

THE COMPLETE DEVELOPMENT OF LARVAL CARIBBEAN SPINY LOBSTER *PANULIRUS ARGUS* (LATREILLE, 1804) IN CULTURE

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A B S T R A C T

The Caribbean spiny lobster (*Panulirus argus*) is the most widespread, commercially important, and extensively studied spiny lobster in the western hemisphere, yet until now it has never been successfully reared through all its planktonic (phyllosomal) stages from egg to early benthic juvenile. Here we describe the development of phyllosomal *P. argus* in culture including the growth, duration, and morphology for 10 distinct stages. Phyllosomata were cultured from egg to juvenile in two ways: 1) in individual cultures using small glass bowls (120 and 400 mL) to determine individual growth, and 2) in group culture using a 40 L elliptical tank to obtain samples for morphological descriptions. Six of the 20 phyllosomata cultured individually (at 25–27°C) metamorphosed after 18–21 molts (mean = 20) to the puerulus stage at 140–198 days (mean = 174 days). Body lengths of the final stage phyllosomata and pueruli ranged from 25.6 to 28.2 mm (mean = 27.0 mm) and 16.4 to 17.5 mm (mean = 17.0 mm), respectively. Of the 550 mass cultured (at 25°C) phyllosomata, 146 were sampled for morphological examination and subsequently divided into 10 stages, each described and illustrated herein. This is the first of the five *Panulirus* species known from the Atlantic Ocean to be cultured completely from hatch to settlement. This success is crucial for future research on larval behavior and dispersal and may renew interest in aquaculture of this economically consequential species.

KEY WORDS: Decapoda, larval development, life history, lobster biology, *Panulirus argus*

INTRODUCTION

The Caribbean spiny lobster (*Panulirus argus* Latreille, 1804) is the most abundant species of spiny lobster in the Western Atlantic, with a broad geographic range that extends from the southeastern U.S. and Bermuda, to the Gulf of Mexico, the Caribbean Sea, and the northeastern coast of Brazil (Williams, 1988). Wherever it occurs, *P. argus* supports economically important fisheries, which is reflected in fishery landings statistics (35,665 metric tons in 2004) that place it first among tropical spiny lobster species worldwide (57% of total catch) (FAO, 2006). Its large size, abundance and ubiquitous distribution also make it an ecologically consequential species as both predator and prey in the shallow tropical waters in which its benthic stages are found (reviewed in Moe, 1991; Butler and Herrnkind, 2000; Butler et al., 2006). Like all spiny lobsters, *P. argus* has a complex life cycle including: planktonic larvae (phyllosoma; plural: phyllosomata) and postlarvae (puerulus; plural: pueruli); early benthic juveniles that are found in shallow, vegetated coastal habitats; crevice-dwelling juveniles that also occur in shallow coastal areas; and coral reef dwelling adults. The biology, ecology, and fishery dynamics of benthic juvenile and adult *P. argus* are comparatively well known (see Butler and Herrnkind, 2000; Butler et al., 2006 for reviews), and studies conducted over the past decade or so have greatly improved our knowledge of the transitory postlarval stage (reviewed in Butler and Herrnkind, 2000; Phillips et al., 2006). Yet, our understanding of even the most basic aspects of the biology and population dynamics of the more elusive, pelagic phyllosomal stages of *P. argus* is rudimentary (see Phillips and McWilliam, 1986; Phillips et al., 2006).

For some palinurid lobsters, phyllosomal development and duration have been documented in studies using laboratory cultures [*P. japonicus* von Siebold, 1824): Yamakawa et al., 1989; Matsuda and Takenouchi, 2006; *P. longipes* (Milne-Edwards, 1868): Matsuda and Yamakawa, 2000; *P. penicillatus* (Olivier, 1791): Matsuda et al., 2006; also see table 7.1 in Phillips et al., 2006], that have illuminated key aspects of their early-life histories (e.g., larval duration, growth, survivorship). However, until now no one has cultured *P. argus* from egg to juvenile so the number of instars, pelagic larval duration (PLD), growth, survivorship, and morphological features of each phyllosomal stage are as yet undescribed.

Several unpublished attempts at culturing *P. argus* have been made over the years with only limited success at rearing the phyllosomata through the very early stages (Moe, 1991). Early and some late-stage phyllosomal specimens obtained from either freshly hatched eggs or from plankton tows have been observed and described (Crawford and DeSmidt, 1923; Gurney, 1936; Lebour, 1950); however, many figures and descriptions from these studies are incomplete. Only one published study by Lewis (1951) contains a much more panoptic description of the phyllosomal stages of *P. argus* collected from plankton tows in the Florida current and West Indies ($n = 300$ specimens, R/V Atlantis). Although findings from that study described 11 phyllosomal stages and a puerulus stage (companion paper, Lewis et al., 1952), the descriptions are potentially confounded by specimens from two other co-occurring genera, *Scyllarus* spp. and *Thenus* spp. (both slipper lobsters), and at least one congener, *P. guttatus*

(Latereille, 1804). From those plankton collections, Lewis was unable to establish the age or duration of each phyllosomal stage. Current estimates of PLD for *P. argus*, extrapolated from modal progressions of phyllosomal stages from plankton samples, is 6-12 months (Lewis, 1951; Sims and Ingle, 1966; Farmer et al., 1989). Estimates of PLD and stage-specific phyllosomal duration, growth, mortality, and behavior are important for aquaculture and for physical transport models that include biological inputs when estimating dispersal and population connectivity (Katz et al., 1994; Hinckley et al., 1996; Chiswell and Booth, 1999; Stockhausen et al., 2000; Griffin et al., 2001; Cowen et al., 2006).

The aim of this study was to determine the growth, phyllosomal duration, number of stages, mortality, and morphological characteristics of phyllosomal *P. argus* in laboratory culture. We also quantified ontogenetic changes in phyllosomal vertical migratory behavior by measuring their swimming response to light intensities and spectra indicative of different depths in the sea, and we compared those results with field observations of size-specific phyllosomal depth distributions. The results on phyllosomal behavior will be reported in a separate paper.

MATERIALS AND METHODS

Terminology

For purposes of clarity, the term 'instar' refers to the intermolt period between two successive ecdyses, whereas 'stage' denotes one or more specific morphological characteristics unique to that phyllosoma. Thus, a stage can include one or more instars (Mikami and Greenwood, 1997) depending on its duration. The nektonic or puerulus stage is defined here as the transitional phase between the planktonic and benthic life stages and is specific to species in the family Palinuridae (Phillips and McWilliam, 1986; Jeffs et al., 2005).

Adult and Phyllosomal Source

Adult male and female spiny lobsters were collected by divers from coral reefs near Long Key, FL USA (24°44'20"N, 80°59'37"W) in mid-May of 2005 and transported in coolers by boat to the Keys Marine Laboratory (Long Key, FL USA) where they were sorted, measured, and assessed for their reproductive condition, e.g., visible eggs, fresh spermatophores, ovary color, similarly to methods of MacDiarmid and Butler (1999). Animals were placed into multiple 850 L circular holding tanks with artificial shelters, running seawater (32-35 psu, 27-29°C), ambient light, and fed frozen squid and shrimp three times weekly. After ~three weeks, eight females (four with external eggs and four with a spermatophore but no eggs) and four males were placed into plastic bags infused with 100% oxygen, packed into styrofoam boxes, and transported by airplane from Miami, FL USA to Osaka, Japan. Upon their arrival in Japan, lobsters were placed in oxygenated 200 L tanks and transported by automobile to the Fisheries Research Division, Mie Prefectural Science and Technology Promotion Center (MPSTPC) in Mie Japan where phyllosomata were cultured. Adult lobsters were held in a 3000 L temperature controlled (26.5 ± 0.5°C) flow-through seawater tank, fed fresh mussel (*Mytilus galloprovincialis*) and frozen krill. The four females without eggs spawned (i.e., extruded their eggs) on June 3-4; their embryos were sampled and monitored throughout the gestation period, i.e., the onset of eyespots and changes in color, to estimate when hatching would occur (Tong et al., 2000). Just prior to hatching, one of these females (carapace length (CL) = 74.6 mm) was isolated in a tank so we could collect phyllosomata. On the morning of June 28, ~300,000 newly hatched phyllosomata were observed at the tank's surface. A total of 570 phyllosomata were collected from those that showed strong positive response to a small halogen light (4W) and these were designated for culture.

Phyllosomal Culture

Phyllosomata were cultured under two treatment regimes: 1) individual cultures using small glass bowls (120 and 400 mL) in a static-seawater

system so we could determine individual growth, and 2) a group culture using a 40 L acrylic elliptical tank (see Matsuda and Takenouchi, 2005 for tank details) equipped with flow-through seawater from which we obtained samples for morphological observations and measurements. A total of 20 and 550 newly hatched phyllosomata were used for individual and group cultures, respectively. Culturing methods in this study were similar to those used for phyllosomata of *P. japonicus* and *P. penicillatus* (see Matsuda and Takenouchi, 2005 and Matsuda et al., 2006 for details). Lighting conditions were controlled using full-spectrum fluorescent bulbs equipped with electric timers with photoperiods for both treatments regulated at 12L : 12D. Light intensity during the light phase measured ~30 μmol/m²/s for individual cultures and 5 μmol/m²/s for the group culture.

Individual Culture of Phyllosomata

For individual cultures, 20 phyllosomata were placed into 120 mL glass bowls with 100 mL of seawater until the 70th day of culture, after which animals were transferred into 400 mL glass bowls with 350 mL of seawater. Seawater was changed daily in each bowl after checking for exuviae and mortalities. Culturing vessels were placed in a temperature-regulated water bath (Model RZ-150Y, Rei Sea Ltd., Tokyo, Japan) and maintained at 27°C until 83 days after hatching (DAH) and thereafter kept at 25°C. Intermolt period and molt increment (change in body length; BL) were recorded for each phyllosoma.

Individually cultured phyllosomata from first to fourth instar were fed daily two-day old *Artemia* spp. (~1.0 mm BL), which were cultured with the diatom, *Phaeodactylum tricornutum*, at a density of one individual per mL. Upon reaching the fifth instar, phyllosomata were fed a combination of juvenile or adult *Artemia* cultured with the diatom, along with finely minced mussel gonad. *Artemia* size was gradually increased to 7-9 mm BL as phyllosomata developed; accordingly, *Artemia* density was decreased to 0.1 individuals per mL. Mussel gonad, fed at rations of 10-12 pieces per glass bowl, was also increased from ~1 to ~4 mm³ as phyllosomata grew. Dead *Artemia* and uneaten mussel gonad were removed and replaced with fresh material daily.

Group Culture of Phyllosomata

Newly hatched phyllosomata ($n = 550$) were reared in a 40 L acrylic culture tank (24-25°C; salinity 33-35 psu) with flow-through seawater (60-90 L/h). Phyllosomata were fed similarly to those in individual cultures. *Artemia* densities for group cultures were decreased from 1.0 to 0.03 individuals per mL relative to increases in *Artemia* BL. Approximately 50-60 pieces of minced mussel gonad were prepared and fed once daily. Survival rate (S) for group cultures was calculated as follows:

$$S(\%) = 100 \times \prod_{i=0}^{n-1} S_i$$

where S_i is the survival rate during the period from i th sampling to $(i + 1)$ th for all morphological observations.

Water Treatment

Seawater (33-35 psu) for both the individual (daily water changes) and group cultures (continuous flow) was filtered through a 0.2 μm membrane or cartridge filters that was washed and cleaned at regular intervals. The antibiotic chloramphenicol was added once each week at a concentration of 10 mg liter⁻¹ for 24 h to ameliorate bacterial outbreaks in both culture systems (see Fisher and Nelson, 1978). When serious necrosis of the pereopods and antennules of phyllosomata were observed (~30-150 DAH in the group culture, see results) chemical dosing was increased to twice each week at the same concentration.

Puerulus Culture

Pueruli that metamorphosed in the individual and the group cultures were placed individually in 400 mL glass bowls and cultured in a static-seawater system until they molted to the juvenile stage (see Matsuda et al., 2006). Pueruli do not feed, so were not provided with food (Nishida et al., 1990; Lemmens, 1994; Jeffs et al., 2005). Seawater temperature was kept at 25°C for pueruli from the individual cultures. Pueruli from the group culture were randomly divided into two groups: one reared at 25°C and the other at 27°C.

Morphological Measurements

After each ecdysis, the body length of individually cultured phyllosomata was measured from the anterior margin of the cephalic shield between the

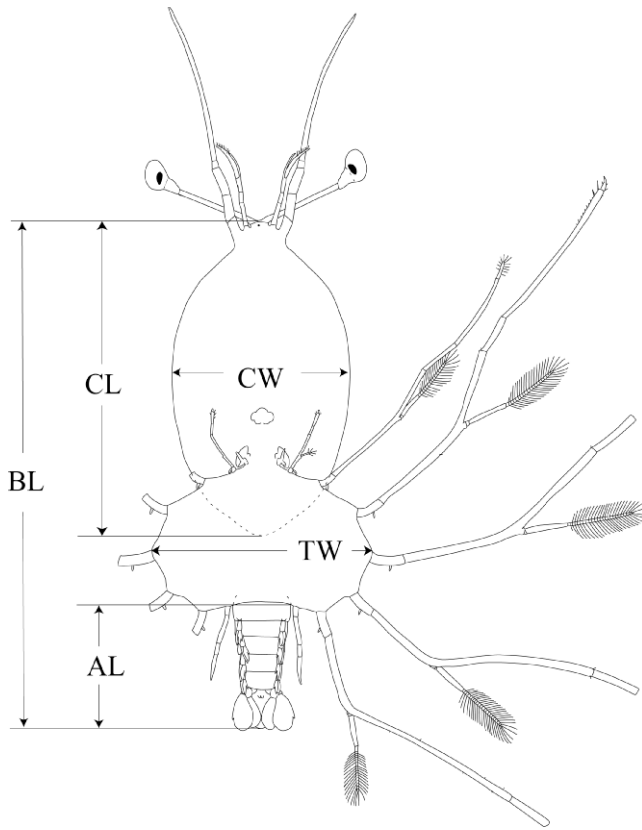


Fig. 1. Diagram showing measurements of *Panulirus argus* phyllosomata. BL: Body length; CL: Cephalic shield length; CW: Cephalic shield width; TW: Thorax width; AL: Pleon length.

eyestalks to the posterior end of the pleon (Fig. 1). BL of pueruli was measured between the anterior margin of the supraorbital plate (which develops into supraorbital spines) to the posterior margin of the telson.

From the group culture, 10 phyllosomata of each instar (1-5) were sampled at regular intervals. Since the number of instars for each phyllosoma could not be recognized beyond the 5th instar, 7-10 phyllosomata were randomly sampled every two weeks between 49-183 DAH thereafter. Beyond 184 DAH, 12 phyllosomata were sampled 341 days after hatch until the completion of culture, at which time 149 phyllosomata were sampled from the group culture, fixed in 5% buffered formalin and then archive-preserved in 70% ethanol.

Body dimensions of specimens preserved were measured as follows (Fig. 1): BL, as mentioned previously; cephalic shield length (CL), from the anterior margin between the eyestalks to the posterior margin of the cephalic shield; cephalic shield width (CW), at the widest section of the cephalic shield; thorax width (TW), at the widest section of the thorax; and abdominal length (AL), from a level line with the base of the pleon to the posterior end of the pleon. Whole body and appendages of phyllosomata were quantified according to Matsuda and Yamakawa (2000). The number of pairs of exopodal natatory setae on the 2nd-3rd maxillipeds and 1st-4th pereopods were also counted (coupled setae on a segment of exopod were counted as one pair, and a non-coupled seta was counted as 1/2). Mandibles, 1st and 2nd maxillae, and 1st maxilliped were not described in this study since their small structure precluded accurate and detailed drawings.

For pueruli from the group culture, BL, cephalothorax length (CL) and antenna length (ANL) were measured: BL, as mentioned before; CL, from the anterior margin of the supraorbital plate to the posterior margin of cephalothorax; ANL, from the posterior margin of basal (5th) segment of antenna to the tip. Molt cuticles of individuals that reached the juvenile stage in the group culture were used for measurements and observations after being fixed in 5% buffered formalin and then archive-preserved in 70% ethanol. Whole body and appendages of pueruli were observed

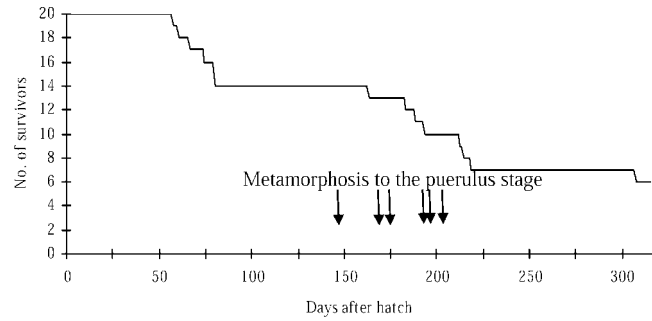


Fig. 2. Survival of phyllosomata of *Panulirus argus* cultured individually.

according to previous studies (Briones-Fourzán and McWilliam, 1997; Inoue et al., 2002), but mandibles, 1st and 2nd maxillae and 1st maxilliped were not observed as in the case with the phyllosoma phase. Measurements and drawings of all phyllosomata and pueruli were made with a Nikon profile projector (model V-12A, Nikon Ltd., Japan) and later digitized using Adobe Illustrator CS2 (Adobe Systems Inc., San Jose, CA USA).

RESULTS

Individual Culture

Six of the 20 individually cultured phyllosomata metamorphosed successfully to the puerulus stage after 140-198 days (mean = 174 days) (Fig. 2). BLs for the final phyllosomal instar ranged from 25.6-28.2 mm (mean = 27.0 mm) and phyllosomata passed through 18-21 instars (mean = 20). Several white horizontal bands appeared on each antenna of the final larval instars and were observed on pueruli as well. The fourteen phyllosomata that did not survive died after 57-308 DAH. The apparent cause of death was bacterial infection, as indicated by cloudiness in the antennal gland, midgut gland, and intestine, and complications due to molting as seen in similar culture studies (Matsuda and Yamakawa, 2000).

The mean BL for the 1st instar (newly hatched) phyllosomata in individual cultures was 1.62 mm (range = 1.56-1.66 mm, $n = 20$). BL increased sigmoidally with development throughout the phyllosoma phase except for the 23rd-25th instars (Fig. 3). The duration of each instar was relatively constant at 6-7 days until the 12th instar, after which instar duration increased gradually to ~two weeks at the 19th instar (Fig. 4).

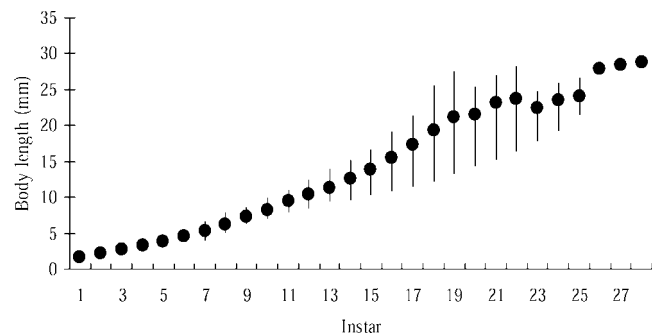


Fig. 3. Relationship between body length and instar for individually cultured *Panulirus argus* phyllosomata. Circles (●) and vertical bars indicate the mean and the range of body length.

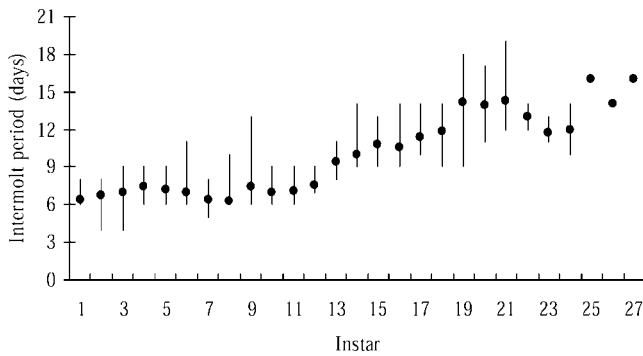


Fig. 4. Relationship between intermolt period and instar for individually cultured *Panulirus argus* phyllosomata. Circles (●) and vertical bars indicate the mean and the range of intermolt period.

Group Culture

For the first month of the study, 10-30 phyllosomata died per day due to unknown causes. An additional episode of disease that caused necrosis of the pereiopods and antennules of phyllosomata in group culture appeared and continued until ~150 DAH. Survival of the phyllosomata in group culture was 47% at 30 DAH, 36% at 60 DAH, 28% at 100 DAH, and 23% at 150 DAH. A total of 13 phyllosomata from the group culture metamorphosed successfully to the puerulus stage after 152-311 DAH (mean = 223.0 days).

Lewis (1951) assigned phyllosomata obtained from plankton tows to 11 stages based on body shape and the development of antennule, antennae, and pereiopods. However, there are many differences in the development of appendages noted in his study compared to the present study. We assigned 146 *P. argus* phyllosomata to 10 stages according to staging criteria modified from Lewis (1951) and Matsuda et al. (2006) (Table 1). A summary of developmental traits is given in Table 2, and various body dimensions for each phyllosoma stage are presented in Table 3. Descriptions of each developmental stage are provided in Appendix I.

Newly hatched phyllosomata were positively phototactic for ~60 DAH. Up to 60 DAH, phyllosomata typically aggregated in patches near the surface of the water during the day, but after 60 DAH they became negatively phototactic and gathered on the bottom of the tank to escape illumination from above.

Pueruli

The BL of pueruli that metamorphosed in the individual ($n = 6$) and group cultures ($n = 13$) measured from 16.4-17.5 mm (mean = 17.0 mm) and from 15.7-17.9 mm (mean = 17.0 mm), respectively; whereas their CL measured 6.20-6.75 mm, (mean = 6.34) for individually cultured animals and 6.00-6.70 mm, (mean = 6.35) for group-cultured animals. Of the six pueruli from the individual cultures, one puerulus died one day following metamorphosis and five molted to the first juvenile instar 15-26 days after metamorphosis (mean = 22.6 days). Of the 13 pueruli obtained from the group culture, one puerulus died four days post metamorphosis; six reached the juvenile stage 16-26 days post metamorphosis (mean = 20.7 days) at 25°C while six molted

Table 1. Phyllosoma key to stages of *Panulirus argus* modified from key for *Panulirus longipes* by Matsuda and Yamakawa (2000).

1.	Eyestalk unsegmented	Stage I
	Eyestalk segmented	2
2.	Exopod of 3rd pereiopod not setose	Stage II
	Exopod of 3rd pereiopod setose	3
3.	Fifth pereiopod absent	Stage III
	Fifth pereiopod present	4
4.	Exopod of fourth pereiopod not setose	Stage IV
	Exopod of fourth pereiopod setose	5
5.	Telson not differentiated	Stage V
	Telson differentiated	6
6.	Uropod bud unclft	Stage VI
	Uropod bud cleft or bifid	7
7.	Pleopod bud unclft	Stage VII
	Pleopod bud cleft or bifid	8
8.	Exopod of 2nd maxilliped not setose	Stage VIII
	Exopod of 2nd maxilliped setose	9
9.	Gill bud absent or present as papilla or unilobed bud	Stage IX
	Coxae of 1st to 4th pereiopods with bilobed gill buds	Stage X

to the juvenile stage 11-18 days post metamorphosis (mean = 15.0 days) at 27°C. Pueruli used their pleopods to propel themselves forward in the vessels or stayed near the shelter during the daytime until 2-3 days after metamorphosis, after which they crawled into the shelter and became cryptic.

Pueruli were completely transparent except for their brown eyes and red pigments at the tip of their antennae in addition to 6-7 white horizontal bands running the length of their antennae. Pigment gradually appeared under the cuticle of each puerulus; the first pigment appeared as white bands on the anterior margin of the eye-stalk 2-3 days after metamorphosis (at 25°C). The spines on the basal segments of antennae then became tinged with yellow 6-7 days after metamorphosis and small patches of white pigment emerged on the carapace behind the eyes. After that, red pigments appeared on the lateral edges of the carapace and pleon while the center of the carapace and pleon remained transparent. The center of the carapace and pleon turned white just before molting to the 1st instar juvenile stage, and the hepatopancreas became visible as a whitish yellow V-shape organ (see Jeffs et al., 1999). A complete description of the puerulus stage is provided in Appendix I.

DISCUSSION

Although *P. argus* sustains one of the most significant lobster fisheries in the world, comprising nearly 46% of the total catch for all spiny lobsters (FAO, 2006), a complete pelagic description and information on phyllosomal development, duration, and growth has been unavailable because this species had never been cultured through all its phyllosomal stages. For the first time, we have successfully cultured *P. argus* from egg to the early benthic juvenile stage and have obtained estimates of phyllosomal duration, growth, and the number of instars and stages. This species is the fifth documented of 21 extant *Panulirus* spp. to be cultured completely from hatch to settlement stage (*P. japonicus*: Yamakawa et al., 1989; Kittaka and Kimura, 1989; *P. longipes*: Matsuda and Yamakawa, 2000; *P. homarus* (Linnaeus, 1758): Sekine and Murakami (personal

Table 2. Developmental summary characteristics for phyllosomata of *Panulirus argus*. (biram) biramous; (diff) differentiated; (exop) exopod; (fs) fringing setae; (Its) long terminal setae; (ped) peduncle; (rect) rectangular; (rud) rudimentary; (seg) segmented; (segs) segments; (st) strong terminal spine; (tps) terminal plumose setae; (unseg) unsegmented. =, same as in the previous stage. *1: Integral numbers indicate the number of paired setae; 0.5 denotes the existence of non-paired seta.

Stage	Eyestalk	Antennule	Antenna	First maxilla			Second maxilla	First maxilliped	Fourth pereiopod	Fifth pereiopod	Ventral coxal spine		
				Coxal endite	Basal endite						First pereiopod	Second pereiopod	Third pereiopod
I	Unseg	Unseg	Unseg	2 Its	2 st	4 tps	Bud	Absent	Absent	Present	Present	Present	
II	Seg	=	=	=	=	=	=	=	=	=	=	=	
III	=	=	=	=	=	3-4 tps	Small bud	Bud	=	=	=	=	
IV	=	1-3 segs	=	=	=	=	Minute bud	Bud or 2 segs	Bud	=	=	=	
V	=	3-4 segs	1-2 segs	=	2-3 st	1-4 tps	=	5 segs	=	=	=	=	
VI	=	4 segs	1-3 segs	=	=	0 tps	Bud	=	=	Present or absent	Present or absent	Present or absent	
VII	=	=	2-5 segs	=	3 st	=	Elongated bud	=	=	=	=	Absent	
VIII	=	=	5 segs	=	=	0-14 fs	Elongated bud or 2 lobed bud	=	Bud or 2 segs	Absent	Absent	=	
IX	=	=	=	=	=	8-43 fs	2-3 lobed bud	=	2-4 segs	=	=	=	
X	=	=	=	=	=	25->80 fs	3 lobed bud	=	4-5 segs	=	=	=	

communication); *P. penicillatus*: Matsuda et al., 2006) and the first of the five species of *Panulirus* inhabiting the Atlantic Ocean.

Phyllosomal Duration and Growth

Our results demonstrate that *P. argus*, along with *P. homarus* and *P. ornatus* (Fabricius, 1798), exhibit the shortest PLD among the nine panulirid lobsters whose PLDs have been estimated, largely based on phyllosomal size structure from plankton samples or the elapsed time between hatching season and settlement (Inoue, 1980; Phillips and Sastry, 1980; Dennis et al., 2001). The mean PLD for *P. argus* was determined to be 174 days, with a minimum duration of 140 days in the laboratory. This minimum PLD is shorter than that of *P. japonicus* (245 days, Matsuda and Takanouchi, 2006), *P. longipes* (284 days, Matsuda and Yamakawa, 2000) and *P. penicillatus* (256 days, Matsuda et al., 2006), which were cultured under similar conditions. Even considering that the seawater temperature during culture of *P. argus* phyllosomata was $\sim 1^\circ\text{C}$ higher than that for the other species, *P. argus* has a considerably reduced PLD, fewer molts (mean = 20; range: 18-21), and a smaller final instar size (mean BL = 27.0 mm; range: 25.6-28.2 mm BL) than the four previously cultured species of *Panulirus*. Moe (1991) cultured newly hatched *P. argus* phyllosomata with diets of wild plankton (*Artemia*, jellyfish, and fish larvae) and obtained 7th instar phyllosomata of about 12 mm body length in less than 81 days; unfortunately these results are unpublished. Those phyllosomata, however, grew as fast or faster compared with those in our study, corroborating our finding that *P. argus* exhibits a shorter pelagic life than previously thought.

From modal progressions of developmental stages of phyllosomata from field samples, the PLD of *P. argus* has previously been estimated at 6-12 months (Lewis, 1951; Sims and Ingle, 1966; Farmer et al., 1989). Our laboratory-based PLD estimate of 6.5 months (range: 4.5-8 months) falls at the low end of those previous estimates. To date, comparative pelagic lifespans in the field and in captivity have been reported for two palinurid lobsters. The pelagic

lifespan for *P. penicillatus* in captivity corresponds accordingly with that of wild-caught specimens (Matsuda et al., 2006), whereas in *P. japonicus* the phyllosomal duration under laboratory conditions is somewhat shorter than that under natural conditions (8-10 months in captivity vs. 1 year in wild) (Matsuda and Takenouchi, 2006; Inoue, 1980). Phillips and Sastry (1980) questioned the validity of PLD for larvae cultured under artificial conditions due to differences in the development between plankton and laboratory-cultured specimens. Cultured larvae, in general, grew sub-optimally and typically differed from wild-caught larvae in minor morphological characteristics. However, recent improvements in culture techniques (e.g., live foods, enhanced water quality, ultra-filtration, disease control) coupled with innovative tank designs for zooplankton (Cox and Johnston, 2003; Raskoff et al., 2003; Matsuda and Takenouchi, 2005) have significantly improved larval production and survivorship (Ritar, 2001; Matsuda and Takenouchi, 2005).

Because of its commercial value, there has been interest in *P. argus* aquaculture for some time (Lellis, 1991; Moe, 1991; Jeffs and Davis, 2003) and with little progress on phyllosomal culture in palinurids, researchers have thus far turned to the capture and grow-out of wild-caught postlarvae and juveniles. However, difficulties in extracting large numbers of juveniles from the wild poses logistical and legal hurdles and may have deleterious ecological impacts on wild populations. Instead, interest worldwide has turned to the capture and culture of wild pueruli for grow-out, which may be a commercially viable and ecologically benign method for aquaculture or for the augmentation of wild stocks (Phillips et al., 2003). However, the low survival of pueruli and early benthic juvenile *P. argus* in the wild (Butler et al., 1997; Butler and Herrnkind, 1997; Acosta and Butler, 1999; Sharp et al., 2000) and the high protein requirements of the fast-growing, predatory juveniles (Herrnkind et al., 1988; Lellis and Russell, 1990; Booth and Kittaka., 2000; Briones-Fourzan et al., 2003) must be seriously evaluated for such enterprises.

Table 2. Continued.

Stage	No. of pairs of natatory setae on exopod of* ¹						Pleopod	Uropod	Telson	Exterior of Pleon	Gill buds
	Second maxilliped	Third maxilliped	First pereopod	Second pereopod	Third pereopod	Fourth pereopod					
I	No exop	3	5	5	Exop bud	Absent	Absent	Absent	Absent	Unseg	Absent
II	=	3	6	5.5-6	Elongated exop bud	=	=	=	=	=	=
III	=	3.5-5	6.5-10	6.5-10	3-7.5	No exop or exop bud	=	=	=	=	=
IV	=	4.5-7	8.5-12.5	71-13	6-10.5	=	=	=	=	=	=
V	=	7-10	11.5-17	12-16.5	9.5-14.5	0.5-9	=	Absent or rud bud	=	=	=
VI	=	9-13.5	14-18	15.5-20	12-17	7-15	=	Bud	Diff	=	=
VII	No exop or rud exop bud	13-16	17.5-21	19-21.5	14-17.5	13.5-16.5	Small bud	Cleft bud or biram	=	=	=
VIII	Exop bud	15.5-19.5	18-25	19-26.5	19.5-23	17.5-22	Bifid or biram	Biram	=	Slight seg or seg	Absent or minute bud
IX	0.5-3.5	16-22.5	20.5-28	19-28	18.5-27	19.5-24.5	+ Rud appendix interna	+ Lateral serration	=	Seg	Absent or unilobed bud
X	2-7	19-24	24-31	25.5-30.5	23.5-28	22-27	+ Appendix interna	=	=	=	Bilobed bud

Phyllosomal Stages

Lewis (1951) described 11 stages of *P. argus* phyllosomata collected from plankton tows in the western Atlantic and Caribbean. Stages I-III of our descriptions correlate fairly well his stages 1-3. Beyond stage III, however, the developmental rate of antennules, antennae, and abdominal segmentation, (traits that Lewis considered important descriptors between stages) differ between the phyllosomata we reared

and his collections. Segmentation of antennules and antennae developed in a relatively short time after stage III in the present study, whereas the phyllosomata described by Lewis appeared to develop appendages incrementally, and segmentation in antennules and antennae in synchrony. For example, Lewis describes stage V phyllosomata as having 2-segmented antennules and 1-segmented antennae, whereas stage VI phyllosomata exhibited 3-segmented antennules

Table 3. Morphometric size comparisons for phyllosomata of *Panulirus argus* reared in the laboratory. (BL) body length; (CL) cephalic shield length; (CW) cephalic shield width; (TW) thorax width; (AL) pleon length.

Stage (N)	I (10)	II (10)	III (28)	IV (19)	V (13)	VI (15)	VII (11)	VIII (21)	IX (14)	X (8)
Body Dimension:										
BL (mm)										
mean	1.60	2.23	3.28	4.57	6.73	9.55	13.19	17.48	22.30	28.78
min.	1.55	2.18	2.56	3.84	5.45	7.60	11.30	15.45	19.10	25.10
max.	1.63	2.28	3.98	5.78	8.50	11.23	16.62	21.50	26.98	32.73
std error	0.01	0.01	0.08	0.14	0.25	0.30	0.32	0.33	0.53	0.82
CL (mm)										
mean	0.93	1.42	2.28	3.36	5.02	7.23	9.79	12.57	15.08	17.88
min.	0.90	1.40	1.68	2.72	4.05	5.75	8.53	11.38	13.36	15.40
max.	0.95	1.46	2.86	4.89	6.45	8.45	12.14	14.52	17.55	19.80
std error	0.00	0.01	0.07	0.14	0.20	0.23	0.20	0.18	0.29	0.45
CW (mm)										
mean	0.73	0.97	1.36	1.81	2.55	3.67	5.21	6.82	8.35	10.16
min.	0.72	0.80	1.11	1.52	2.05	2.88	4.40	6.10	7.49	9.66
max.	0.76	1.01	1.64	2.30	3.35	4.50	6.60	7.80	9.97	11.14
std error	0.00	0.02	0.03	0.05	0.10	0.13	0.15	0.10	0.17	0.20
TW (mm)										
mean	0.53	0.78	1.30	2.01	3.28	4.86	6.74	8.76	10.26	12.25
min.	0.51	0.75	0.96	1.56	2.50	3.75	5.80	7.80	9.13	11.03
max.	0.56	0.82	1.66	2.72	4.30	5.90	7.90	10.05	11.34	13.68
std error	0.00	0.01	0.04	0.08	0.14	0.16	0.17	0.12	0.15	0.26
AL (mm)										
mean	0.23	0.25	0.32	0.38	0.51	0.64	1.05	1.96	3.81	6.92
min.	0.22	0.24	0.28	0.34	0.45	0.55	0.68	1.40	2.55	5.37
max.	0.24	0.26	0.36	0.44	0.58	0.75	1.70	3.44	5.63	8.24
std error	0.00	0.00	0.00	0.01	0.01	0.02	0.07	0.11	0.21	0.32

and 2-segmented antennae. In contrast, the development of antennules and antennae by phyllosomata in our study did not occur in synchrony. There were phyllosomata, for instance, that had 3-4 segmented antennules and 1-segmented antennae. Therefore, the phyllosomata that we cultured could not be unequivocally assigned to stages according to Lewis (1951), especially those beyond stage III, so we propose a new set of criteria modified from those accepted for *P. longipes* (Matsuda and Yamakawa, 2000). Criteria were selected such that overlaps between successive stages in body lengths were minimized. However, the staging criteria for *P. longipes* were not directly applied to *P. argus* phyllosomata because there are stark differences in the development of certain structures. For instance, the staging criteria describing Stage IV for *P. longipes* includes the presence of segmented 4th pereopods without setose exopods. However, there were only a few animals where this was the case for *P. argus* phyllosomata cultured in this study because both the segmentation and setae of exopods on the 4th pereopod appeared almost simultaneously.

Puerulus Stage

Panulirus argus pueruli described and illustrated by Lewis et al. (1952) from collectors along the Florida coast contain many similarities to our specimens, with the exception of a few additional setae on the penultimate segment of the endopod of the 2nd maxilliped on pueruli that we cultured. The body size (CL) of the pueruli that we cultured (mean CL = 6.3 mm, $n = 19$) was also similar as that reported for wild-caught pueruli in other studies (mean CL = 6.1 mm, $n = 25$, Lewis et al., 1952; mean CL = 6.1 mm, $n = 321$, Sweat, 1968; mean CL = 6.1 mm, $n = 597$, Yeung et al., 2001; mean CL = 6.2 mm, $n = 925$, Goldstein, 2007).

McWilliam (1995) classified *Panulirus* pueruli into four groups (P1-P4) based on selected morphological characteristics, including: sternal spines, apex of antennal flagellum, antenna length relative to BL and exopod condition of 2nd and 3rd maxillipeds. For example, Lewis et al. (1952) characterized *P. argus* pueruli they captured as possessing no diagnostic sternal spines, tapered antenna and long exopods on 2nd and 3rd maxillipeds, including a relatively shortened antenna, ~1.5 times as long as BL, which would place these in group P1. The pueruli that we reared developed in accordance with the characteristics that McWilliam described, except that the ratio of antennal length to BL (about 1.3) in our specimens was slightly smaller (~ 1.5) than that described by Lewis et al. (1952). McWilliam (1995) suggested the possibility that small, but nondiagnostic posterolateral sternal spines may occur in the puerulus phase of group P-1, although Lewis et al. (1952) did not mention whether the small sternal spines were present; they were in the pueruli we cultured.

CONCLUSIONS

Our successful culture of *P. argus* from egg to early benthic juvenile provides the first complete description of the phyllosomal and postlarval stages of the most economically important species of spiny lobster in the western hemisphere. Our estimates of PLD for this species are shorter than previously thought and among the shortest for palinurids, although still appreciably longer than those

reported for nearly all marine fishes and invertebrates. The information reported here on PLD, growth, and size-at-age along with as yet unpublished data on ontogenetic changes in vertical migratory behavior, are crucial for the proper modeling of larval dispersal. We are currently incorporating these data into a Lagrangian particle model linked with the Hybrid Coordinate Ocean Model (HYCOM) to generate predictions of *P. argus* larval connectivity among Caribbean regions as has been accomplished for several coral reef fishes (Cowen et al., 2006). Understanding the potential population connectivity and local retention of *P. argus* within the Western Atlantic is of paramount importance for management of this valuable fishery species.

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APPENDIX I

Phyllosomal Descriptions

Phyllosoma Stage I ($n = 10$).—Eye (Fig. 5a). Eyestalk unsegmented.

Cephalic shield (Fig. 5a). Pear-shaped in outline, mean value of CW/CL 0.790 (range = 0.766-0.809), distinctly wider than thorax.

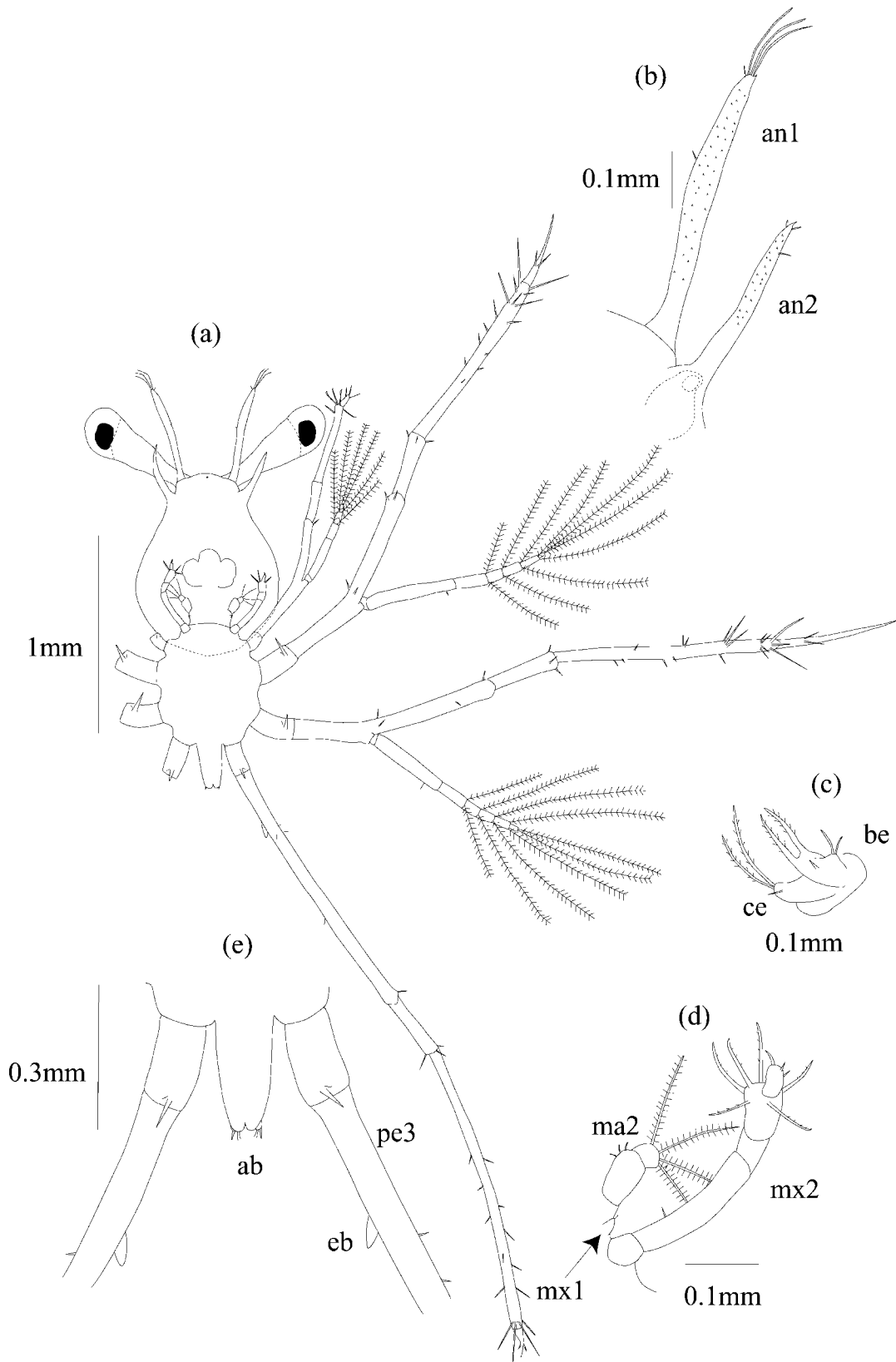


Fig. 5. Phyllosoma Stage I of *Panulirus argus*. a, ventral view; b, left antennule (an1) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, 3rd pereiopod (pe3) with exopod bud (eb) and pleon (ab), ventral.

Antennule (Fig. 5b). Uniramous and unsegmented, with scattered small spines; 3 long sensory setae and 1 short seta present at distal end; 1 short seta present at position of future segmentation (middle of antennule).

Antenna (Fig. 5b). Uniramous, with scattered small spines, shorter than antennule.

First maxilla (Fig. 5c). Coxal endite with 2 long serrated terminal setae and 1 short subterminal seta; basal endite with 2 strong serrated terminal spines and 1 short subterminal seta, along with 2 short setae on vestigial palp.

Second maxilla (Fig. 5d). 2-segmented; larger basal segment with 3 short setae on anterior margin; smaller distal segment bearing 4 long plumose setae.

Maxillipeds (Fig. 5a-d). 1st maxilliped present as small bud with 1 seta at top, located near coxa of 2nd maxilla; 2nd maxilliped 5-segmented, without exopod; 3rd maxilliped well-developed, having exopod bearing 3 pairs of natatory plumose setae.

Pereiopods (Fig. 5a-e). 1st and 2nd pereiopods 5-segmented, exopod with 5 pairs of natatory plumose setae; exopod of 3rd pereiopod present as small bud; each 1st-3rd pereiopod with 1 ventral coxal spine and 1 accessory seta; 4 and 5 pereiopods absent.

Pleon (Fig. 5e). Longer than coxa of 3rd pereiopod, bearing 1 postero-lateral spine with 2-3 short basal setae at each side; pleopod, uropod and telson not differentiated.

Phyllosoma Stage II ($n = 10$).—Eye (Fig. 6a). Eyestalk segmented, approx. 1/3 length of whole eye.

Cephalic shield (Fig. 6a). Becoming elongated, mean value of CW/CL 0.680 (range = 0.571-0.704).

Antennule (Fig. 6b). With 4 long sensory setae and 1 short seta at distal end, plus 1 subterminal seta.

Antenna (Fig. 6b). No marked change.

First maxilla (Fig. 6c). No marked change.

Second maxilla (Fig. 6d). No marked change.

Maxillipeds (Fig. 6a-d). No marked change.

Pereiopods (Fig. 6a). Exopods of 1st and 2nd pereiopods with 6 and 5.5-6 pairs of natatory plumose setae, respectively; exopod of 3rd pereiopod as long as pleon, still without plumose setae.

Pleon (Fig. 6e). No marked change.

Phyllosoma Stage III ($n = 28$).—Eye (Fig. 7a). Eyestalk becoming relatively longer than in Stage II.

Cephalic shield (Fig. 7a). Becoming more elongated, mean value of CW/CL 0.602 (range = 0.544-0.661), still slightly wider than or as wide as thorax.

Antennule (Fig. 7b). With 1 subterminal sensory seta.

Antenna (Fig. 7b). No marked change.

First maxilla (Fig. 7c). Coxal endite with 1-2 short subterminal setae.

Second maxilla (Fig. 7d). No marked change.

Maxillipeds (Fig. 7a-d). 1st maxilliped becoming relatively smaller than in Stage II; exopod of 3rd maxilliped with 3.5-5 pairs of natatory plumose setae.

Pereiopods (Fig. 7a-e). Exopod of 3rd pereiopod with 3-7.5 pairs of natatory plumose setae; 4th pereiopod present as small bud without exopod or as elongated bud with minute exopod bud at base of pleon, shorter than 1/2 length of pleon.

Pleon (Fig. 7e). No marked change.

Phyllosoma Stage IV ($n = 19$).—Eye (Fig. 8a). Eyestalk approx. 1/2 length of whole eye.

Cephalic shield (Fig. 8a). Mean value of CW/CL 0.543 (range = 0.417-0.589), medial part in posterior margin slightly projecting posteriorly, slightly narrower than thorax.

Antennule (Fig. 8b). 1-3-segmented, inner flagellum present as minute lump or round process at the middle; distal segment with 1-2 rows of subterminal sensory setae.

Antenna (Fig. 8b). No marked change.

First maxilla (Fig. 8c). Basal endite with 2 strong serrated terminal spines and 1-2 short subterminal setae, along with 2 short setae on vestigial palp.

Second maxilla (Fig. 8d). Distal segment bearing 0-4 long plumose setae.

Maxillipeds (Fig. 8a-d). 1st maxilliped minute bud, apical seta disappearing in many individuals.

Pereiopods (Fig. 8a-e). 4th pereiopod 2-segmented in advanced individuals, exopod bud without plumose setae; 5 pereiopod present as small bud at base of pleon.

Pleon (Fig. 8e). No marked change.

Phyllosoma Stage V ($n = 13$).—Eye (Fig. 9a). Eyestalk slightly longer than 1/2 length of whole eye.

Cephalic shield (Fig. 9a). This stage, together with stage VI, having relatively the narrowest cephalic shield, mean value of CW/CL 0.508 (range = 0.495-0.526), noticeably narrower than thorax.

Antennule (Fig. 9b). 3-4-segmented, bearing 2-4 rows of subterminal sensory setae.

Antenna (Fig. 9b). With a segmentation at the middle in advanced individuals.

First maxilla (Fig. 9c). Coxal endite with 1-4 short subterminal seta; basal endite with 2-3 strong serrated terminal spines and 3-4 subterminal short setae.

Second maxilla (Fig. 9d). Basal segment with 2-3 short setae on anterior margin; distal segment lacking long plumose setae in many individuals.

Maxillipeds (Fig. 9a-d). No marked change.

Pereiopods (Fig. 9a-e). 4th pereiopod 5-segmented, exopod with 0.5-9 pairs of plumose setae; 5th pereiopod located slightly at distance from base of pleon in some individuals, 1/5 length of pleon.

Pleon (Fig. 9e). Uropod differentiated as faint swelling or rudimentary bud in many individuals; pleopod and telson absent.

Phyllosoma Stage VI ($n = 15$).—Eye (Fig. 10a). Eyestalk elongated.

Cephalic shield (Fig. 10a). Mean value of CW/CL 0.508 (range = 0.493-0.533).

Antennule (Fig. 10b). 4-segmented; inner flagellum present as finger-like process on antero-lateral margin of 3rd segment; 4th (distal) segment with 2-5 rows of subterminal sensory setae.

Antenna (Fig. 10b). 1-3-segmented.

First maxilla (Fig. 10c). Coxal endite with 3-5 short subterminal setae.

Second maxilla (Fig. 10d). Somewhat broader, lacking apical plumose setae, with 1-4 short setae on anterior margin of basal segment.

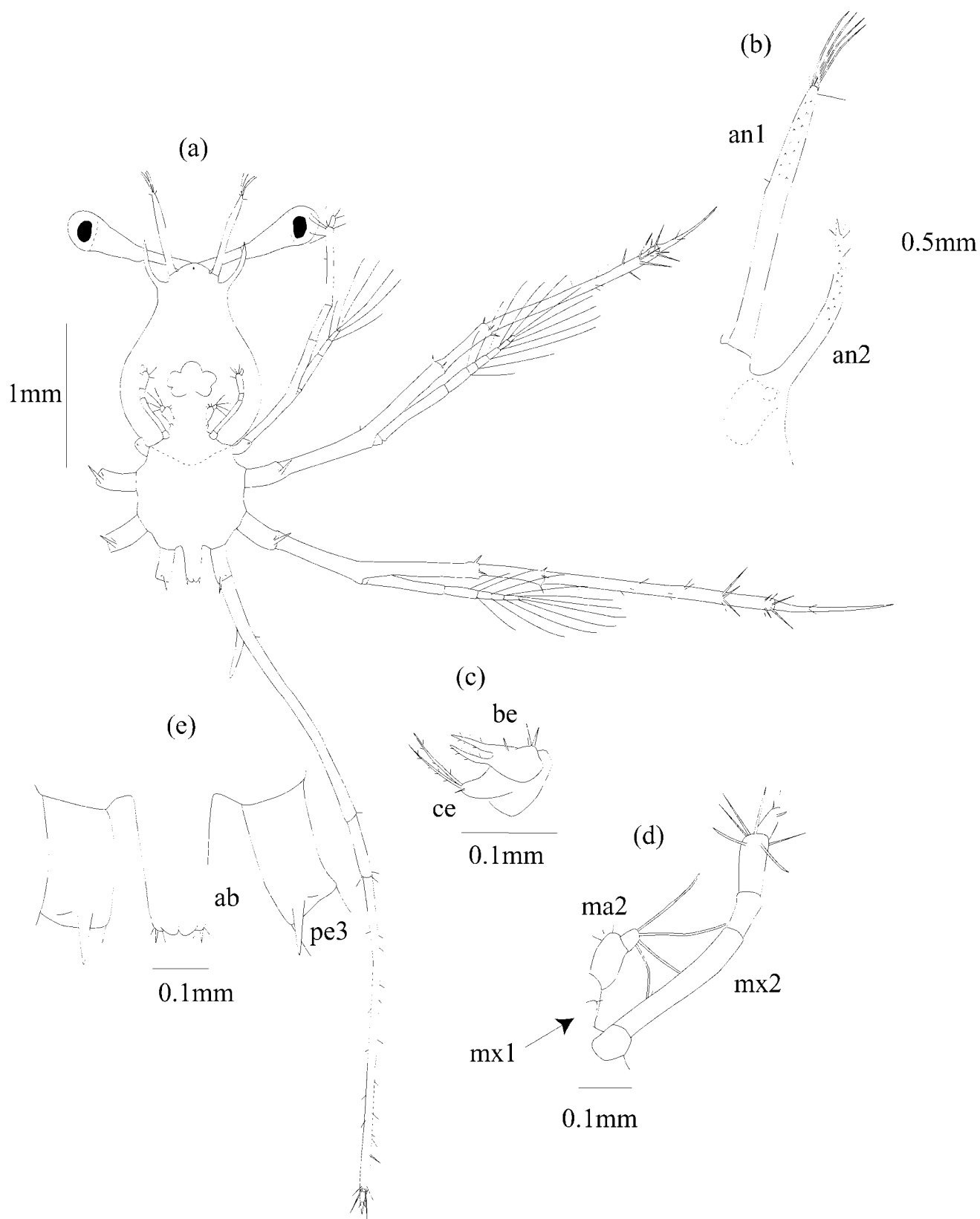


Fig. 6. Phyllosoma Stage II of *Panulirus argus*. a, ventral view; b, left antennule (an1) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, coxa of 3rd pereiopod (pe3) and pleon (ab), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

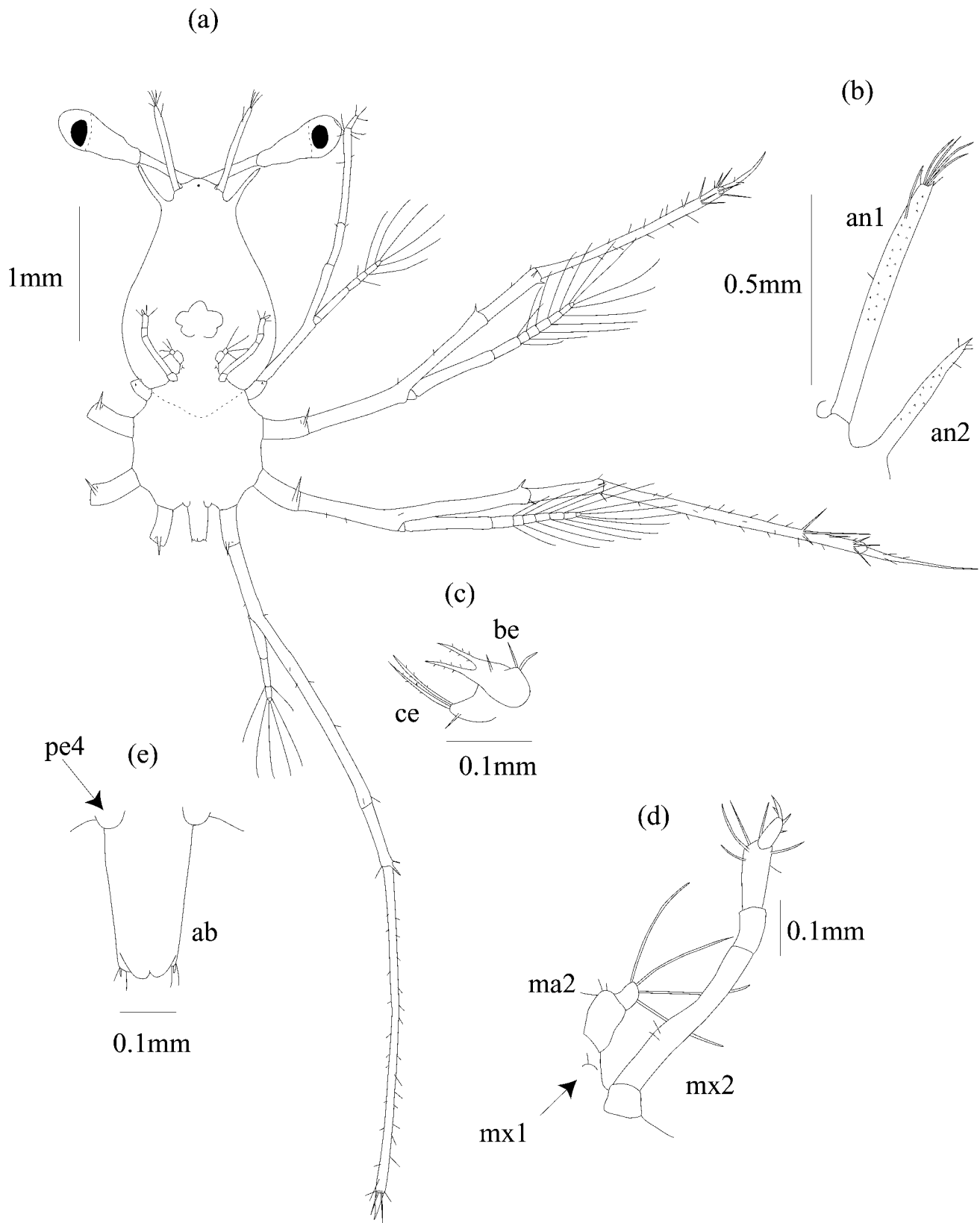


Fig. 7. Phyllosoma Stage III of *Panulirus argus*. a, ventral view; b, left antennule (an1) and antenna (an2), ventral view; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, 4th pereiopod (pe4) and pleon (ab), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

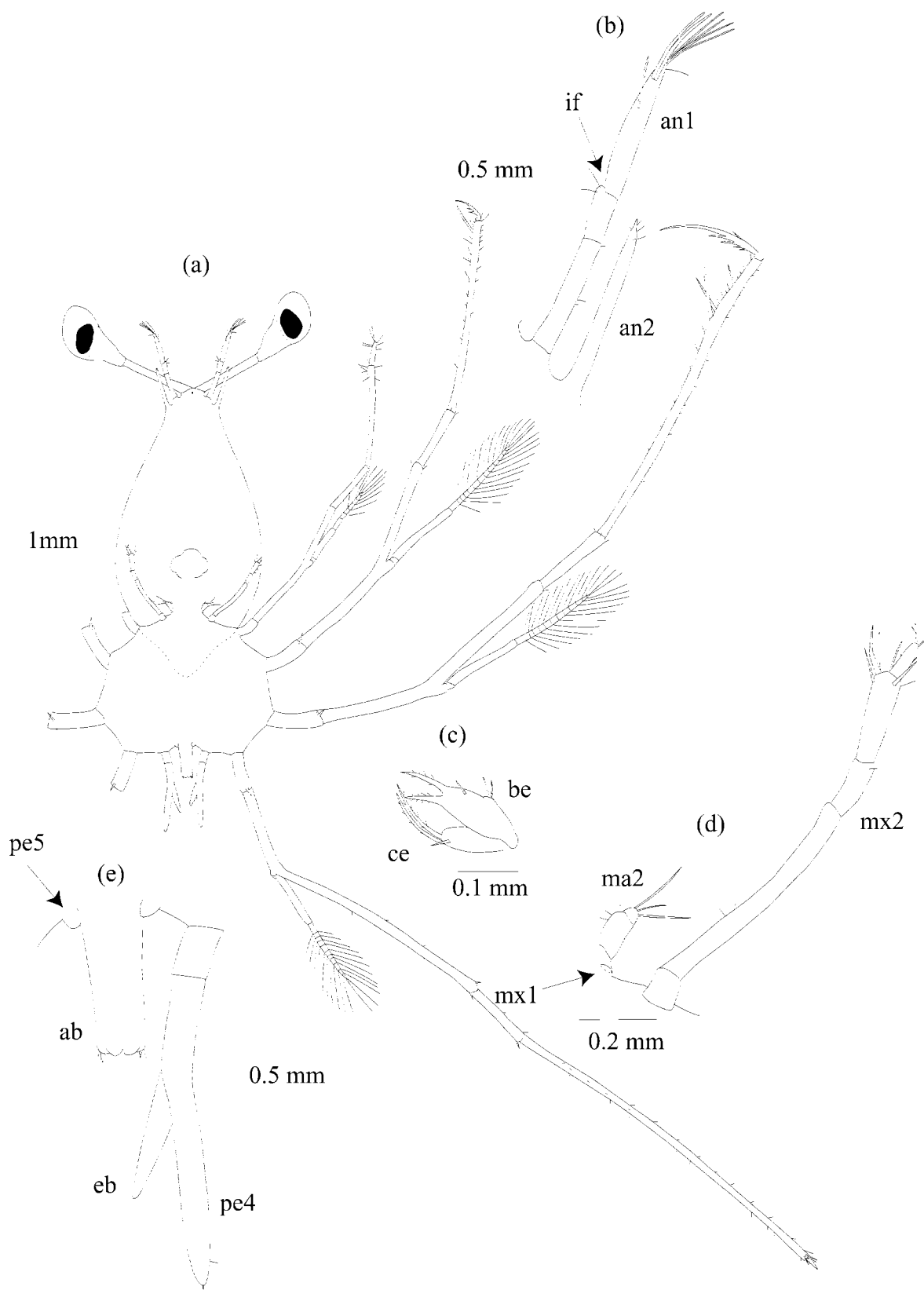


Fig. 8. Phyllosoma Stage IV of *Panulirus argus*. a, ventral view; b, left antennule (an1) with rudimentary inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, 4th pereiopod (pe4) with exopod bud (eb), 5th pereiopod (pe5) and pleon (ab), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

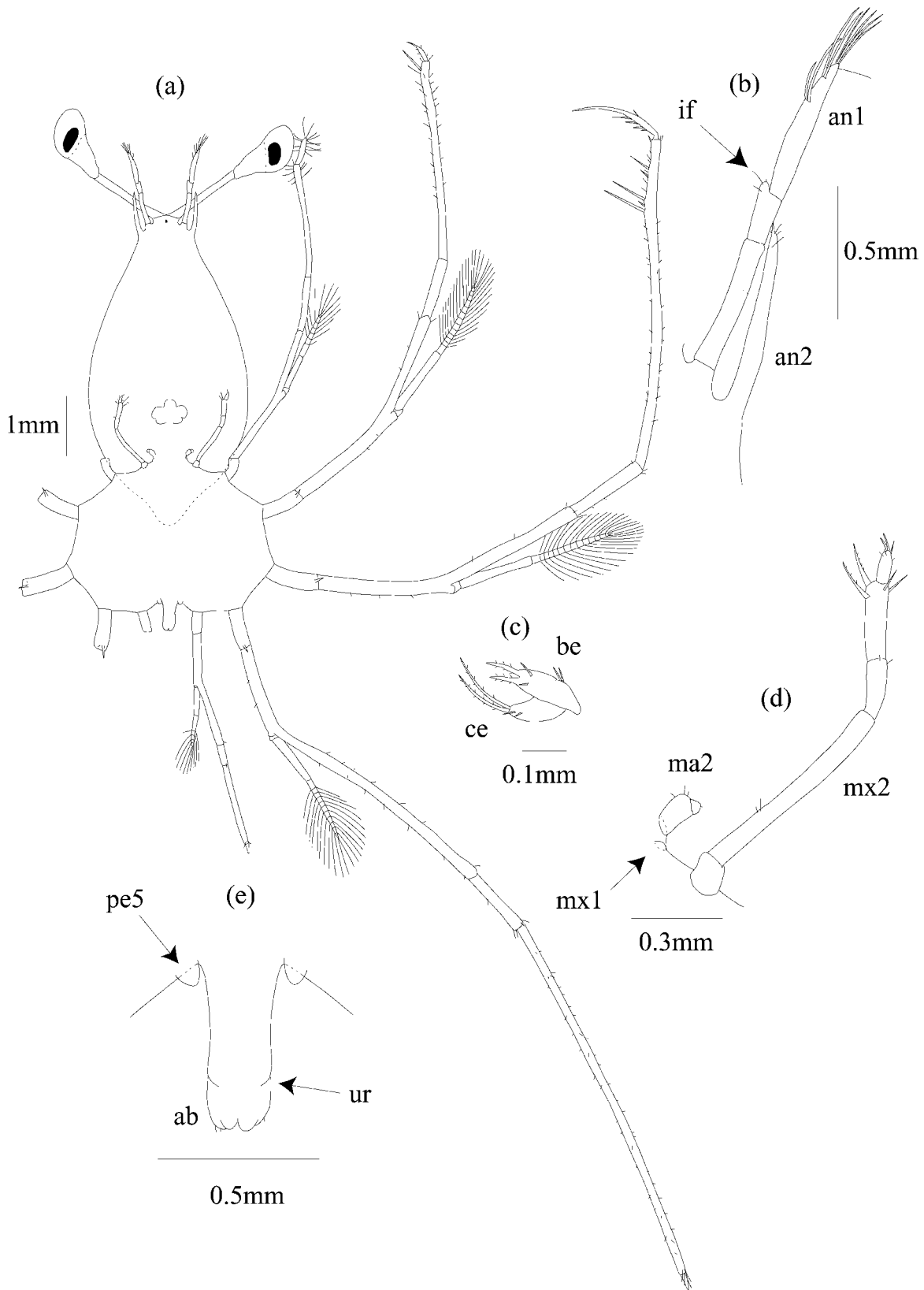


Fig. 9. Phyllosoma Stage V of *Panulirus argus*. a, ventral view; b, left antennule (an1) with minute inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), rudimentary 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, ventral view of 5th pereiopod (pe5) and pleon (ab) with rudimentary uropod (ur). Setules on plumose setae of pereiopods are not shown.

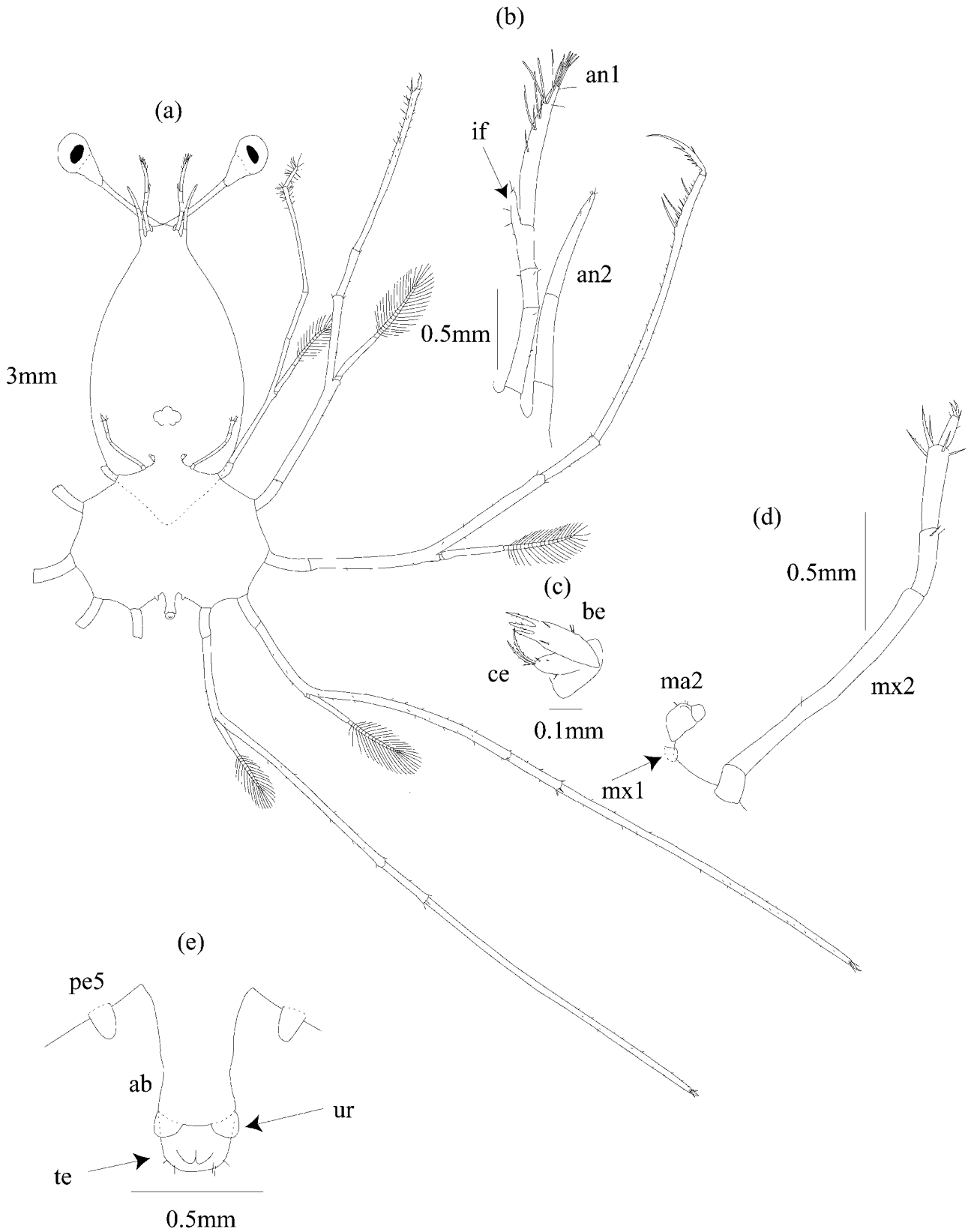


Fig. 10. Phyllosoma Stage VI of *Panulirus argus*. a, ventral view; b, left antennule (an1) with inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); e, 5th pereiopod (pe5) and pleon (ab) with uropod (ur) and telson (te), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

Maxillipeds (Fig. 10a-d). 1st maxilliped developing to conical bud agian.

Pereiopods (Fig. 10a-e). 5th pereiopod located at distance from base of pleon, around 1/7 length of pleon; ventral coxal spines on 2nd-3rd pereiopods disappearing in many individuals.

Pleon (Fig. 10e). Broadened at base and minimum width at middle of length; uropod bud; telson differentiated; pleopod absent.

Phyllosoma Stage VII ($n = 11$).—Eye (Fig. 11a). Eyestalk around 3/5 length of whole eye.

Cephalic shield (Fig. 11a). Lemon-shaped in outline, becoming relatively wider than in the previous stage, mean value of CW/CL 0.531 (range = 0.507-0.593), maximum width located near to middle of length.

Antennule (Fig. 11b). 4th segment with 6-9 rows of subterminal sensory setae.

Antenna (Fig. 11b). 2-5-segmented, as long as antennule.

First maxilla (Fig. 11c). Coxal endite with 4-7 short subterminal setae; basal endite with 3 strong serrated terminal spines.

Second maxilla (Fig. 11d). Distal segment expanding posteriorly in some individuals.

Maxillipeds (Fig. 11a-d). 1st maxilliped elongated bud; exopod of 2nd maxilliped present as minute protuberance in advanced individuals.

Pereiopods (Fig. 11a-e). 5th pereiopod elongated, 1/6-1/3 length of pleon; ventral coxal spines on all pereiopods absent in most individuals; minute sternal spines present near the coxae of 2nd-3rd pereiopods in well-advanced individuals.

Pleon (Fig. 11e). Pleopod 2-4 pairs of small buds; uropod cleft bud or biramous.

Phyllosoma Stage VIII ($n = 21$).—Eye (Fig. 12a). Eyestalk relatively longer than in the previous stage.

Cephalic shield (Fig. 12a). Mean value of CW/CL 0.543 (range = 0.520-0.568).

Antennule (Fig. 12b). Inner flagellum elongated, 2/5-1/2 length of 4th (distal) segment; 4th segment with 9-12 rows of subterminal sensory setae.

Antenna (Fig. 12b). 5-segmented, longer than antennule.

First maxilla (Fig. 12c). Coxal endite with 5-8 short subterminal setae; basal endite no marked change.

Second maxilla (Fig. 12d). Distal portion expanding widely and posteriorly more than in Stage VII, bordered by several short setae in some individuals.

Maxillipeds (Fig. 12a-d). 1st maxilliped elongated bud, with short lobe on lateral margin in advanced individuals; exopod of 2nd maxilliped present as bud without plumose setae.

Pereiopods (Fig. 12a-e). 5th pereiopod elongated bud, 1-2-segmented, about 1/3-1/2 length of pleon, ventral coxal spines on all pereiopods absent; minute sternal spines present near the coxae of 1st-4th pereiopods in many individuals.

Pleon (Fig. 12e). Weakly or distinctly segmented; pleopod 4 pairs of bifid bud or biramous; uropod segmented and biramous.

Gill buds. Rudimentary bud on 1st-3rd pereiopods present in well-advanced individuals.

Phyllosoma Stage IX ($n = 14$).—Eye (Fig. 13a). Eyestalk elongated.

Cephalic shield (Fig. 13a). Becoming relatively wider than in the previous stage, mean value of CW/CL 0.554 (range = 0.529-0.577), maximum width located slightly anterior part of the shield.

Antennule (Fig. 13b). Inner flagellum elongated, 1/2-3/5 length of 4th segment; 4th segment with 11-15 rows of subterminal sensory setae, lacking terminal sensory setae in some individuals.

Antenna (Fig. 13b). About 1.5-2.3 times as long as antennule.

First maxilla (Fig. 13c). No remarked change.

Second maxilla (Fig. 13d). Distal portion greatly expanding posteriorly, fringed with 8-43 short setae; anterior margin of proximal portion with a knob, bearing 1-6 short setae.

Maxillipeds (Fig. 13a-d). 1st maxilliped trilobed bud; exopod of 2nd maxilliped with 0.5-3.5 pairs of plumose setae.

Pereiopods (Fig. 13a-e). 5th pereiopod 2-4-segmented, longer than 1/2 length of pleon; minute sternal spines present near the coxae of 1st-4th pereiopods in most individuals.

Pleon (Fig. 13e). Segmentation well-developed; both rami of pleopod elongated, inner ramus with rudiment of appendix interna in well-advanced individuals; uropod with 1 serration on lateral margin of each outer ramus.

Gill buds. Gill buds present as papilla or unlobed bud on 2nd and 3rd maxillipeds and 1st-5th pereiopods in most individuals.

Phyllosoma Stage X ($n = 8$).—Eye (Fig. 14a). Eyestalk around 2/3 length of whole eye.

Cephalic shield (Fig. 14a, b). Mean value of CW/CL 0.569 (range = 0.545-0.627).

Antennule (Fig. 14c). Inner flagellum on antero-lateral margin of 3rd segment longer than half length of 4th segment; 4th segment with 13-17 rows of subterminal sensory setae, lacking terminal sensory setae in most individuals.

Antenna (Fig. 14c). About 2.2-3.0 times as long as antennule.

First maxilla (Fig. 14d). Coxal endite with 2 long serrated terminal setae and 8-12 short subterminal setae; basal endite with 3 strong serrated terminal spines and 4-5 short subterminal setae.

Second maxilla (Fig. 14e). Distal portion fringed with 25 or more than 80 short setae; anterior margin of proximal portion with 4-7 short setae.

Maxillipeds (Fig. 14a-e). 1st maxilliped trilobed bud; middle lobe reaching lateral margin of 2nd maxilla, posterior lobe expanding greatly; exopod of 2nd maxilliped with 2-7 pairs of plumose setae.

Pereiopods (Fig. 14a-f, g). 5th pereiopod 4-segmented in many individuals, additionally with a slight segmentation near distal end in some individuals; minute sternal spines present near the coxae of 1st-4th pereiopods in most individuals.

Pleon (Fig. 14f, g, h). Pleopod segmented, inner and outer rami bearing no setae on the margin, inner ramus having

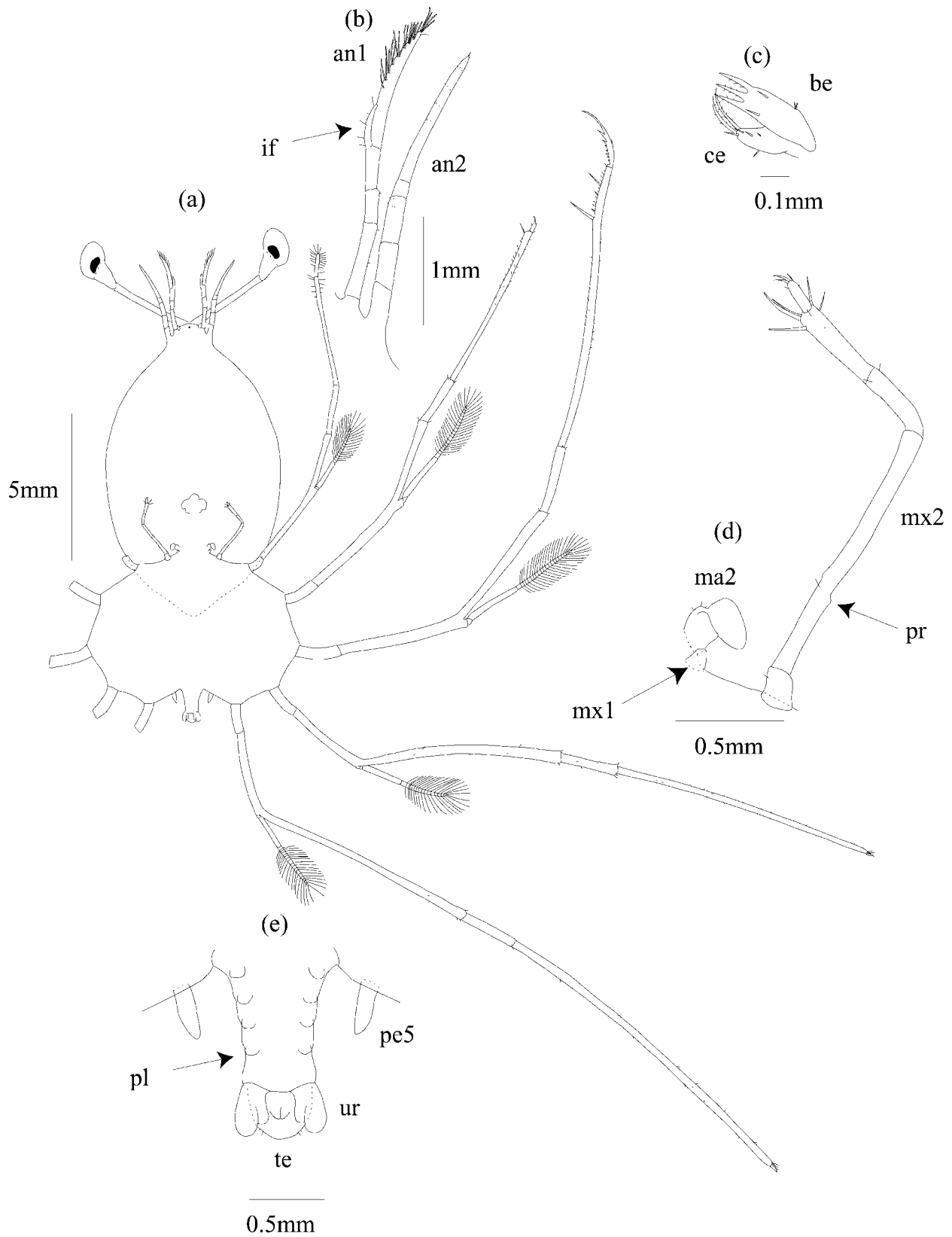


Fig. 11. Phyllosoma Stage VII of *Panulirus argus*. a, ventral view; b, left antennule (an1) with inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2) with slight protuberance (pr) developing exopod; e, 5th pereiopod (pe5) and pleon (pl: pleopod, ur: uropod, te: telson), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

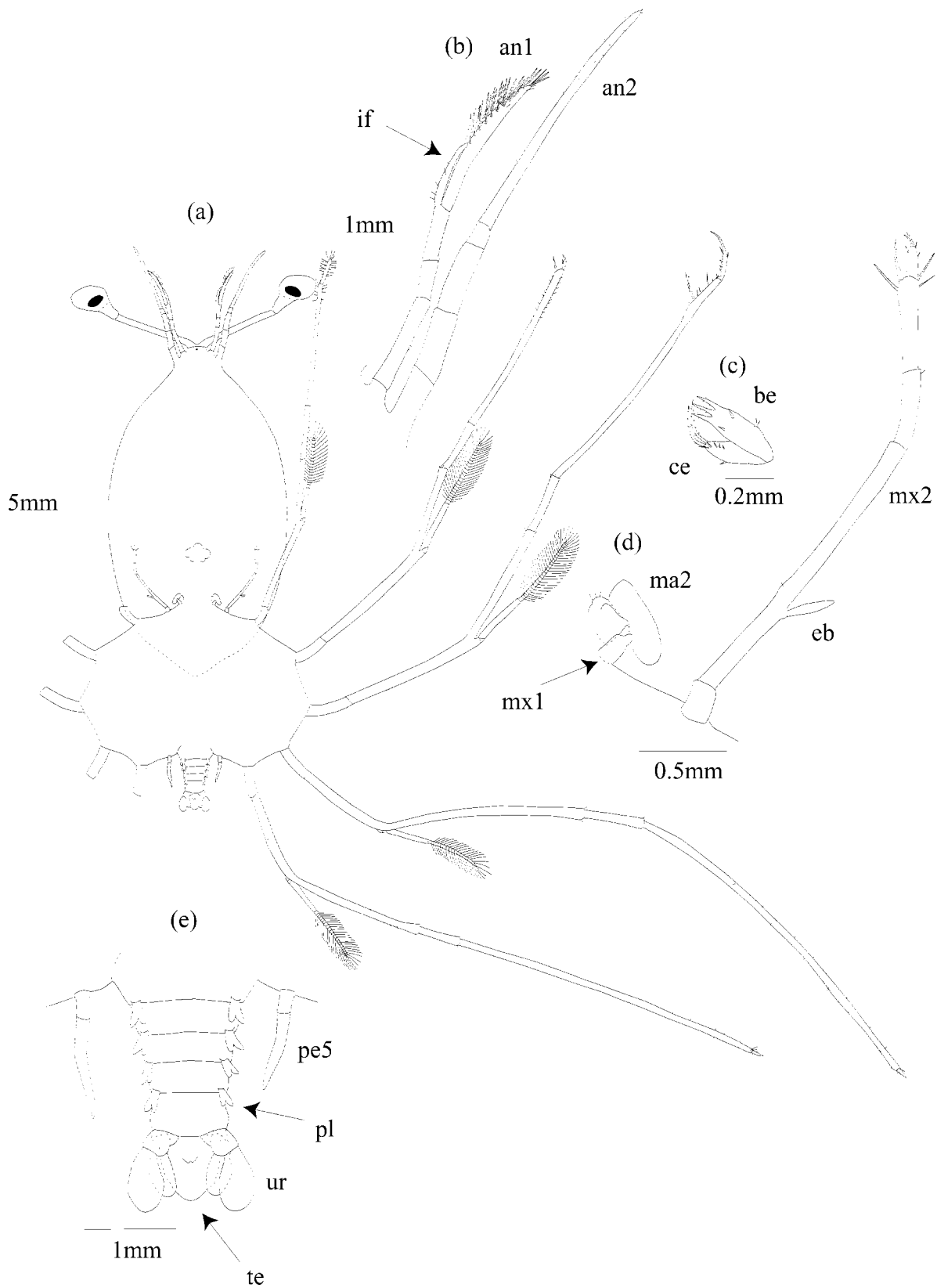


Fig. 12. Phyllosoma Stage VIII of *Panulirus argus*. a, ventral view; b, left antennule (an1) with inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1), and 2nd maxilliped (mx2) with exopod bud (eb); e, 5th pereiopod (pe5) and pleon (pl: pleopod, ur: uropod, te: telson), ventral. Setules on plumose setae of exopod are not shown.

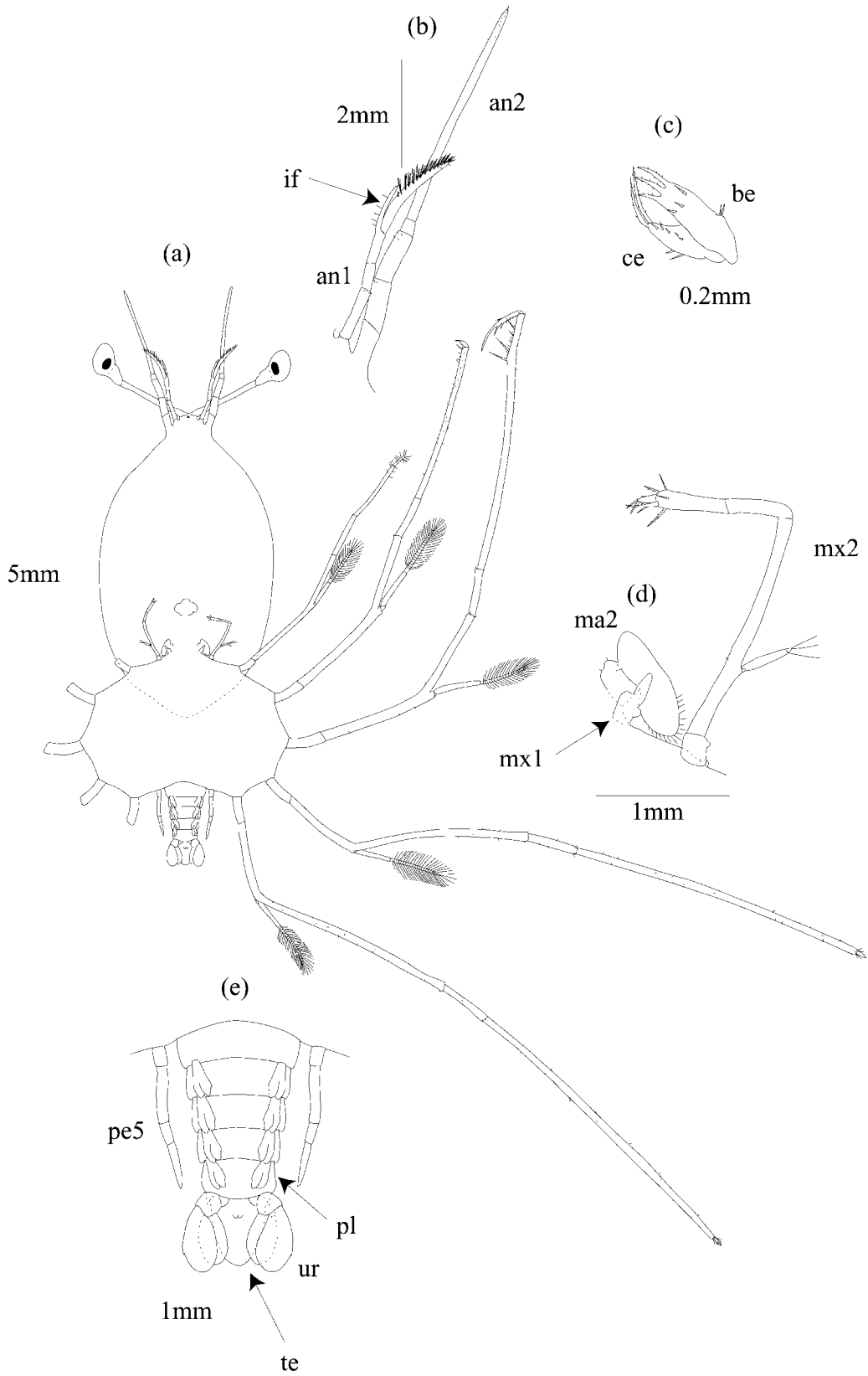


Fig. 13. Phyllosoma Stage IX of *Panulirus argus*. a, ventral view; b, left antennule (an1) with inner flagellum (if) and antenna (an2), ventral; c, coxal and basal endites (ce, be) of left 1st maxilla, ventral; d, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2) with setaceous exopod; e, 5th pereiopod (pe5) and pleon (pl: pleopod, ur: uropod, te: telson), ventral. Setules on plumose setae of exopod of pereiopod are not shown.

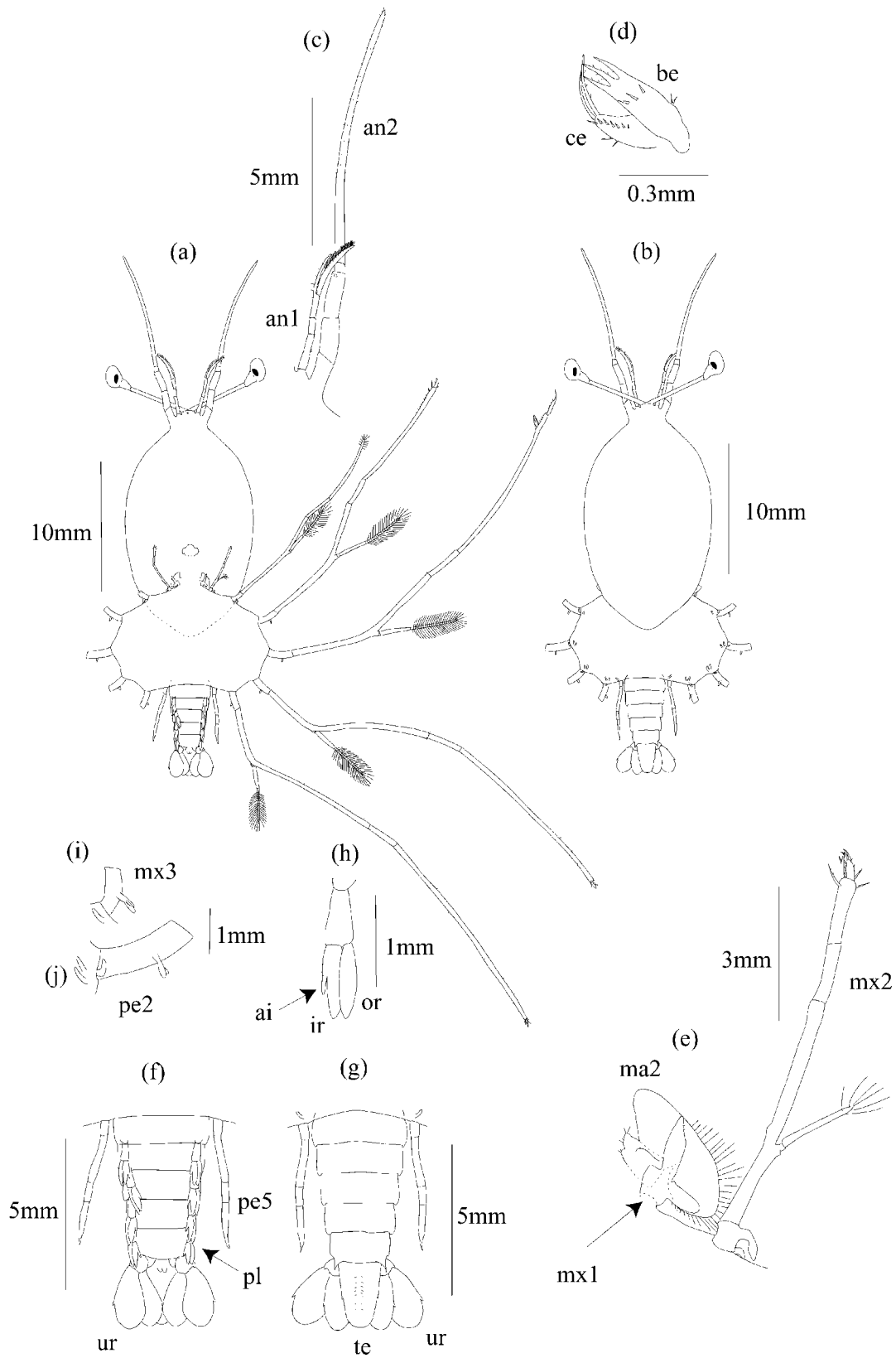


Fig. 14. Phyllosoma Stage X of *Panulirus argus*. a, ventral view; b, dorsal view; c, left antennule (an1) and antenna (an2), ventral; d, coxal and basal endites (ce, be) of left 1st maxilla, ventral; e, ventral view of left 2nd maxilla (ma2), 1st maxilliped (mx1) and 2nd maxilliped (mx2); f, 5th pereiopod (pe5) and pleon (pl: pleopod, ur: uropod), ventral; g, 5th pereiopod and pleon (ur: uropod, te: telson), dorsal; h, left 1st pleopod (or: outer ramus, ir: inner ramus) and appendix interna (ai), ventral; i, j, gill buds on dorsal surface of left 3rd maxilliped (mx3) and 2nd pereiopod (pe2). Setules on plumose setae of exopod of pereiopod are not shown.

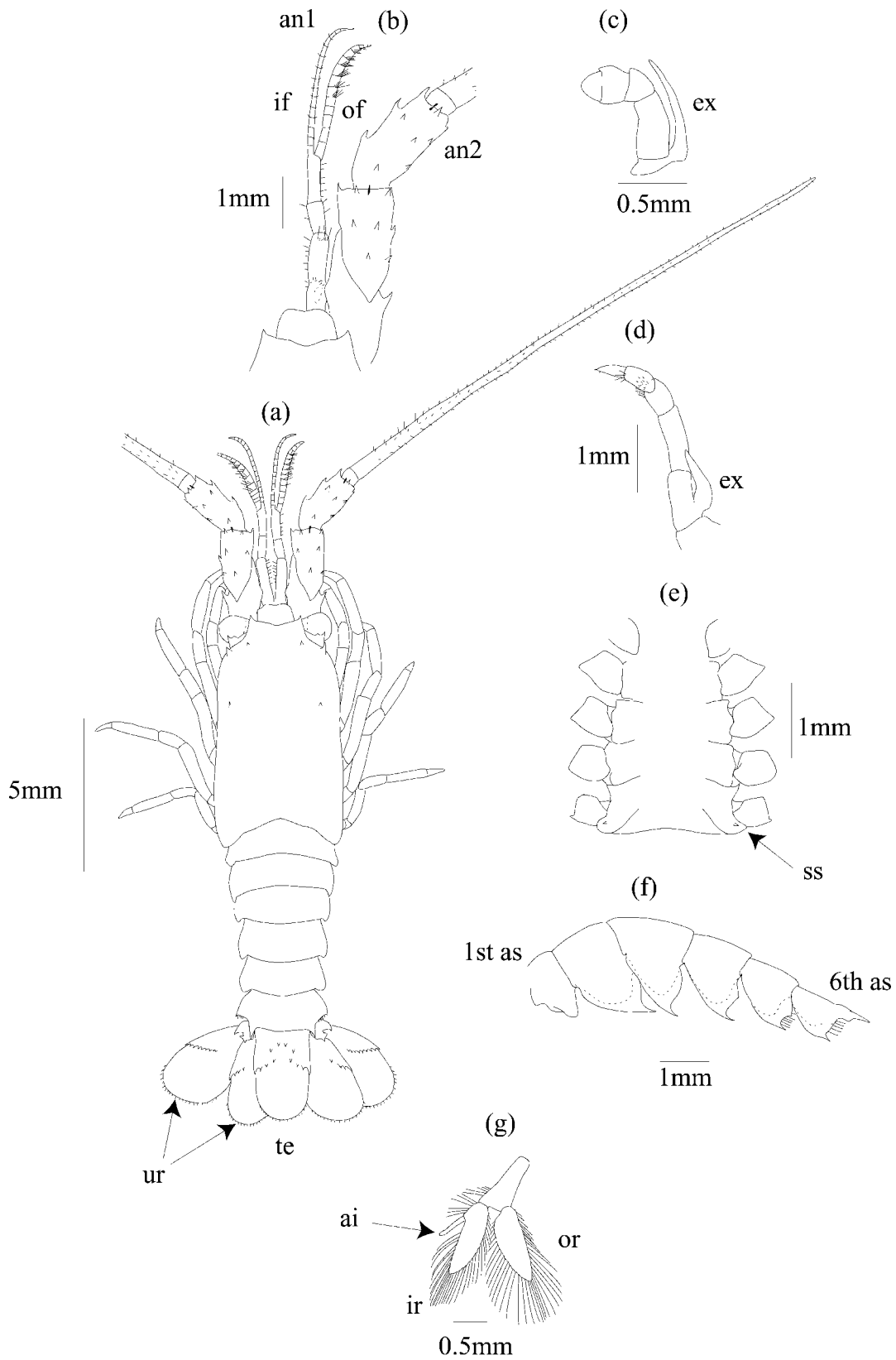


Fig. 15. Puerulus Stage of *Panulirus argus*. a, dorsal view (ur: uropod, te: telson); b, right antennule (an1) with inner flagellum (if) and outer flagellum (of) and antenna (an2), dorsal; c, ventral view of left 2nd maxilliped with exopod (ex); d, left 3rd maxilliped with exopod (ex), ventral; e, ventral thoracic sternum (ss: sternal spine); f, lateral view of pleon (as: abdominal somite); g, right 2nd pleopod (or: outer ramus, ir: inner ramus) and appendix interna (ai), ventral.

elongated appendix interna without anchorshaped hooks (cincinnuli), appendix interna not segmented or slightly segmented from inner ramus in advanced individuals; uropod having serrations on lateral margins of inner and outer rami; telson bearing 7-8 pairs of short setae longwise on middle area; 5 segment of pleon with postero-lateral projections.

Gill buds (Fig. 14i, j). Full complement of gill buds present on 2nd-3rd maxillipeds and 1st-5th pereopods, gill buds on coxae of 2nd-3rd maxillipeds and 1st-4th pereopods bilobed.

Puerulus Description

Puerulus Stage ($n = 13$).—Cephalothorax (Fig. 15a). 4 pairs of major spines (suborbital spine, antero-lateral spine, spine posterior to antero-lateral spine and branchial spine) on cephalothorax; supraorbital plate with slight projection on antero-lateral margin; cervical groove and median carina invisible.

Antennule (Fig. 15b). Peduncle with 3 segments; proximal segment having some relatively long setae and some short setae on anterior margin, several short setae on inner lateral margin and a few setae on outer lateral margin; inner flagellum slightly longer than outer one, outer flagellum having 14-15 segments, dense rows of setae on anterior margin of 4th-11th segments.

Antenna (Fig. 15b). ANLp 20.2-25.5 mm, 1.2-1.4 times (mean = 1.3) as long as BLp, having peduncle with 4

segments and long tapered flagellum; 1st segment with antero-lateral spine; 2nd segment with 8 spines on dorsal surface; 3rd segment with 8-10 strong spines on dorsal surface and 1 rounded spine on antero-lateral margin.

Maxillipeds (Fig. 15c, d). 2nd maxilliped with long exopod reaching anterior margin of carpus, lacking any setae; propodus and carpus of 3 maxilliped with several setae on anterior margin, exopod reaching middle of merus.

Thoracic sternum (Fig. 15e). Rounded protuberances near bases of 2nd to 5th pereopods on thoracic sternum, small posterolateral sternal spines near base of 5th pereopod.

Pleon (Fig. 15a-f, g). 2nd to 6th pleural plates produced into recurved spines, lateral margin of 5th and 6th plates bearing some setae; posteriorly directed strong spine projecting on postero-lateral margin of 6th abdominal somite; posterior margin of abdominal tergites of 2nd to 5th somites fringed with minute setae; posterior margin of 6th tergite without serrations; pleopods present on 2nd to 5th somites, inner and outer rami with plumose setae, inner ramus having appendix interna with cincinnuli; outer and inner rami of uropod bearing 9 and 4 spines, respectively, on anterior margin of calcified part; telson having 3 pairs of spines on central area of calcified part and 3 spines on each right and left anterior margin of calcified part.

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