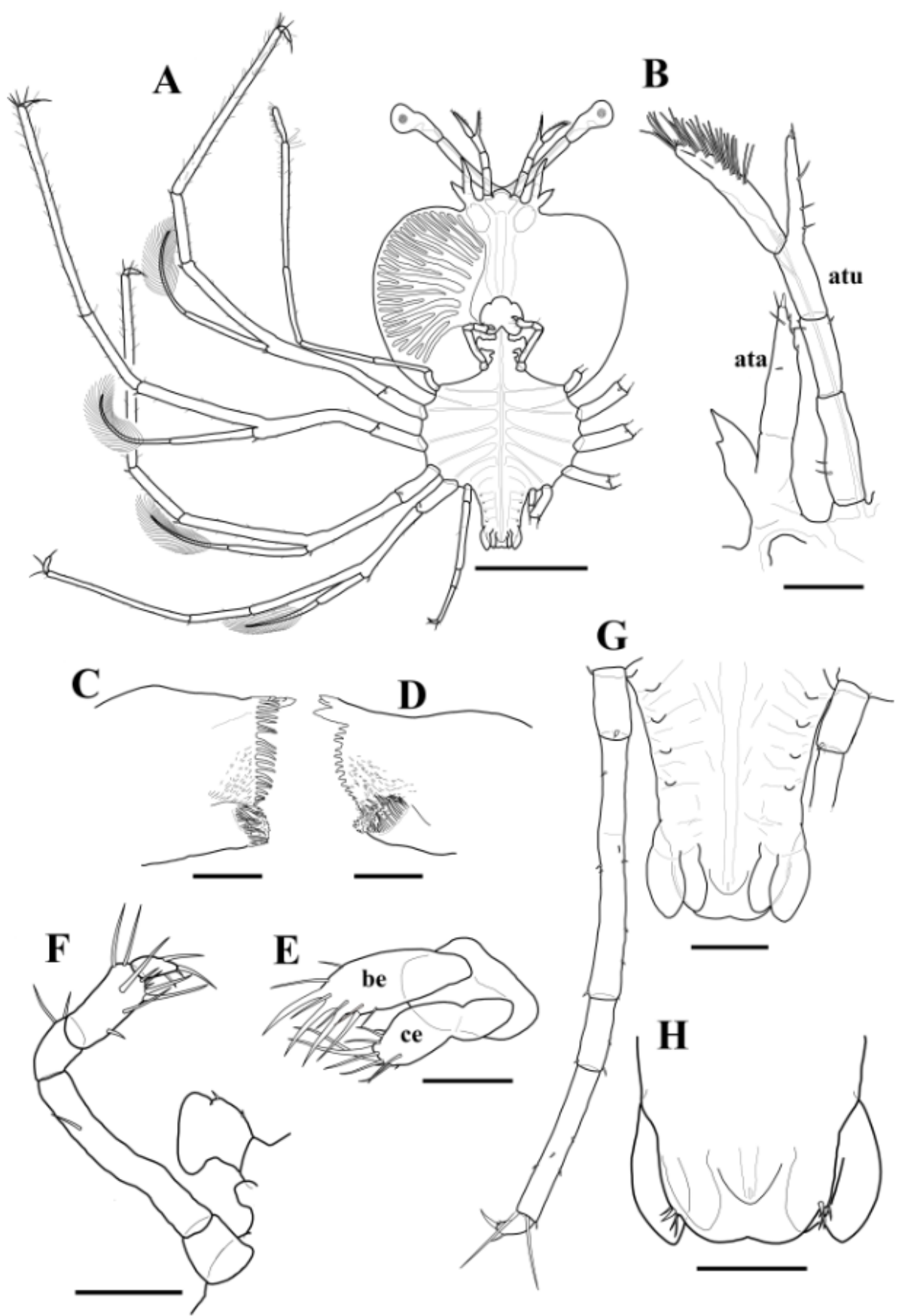
Figure 1

Figure 2

Figure 3

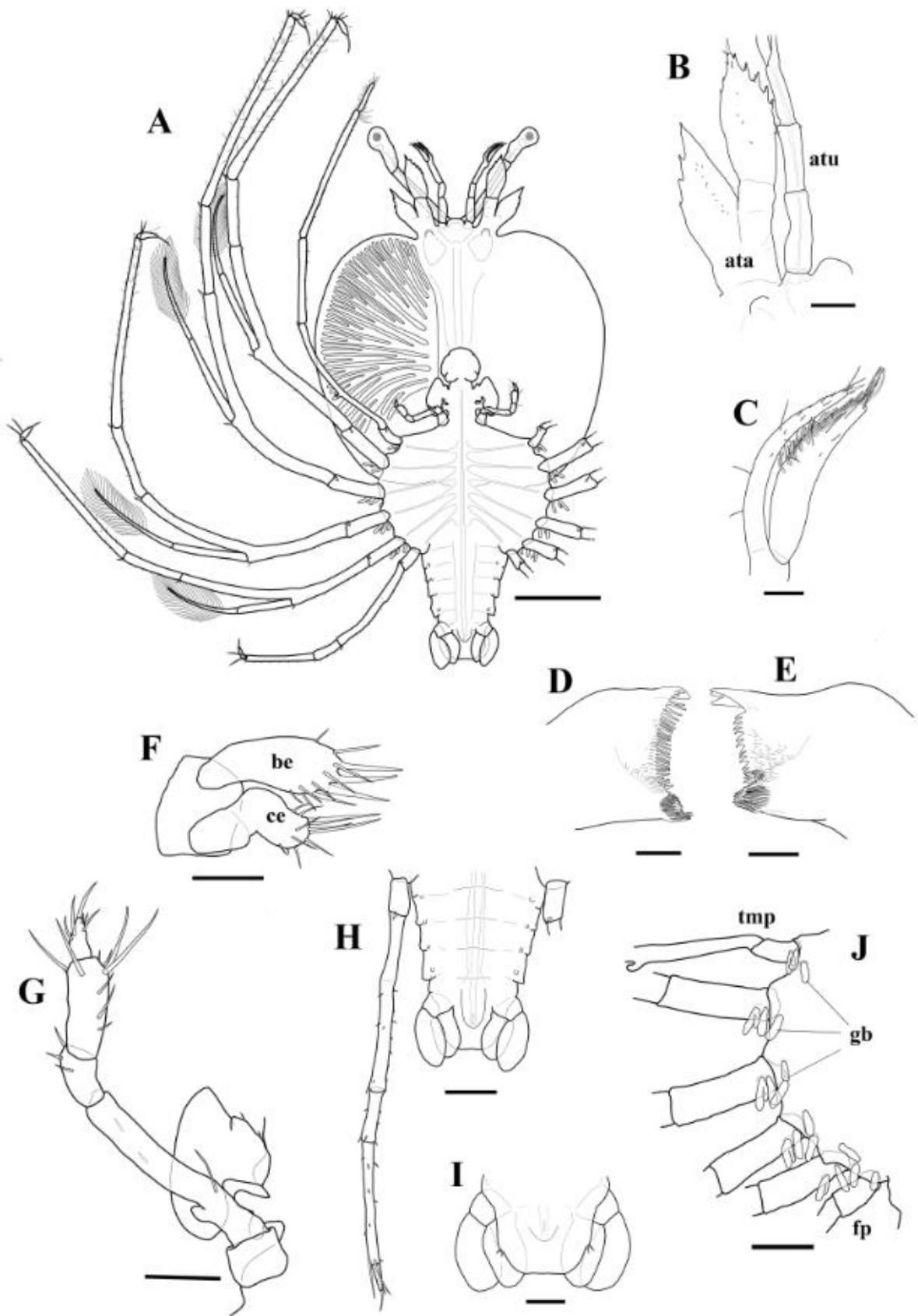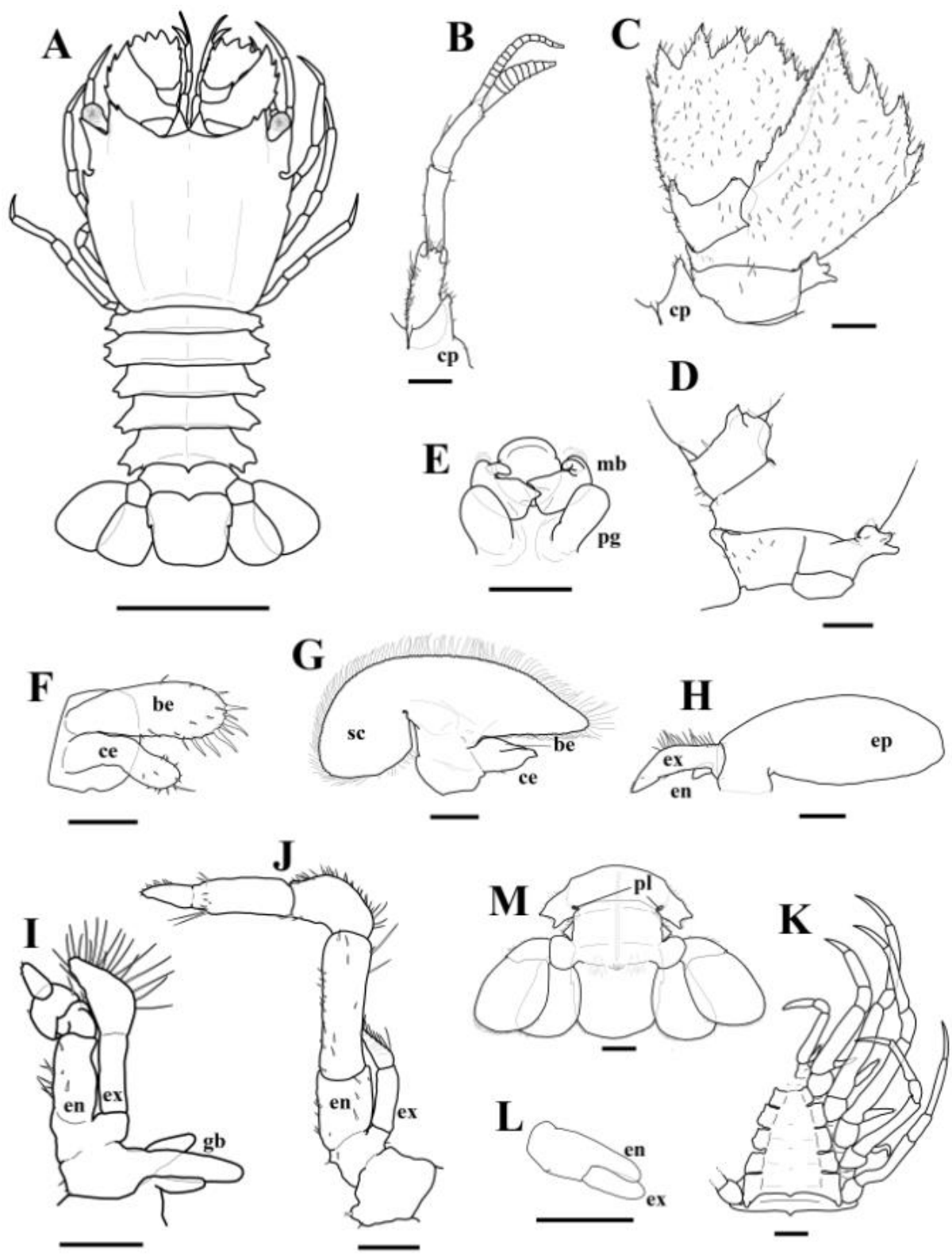Figure 4

Figure 5

Figure 6

Figure 7

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