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## Description of the newly-hatched juvenile of *Aegla perobae* (Crustacea: Decapoda: Aeglidae)

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### Abstract

The present paper contains the complete description of the external morphology of the first juvenile stage of *Aegla perobae* analysed through light microscopy (LM) and scanning electron microscopy (SEM). Newly-hatched juveniles were obtained from ovigerous females kept under laboratory conditions. Hatching is asynchronous, taking 2–4 days for all juveniles of a single brood to hatch. Average carapace dimensions are 1.54 mm wide and 1.69 mm long (rostrum excluded). Morphology of the carapace, of the cephalothoracic appendages (antennule, antenna, mandible, maxillule, maxilla, maxillipeds, and pereopods), of the pleon, and of the tail fan (telson plus uropods) are described in detail. *Aegla perobae* juveniles can be readily differentiate from the first juveniles of other aeglids species described so far by the upwardly curved condition of the distal region of the rostrum and the distinct groove along the orbital sinus produced the elevated free in this area. Pleopods 2–5 are present as rudimentary digitiform buds. Rudimentary pleopods are still present in adult males of the species, a trait not yet described in freshwater aeglids. This curious condition is compared and discussed in the light of the current knowledge of early postembryonic developmental patterns found in other anomurans.

**Key words:** Anomura, external morphology, direct development, pleopods, SEM

### Introduction

The marine origin of the family Aeglidae Dana 1852, probably in the Indo-Pacific region, is supported by evidence from fossil material attributed to the extinct genera *Haumuriaegla* and *Protaegla* (Feldmann 1984; Feldmann *et al.* 1998). The only extant genus, *Aegla* Leach 1820, is unique because it is entirely adapted to freshwater habitats and is endemic to temperate and subtropical regions of continental South America (Schmitt 1942; Bond-Buckup *et al.* 2008). Pérez-Losada *et al.* (2004) demonstrated that the colonization of freshwater by aeglids, and the point of origin of *Aegla*, probably took place along the Pacific coast of South America as a consequence of several marine transgressions that covered vast low lying areas of western South America periodically during the Late Cretaceous–Early Tertiary Period (about 90–60 mya).

*Aegla* is also remarkable in that it is the only confirmed anomuran taxon with direct postembryonic development, characterized by the complete suppression of free-swimming larval stages (Rabalais & Gore 1985), although rudimentary larval traits can be recognized during embryonic development within the egg (Lizardo-Daudt & Bond-Buckup 2003). The hatching form is an epibenthic juvenile that very much resembles the adult in general morphology (Francisco *et al.* 2007; Moraes & Bueno 2013).

Newly-hatched juveniles remain under maternal care in the brooding chamber formed by flexure of the pleon of the female for a few days before leaving their mother and starting to explore the surroundings (Bahamonde & López 1961; Rodrigues & Hebling 1978; Bueno & Bond-Buckup 1996; Bond-Buckup *et al.* 1999; López-Greco *et al.* 2004; Francisco *et al.* 2007). Young juveniles avoid being carried away by the water current by hiding under rocks and pebbles or in shallow areas with low water flow velocity (López 1965). Due to their limited capacity for dispersal, the recruits tend to remain near the parental population (Bueno *et al.* 2014).

Seventy-five species of *Aegla* have been described so far, and complete descriptions and illustrations of newly-

hatched juveniles are available for six species from Brazil only: *Aegla prado* Schmitt 1942, *A. violacea* Bond-Buckup & Buckup 1994, *A. platensis* Schmitt 1942, *A. franca* Schmitt 1942, *A. schmitti* Hobbs III 1979, and *A. paulensis* (Bond-Buckup *et al.* 1996; Bueno & Bond-Buckup 1996; Bond-Buckup *et al.* 1999; Francisco *et al.* 2007; Teodósio & Masunari 2007; Moraes & Bueno 2013). Furthermore, morphological descriptions of newly-hatched juveniles of *A. ligulata* Bond-Buckup & Buckup 1994 and *A. longirostri* Bond-Buckup & Buckup 1994 are also available, but the corresponding illustrations were not provided (Bond-Buckup *et al.* 1999).

*Aegla perobae* Hebling & Rodrigues 1977 is endemic to the cuesta of São Pedro, in São Paulo state, Brazil (Hebling & Rodrigues 1977; Rodrigues & Hebling 1978; Bueno *et al.* 2014). The reproductive period occurs during the cold dry period of the year (mid-autumn till late winter) with the production of one single egg batch, and therefore, one single cohort of juveniles per year (Bueno *et al.* 2014). Newly-hatched juveniles were obtained by Rodrigues & Hebling (1978) under laboratory condition, but apart from the illustration of the juvenile in dorsal view presented therein, a complete and detailed morphological description is not yet available.

In this paper, we provide the complete description of the external morphology of the newly-hatched juvenile of *Aegla perobae* as seen through Light and Scanning Electron Microscopy. The morphology and state of development of selected appendages and structures observed in newly-hatched aeglid juveniles are compared and discussed in the light of current knowledge of early postembryonic developmental patterns found in other anomurans, with special emphasis on the pairs of pleopods.

## Material and methods

Ovigerous females carrying eggs in the final embryonic developmental stage [see Bueno & Shimizu (2008) for egg development categories] were sampled at the type-locality (22°31'26.6"S, 047°56'37.6" W) in July 2008 and in July 2010, and transported to and maintained alive at the University of São Paulo according to procedures and techniques described by Francisco *et al.* (2007) and Moraes & Bueno (2013). Females were checked daily for newly-hatched juveniles in the brooding chamber. Approximately 130 newly-hatched juveniles were obtained from eight ovigerous females and fixed by graded ethanol series (7.5%–15%–30%, 10 minutes each step) and stored in 50% ethanol solution. Carapace length (CL) was measured from the posterior border of the orbital sinus to the mid-posterior border of the cephalothorax; carapace width (CW) was measured as the largest transverse distance (Francisco *et al.* 2007; Moraes & Bueno 2013).

Specimens selected as best for dissection were later stored in 1:1 70% ethanol and glycerine solution and cleared in 3% potassium hydroxide (KOH) solution before dissection. Cephalothoracic appendages (antennule, antenna, mandible, maxillule, maxilla, maxillipeds, pereopods), and the tail fan (telson and uropods) were mounted in glycerine in semi-permanent preparations according to Moraes & Bueno (2013). Observations and line drawings of the appendages and whole specimen in dorsal view were made with the aid of a stereoscopic microscope (Zeiss Stemi V6) and a compound phase contrast microscope (Zeiss Axioskop 2 plus) with drawing tube. Scale bars (in millimetres) were made with scale slide (Graticules Ltd, Tonbridge Kent). Line drawings were scanned at 600 dpi and edited in Adobe Photoshop 7.0.1 software at 1200dpi.

Fifteen newly-hatched specimens were cleaned by immersion in contact-lens solution, dehydrated (graded ethanol series: 7.5%, 10%, 15%, 30%, 50%, 70%, 90% and 100%, three times of 10 minutes each one; and critical-point), coated with gold palladium (Sputter Coater, Balzers SCD 050), observed and photographed in a DSM 940 Zeiss Scanning Electron Microscope of the Laboratory of Electron Microscopy of the Institute of Biosciences, University of São Paulo.

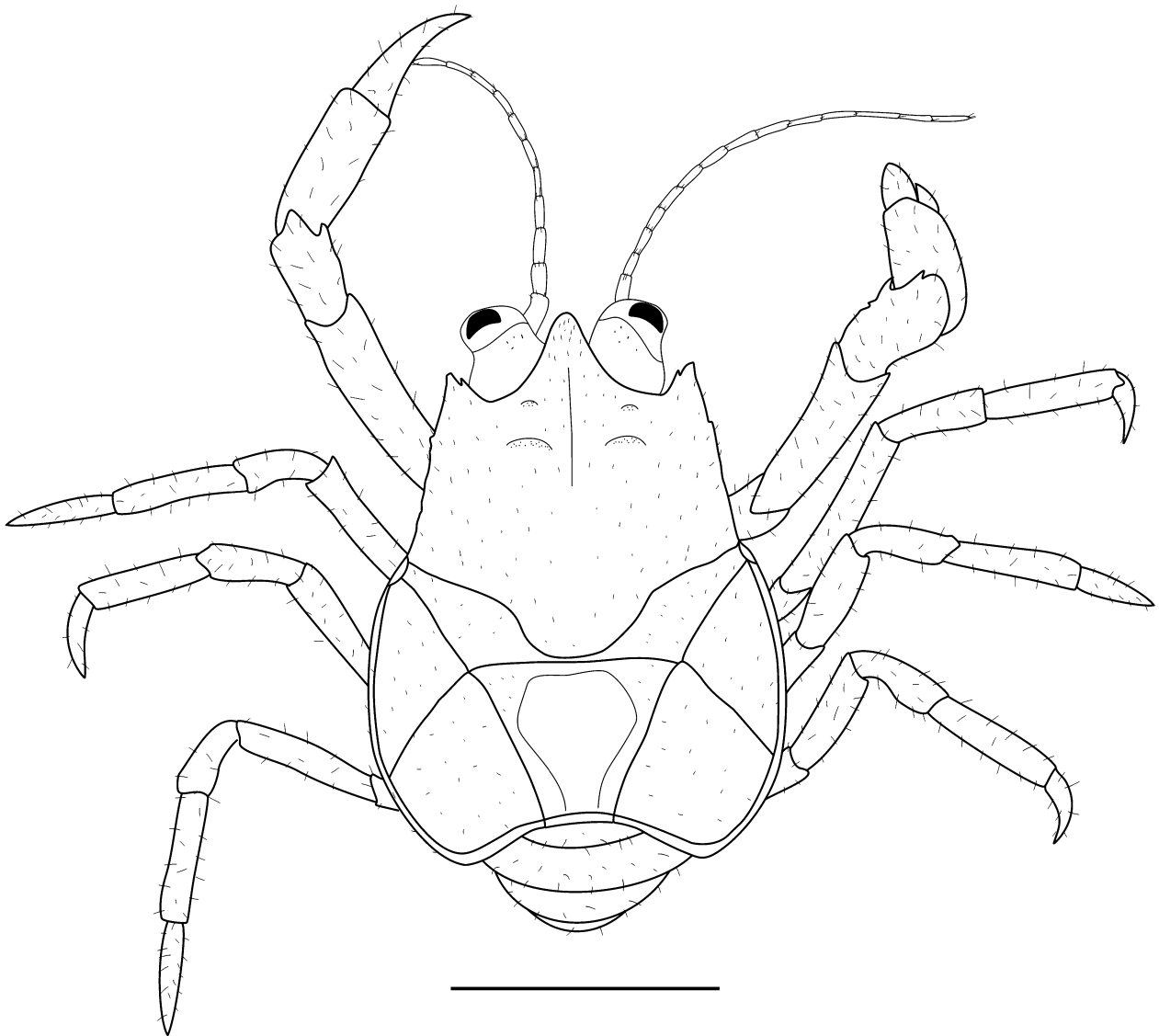
Terms related to carapace morphology followed description of the adult form by Martin & Abele (1988). Interpretation of lamellar lobe (sensu Martin & Abele 1988) of the first pair of maxillipeds as epipod followed Schnabel & Ahyong (2010). Morphological descriptions of setae and pores followed Moraes & Bueno (2013). Names of taxa of Anomura in the superfamilial and familial ranks follow Ahyong *et al.* (2010), Schnabel & Ahyong (2010) and Schnabel *et al.* (2011).

Specimens of newly-hatched juveniles of *A. perobae* were deposited as voucher materials at the Museu de Zoologia da Universidade de São Paulo (MZUSP 25137 and MZUSP 28394).

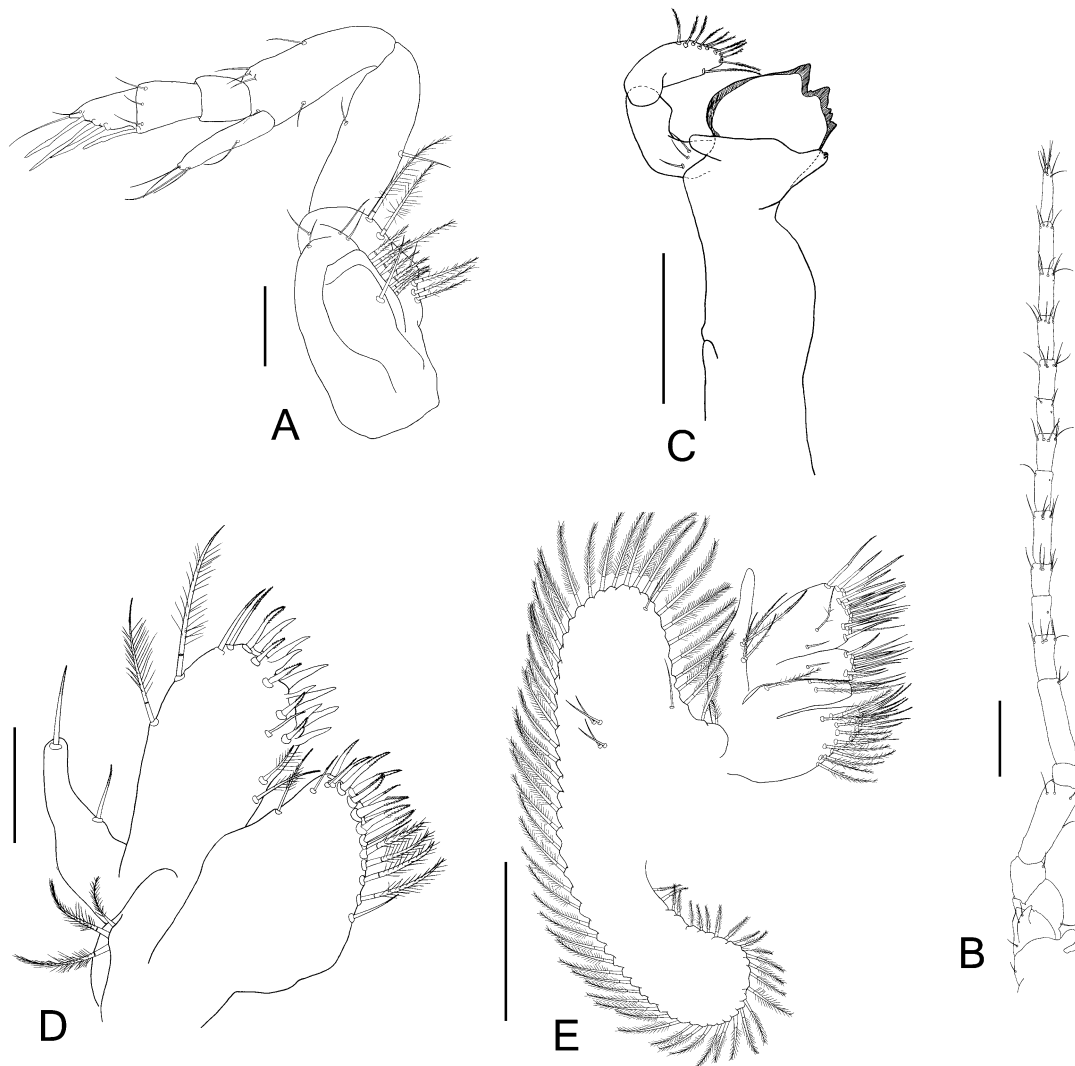
## Results

Postembryonic development in *Aegla perobae* is epimorphic. Hatching is asynchronous taking approximately 2–4 days for all juveniles from a single brood to hatch.

**Carapace** (Figs 1, 6, 7): subcylindrical, slightly longer (mean: 1.69 mm; range: 1.61–1.77 mm) than wide (mean: 1.54 mm; range: 1.40–1.67 mm). Rostrum triangular and curved upward distally; with carina along its length, except on distal third (Fig. 7c). Tip of anterolateral spines rounded and almost reaching base of cornea (Fig. 7b). Orbital spines, when present, rudimentary and defining a small extraorbital sinus (Fig. 7a) or coalesced with anterolateral spines thus defining no extraorbital sinus (Fig. 7b). Orbital sinus well-developed, wide, U-shaped, elevated margin defining distinct groove (Fig. 7a). Epigastric prominences small. Protogastric lobes conspicuous and granulate. Hepatic lobes not distinguishable. Epibranchial tooth rudimentary. Cervical groove distinct and gastric area elevated. Areola large and trapezoidal. Cardiac area well-defined and trapezoidal. Dorsal grooves discernible: *linea aeglica dorsalis* (lad), *linea aeglica lateralis* (lal), *branchial linea* (brl), *transverse dorsal linea* (tdl) and *dorsal longitudinal linea* (dll), the latter visible as a subtle suture running obliquely and parallel to each side of the areola. Recognized lateral grooves: *linea aeglica* (la), *linea aeglica ventralis* (lav) and *linea aeglica posterioris* (lap). Type 3 pores (sensu Moraes & Bueno 2013) scattered across general surface of carapace, mainly in the rostral area (Fig. 12d).



**FIGURE 1.** Dorsal view. *Aegla perobae* newly-hatched juvenile. Scale = 1.0 mm.



**FIGURE 2.** A) Antennule. B) Antenna. C) Mandible. D) Maxillule. E) Maxilla. *Aegla perobae* newly-hatched juvenile. Scale: A, D = 0.1 mm; B, C, E = 0.2 mm.

**Sternum** (Fig. 9a): Sternites 3 through 8 visible only. Sternum width increases slightly towards posterior end. Ornamentations of the anterior margins of the third and fourth segments not completely developed. Coxo-sternal depression distinct.

**Pleon** (Fig. 9b–c): with 6 somites, the second being the largest. Width of third to sixth somites decreasing progressively towards posterior end. Simple setae distributed dorsally on all somites.

**Telson** (Figs 5, 9d): laminar, subtriangular, rudimentary longitudinal groove on proximal third. Surface covered with 21–23 simple setae and 12–15 long plumose setae along distal edge.

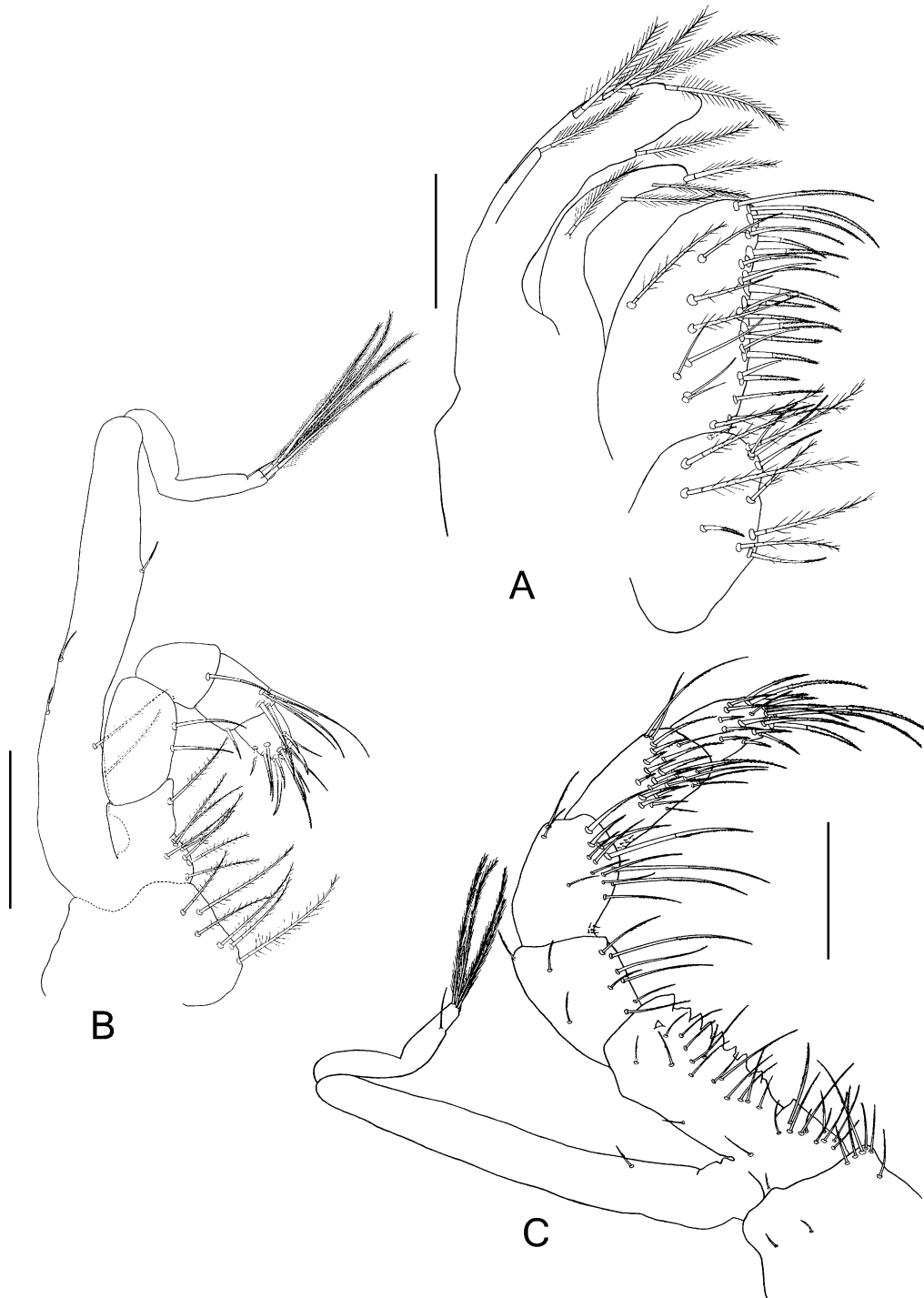
**Eye** (Fig. 7f): well-developed with 4–7 simple setae dorsally on the peduncle.

**Antennule** (Figs 2a, 8a–b, 10d, 11f): Uniramous. Basal segment globose, with 5–8 simple setae, group of 13–15 pappose setae (7 of them forming a fringe). Peduncle: proximal segment with 2 simple setae; distal segment with 1–2 simple setae mesially and 3–5 pappose (distal half) setae near dorsal and ventral flagella, respectively. Dorsal flagellum three-articulated: proximal article bare; mesial article with 3 simple setae, 1 aesthetasc distally and one pore type 1; and distal article with 2 simple setae and 3 aesthetascs. Ventral flagellum with 1–2 mesial, 2 subapical and 1–2 apical simple setae, and one pore type 1 (Fig. 8a–b).

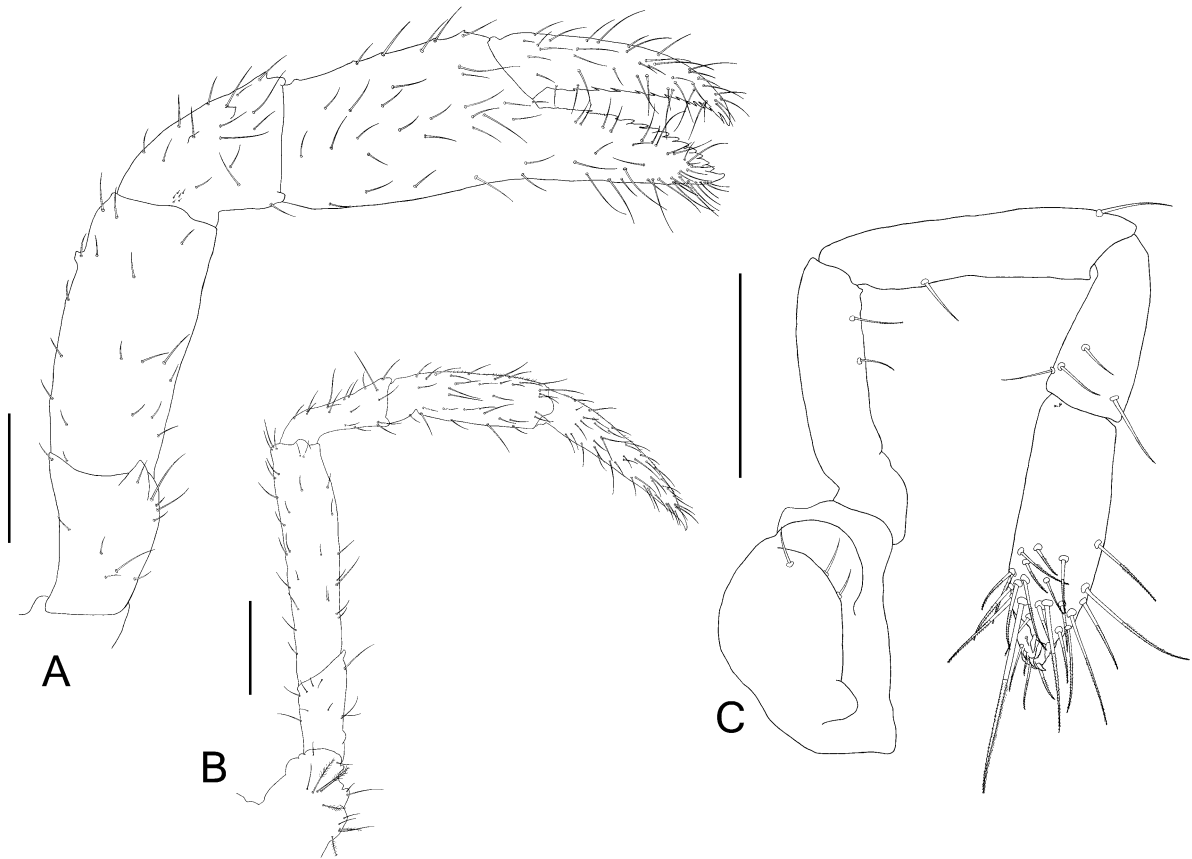
**Antenna** (Figs 2b, 12a): Uniramous. Peduncle 5-segmented. First segment with 1 simple seta, second and third segments with 4–8 simple setae, fourth segment with 1–3 simple setae, and fifth segment with 4–7 simple setae. Flagellum long, multi-articulated, with 13–14 articles; proximal article shortest and lacking setae; remaining articles with variable number of simple setae (maximum of 6) on distal margin except for apical article, which

exhibits up to 9 simple setae on distal third. All three distinct types of pore sensilla were observed in several articles of the flagellum: type 1 pore sensilla are found at the distal half of the flagellum, only 1 per article; type 2 pore sensilla are scattered along the article, more than one per article; type 3 pore sensilla rarest.

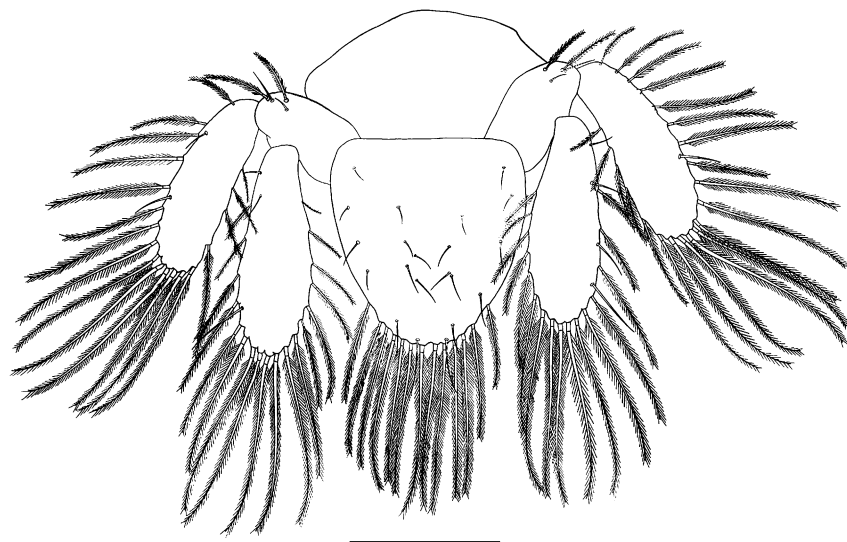
**Mandible** (Figs 2c, 8c, 11d): Uniramous. Molar process rudimentary. Incisor process well-developed, with sclerotized teeth asymmetrically and complementarily arranged between left and right side along grinding margin. Mandibular palp (endopod) 2-segmented: proximal segment with 3 simple setae near proximal margin and 0–1 simple setae subdistally; distal segment with 10–11 serrulate setae (Fig. 11d).



**FIGURE 3.** A) First maxilliped. B) Second maxilliped. C) Third maxilliped. *Aegla perobae* newly-hatched juvenile. Scale: A = 0.1 mm; B, C = 0.2 mm.



**FIGURE 4.** A) Cheliped. B) Second pereopod. C) Fifth pereopod. *Aegla perobae* newly-hatched juvenile. Scale: A, B = 0.3 mm; C = 0.2 mm.

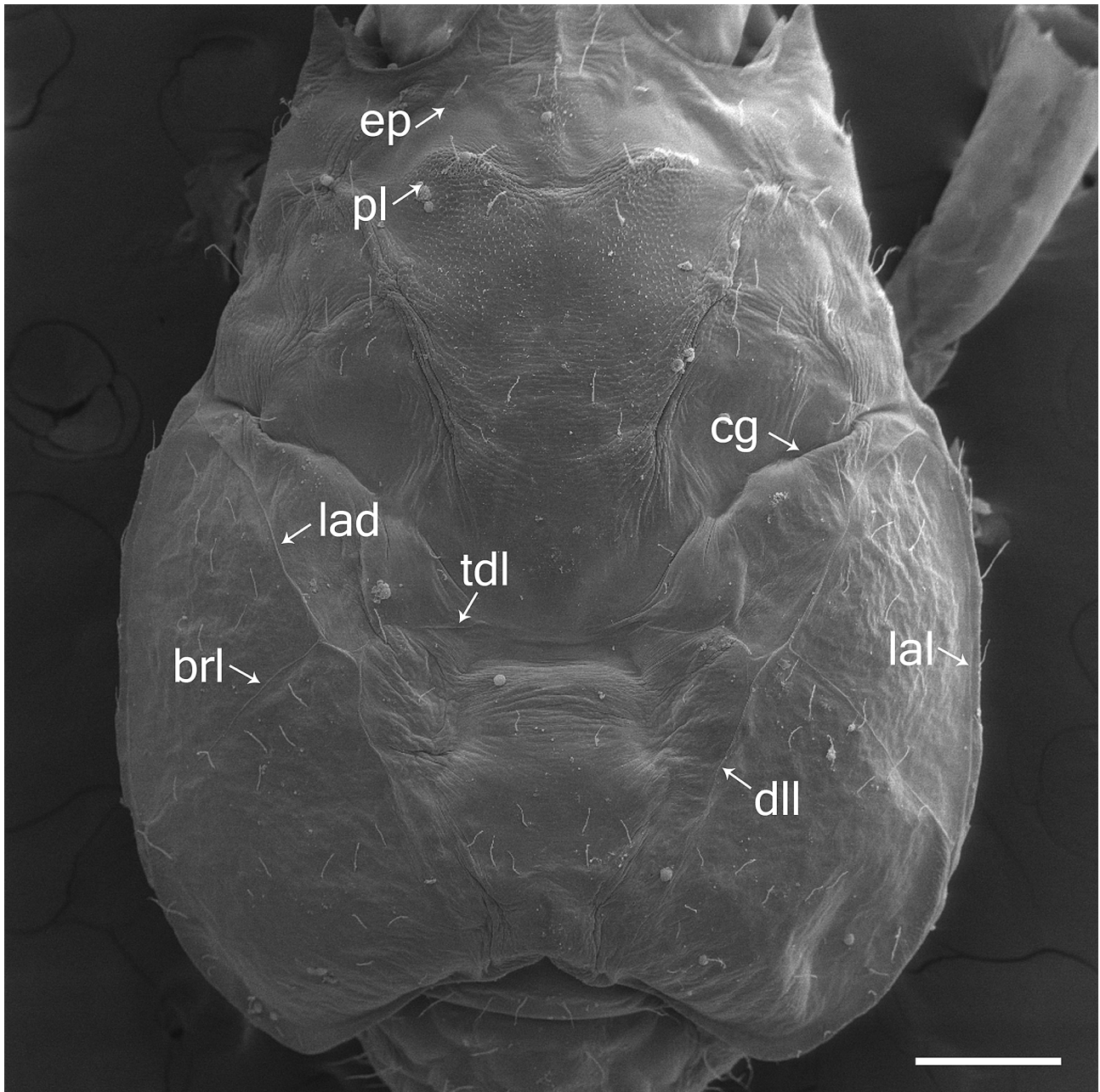


**FIGURE 5.** Telson and Uropods. *Aegla perobae* newly-hatched juvenile. Scale = 0.3 mm.

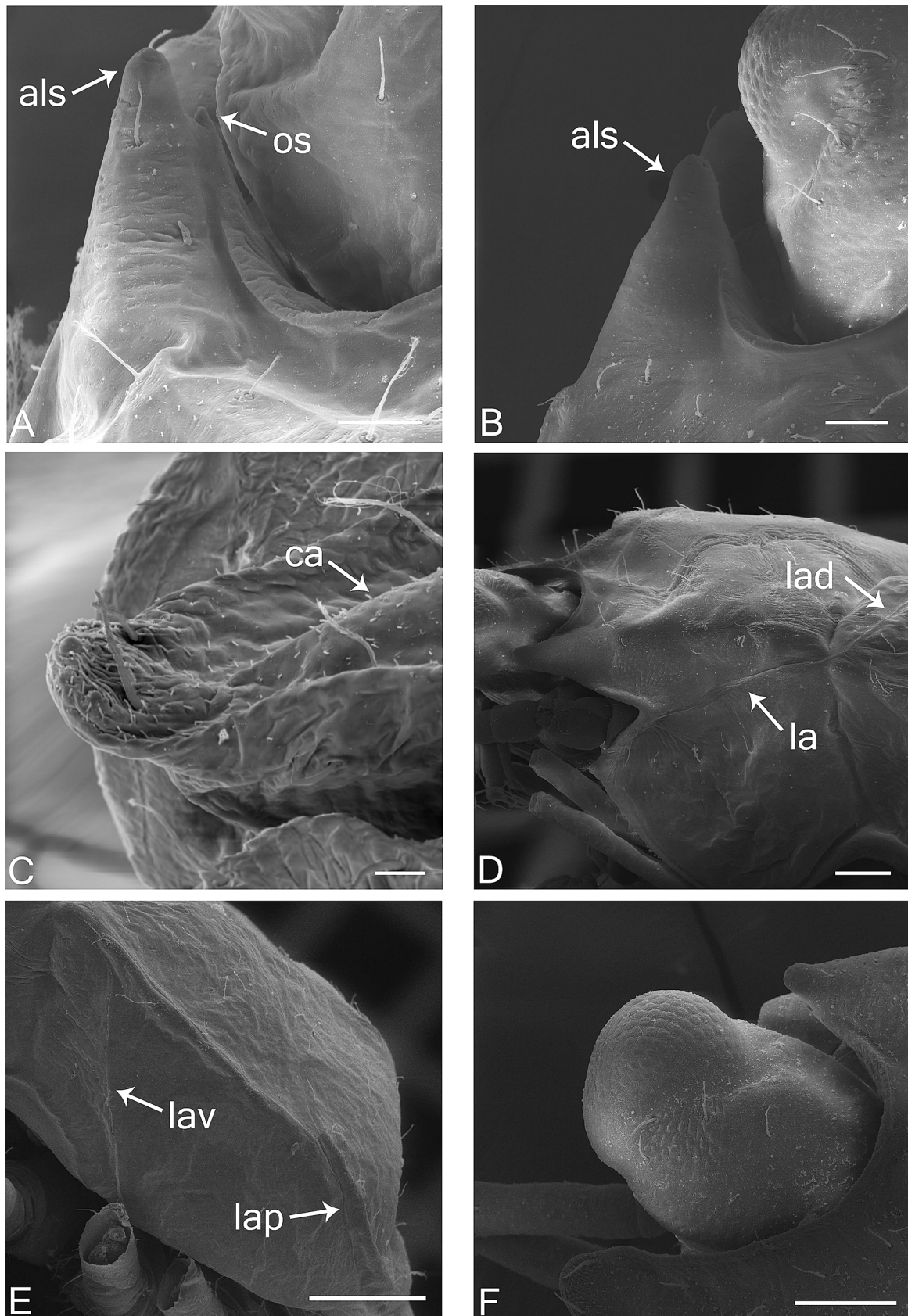
**Maxillule** (Fig. 2d, 10e, 11c): Uniramous. Protopod with 2–3 pappose setae. Coxal endite with 3–5 pappose setae, 0–2 papposerrate setae and 10–14 serrate setae. Basal endite with 0–2 short serrate setae, 3–5 papposerrate setae, 5–7 serrate setae and 9 cuspidate setae. Endopod 1-segmented with serrate setae: 0–2 mesially, 1 subapically and 0–1 apically.

**Maxilla** (Fig. 2e, 10b): Biramous. Coxal endite bilobed: proximal lobe with 10 pappose setae, 7 serrate setae and 1 simple seta bearing terminal pore and small scaly outgrowths subdistally; distal lobe with 3 pappose setae, 1 serrate seta and 2 simple setae with terminal pore and small scaly outgrowths subdistally. Basal endite bilobed: proximal lobe with 1 simple seta, 3 serrate setae and 8 simple setae (bearing terminal pore and small scaly outgrowths subdistally); distal lobe with 1 simple seta, 1 papposerrate seta, 9 serrate setae and 12 simple setae with terminal pore and small scaly outgrowths subdistally. Endopod 1-segmented, with 4 papposerrate setae. Exopod (scaphognathite) with 5 simple setae on the surface and a fringe of 65–70 plumose setae marginally.

**First Maxilliped** (Figs 3a, 8d, 10f): Biramous. Coxal endite with 3–5 pappose, 0–1 papposerrate and 5–7 serrate setae. Base with incipient epipod (= lamellar lobe) (Fig. 8d). Basal endite with 3–4 simple, 1–2 pappose, 3–5 papposerrate and 25–28 serrate setae. Endopod 1-segmented with 2–4 plumose setae. Exopod 1-segmented with 0–2 pappose setae, 4–6 plumose setae, 0–2 short serrate setae.

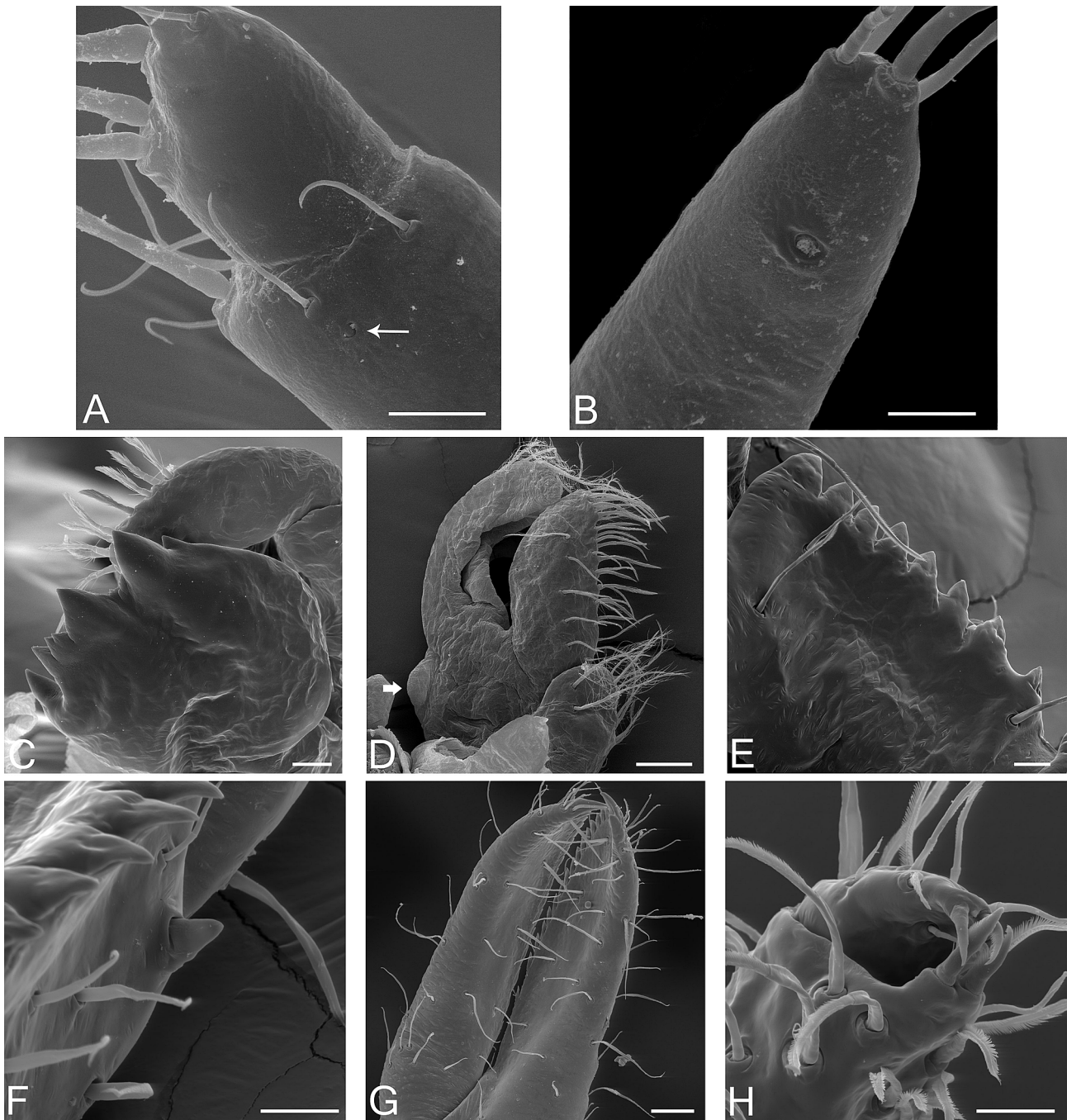


**FIGURE 6.** Dorsal view. *Aegla perobae* newly-hatched juvenile. brl = branchial linea; cg = cervical groove; dll = dorsal longitudinal linea; ep = epigastric prominence; lad = linea aeglica dorsalis; lal = linea aeglica lateralis; pl = protogastric lobe; tdl = transverse dorsal linea. Scale = 200  $\mu$ m.



**FIGURE 7.** A) Anterolateral and orbital spines. B) Anterolateral spine and orbital spine absent. C) Rostrum curved up with carina. D) Carapace anterolateral view. E) Carapace posterolateral view. F) Eye with simple setae. *Aegla perobae* newly-hatched juvenile. als = anterolateral spine; ca = carina; la = *linea aeglica*; lad = *linea aeglica dorsalis*; lap = *linea aeglica posterioris*; lav = *linea aeglica ventralis*; os = orbital spine. Scale: A, B = 50  $\mu$ m; C = 20  $\mu$ m; D, F = 100  $\mu$ m; E = 200  $\mu$ m.





**FIGURE 8.** A) Antennule: aesthetascs and pore type 1 (thin arrow) of dorsal flagellum. B) Antennule: pore type 1 of ventral flagellum. C) Mandible. D) First maxilliped with rudimentary lamellar lobe (thick arrow). E) Third maxilliped: ischiobasis with *crista dentata*. F) Third maxilliped: ischiobasis with corneous tooth. G) Cheliped distal region. H) Fifth pereopod distal region. *Aegla perobae* newly-hatched juvenile. Scale: A, C, E, F, H = 20  $\mu\text{m}$ ; B = 10  $\mu\text{m}$ ; D, G = 50  $\mu\text{m}$ .

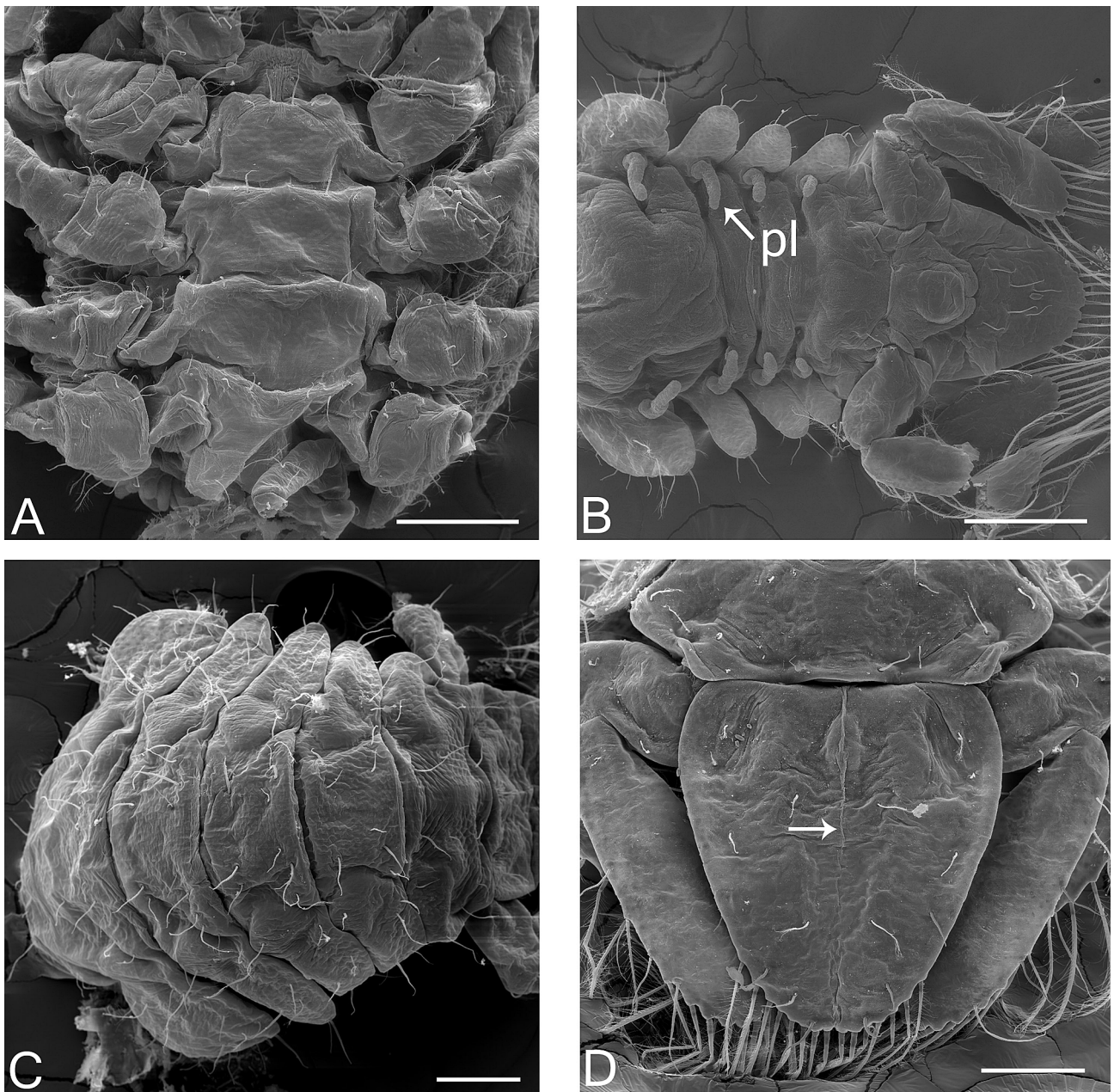
**Second Maxilliped** (Figs 3b, 10c, 11a, 11b): Biramous. Protopod with 6–7 pappose setae. Endopod 5-segmented: ischiobasis with 5–9 pappose setae, 0–2 papposerrate setae and 0(3) serrate setae; merus with 2–4 serrate setae; carpus with 1 serrate seta and 2–3 minute simple setae; propodus with 7–9 serrate setae and 1–2 minute simple setae; dactylus with 10–12 serrate setae. Exopod 2-segmented: proximal segment with 2 pappose and 2–4 short serrate setae; distal segment (“flagellum”) with 1–2 short simple setae and 4 long plumose setae.

**Third Maxilliped** (Figs 3c, 8e–f, 10a): Biramous. Coxa with 0–3 pappose, 0–1 papposerrate and 7–11 serrate setae. Endopod 5-segmented; ischiobasis with 24–31 serrate setae on the ventral surface, *crista dentata* (Fig. 8e) with 8–10 corneous teeth along the inner margin, and 1 corneous tooth on the ventral surface (Fig. 8f); merus with 9–11 serrate setae; carpus with 15–17 serrate and 3–5 minute simple setae; propodus with 22–27 serrate setae and

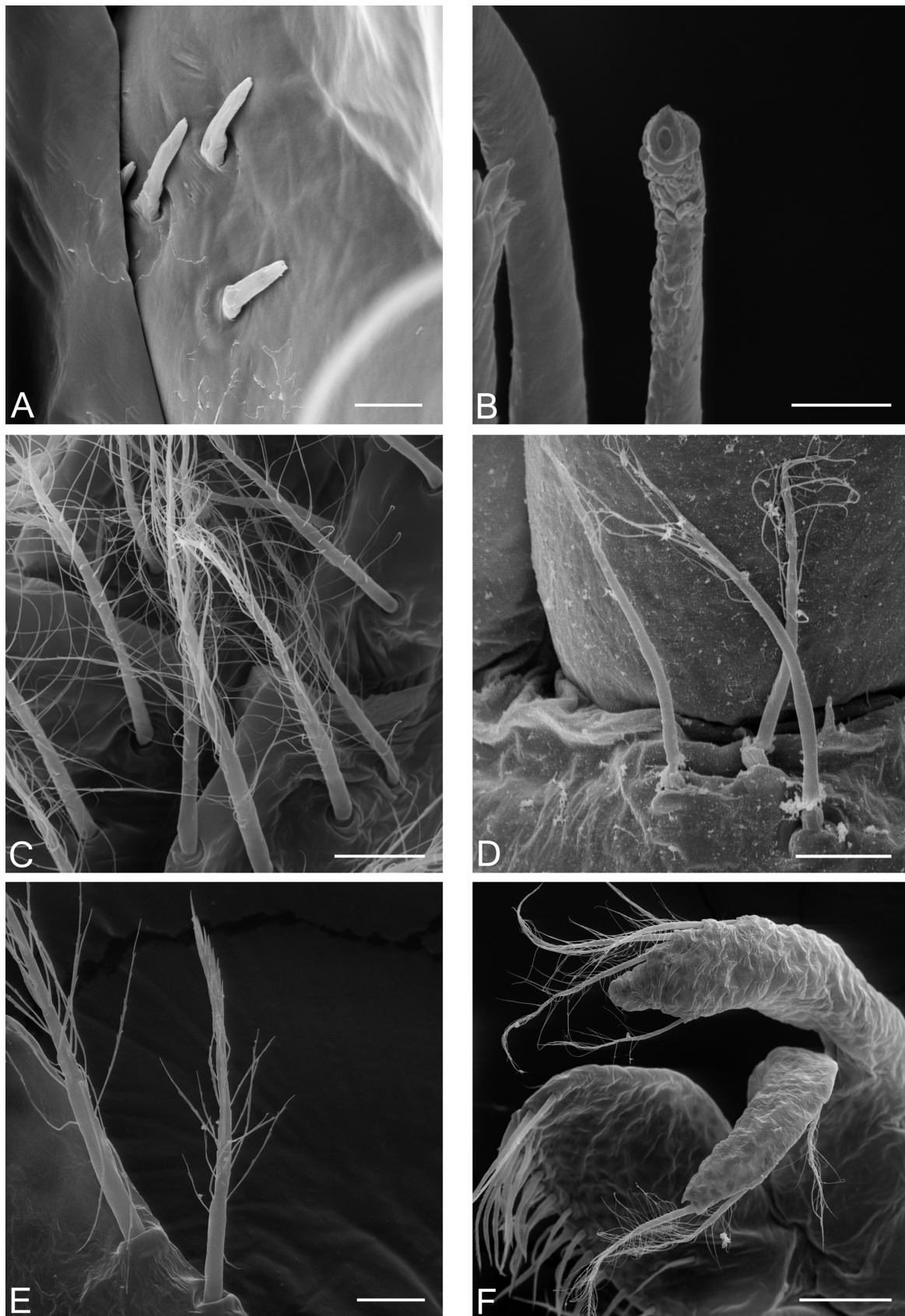
2–4 minute simple setae (Fig. 10a); dactylus with 17–22 serrate setae. Exopod 2-segmented: proximal segment with 1 serrate seta, and distal segment (“flagellum”) with 1–2 short plumose setae and 4 long plumose setae.

**Cheliped** (Figs 4a, 8g): Uniramous, 6-segmented, with several simple setae distributed in all segments. Coxa with 4 pappose setae. Ischiobasis subrectangular without corneous teeth. Merus with 1 corneous tooth on the dorsal margin. Carpus trapezoidal with 2 corneous teeth on the distal region of dorsal margin, and 6–7 minute simple setae on the proximal region (near articulation with merus). Propodus subrectangular with 2 corneous teeth on the distal region of dorsal margin, and 6 minute simple setae on proximal region (near articulation with carpus). Dactylus subtriangular. Cutting edge of both fixed (propodus) and movable (dactylus) fingers with row of short robust denticles obliquely and serially arranged.

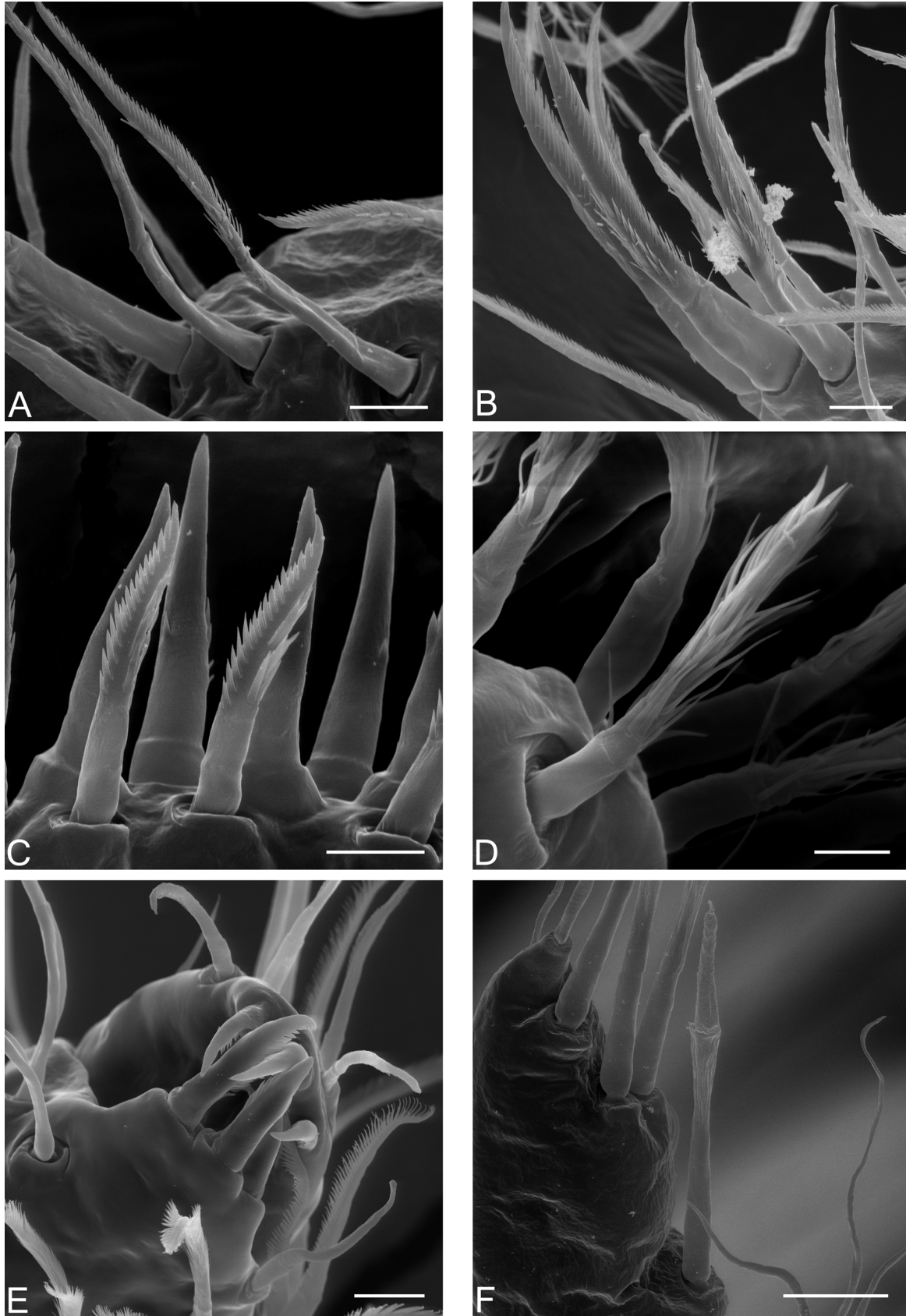
**Second, third and fourth pereopods** (Fig. 4b): Uniramous, 6-segmented. Coxa with several simple setae sparsely distributed and 4 pappose setae. Ischiobasis, merus, carpus and propodus subrectangular with several simple setae sparsely distributed. Dactylus subtriangular with several simple setae sparsely distributed.



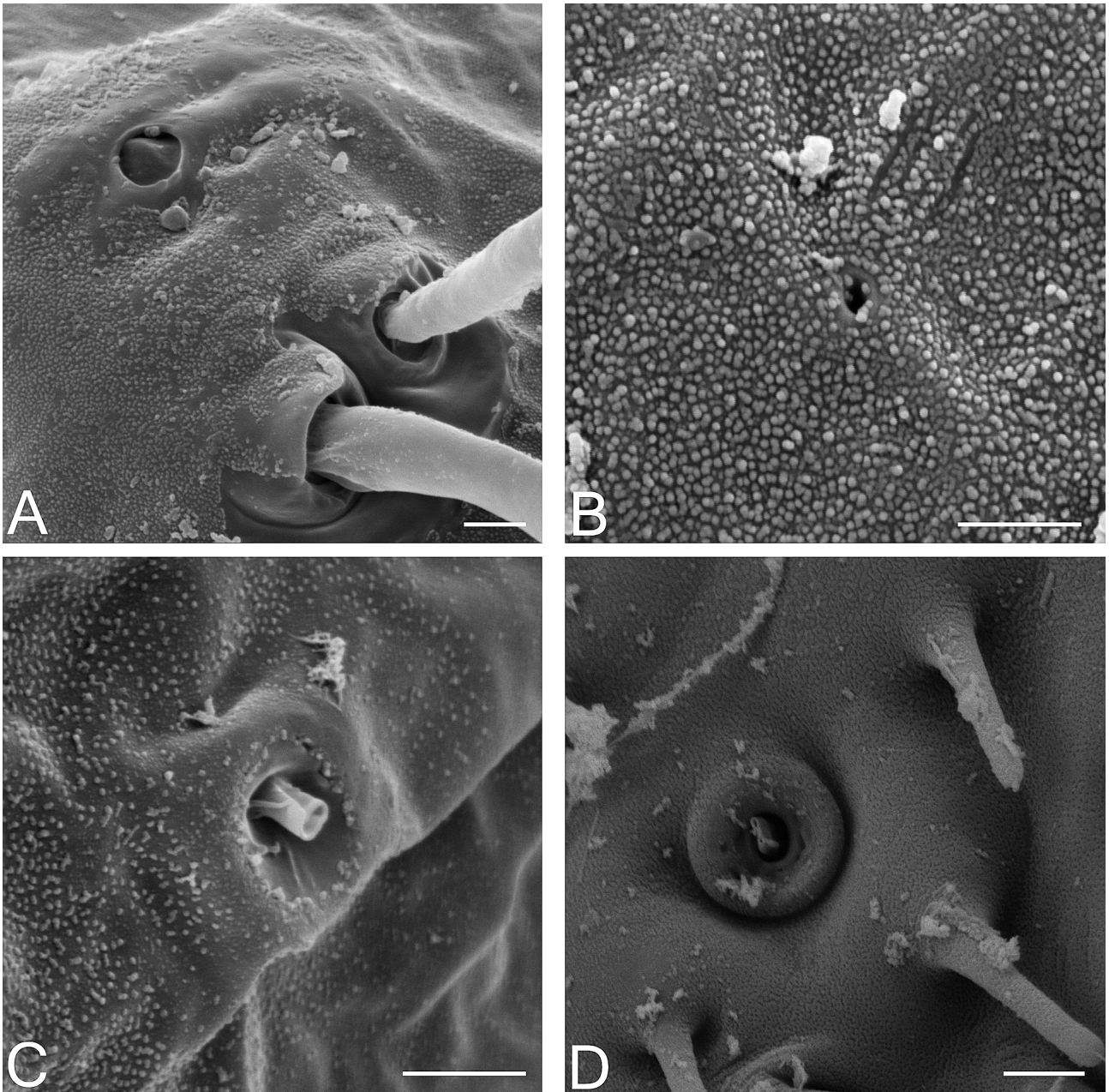
**FIGURE 9.** A) Sternum. B) with rudimentary pleopods (pl). C) Pleon dorsal view. D) Telson with rudimentary longitudinal groove (arrow). *Aegla perobae* newly-hatched juvenile. Scale: A, B = 200  $\mu$ m; C, D = 100  $\mu$ m



**FIGURE 10.** A) Minute simple setae of third maxilliped endopod propodus. B) Simple seta with terminal pore and scaly of maxilla endites. C) Pappose setae of second maxilliped. D) Pappose setae (distal half) of antennule. E) Papposerrate seta of maxillule basal endite. F) Plumose setae of first maxilliped. *Aegla perobae* newly-hatched juvenile. Scale: A = 5  $\mu\text{m}$ ; B = 2  $\mu\text{m}$ ; C = 20  $\mu\text{m}$ ; D, E = 10  $\mu\text{m}$ ; F = 50  $\mu\text{m}$ .



**FIGURE 11.** A) Serrate seta of second maxilliped endopod. B) Serrate setae of second maxilliped endopod. C) Cuspidate setae of maxillule basal endite. D) Serrulate seta of mandible palp. E) Stout serrate setae of fifth pereiopod propodus and dactylus. F) Aesthetasc of antennule dorsal flagellum. *Aegla perobae* newly-hatched juvenile. Scale: A, B, C, E = 10  $\mu\text{m}$ ; D = 5  $\mu\text{m}$ ; F = 20  $\mu\text{m}$ .

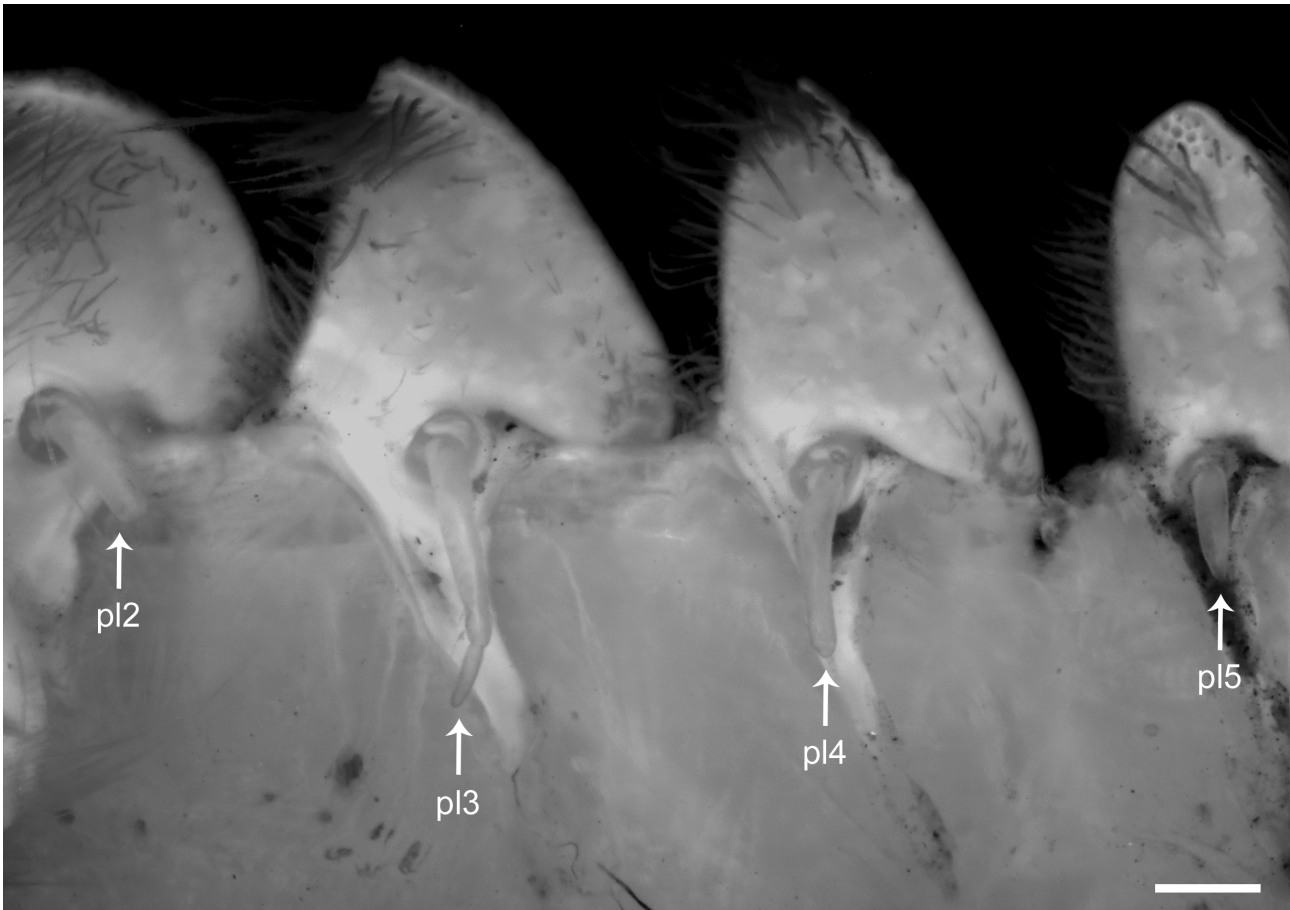


**FIGURE 12.** A) Pore type 1 of antenna. B) Pore type 2 of antenna. C) Pore type 3 of antennule (lateral view). D) Pore type 3 of rostrum distal region. *Aegla perobae* newly-hatched juvenile. Scale = 2  $\mu$ m.

**Fifth pereopod** (Figs 4c, 8h, 11e): Uniramous. Reduced in size as compared to other pairs of pereopods. Dactylus and fixed finger of propodus forming minute chela (Fig. 8h). Protopod with 3 simple setae. Ischium with 1–2 serrate setae. Merus with 2 serrate setae. Carpus with 4 serrate setae. Propodus with 21–25 serrate, 3 stout serrate setae and 2 minute simple setae. Dactylus with 1 simple seta, 4–5 serrate setae and 3 stout serrate setae (Fig. 11e).

**Pleopods** (Fig. 9b): Uniramous, rudimentary, 1-segmented and digitiform. Present on pleonal somites 2 through 5; one pair per segment.

**Uropods** (Fig. 5): Biramous. Protopod with 2–4 simple and 2 plumose setae. Endopod with 3–6 simple setae and 14–18 plumose setae. Exopod with 1–2 simple setae and 18–23 plumose setae along free margin. Distalmost group of plumose setae on both endopod and exopod are the longest.



**FIGURE 13.** Rudimentary uniramous pleopods 2–5 (one side shown only) in the abdomen of an adult male of *Aegla perobae*. All pleopods are 1-segmented except pleopod 3 which is 2-segmented. Scale = 0.5 mm.

## Discussion

Excluding freshwater aeglids, the postembryonic development pattern in marine anomurans is indirect, meaning that there is a larval phase in which the hatching form is typically a zoea. The type of development during the zoeal phase may be either regular or abbreviated, depending on the size and number of eggs, mode of feeding of the newly-hatched larva, the total number of zoeal stages and the state of development of larval structures between comparable larval stages. Regardless of the developmental pattern, however, the zoeal phase is followed by one megalopal stage before the subsequent appearance of the juvenile, or “first crab”, the ontogenetically equivalent instar to the first juvenile of *Aegla*.

Several anomuran families exhibit the regular developmental pattern, such as in the Galatheidae (Fagetti & Campodonico 1971; Christiansen & Anger 1990; Fujita & Shokita 2005; Fujita 2010), Porcellanidae (Fujita *et al.* 2002; Fujita & Osawa 2005), Hippidae (Knight 1967), Coenobitidae (Brodie & Harvey 2001) and Paguridae (McLaughlin *et al.* 1989; Barria *et al.* 2006). A case of extremely abbreviated development, however, has been reported for an undescribed species of the diogenid crab of the genus *Calcinus* Dana 1851 (Calado *et al.* 2006).

Abbreviated larval development has been reported in the families Chirostylidae (Clark & Ng 2008; Fujita & Clark 2010), Lomisidae (Cormie 1993; McLaughlin *et al.* 2010) and some species of Lithodidae (Haynes 1982; Crain & McLaughlin 2000a, b; McLaughlin *et al.* 2003). Unfortunately, the developmental pattern in the two marine fossil aeglids *Haumuriaegla* Feldmann 1984 and *Protaegla* Feldmann *et al.* 1998 is not known. In recent works on phylogenetic relationships amongst anomuran superfamilies, Aegloidea has been determined either as sister group to the clade Lithodoidea-Hippoidea (McLaughlin *et al.* 2007) or as sister taxon to Lomisoidea, with the clade Aegloidea/Lomisoidea allocated as sister group to Chirostyloidea (Schnabel *et al.* 2011).

In freshwater aeglids, the female provides protection to the newly-hatched juveniles for a few days in the brood

chamber formed by the flexed pleon (López-Greco *et al.* 2004). Very few examples of parental care in non-aeglid anomurans are known, and are referred to as extended parental care (XPC) because it is extended up to or beyond the first juvenile instar (Thiel 2003). An example of XPC was reported for an undescribed marine diogenid hermit crab, whose zoea larvae hatch at an advanced stage (= abbreviated larval development), and remain under protection inside the gastropod shell inhabited by its mother, until the juvenile stage is reached and they become capable of choosing their own gastropod shell (Calado *et al.* 2006). The term XPC, however, cannot be applied to freshwater aeglids, because there is no free larval form involved. Direct development followed by parental care is not unique to living aeglids. Similar life strategies have also evolved independently in freshwater brachyurans and some freshwater crayfishes (Hobbs 1972; Jones 1995; Scholtz & Kawai 2002; Burton *et al.* 2007; Vieira 2013) and are viewed as key features associated with the process of colonization and successful adaptation to freshwater habitats in decapods (Vogt 2013).

Upon hatching, the epibenthic freshwater aeglid juveniles already exhibit several advanced morphological features as compared to larval stage of other anomurans. Among these features worth citing we may include the stalked eyes, antennule with two rami and bearing aesthetascs, segmented mandibular palp, well-developed biramous and setose third maxilliped with *crista dentata* on the endopod, the full complement of well-developed and functional pereopods (including the minute terminal chela of the fifth pair), six pleonal somites, and well-formed tail fan (Bond-Buckup *et al.* 1996; Bueno & Bond-Buckup 1996; Bond-Buckup *et al.* 1999; Francisco *et al.* 2007; Teodósio & Masunari 2007; Moraes & Bueno 2013). Even the sutures, or lineae, on the carapace that so well characterize the genus *Aegla* [see Martin & Abele (1988) for morphological details of adult aeglids] are clearly discernible (Moraes & Bueno 2013; this paper). Francisco *et al.* (2007) failed to mention the presence of the *lineae aeglicae* on the carapace of *Aegla franca*, even though these lineae were clearly visible in SEM preparations of this species (Bueno, personal observation). It is possible that the presence of the complete set of *lineae aeglicae* in the first juvenile instar might be a feature common to all freshwater aeglids, as a result of the direct type of postembryonic development they all share.

Mouthparts in the newly-hatched juvenile of freshwater aeglids are well-developed and richly setose. Morphological traits that characterize an advanced state of development are: mandible with palp showing the characteristic number of segments particular to the taxon, endites of the maxillule and the maxillae exhibiting rich assortment of setae morphology for food handling and processing, including special setae with terminal pore in the maxillary endites with possible chemoreceptive function, and third maxilliped with *crista dentata* on the endopod (Francisco *et al.* 2007; Moraes & Bueno 2013).

Although there are no studies specifically conducted on the feeding mode of the first juvenile of freshwater aeglids, the morphology of the mouthparts strongly suggests that these appendages are already functional, so these juveniles could make immediate use of exogenous food particles, as suggested for *Aegla schmitti* by Teodósio & Masunari (2007). The only apparent exception being the rudimentary condition of the mandibular incisor process in *Aegla franca*, which, according to Francisco *et al.* (2007), could be associated with a brief period of lecithotrophy mode of feeding of the newly-hatched juvenile while still in the brood chamber during maternal care (Francisco *et al.* 2007).

One of the most intriguing findings was the observation of four pairs of uniramous finger-shaped pleopod buds in the newly-hatched juvenile of *Aegla perobae*. Similar condition has recently been reported in the first juvenile of *Aegla paulensis* as well (Moraes & Bueno 2013). In the description of the juvenile of *A. franca*, the pleopods are not mentioned at all (Francisco *et al.* 2007), but examination of the original material confirmed the presence of pleopod buds in this species too. However, pleopods are reported to be absent in newly-hatched juveniles of *A. platensis*, *A. longirostri*, *A. ligulata*, *A. prado*, *A. violacea* and *A. schmitti*, with no change in this condition in the second juvenile instar of the last two species mentioned (Bond-Buckup *et al.* 1996; Bueno & Bond-Buckup 1996; Bond-Buckup *et al.* 1999; Teodósio & Masunari 2007).

In adults of living aeglids, pleopods constitute a sexually dimorphic trait frequently used for quick sex determination. The first pair of pleopods is absent in adult *Aegla* of both sexes. The second through the fifth pairs of pleopods, however, are uniramous, 2-segmented, and used for egg incubation in adult females, while in adult males, these pairs of pleopods are lacking altogether or reduced to small calcified knobs (Martin & Abele 1988).

The ontogenetic implications of the presence of pleopod buds in some juvenile aeglids should be investigated further. One possible scenario suggested by Moraes & Bueno (2013) would be that it might involve further growth of the pleopods until they attain full development in adult females, or might regress to calcified knobs in adult

males. Adult males of *Aegla perobae*, however, still have rudimentary pleopods exhibiting varying degrees of development (Fig. 13). Although this morphological trait is indeed a remarkable feature per se for this condition has not yet been described in adult males of any other freshwater aeglid species, it should not be viewed as an evidence of possible correlation regarding the presence of rudimentary pleopods in both juvenile and adult males until more investigation is extended to other species.

In non-aeglid anomurans, pleopods 2–5 are absent (regular development pattern) or present as buds or incompletely developed rudiments (abbreviated development pattern) in the first zoeal instar, that gradually develop to non-functional appendages during larval development, and attain full development to become functional at the megalopal stage (Pike & Wear 1969; Haynes 1982; Stuck & Truesdale 1986; Christiansen & Anger 1990; Brodie & Harvey 2001; Harvey 1992; Cormie 1993; Hernández *et al.* 2002; Barria *et al.* 2006; Fujita & Clark 2010; Baba *et al.* 2011).

During the early juvenile phase, development of the pleopod proceeds according to the adult characteristics of the taxon. In hermit crabs, for example, morphological modifications of the pleopods associated with the spiralling of the pleon take place early in the juvenile phase (McLaughlin *et al.* 1989; McLaughlin *et al.* 1993; Gherardi & McLaughlin 1995). In lithodoids, the presence or the absence of pleopods in adult females and males, respectively, is a dimorphic trait (McLaughlin *et al.* 2007). During the early postembryonic development, pleopod buds may or may not attain their maximum development before they gradually reduce to rudiments or are completely lost during early crab stages (Haynes 1968; Crain & McLaughlin 2000a, b; McLaughlin & Paul 2002; McLaughlin *et al.* 2003). In *Lithodes aequispinus* Benedict 1895, pleopods redevelop only in females and on the left side of the pleon, and will serve for egg incubation purposes in adults (McLaughlin & Paul 2002).

Pleopods are also a sexually dimorphic trait in brachyurans. The postembryonic development in the freshwater trichodactylid crab, *Dilocarcinus pagei* Stimpson 1861, is direct and the newly-hatched juvenile bears four pairs of rudimentary pleopods (Vieira *et al.* 2013). Sexual differentiation involving these pleonal appendages already starts in the second juvenile stage through the retention of the first two pairs to be later modified as gonopods in males, while the pairs of pleopods 2–5 become biramous in females after the sixth juvenile stage (Vieira *et al.* 2013).

SEM techniques have opened new possibilities of detailed investigations on the morphology of newly-hatched aeglids, with special contributions regarding carapace texture and ornamentations, setal morphology (types and location on cephalothoracic appendages) and pore sensilla (on sensorial appendages) details. Unfortunately, the use of SEM techniques has only recently been introduced in the study of newly-hatched juveniles of aeglids, thus limiting morphological comparisons to four species only: *Aegla prado*, *A. franca*, *A. paulensis* and *A. perobae* (Bond-Buckup *et al.* 1996; Francisco *et al.* 2007; Moraes & Bueno 2013; this paper).

One feature that can be seen is the reduced and coalesced condition of the orbital spine, which, with the anterolateral spine, produces an incipient extraorbital sinus in the juvenile (Fig. 7a). For *Aegla perobae* juvenile, the orbital spine was absent in some individuals, and, when it occurred it was small (Fig. 7a–b). Another specific characteristic of *A. perobae* easily observed by SEM is the elevated border of the orbital sinus, defining distinct groove along the orbital sinus, mainly when orbital spine is present (Fig. 7a).

Figures 10 and 11 show a selection of setal morphology found in the juvenile of *Aegla perobae*. Some types of setae are only clearly distinguishable through SEM techniques, such as the minute simple setae (Fig. 10a), which have also been reported in newly-hatched juvenile of *Aegla paulensis* (Moraes & Bueno 2013). Because these setae are located in the inner side at the articulation region between segments of the endopod of the second and third pairs of maxillipeds and the first (= chelipeds) and fifth pairs of pereopods, Moraes & Bueno (2013) have suggested that they may serve as mechanoreceptors of stretching and bending movement between specific segments.

Observations through SEM techniques also confirmed the presence of pappose setae (distal half) on the antennule and the serrulate setae on the mandibular palp, which have previously been reported in *Aegla paulensis* (Moraes & Bueno 2013). SEM analyses still allowed the observation on the variation among species in the number of simple setae with terminal pore in the endites of the maxilla, being very similar and numerous in *Aegla perobae* (n= 23) and *A. paulensis* (n= 20–23), but less frequent in *A. franca* (n = 10–12).

Pore sensillae in aeglids were first described in *Aegla franca* on both pairs of sensorial appendages (Francisco *et al.* 2007). While one single type of pore was recognized in that species, three different types were reported in *A. paulensis* (Moraes & Bueno 2013) and *A. perobae* (this paper; Fig. 12). Based on morphology and distributional pattern, type 1 pore sensillum corresponds to those reported in *A. franca* by Francisco *et al.* (2007). Pore sensilla of



types 2 or 3 were observed on the antennae and carapace in *A. paulensis* and on both pairs of sensorial appendages (antennule and antenna) and carapace to *A. perobae* (this paper).

In *Aegla perobae*, some structures show modification during ontogenetic development. For example, the dorsal carina does not reach the apex of the rostrum in juveniles (this paper), while in adults the dorsal carina extends throughout its length (Bond-Buckup & Buckup 1994). Also, the markedly trapezoidal shape of the areolar area in the juveniles contrasts sharply with the rectangular shape of the adult form (Bond-Buckup & Buckup 1994). The incipient epipod on the protopod of the first maxilliped develops into the conspicuous lamellar lobe found in the adult (Martin & Abele 1988). Although Martin & Abele (1988) indicate that the lamellar lobe derives from the basal portion of the exopod, we follow the interpretation suggested by Schnabel & Ahyong (2010) that this lamellar lobe would actually correspond to an epipod, and would be homologous to the epipod found in other anomuran families (Schnabel & Ahyong 2010; Baba *et al.* 2011).

As a final remark, one might be misled by the apparent similarity of the general morphology of body and appendages, which appear at first as very conservative among juveniles of aeglid species and may question their potential as informative characters. However, one should bear in mind that the description of newly-hatched juveniles of aeglids is still only beginning, and that only few species from Brazil have been investigated so far. As descriptions of the first juvenile of other aeglid species continues to be published, a rich picture on juvenile morphological variability might present itself, and which may well reflect the variability already recognized in the adults. Raising and describing aeglid juveniles beyond the newly-hatched form is also strongly desirable and recommended so as allow a clear understanding of the ontogenetic developmental modifications of selected features, especially those associated with sexual dimorphism, such as the pleopods.

Only after such studies are expanded to include other aeglid species, including those from Chile and Argentina, will strong and informative data be available for comparative phylogenetic studies regarding early postembryonic data within the Aegliidae. Also, comparative studies of early life stages should be warranted, since these are important tools for the understanding of phylogenetic relationship among anomurans and other decapods crustaceans.

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