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Original Article

Reconstructing the life cycle of the isopodan group Aegidae with morphological descriptions and the importance of immature stages

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ABSTRACT

A collection of various developmental stages of Aegidae is presented and described, with the first description and photographs of eggs and embryos of this group. Intra-specific variation among specimens and developmental stages is described, as well as inter-specific, ontogenetic variation between immature stages and their better-known adult stages. Developmental stage differentiation of these opportunistic feeders is compared to that of the closely related parasitic representatives of Cymothoidae. This study is the first to attempt to provide the life cycle of these animals, which include well-documented and described immature stages.

KEYWORDS

Cymothoida, development, embryo, manca, ontogeny

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INTRODUCTION

A few crustacean groups are rather highly diversified and species rich, including Isopoda. Inhabiting nearly every environment on earth, animals of this group have developed various specialized and unique morphological characters, as well as remarkable, unusual, and complex developmental patterns and variation, in addition to an array of feeding- and life habits. Yet, many species of Isopoda are so far, only known by a single ontogenetic stage, in most cases an adult male or female specimen, with little to nothing known about the immature and embryonic stages. This seems correlated to the fact that isopodan crustaceans are generally considered as "direct developers" (see Haug, 2019 for challenges to the term). Yet, it is well known that within Isopoda, some lineages are characterized by a distinct differentiation between the adults and immatures concerning their morphology and ecology; immatures in such cases are referred to as larvae (Boyko and Wolff, 2014; Haug, 2020; Van der Wal and Haug, 2020). Larvae are well known in representatives of the group Epicaridea (Boyko and Wolf, 2014) and have even been found in the fossil record (Serrano-Sanchez et al., 2016; Schädel et al., 2019; 2021). Immatures in the group Cymothoidae are also differentiated from their adults (van der Wal and Haug, 2020); this differentiation has also been recognized in fossil representatives (van der Wal et al., 2021). Cymothoidae and Epicaridea are considered by some to be closely related (Dreyer and Wägele, 2002; Brandt and, Poore 2003; Nagler et al., 2017; Hua et al., 2018). Representatives of both groups are highly specialized parasites as adults; hence the variation of developmental stages documented for these groups, has likely evolved in correlation to this specific lifestyle. To further understand the evolutionary correlation between developmental differentiation and lifestyle or parasitic strategy, other closely related groups that show less specialized types of parasitism should be highly informative.

Aegidae is a candidate group for such an approach (Nagler et al., 2017). Unfortunately, the immature stages of Aegidae are seldom encountered, or intentionally overlooked (Jones, 2008), especially within taxonomic, phylogenetic, and ecological works. This is probably due to the notion that immature stages should have the general appearance of adult stages and are therefore unimportant or uninformative (Hale, 1925), or that they are indistinguishable between species (Miller, 1968). The resulting lack of knowledge leaves a large gap in the understanding of changes in ecological roles and morphology through development and hampers evolutionary comparisons.

Most aspects of the life cycle of Aegidae are largely unknown (Wägele, 1989). Brusca and Iverson (1985) and Sars (1897) stated that species of Aegidae show little sexual dimorphism, or that these differences are not prominent. Unlike many terrestrial and parasitic groups of Peracarida, representatives of Aegidae do not seem to be hermaphroditic, but rather develop as separate sexes (Wägele, 1990; Ramdane and Trilles, 2008), which is usually the case with non-parasitic marine representatives of Isopoda (Johnson, 2001). Immature stage specimens are usually referred to with the umbrella terms 'manca', 'juvenile' or simply 'larvae' (Pillai, 1964; Williams and Bunkley-Williams, 1980; Bakenhaster, 2004; Trilles and Justine, 2006; Čolak et al., 2019) with insufficient substantiation given for the interpretation of the developmental stage, other than the overall body size and the presence or absence of the seventh pair of trunk appendages (8^{th} pair of thoracopods). These smaller sized individuals have rarely been described or illustrated, with only a few publications providing some information on the morphological characters of at least one immature stage specimen (see Bruce, 1988; Sars, 1987; Kensley, 2004; Brusca and France, 1992; Bruce, 2009; Shimomura and Bruce, 2019). The early works of Schioedte and Meinert (1884) provide more comprehensive descriptions and illustrations of some non-adult stages.

Here, we provide the first comprehensive description and high-quality photographs of immature stages of six species of Aegidae. Additionally, we contribute some insight into ontogenetic and inter-specific variation and their importance, with the focus on immature stages.

MATERIAL AND METHODS

Material

Selected material containing possible immature stages of Aegidae was loaned from the National Institute of Water & Atmospheric Research Ltd (NIWA), New Zealand. A total of 20 specimens of 6 different species were examined. The species were already identified upon loan of the material, as the collections also contain adult specimens, which had been examined by Bruce (2009). Therefore, only the immature specimens were subjected to full documentation and dissection. Morphological descriptions are provided here for immature stages of the examined species. References to the descriptions for adult stages are provided in the remarks.

Documentation methods

All specimens were kept submerged in 70% ethanol throughout the documentation process to maintain preservation of the material. Individual specimens were documented and photographed using a Keyence VHX-6000 Digital Microscope with Z-stack function, resulting in full-focus composite images. The total length of each specimen was recorded using the scaling and measuring function on the Keyence VHX-6000. After thorough photographic documentation of each specimen, mouthparts and in some cases, pleon appendages, were dissected to be used for morphological description and comparison. Mouthparts were cleaned and mounted to be photographed using an inverse fluorescence microscope BZ-9000 (BIOREVO, Keyence) with fluorescence (with DAPI filter) and brightfield settings. These settings were used in combination to achieve composite images with full visibility of small structures along the outlines of the structure, along with the overall surface of the structure. Dissected parts were collected and stored in vials along with each representative specimen and collection number. Image processing and editing, as well as arrangement of figure plates, was done using the software programs Affinity Photo and Affinity Designer. Measurements, ratios and scale bars were calculated and generated using Fiji (open source, GNU General Public License).

Terminology

Specialised terminology often prohibits communication beyond a specific taxonomic border. The specimen descriptions herein comprise terminology used for the general Eumalacostraca body organization and articulation based on Walossek (1999), and as used by Nagler et al. (2019) and van der Wal et al. (2021).

The following terminology is used herein: head (in literature also referred to as cephalon or cephalothorax) with the clypeus (sclerotised plate) that bears the labrum ('upper lip'). The head further bears the ocular segment and six post-ocular segments, including appendages antennula, antenna, mandible, maxillula, maxilla and maxilliped; the anterior trunk (in literature also referred to as the posterior thorax or pereon) of seven segments (thoracomeres, also referred to as pereonites), each with one pair of appendages (thoracopods, also referred to as pereopods); a posterior trunk (pleon) comprising five anterior segments (pleomeres, or also pleonites), each with one pair of appendages (pleopods) and the sixth pleon segment conjoined to the telson forming the pleotelson, with one pair of appendages (uropods).

Staging of immature individuals

The ontogenetic staging of specimens is based on the descriptions of stages provided and described in van der Wal and Haug (2020) for Cymothoidae, a closely related group to Aegidae. Immature stage 1 refers to individuals that have hatched from the egg and are initially still inside the brood pouch of the female. Individuals in this stage have distinctly developed appendages and large eyes, but lack the last (7th) pair of pereopods. Immature stage 1 moults into immature stage 2, which is released from the brood pouch. This stage still has prominent eyes and lacks the last (7th) pair of pereopods. Immature stage 3 individuals also have large eyes, but differ from the earlier stages by possessing a pair of fully developed last (7th pair) pereopods. Additionally, the body is usually more streamlined. In the next stage the transformation to adult stages begins.

RESULTS

For full synonymies of all species examined, refer to Bruce (2009).

Descriptions

Aega monophthalma Johnston, 1834

Material examined. Immature male stage 3 (26.5 mm total length, 11.54 mm wide, excluding laterally visible coxae), Fig. 1. NIWA Cat. No. 23759. Collected at North Norfolk Ridge, 28°51.21'S 167°42.53'E, coll. R/V "Tangaroa", on 15 May 2003.

Immature male stage 3 NIWA 23759 (Fig. 1)

Body ovoid, longer than wide, 2.3 ×, slightly ventrally curved, widest at trunk segment 5, most narrow at trunk segment 7 (Fig. 1A, B). Head wider than long, 2.33 ×, anterior margin broadly rounded, not ventrally folded. Eyes medially united, extending backwards, surpassing anterior margin of trunk segment 1; longer than wide, 3.45 ×; each eye made up of ~ 23 transverse rows of ommatidia, each row with ~ 36 ommatidia (Fig. 1A–C). Frontal lamina longer than wide, 1.63 ×, anterior margin with medial protrusion (Fig. 1D). Clypeus, labrum with indistinct margins.

Antennula 2.34 mm long, consisting of 10 articles, extending to middle of eye, with plumose setae on articles 1–3, with tufts of long setae on articles 5–10 (Fig. 1E); article 1 longer than wide, 1.14 ×, with simple setae; article 2 longer than wide, 1.11 ×, with disto-lateral protrusion; article 3 longer than wide, 1.66 ×, with individual simple setae; article 4 short, wider than long, 2.22 ×. Antenna 5.16 mm long, longer than antennula, consisting of 20 articles, extending to middle of anterior trunk segment 1, with plumose setae on articles 4–5, with simple setae on articles 6–20, terminal article with 1–5 short simple setae (Fig. 1F); article 1 wider than long, 1.63 ×; article 2 wider than long, 2.48 ×; article 3 wider than long, 1.2 ×; article 4 longer than wide, 1.67 ×. Mandible coxa 1.39 mm long; molar process present, ending in an acute incisor (Fig. 1G). Mandible palp 2.08 mm long; article 1 longer than wide, 3.77 ×; article 2 (slightly broken) longer than wide, 6.77 ×, with 3 long disto-lateral setae; article 3 longer than wide, 3.27 ×, with 13 serrate setae. Maxillula 1.13 mm long, with endite, terminating distally in 7 robust setae (Fig. 1H). Maxilla 1.28 mm long; lateral lobe with 2 recurved robust setae; mesial lobe 3 recurved robust setae (Fig. 1I). Maxilliped 1.69 mm long, consisting of 5 articles, with endite on article 1 (Fig. 1J); article 3 with 3 recurved robust setae; article 4 with 4 recurved robust setae; palp article 5 with 3 recurved robust setae.

Anterior trunk longer than pleon length, 1.78 ×. Anterior trunk segment 1 anterior border straight, anterolateral angle encompassing posterior margins of eyes. Anterior trunk appendages 7 pairs, posterior pair underdeveloped (Fig. 1B, K). Coxae 2–3 with posteroventral angles rounded; coxae 4–7 posteriorly pointed; coxa 7 smaller than remaining coxae (underdeveloped); all extending past respective anterior trunk segment margins. Trunk appendage 7 present, largely underdeveloped (Fig. 1K).

Pleon segments subequal in length; pleon segment 1 not concealed by anterior trunk segment 7, visible in dorsal view; pleon segment 5 overlapped by lateral margins of pleon segment 4, posterior margin slightly convex. Penial openings present (Fig. 1L) on posterior margin of sternite 7, set apart. Pleon appendage 2 with appendix masculina (Fig. 1M).

Pleotelson wider than long, 1.21 ×; dorsal surface with 2 sub-medial depressions, with longitudinal carina; lateral margins evenly rounded, slightly convex, posterior margin converging to medial point. Uropods more than half the length of pleotelson.

Remarks. For species descriptions and illustrations of adult specimens, see for example Johnson (1834), Treat (1980), Kensley (1978), and Bruce (2009). Specimen NIWA 23759 is an immature male stage 3 ('juvenile'). This interpretation is substantiated by the largely underdeveloped pair of trunk appendage 7 as well as the presence of visible penial openings on sternite 7 with an appendix masculina on the medial margin of pleon appendage 2.

Ontogenetic intra-species variation. Immature male stage 3 of *A. monophthalma* differs from its adult counterparts by having a smaller overall body size; a more evenly ovoid body, compared to the egg-shaped adult male examined in Bruce (2009) and the elongate adult illustrated by Johnston (1834); more ommatidia; fewer antennula and antenna articles than that of an adult male; a maxillula with endite; narrower coxae (especially coxae 4–6, best visible from lateral view); with coxa 7 largely underdeveloped, not visible and almost completely concealed by coxa 6 in lateral view; pleon appendage endo- and exopods proximally covered in setae, versus a few single setae on those of an adult male; appendix masculina shorter than that of an adult male. The remaining mouthparts are similar to that of an adult male.

Aegapheles mahana Bruce, 2009

Material examined. Immature male stage 3 (21.0 mm total length, 7.36 mm wide, excluding laterally visible coxae), Fig. 2. NIWA Cat. No. 17943. Collected at South Norfolk Ridge, 33°22.61'S 170°12.70'E, coll. R/V "Tangaroa", 1 June 2003.

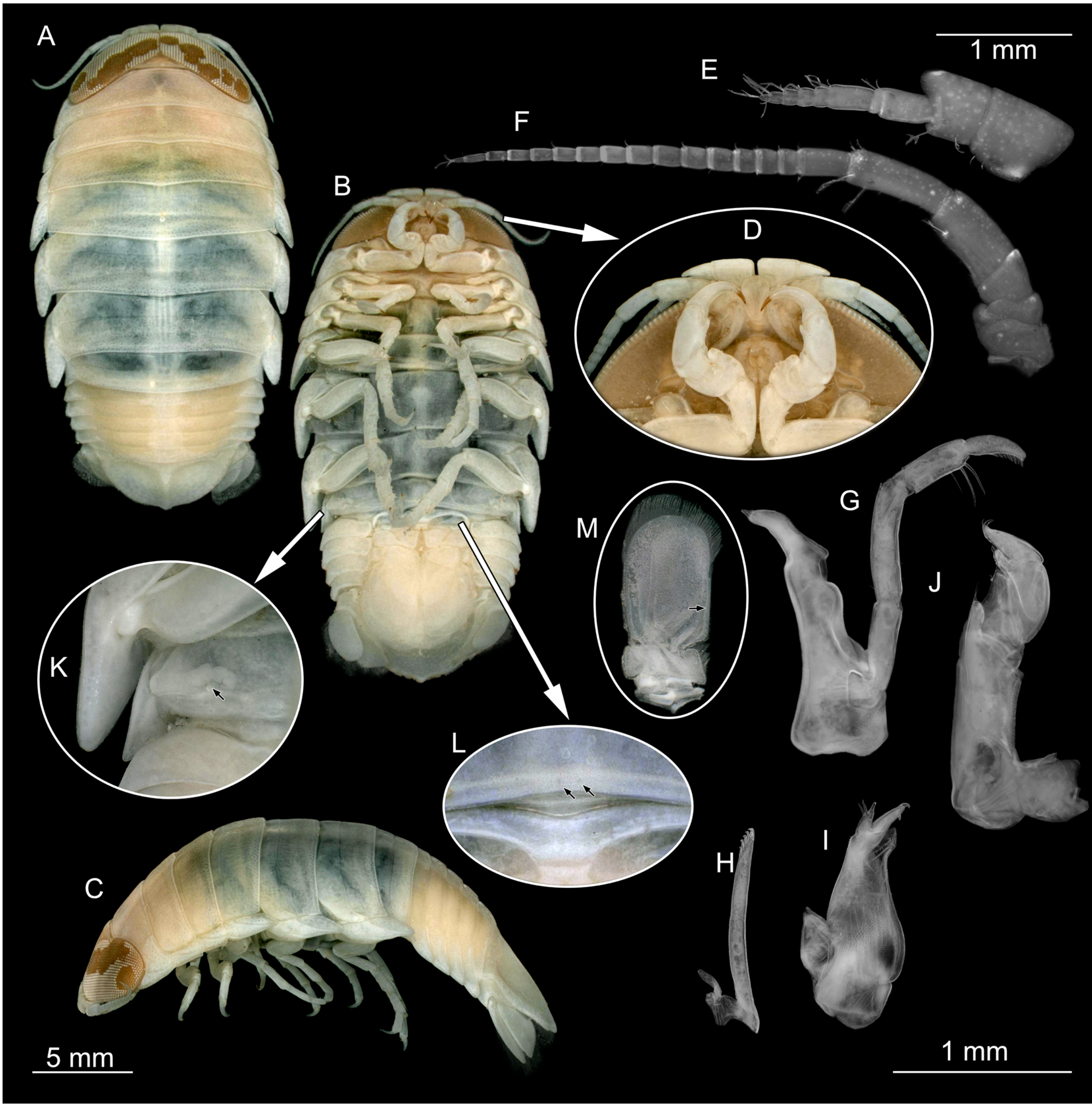

Figure 1. *Aega monophthalma* Johnston, 1834 immature male stage 3 (NIWA 23759). **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. **D**, Anteroventral view. **E**, Antennula. **F**, Antenna. **G**, Mandible. **H**, Maxillula. **I**, Maxilla. **J**, Maxilliped. **K**, Close-up of underdeveloped thoracopod 7. **L**, Close-up of penial openings. **M**, Pleon appendage 2 with appendix masculina. Scales: **A–C,** 5 mm; **E–F,** 1 mm (top, right); **G–J,** 1 mm (bottom, right).

Immature male stage 3 NIWA 17943 (Fig. 2)

Body elongate, longer than wide, 2.9 ×, widest at trunk segment 5, most narrow at trunk segment 7 (Fig. 2A–C). Head wider than long 3.67 ×, anterior margin broadly rounded, not ventrally folded. Eyes medially united, extending backwards, surpassing anterior margin of trunk segment 1; longer than wide, 2.91 ×, each eye made up of ~ 9 transverse rows of ommatidia, each row with ~ 22 ommatidia (Fig. 2A–C). Frontal lamina longer than wide, 1.1 ×, anterior margin rounded (Fig. 2D). Clypeus, labrum with indistinct margins.

Antennula 2.84 mm long, consisting of 12 articles, extending to middle of eye, with individual simple setae on articles 1, 3, 7–12 (Fig. 2E); article 1 longer than wide, 1.28 ×, with marginal simple setae; article 2 longer than wide, 1.29 ×, with disto-lateral protrusion;

article 3 longer than wide, 2.66 ×; article 4 short, wider than long, 2.15 ×. Antenna 5.24 mm long, longer than antennula, consisting of 18 articles, extending almost to posterior margin of anterior trunk segment 1, with plumose setae on article 5, tufts of setae on articles 6–18, terminal article with 1–5 short simple setae (Fig. 2F); article 1 as long as wide; article 2 wider than long, 1.65 ×; article 3 as long as wide; article 4 longer than wide, 2.19 ×. Mandible coxa 1.38 mm long, molar process present, ending in an acute incisor (Fig. 2G). Mandible palp 1.58 mm long; article 1 longer than wide, 3.31 ×; article 2 longer than wide, 4.06 ×, with 7 long disto-lateral setae; article 3 longer than wide, 3.74 ×, with 17 serrate setae. Maxillula 1.12 mm long, with endite, with 8 terminal robust setae (Fig. 2H). Maxilla 1.3 mm long; lateral lobe with 3 recurved robust setae; mesial lobe 2 recurved robust setae (Fig. 2I). Maxilliped 1.68 mm long, consisting of 5 articles, with endite on article 1; article 4 with 6 recurved robust setae; article 5 with 5 recurved robust setae (Fig. 2J).

Anterior trunk longer than pleon length, 1.43 ×. Anterior trunk segment 1 anterior border slightly convex, anterolateral angle encompassing posterior margins of eyes. Anterior trunk appendages 7 pairs, posterior pair underdeveloped (Fig. 2K). Coxae 2–3 with posteroventral angles rounded; coxae 4–7 posteriorly pointed; coxa 7 smaller than remaining coxae (underdeveloped, Fig. 2K); all extending past respective anterior trunk segment margins. Trunk appendage 7 present, underdeveloped; all articles longer than wide: basipod 3.2 ×, ischium 2.12 ×, merus 2.28 ×, carpus 3.03 ×, propodus 3.91 ×, dactylus 2.43 ×.

Pleon segments subequal in length; pleon segment 1 not concealed by anterior trunk segment 7, visible in dorsal view; pleon segment 5 longest, posterior margin slightly convex. Penial tubercles present on posterior margin of sternite 7, penial openings set apart (Fig. 2K). Pleon appendage 2 with appendix masculina (Fig. 2L).

Pleotelson longer than wide, 1.15 ×, dorsal surface smooth, lateral margins weakly convex, posterior margin converging to medial point or triangular. Uropods same length or slightly longer than the pleotelson, not extending to pleotelson posterior margin.

Remarks. For species descriptions and illustrations based on adult male specimens, see Bruce (2009). Specimen NIWA 23759 is an immature male 3 ('juvenile' or young male). This interpretation is substantiated by the presence of penial processes and appendix masculina, but with an underdeveloped pair of trunk appendage 7.

Ontogenetic intra-species variation. The examined specimen is morphologically very similar to that of the described and illustrated holotype adult male in Bruce (2009). Some minor differences to the adult male include a smaller overall body size; less antennula and antenna articles; maxillula with an endite; an underdeveloped trunk appendage 7; penial openings more posterior on sternite segment 7.

Aegiochus antarctica **(Hodgson, 1910)**

Material examined. Eggs (~2.25 mm total length), embryos (~2.35 mm total length, ~1.7 mm wide), Fig. 3; immature stage 2 (5.7 mm long, 3.05 mm wide), Fig. 4. NIWA Cat. No. 23671. Collected at Pennell Bank, 74°30'S 179°40'E, 15 January 1959. Immature stage 1 (4.48 mm total length, 2.15 mm wide), Fig. 5. NIWA Cat. No. 23664. Collected at the Balleny Islands 65°24.76'S 160°53.22'E, 7 March 2004.

Additional material examined (not described). Adult male (15.0 mm total length, 7.9 mm wide), ovigerous female (20.1 mm total length, 10.2 mm wide), gravid female (22.74 mm total length, 11.26 mm wide), NIWA Cat. No. 23671. Collected at Pennell Bank, 74°30'S 179°40'E, 15 January 1959.

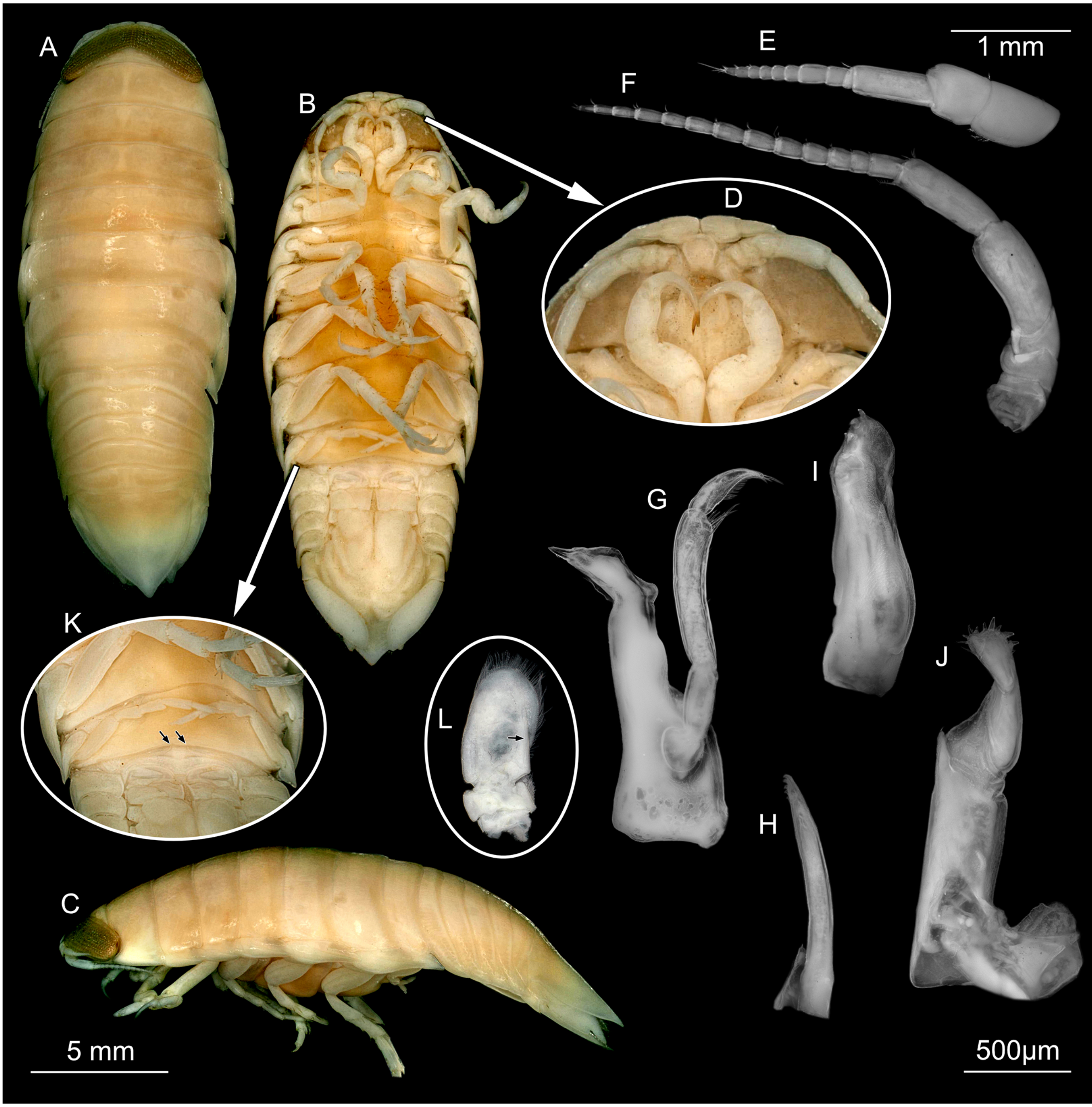

Figure 2. *Aegapheles mahana* Bruce, 2009 immature male stage 3 (NIWA 17943). **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. **D**, Anteroventral view. **E**, Antennula. **F**, Antenna. **G**, Mandible. **H**, Maxillula. **I**, Maxilla. **J**, Maxilliped. **K.** Close-up of underdeveloped thoracopod 7 and penial tubercules. **L**, Pleon appendage 2 with appendix masculina. Scales: **A–C,** 5 mm; **E–F,** 1 mm; **G–J,** 500 µm.

Eggs NIWA 23671 (Fig. 3A–E)

Egg mostly comprised of yolk. Dorsal organ not visible. Germline visible on ventral surface. Germ disc visible ventrally as accumulation of cells, precursor for germband development (Fig. 3D, E). Anterior and posterior ends distinguishable (Fig. 3C). Development in dorsally folded orientation. Ectoteloblasts visible. Single uniform membrane (egg membrane) visible, in close contact with yolk (Fig. 3A–D). No appendage subdivision.

Embryos NIWA 23671 (Fig. 3F–I)

Embryos slightly elongate; segmentation, early development of trunk appendages. Tergites not fully distinguishable (dorsal closure not yet complete, Fig. 3F–G). Frontal head lobes developed. Body

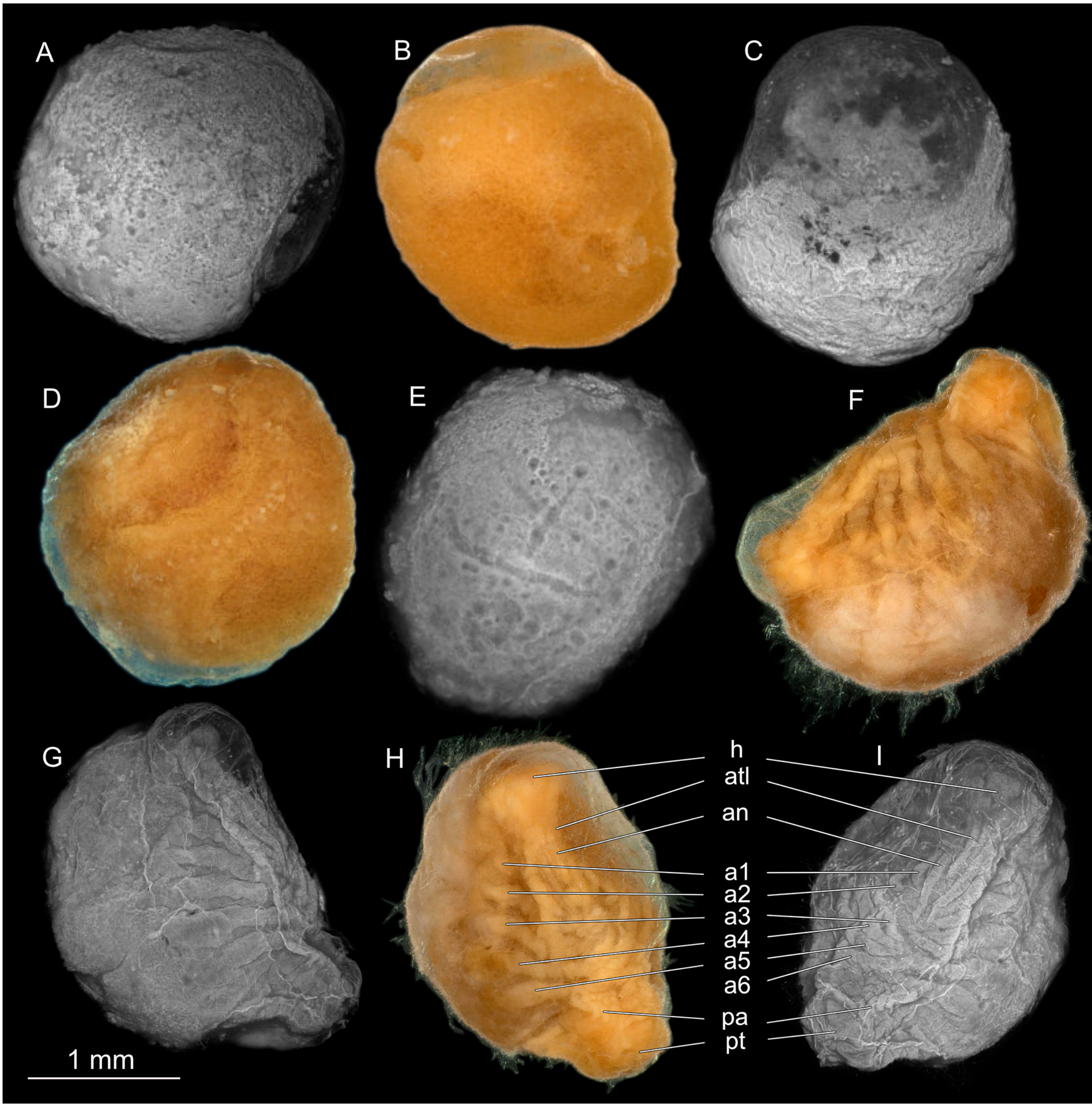

Figure 3. *Aegiochus antarctica* (Hodgson, 1910) (NIWA 23671). **A–E**, Eggs. **F–G**, Embryo lateral view. **H–I**, Embryo ventral view. h, head; atl, antennula; an, antenna; a1–6, trunk appendage 1–6; pa, pleon appendages; pt, pleotelson.

covered in single encompassing membrane; outer surface covered with fine, simple setae (Fig. 3F, H).

Immature stage 2 NIWA 23671 (Fig. 4)

Body ovoid, longer than wide, 1.87 ×, widest at trunk segment 5, most narrow at trunk segment 1 (Fig. 4A, B). Head wider than long, 3.29 ×, triangular, with blunt rostrum, slightly folded ventrally. Eyes small, set wide apart, longer than wide, 4.26 ×, ommatidia not clearly visible for counting. Frontal lamina wider than long, 1.42 ×, anterior margin truncated triangular (Fig. 4C). Clypeus, labrum with distinct margins.

Antennula 1.85 mm long, consisting of 14 articles, extending to middle of anterior trunk segment 2, with plumose setae on articles 1–3, tufts of setae on articles 5–14 (Fig. 4D); article 1 as long as wide; article 2 as long as wide; article 3 longer than wide, 1.98 ×; article 4 short, wider than long, 2.9 ×. Antenna 2.46 mm long, longer than antennula, consisting of 16 articles, extending to postero-lateral margin of anterior trunk segment 2, with tufts of setae on articles 4–16, terminal article terminating with 6–10 short simple setae (Fig. 4E); article 1 wider than long, 1.59 ×; article 2 wider than long, 1.32 ×; article 3 wider than long, 1.19 ×; article 4 longer than wide, 1.65 ×. Mandible coxa 0.63 mm long, molar process present, ending in an acute incisor (Fig. 4F). Mandible palp 0.68 mm long; article 1 longer than wide, 1.65 ×; article 2 longer than wide, 2.71 ×, with 5 long disto-lateral setae; article 3 longer than wide, 1.97 ×, with 21 serrate setae. Maxillula 0.46 mm long, with endite, with 4 terminal robust setae (Fig. 4G). Maxilla 0.4 mm long (Fig. 4H); lateral lobe with 2 recurved robust setae; mesial lobe 2 recurved robust setae. Maxilliped 0.72 mm long, consisting of 5 articles, with endite on article 1 (Fig. 4I); article 4 with 5 recurved robust setae; article 5 with 4 recurved robust setae.

Anterior trunk as long as pleon length. Anterior trunk segment 1 anterior border straight, anterolateral angle narrowly rounded. Anterior trunk appendages 6 pairs, each with 7 articles. Coxae 2–3 with posteroventral angles rounded; coxae 4–7 posteriorly pointed; coxa 7 smaller than remaining coxae (underdeveloped); all extending past respective anterior trunk segment margins. Trunk appendage 7 not developed.

Pleon segments subequal in length, pleon pleon segment 5 longest; segment 1 largely concealed by underdeveloped trunk segment 7, slightly visible in dorsal view; pleon segment 5 longest, posterior margin slightly convex. Penial structures absent (Fig. 4J). Pleon appendage 2 without appendix masculina (Fig. 4K).

Pleotelson wider than long, 1.4 ×, dorsal surface smooth, lateral margins with serrations, posterior margin triangular. Uropods same length or slightly longer than the pleotelson.

Immature stage 1 NIWA 23664 (Fig. 5)

Body medially ovoid, longer than wide, 2.08 ×, widest at trunk segment 5, most narrow at trunk segment 1 (Fig. 5A–C). Head wider than long, 2.4 ×, frontal margin subtriangular, rostrum slightly folded ventrally. Eyes small, set wide apart, folded latero-ventrally with head, longer than wide, 1.3 ×, each row with ~ 11 ommatidia (Fig. 5A–C). Frontal lamina wider than long, 1.39 ×, anterior margin with median point (Fig. 5D). Clypeus indistinct margins, labrum indiscernible.

Antennula 1.44 mm long, consisting of 12 articles, extending to posterior end of anterior trunk segment 1, with tuft of setae on distal most article (Fig. 5E); article 1 longer than wide, 1.27 ×, with rounded proximal end; article 2 as long as wide; article 3 longer than wide, 2.1 ×; article 4 longer than wide, 1.26 ×. Antenna 1.73 mm long, longer than antennula, consisting of 15 articles, extending to postero-lateral margin of anterior trunk segment 3, with tufts of setae on articles 14–15 (Fig. 5F); article 1 wider than long, 1.83 ×, article 2 wider than long, 2.15 ×; article 3 wider than long, 1.4 ×, article 4 longer than wide, 1.5 x. Mandible coxa 0.44 mm long, molar process present, ending in an acute incisor (Fig. 5G). Mandible palp 0.5 mm long; article 1 longer than wide, 1.8 ×; article 2 longer than wide, 3.1 ×, with 4 short, disto-lateral setae; article 3 longer than wide, 3.14 ×, with 11 serrate setae. Maxillula 0.36 mm long, with endite, with 4 terminal robust setae (Fig. 5H). Maxilla 0.34 mm long (Fig. 5I). Maxilliped 0.53 mm long, consisting of 5 articles, with endite on article 1; article 2 with 1 seta; article 3 with 1 recurved robust seta; article 4 with 2 recurved robust setae; article 5 with 2 recurved robust setae (Fig. 5J).

Anterior trunk longer than pleon, 1.38 ×. Anterior trunk segment 1 anterior border straight, anterolateral angle pointed, not produced. Anterior trunk appendages 6 pairs, each with 7 articles (Fig. 5B). Coxae 2–3 with posteroventral angles acute, posteriorly produced; coxae 4–7 posteriorly pointed, coxa 7 not developed, all extending past respective anterior trunk segment margins. Trunk appendage 7 absent, not developed.

Pleon segments subequal in length, pleon segment 5 longest; pleon segment 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleon segment 5 free, not overlapped by lateral margins of pleon segment 4 or longest, posterior margin straight with slight medial protrusion. Penial structures absent. Pleon appendage 2 without appendix masculina (Fig. 5K).

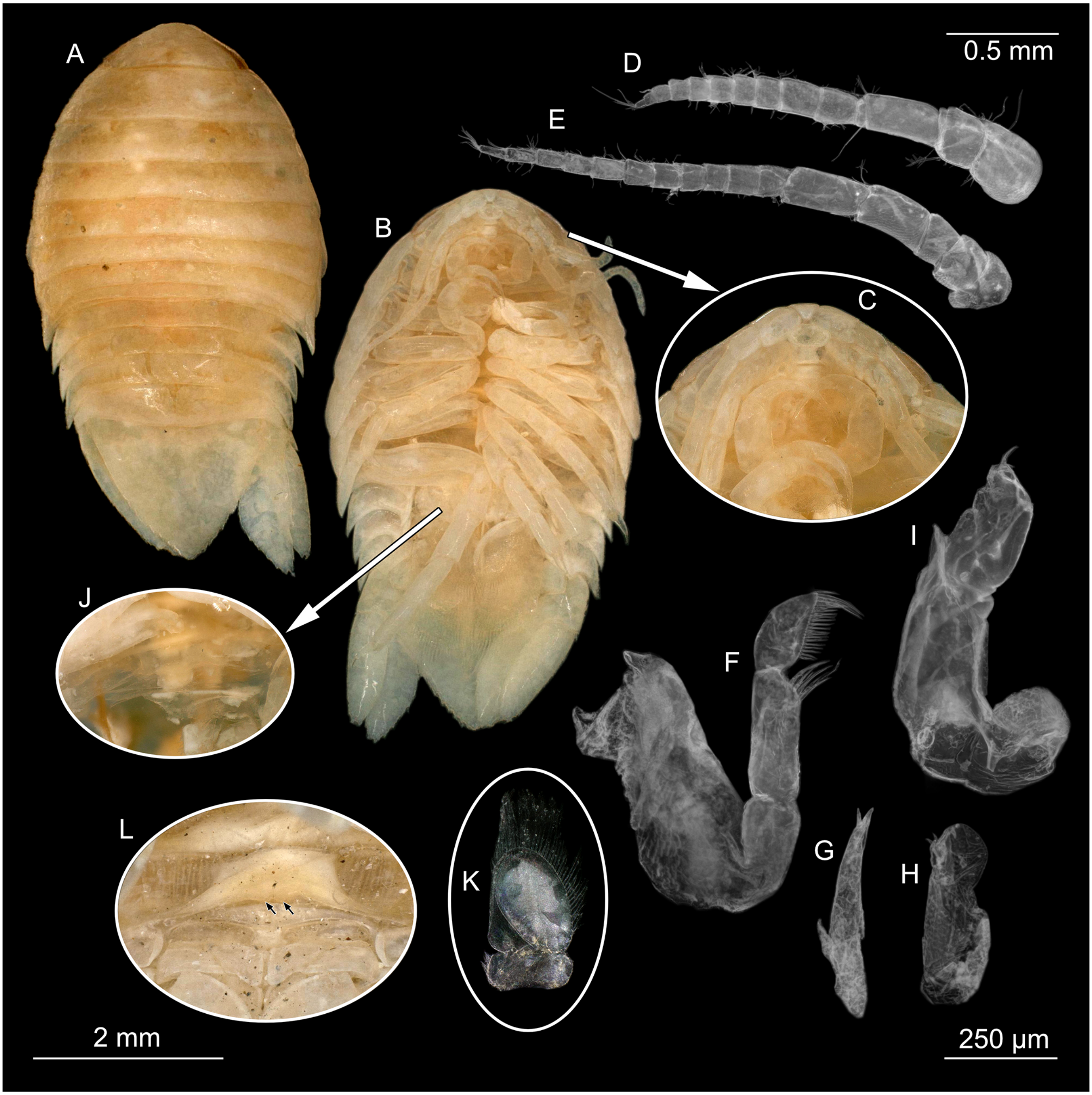

Figure 4. *Aegiochus antarctica* (Hodgson, 1910) immature stage 2 (NIWA 23671). **A**, Dorsal view. **B**, Ventral view. **C**, Anteroventral view. **D**, Antennula. **E**, Antenna. **F**, Mandible. **G**, Maxillula. **H**, Maxilla. **I**, Maxilliped. **J**, Close-up of sternite 7 (without penes). **K**, Pleon appendage 2 without appendix masculina. **L**, Example of penial lobes of adult male. Scales: **A–B,** 2 mm; **D–E,** 0.5 mm (top, right); **F–I,** 250 µm.

Pleotelson wider than long, 1.18 ×, dorsal surface transparent, lateral margins straight, posterior margin triangular. Uropods same length, slightly longer than the pleotelson.

Remarks. All specimens from the collections NIWA 23664 and NIWA 23671 were identified as *A. antarctica* upon loaning of the material. For species descriptions and illustrations of adult representatives of *A. antarctica*, see for example Hodgson (1910), Kussakin (1967), Schultz (1978), Wägele (1990), and Bruce (2009). The morphology of the examined specimens corresponds well with the illustrations and descriptions of adult representatives of *A. antarctica* as given by previous authors and are considered to be correctly identified. Immature stage 2 (NIWA 23671) is the first hatched ('post-marsupial') stage, based on the underdeveloped posteriormost trunk segment,

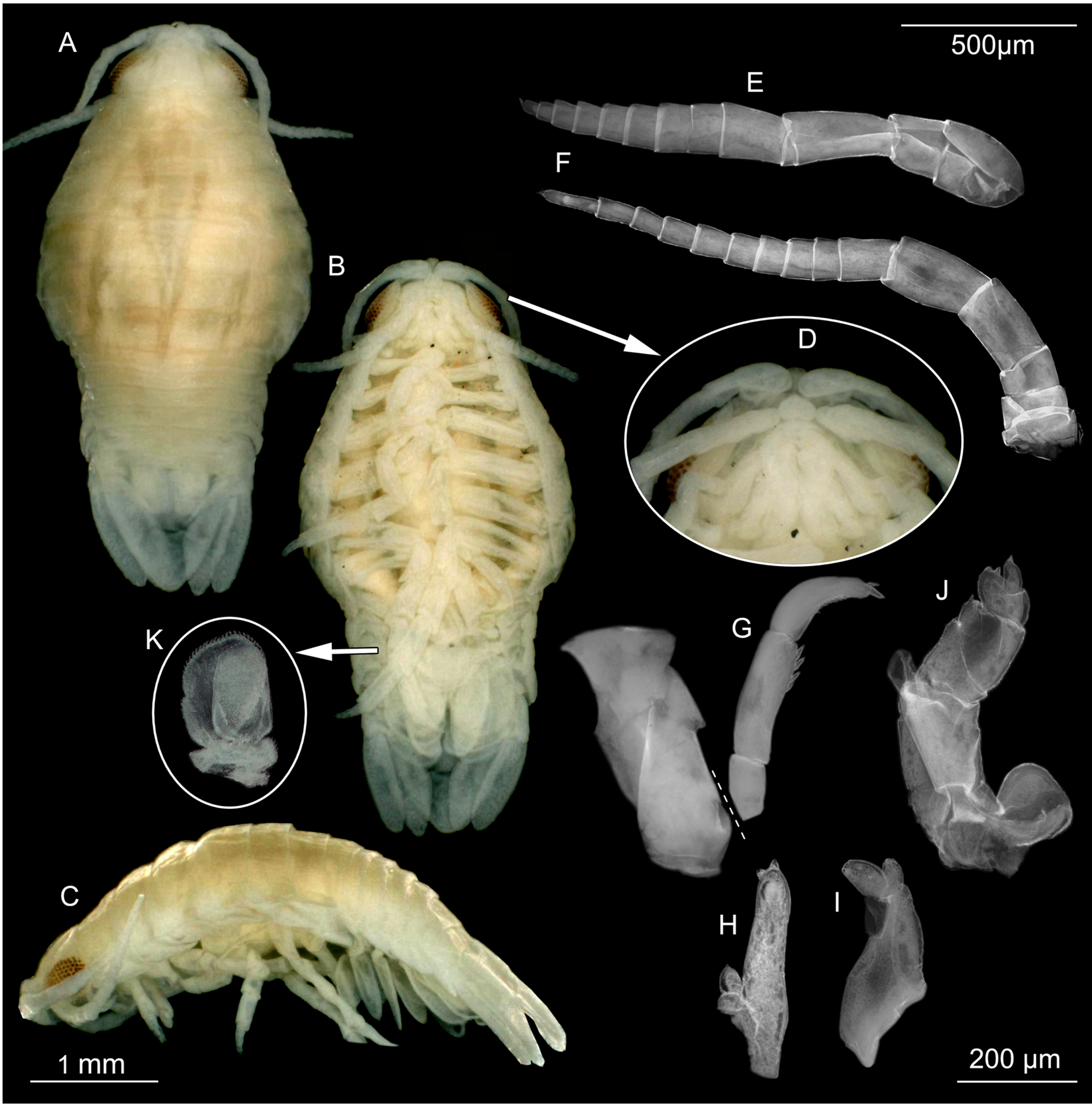

Figure 5. *Aegiochus antarctica* (Hodgson, 1910) immature stage 1 (NIWA 23664). **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. **D**, Anteroventral view. **E**, Antennula. **F**, Antenna. **G**, Mandible. **H**, Maxillula. **I**, Maxilla. **J**, Maxilliped. **K**, Pleon appendage 2 without appendix masculina. Scales: **A–C,** 1 mm; **E–F,** 500 µm; **G–J,** 200µm.

as well as the absence of trunk appendage 7 and all external sexual structures. Specimen NIWA 23664 is an immature stage 1 individual (pre-manca), retrieved from the brood pouch of a gravid female specimen.

Ontogenetic intra-species variation. Wägele (1990) studied the reproduction and growth of *A. antarctica* under laboratory conditions and provided valuable insight into the size ranges of different developmental stages, growth rates and internal anatomy of adult specimens. Unfortunately, no illustrations of the specimens were provided. The eggs of *A. antarctica* studied by Wägele (1990), measured on average 2.36 mm in length, similar to the examined egg specimens. The study did unfortunately not follow further embryonic development, but could show that it takes an individual a minimum of 32 months to develop from an egg to being released from the brood pouch.

An example of the penes of an adult male is provided (Fig. 4L), as there is no illustration in literature, showing this structure for *A. antarctica*. Here, the penes form lobes at the posterior margin of sternite 7, unlike the small openings of the other male specimens from the examined species. This specimen is one of a collection of specimens that contains a range of developmental stages, all under the collection number NIWA 23671. Immature stage 1 (NIWA 23664) was removed from the brood pouch of a gravid female, therefore, the specimen has not yet been released from the brood pouch. During this stage, trunk segment 7 is largely underdeveloped, trunk appendage 7 not developed, and no external sexual structures have developed.

Some developmental variation is noted between the immature stage 1 individual (NIWA 23664) and the immature stage 2 individual (NIWA 23671), including: a medially ovoid body shape of an immature stage 1, tapering towards the anterior and posterior ends, whereas that of immature stage 2 is uniformly ovoid; variation in the shape of the maxilla; immature stage 1 with anterior trunk segments subequal in length versus the longer trunk segment 1 and short segments 5 and 6 of immature stage 2; variation in the shape of the pleon and pleon segments posterolateral angles; variation in the shape of the uropods, especially the distal region of the exopod; and variation in the shape of the pleon appendages.

Apart from the external sexual structures and the underdeveloped structures, the immature stage 2 of *A. antarctica* show only minor variation to adult counterparts, most notably by the smaller trunk to pleon length ratio; the body being less elongate; and having more setae on swimming appendages such as the pleon appendages and uropods.

Aegiochus kanohi **Bruce, 2009**

Material examined. Immature male stage 3 (6.9 mm total length, 2.8 mm wide), Fig. 6. NIWA Cat. No. 24023. Collected north of Chatham Rise, 43°04.00'S 178°38.99'W, 13 September 1963.

Additional material examined (not described). Adult male (8.8 mm total length, 3.3 mm wide, excluding laterally visible coxae); non-ovigerous female (13.63 mm total length, 5.87 mm wide). NIWA Cat. No. 24023. Collected north of Chatham Rise, 43°04.00'S 178°38.99'W, 13 September 1963.

Immature male stage 3 *(NIWA 24023)* (Fig. 6)

Body slightly medially ovoid, longer than wide, 2.46 ×, widest at trunk segment 5, most narrow at trunk segment 1 (Fig. 6A–D). Head wider than long, 2.51 ×, roughly semi-circular, with narrowly pointed rostrum, rostrum slightly folded ventrally. Eyes medially united, extending backwards, surpassing anterior margin of trunk segment 1, longer than wide, 2.15 ×; each eye made up of ~ 10 transverse rows of ommatidia, each row with ~ 15 ommatidia. Frontal lamina wider than long, 1.43 ×, anterior margin with median point (Fig. 6E). Clypeus, labrum with distinct margins.

Antennula 1.82 mm long, consisting of 15 articles, extending to posterior end of anterior trunk segment 1, with tufts of setae on articles 7–15, tufts of plumose setae on article 2–3 (Fig. 6F); article 1 longer than wide, 1.31 ×, with rounded proximal end; article 2 as long as wide; article 3 longer than wide, 3.14 ×; article 4 short, wider than long, 1.57 ×. Antenna 2.24 mm long, longer than antennula, consisting of 17 articles, extending to postero-lateral margin of anterior trunk segment 2, with plumose setae on articles 4 & 5, tufts of setae on articles 8–17 (Fig. 6G); article 1 wider than long, 1.34 ×; article 2 wider than long, 1.71 ×; article 3 as long as wide. Mandible coxa 0.62 mm long, molar process present, ending in acute incisor (Fig. 6H). Mandible palp 0.7 mm long; article 1 longer than wide, 3 ×; article 2 longer than wide, 3.1 ×, with 3 long disto-lateral setae; article 3 longer than wide, 2.54 ×, with 11 serrate setae. Maxillula 0.5 mm long, with endite, with 6 terminal robust setae (Fig. 6I). Maxilla 0.5 mm long, lateral lobe with 2 recurved robust setae; mesial lobe 1 recurved robust seta (Fig. 6J). Maxilliped 0.68 mm long, consisting of 5 articles, with endite on article 1 (Fig. 6K); article 4 with 4 recurved robust setae; article 5 with 5 recurved robust setae.

Anterior trunk longer than pleon, 1.36 ×. Anterior trunk segment 1 anterior border straight, anterolateral angle encompassing posterior margins of eyes. Anterior trunk appendages 7 pairs, posterior pair underdeveloped (Fig. 6L). Coxae 2–3 with posteroventral angles with small, produced point;

coxae 4–7 posteriorly pointed, coxa 7 smaller than remaining coxae (underdeveloped), all reaching postero-lateral margin of respective trunk segment. Trunk appendage 7 present, underdeveloped (Fig. 6L); basipod longer than wide, 2.65 ×; ischium as long as wide; merus longer than wide, 1.6 ×; carpus longer than wide, 1.92 ×; propodus longer than wide, 2.18 ×; dactylus longer than wide, 2.25 ×.

Pleon segments subequal in length, pleon segment 5 longest; pleon segment 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleon segment 5 overlapped by lateral margins of pleonite 4 or longest, posterior margin slightly convex. Penes present as lobes on sternite 7 posterior margin, set apart (Fig. 6L); penial tubercles on posterior margin of sternite 7. Pleon appendage 2 with appendix masculina (Fig. 6M).

Pleotelson wider than long, 1.21 ×, dorsal surface smooth, transparent; lateral margins with serrations, posterior margin triangular. Uropods slightly longer than pleotelson.

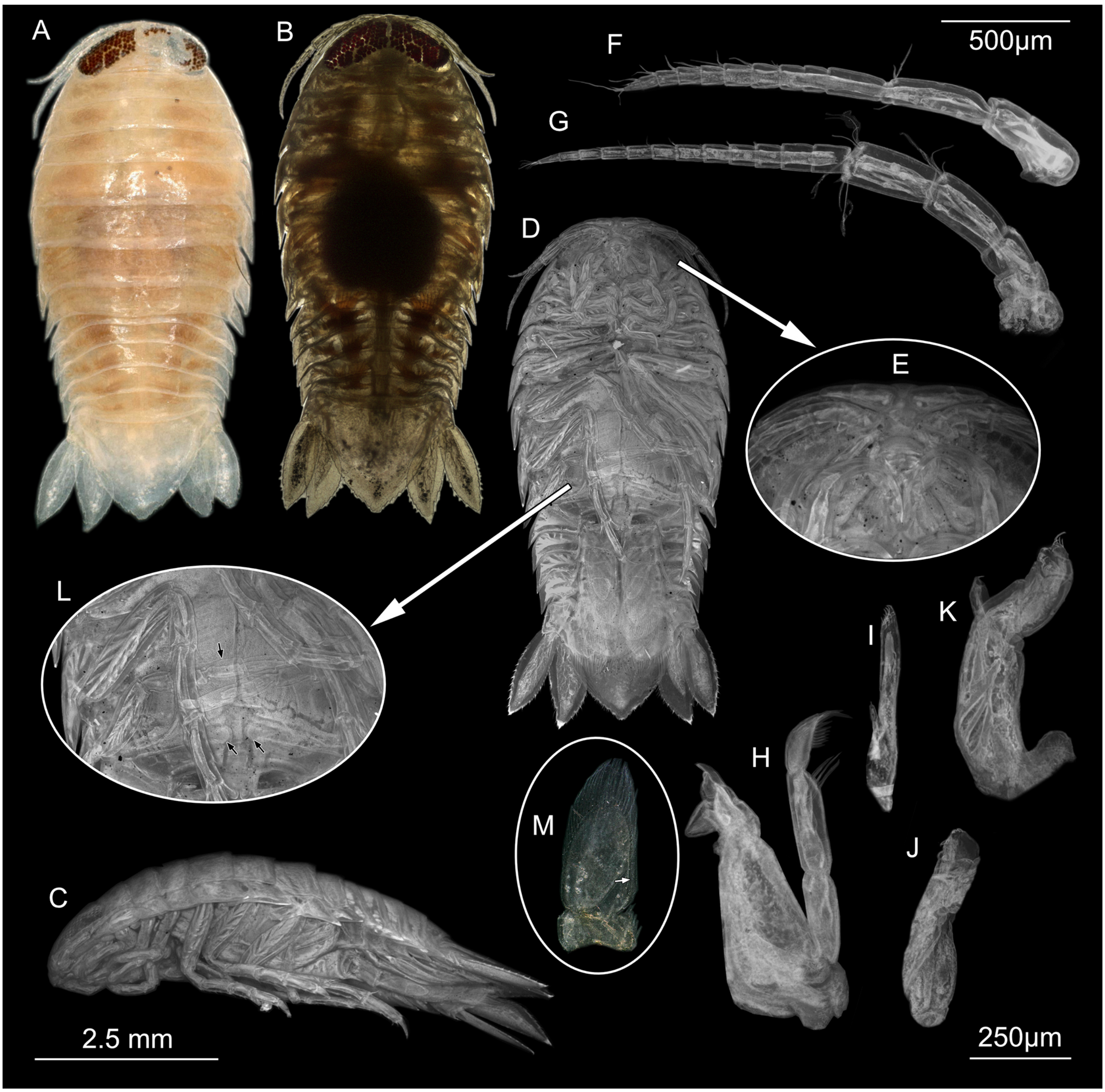

Figure 6. *Aegiochus kanohi* Bruce, 2009 immature male stage 3 (NIWA 24023). **A–B**, Dorsal view. **C**, Lateral view. **D**, Ventral view. **E**, Anteroventral view. **F**, Antennula. **G**, Antenna. **H**, Mandible. **I**, Maxillula. **J**, Maxilla. **K**, Maxilliped. **L**, Close-up of underdeveloped thoracopod 7 and penial lobes. **M**, Pleon appendage 2 with appendix masculina. Scales: **A–D,** 2.5 mm; **F–G,** 500 µm; **H–K,** 250µm.

Remarks. For species descriptions and illustrations of adult specimens, see original species description. The interpretation of immature male stage 3 (NIWA 24023) is substantiated by the underdeveloped pair of trunk appendage 7 and the presence of external male structures. Therefore, indicating an immature male.

Ontogenetic intra-species variation. The collection NIWA 24023 contains an adult male to which the examined immature specimen can be compared, in addition to the illustrated and described type material as given in Bruce (2009). Developmental variation between the immature male stage 3 and an adult male specimen is minimal, with the most noticeable difference in the number of setae on pleon appendages as well as the overall smaller body size, with the immature male stage 3 being slightly medially ovoid, versus a more elongate, rectangular adult male body shape. Collection NIWA 24023 also contains an ovigerous female specimen, evident from the developed oostegites forming the brood pouch, along with the absence of external male structures.

Aegiochus nohinohi Bruce, 2009

Material examined. Immature stage 1 (1.6 mm total length, 0.75 mm wide), Fig. 7; immature stage 2 (3.6 mm total length, 1.6 mm wide), Fig. 8A–D. NIWA Cat. No. 24018. Collected at 43.0667°S 178.6500°E, 13 September 1963.

Additional material examined (not described). Adult male (6.28 mm total length, 2.63 mm wide), Fig. 8E–H; non-ovigerous female (8.61 mm total length, 4.01 mm wide); ovigerous female (8.65 mm total length, 4.47 mm wide). NIWA Cat. No. 24018. Collected at 43.0667°S 178.6500°E, 13 September 1963.

Immature stage 1 (NIWA 24018) (Fig. 7)

Body rectangular, ventrally folded, longer than wide, 2.13 ×, widest at trunk segment 5, most narrow at trunk segment 2 (Fig. 7A–D). Head wider than long 1.28 ×, roughly semi-circular, rostrum folded ventrally. Eyes relatively well-developed, ommatidia not clearly visible for counting. Frontal lamina as long as wide, truncated triangular. Clypeus, labrum indiscernible.

Antennula 0.76 mm long, consisting of 13 articles; extending to middle of anterior trunk segment 2, with tuft of setae on distal most article, without setae (Fig. 7E); article 1 as wide as long; article 2 as long as wide; article 3 wider than long, 1.8 ×; article 4 as long as wide. Antenna 0.92 mm long, longer than antennula, consisting of 17 articles extending to postero-lateral margin of anterior trunk segment 3, without setae, tufts of setae on distal most article (Fig. 7F); article 1 longer than wide, 1.1 ×; article 2 wider than long, 2 ×; article 3 wider than long, 1.7 ×; article 4 wider than long, 1.2 ×. Mandible coxa 0.23 mm long, molar process underdeveloped (Fig. 7G). Mandible palp 0.27 mm long. Maxilla 2.7 mm long (Fig. 7J). Maxilliped 0.3 mm long, consisting of 5 articles, with endite on article 1 (Fig. 8H).

Anterior trunk longer than pleon, 2.9 ×. Anterior trunk appendages 6 pairs, each with 7 articles. Coxae 2–3 with posteroventral angles right-angled; coxae 4–7 posteriorly pointed, coxa 7 not developed; all reaching postero-lateral margin of respective trunk segment.

Pleon segments not well distinguishable. Pleotelson wider than long,1.4 ×, lateral margins slightly damaged and unclear. Uropods half the length of pleotelson.

Immature male stage 2 (NIWA 24018) (Fig. 8A–D)

Body medially ovoid, longer than wide, 2.25 ×, widest at trunk segment 5, most narrow at trunk segment 1 (Fig. 8A–C). Head wider than long, 2.6 ×, triangular, with broadly rounded anterior margin, rostrum slightly folded ventrally. Eyes set apart, not extending past head posterior margin, longer than wide, 1.88 ×, each eye made up of ~ 9 transverse rows of ommatidia, each row with ~ 11 ommatidia. Frontal lamina wider than long, 2.46 ×, anterior margin truncated triangular. Clypeus, labrum indiscernible.

Anterior trunk longer than pleon, 1.73 ×. Anterior trunk segment 1 anterior border straight, anterolateral angle pointed, not produced. Coxae 2–3 with posteroventral angles right-angled; coxae 4–7 with rounded point, coxa 7 smaller than remaining coxae (underdeveloped), all reaching postero-lateral margin of respective trunk segment (Fig. 7B). Trunk appendage 7 not developed.

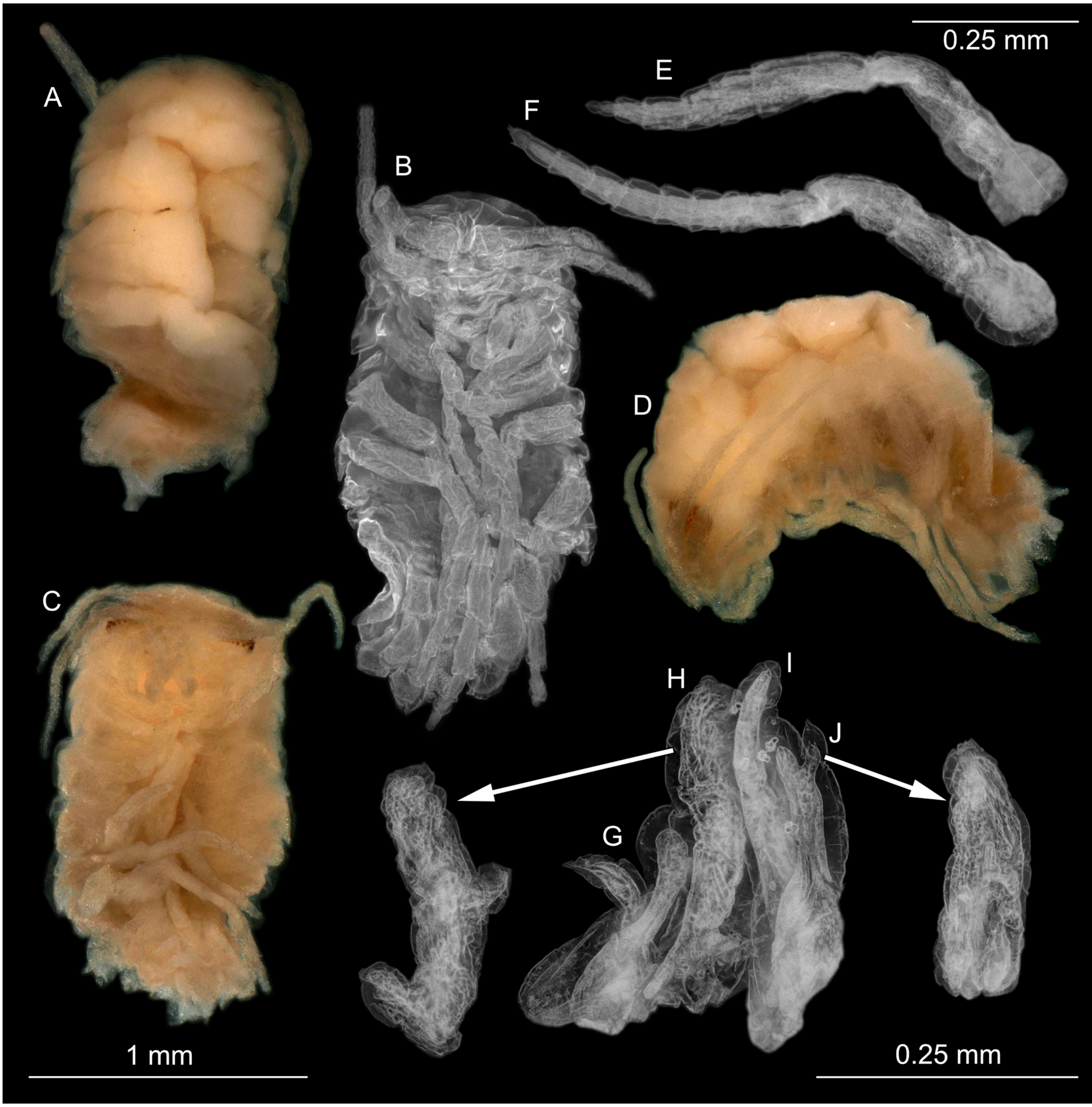

Figure 7. *Aegiochus nohinohi* Bruce, 2009 immature stage 1 (NIWA 24018). **A**, Dorsal view. **B–C**, Ventral view. **D**, Lateral view. **E**, Antennula. **F**, Antenna. **G**, Mandible. **H**, Maxilliped. **I**, Maxillula. **J**, Maxilla. Scales: **A–D,** 1 mm; **E–F,** 0.25 mm (top, right); **G–J,** 0.25 mm (bottom, right).

Pleon segments subequal in length, pleon segment 5 longest; pleon segment 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleon segment 5 free, not overlapped by lateral margins of pleon segment 4, longest or narrowest, posterior margin slightly convex. Penial lobes present (Fig. 8D), small, on sternite 7 posterior margin, medially in contact. Pleon appendage 2 without appendix masculina (possibly damaged).

Pleotelson wider than long, 1.4 ×, dorsal surface smooth, lateral margins straight, with serrations, posterior margin broadly rounded. Uropods same length or slightly longer than pleotelson.

Remarks. For species descriptions and illustrations of adult specimens, see original species description. The immature stage 1 individual ('pre-manca') was removed from the brood pouch of a gravid female as a pre-hatchling. Similar to immature stage 1 individuals from other species, no external sexual structures could be seen in the *A. nohinohi* immature stage 1 specimen. The immature male stage 2 has already been released from the brood pouch of the female and shows underdeveloped, but present penial processes, indicating an immature male. No appendix masculina was present on the dissected pleon attachment 2, possibly damaged or not yet developed. Photographs of an adult male specimen are provided for comparison (Fig. 8E–H).

Ontogenetic intra-species variation. The penes of the adult male are clearly visible as tubular structures on the posterior margin of sternite 7, with penial openings not in contact (Fig. 8F, H). The shape of the appendix masculina can be seen in Bruce (2009). In addition to the underdeveloped external sexual structures, immature male stage 2 shows some additional morphological variation to that of adult specimens, including: an underdeveloped coxa 7, not visible from dorsal or lateral view; and a rounded, blunt pleotelson posterior margin, compared to the posteromedially pointed pleotelson tip of an adult.

Figure 8. *Aegiochus nohinohi* Bruce, 2009 **A–D**, Immature stage 2 (NIWA 24018). **E–H**, Adult male (NIWA 24018). **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. **D**, Close-up of underdeveloped penial lobes. **E**, Dorsal view. **F**, Ventral view. **G**, Lateral view. **H**, Close-up of well-developed penial lobes.

Aegiochus vigilans (Haswell, 1881)

Material examined. Immature female stage 3 (12.8 mm total length, 4.98 mm wide), Fig. 9. NIWA Cat. No. 23779. Collected off Great Barrier Island, North Island, January 2006, coll. Steve Lowe. Coordinates not recorded.

Immature female stage 3 (NIWA 23779) (Fig. 9)

Body elongate, longer than wide, 2.6 ×, widest at trunk segment 5, most narrow at trunk segment 1 (Fig. 9A–C). Head wider than long, 2 ×, roughly semi-circular, with broadly rounded anterior margin, frontal margin rounded to form blunt rostrum, simple, not folded. Eyes medially united, extending past head posterior margin, longer than wide, 2.23 ×, each eye made up of ~ 9 transverse rows of ommatidia, each row with ~ 13 ommatidia. Frontal lamina longer than wide, 1.9 ×, truncated triangular (Fig. 9D). Clypeus, labrum wide, with clear margins.

Antennula 2.18 mm long, consisting of 9 articles; extending to anterior of pereonite 1, distally damaged, with simple setae on articles 7, 9, tufts of plumose setae on article 2–3 (Fig. 9E); article 1 as long as wide; article 2 longer than wide 1.3 ×; article 3 longer than wide, 2.8 ×; article 4 short, wider than long, 2 ×. Antenna 8.82 mm long, longer than antennula, consisting of 42 articles, extending to postero-lateral margin of anterior trunk segment 6, with simple setae on articles 4, 5, 13–18, 21, 23, 25, 28, 31, 39, 42 (Fig. 9F); article 1 as long as wide; article 2 wider than long, 1.5 ×; article 3 longer than wide, 1.3 ×; article 4 longer than wide, 1.9 ×. Mandible coxa 1.3 mm long, molar process present, ending with acute incisor (Fig. 9G). Mandible palp 1.29 mm long; article 1 longer than wide, 2.8 ×; article 2 longer than wide, 3.3 ×, with 17 long disto-lateral setae; article 3 longer than wide, 2.1 ×, with 17 serrate setae. Maxillula 1.04 mm long, without endite, with 7 terminal robust setae (Fig. 9H). Maxilla 1 mm long, lateral lobe with 4 recurved robust setae; mesial lobe 3 recurved robust setae (Fig. 9I). Maxilliped 1.2 mm long, consisting of 5 articles, with endite on article 1 (Fig. 9J); article 3 with 2 recurved robust setae; article 4 with 8 recurved robust setae; article 5 with 4 recurved robust setae.

Anterior trunk longer than pleon, 1.06 ×. Anterior trunk segment 1 anterior border slightly convex, anterolateral angle encompassing posterior margins of eyes. Anterior trunk appendages 7 pairs, posterior pair underdeveloped. Coxae 2–3 with posteroventral angles rounded; coxae 4–7 posteriorly pointed, coxa 7 smaller than remaining coxae (underdeveloped), all reaching postero-lateral margin of respective trunk segment. Trunk appendage 7 present, underdeveloped (Fig. 9K); basipod longer than wide, 3.46 ×; ischium longer than wide, 1.89 ×; merus longer than wide, 1.6 ×; carpus longer than wide, 2 ×; propodus longer than wide, 2.7 ×; dactylus longer than wide, 2.2 ×.

Pleon segments subequal in length, pleon segment 5 longest; pleon segment 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleon segment 5 free, not overlapped by lateral margins of pleonite 4 or longest, posterior margin straight. Penial structures absent. Pleon appendage 2 without appendix masculina (Fig. 9L).

Pleotelson wider than long, 1.1 ×, dorsal surface smooth, lateral margins convex, with serrations, posterior margin converging to posteromedial point or evenly rounded. Uropods same length as pleotelson.

Remarks. For species descriptions and illustrations of adult specimens, see Haswell (1881) Stebbing (1905), Hale (1925), Bruce (1983), Nunomura (1988), and Bruce (2009). The examined immature stage 3 specimen is by all indication, an immature female based on the absence of external male specific structures such as penial structures and appendix masculina, as well as the absence of the male-specific, characteristic “horn-like” structures on the anterior trunk segment 1 and rostrum.

Ontogenetic intra-species variation. Male specimens of *A. vigilans* have a characteristic morphology that is easily distinguished from all other species. The anterior trunk segment 1 of an adult male develops two “forward-projecting processes”, from the anterior margin, each reaching over the eye and head. Additionally, the anterior margin of the head (rostrum) is produced anteriorly, creating an elongated, not ventrally folded rostrum. The presence of these three unique ‘processes’ give the adult male specimens the appearance of having three horns. Immature stage specimens and females lack these characters.

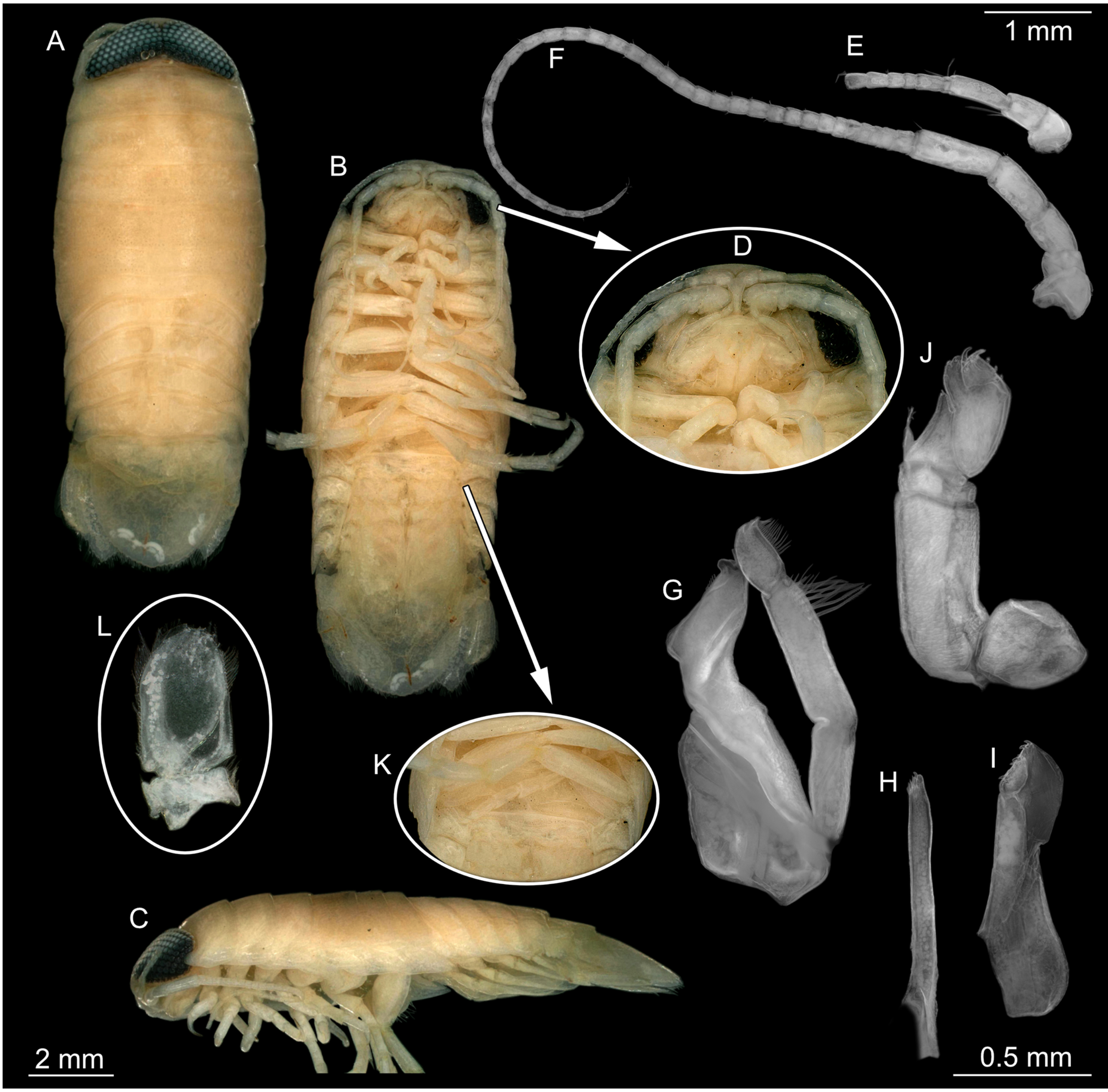

Figure 9. *Aegiochus vigilans* (Haswell, 1881) immature female stage 3 (NIWA 23779). **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. **D**, Anteroventral view. **E**, Antennula. **F**, Antenna. **G**, Mandible. **H**, Maxillula. **I**, Maxilla. **J**, Maxilliped. **K**, Close-up of underdeveloped thoracopod 7. **L**, Pleon appendage 2 without appendix masculina. Scales: **A–C,** 2 mm; **E–F,** 1 mm; **G–J,** 0.5 mm.

The appendix masculina on pleon appendage 2 of adult males are also unusually long and thin, reaching far beyond the proximal margin of the appendage endo- and exopods. This appendix masculina is clearly absent from the examined immature stage specimen. During this developmental stage, these, and the penes should have started to develop. Furthermore, the examined immature stage specimen shares characters with those of other immature stage and female specimens of *A. vigilans*, including: large eyes, covering almost the entire head dorsal area and connected medially; and the long, elongate frontal lamina. The morphology of these structures confirms the interpretation that this specimen would have developed as a female.

Haswell (1881) provided a description and a single dorsal view illustration of what seems to be an immature stage individual, similar in morphology to the examined specimen. Stebbing (1905) later provided a description and illustrations of a male specimen as well as some illustrations of what seems to be a female specimen of *A. vigilans* (described as *Aega ommatophylax*). The dorsal view and mouthpart illustrations of the supposed female specimen are comparably similar in morphology to that of the examined specimen. No indication of size or female specific characters was given for this specimen. The description and illustrations in Hale (1925) are of an ovigerous female specimen, distinguishable from the relatively large size, the oosegites and maxilliped with developed oostegite attached. Bruce (1983) provided a comprehensive description and illustrations of a male specimen and mentioned that the differentiation of sexes only occurs at a later developmental stage when the individual is larger, with the smallest males measuring 12 mm therein. Nunomura (1988) provided a description and illustrations of the species as *Aega giganteocula*, which has been synonymised with *A. vigilans* by Bruce (2009). The description does not distinguish between male and female character states and the illustrations seem to comprise of both male and female structures and/or specimens. The dorsal view illustration therein, indicates a female or immature specimen, based on the absence of the characteristic trunk segment 1 and rostrum morphology of a male.

DISCUSSION

The role of immature stage specimens

Morphological descriptions of species of Aegidae are usually based on a single adult specimen, occasionally with some notes on the variation between the examined adult specimens. Immature stages are largely overlooked and often intentionally disregarded in species descriptions, illustrations, discussions and collection depositions. The lack of knowledge on the immature stages, their development and morphology can sometimes cause misinterpretation or uncertain interpretation of species and their developmental stage.

For example, as the holotype of *Xenuraega ptilocera* Tattersall, 1909 had been lost, Bruce (1993) re-described the species based on a specimen that resembled an immature or male. This specimen has well-developed 7 pairs of trunk appendages with no indication of external sexual structures, making it more likely that this specimen will develop as a female. The original description of *Aegiochus nordenskjoldii* Bovallius, 1885 was unknowingly based on an intermoult specimen, which usually have a unique morphology due to the biphasic moulting process. This specimen and consequently the species, was later reinterpreted as an intermoult stage representative of *Aegiochus ventrosa* (Sars, 1859). *Xenuraega bythionekta* Shimomura and Bruce, 2019 was originally described based on an immature stage specimen, which serves as the holotype. This specimen lacks the 7th pair of trunk appendages and no mention is made of external sexual structures (which have possibly not yet developed), indicating that this specimen is most likely an immature stage 2 (manca). Even with an immature stage specimen, the authors were able to distinguish the species from others by comparing its morphological characters to adult specimens of other species. The holotype of *Rocinela oculata* Harger, 1883 is thought to be an immature stage specimen (Bruce, 1988), but since there is no indication of sexual structures in the original description and all 7 pairs of trunk appendages are developed, this specimen is more likely to be a non-ovigerous or young female.

Through development, immature stage individuals start to represent an adult stage in morphology (either a male or female), with the degree of variation decreasing with development. Based on the results, representatives of Aegidae develop as separate sexes, indicated by the presence or absence of penes and appendix masculina that become visible during the 2nd immature stage.

The comparison between immature stage individuals and adult stage representatives provides a clear indication that immature stage individuals show morphological variation among species, in comparison to the amount of variation noted among their adult counterparts. Variation in adults varies between species but is clearly most pronounced in early immature stage individuals.

Eggs and embryos

In this study we provide the first description and photographs of eggs and embryos of Aegidae and of *A. antarctica* (Fig. 3). The germ band and appendages develop on the outer surface of the early embryo (Fig. 3C, E). The embryos examined herein, show early signs of segmentation, inferring that fertilization has taken place before the collection of the female specimen. In this study, a single brood pouch of *A. antarctica* contained eggs as well as embryos which show early signs of segmentation and development, indicating that a brood may consist of individuals of different embryonic developmental stages or that individuals in the brood possibly do not all develop at the same rate.

The pre-hatch development of Aegidae has never been recorded prior to this study and seems to be similar to that of many ingroups of Isopoda, such as Anthuroidea (Strömberg, 1972); Cymothoidae (Cymothoida, see Bullar, 1878; Bakenhaster et al., 2006); Epicaridea (Cymothoida, see Strömberg, 1972); *Eurydice* Leach, 1815 (Cymothoida, see Jones, 1970), and *Eurydice pulchra* Leach, 1915 (Fish, 1970); *Idotea* Fabricius, 1798 (Valvifera, see Kroer, 1989); Oniscidea (see Wolff, 2009) and *Porcellio* Latreille, 1804 (Oniscidea, see Wolff, 2009; Milatovic et al., 2010); and Sphaeromatidae (Sphaeromatidea, see Holdich, 1968; Wägele, 1987) .

A few studies have presented illustrations or photographs of eggs and embryos of ingroups of Isopoda, to which the herein presented specimens can be compared:

Bullar (1878) provided illustrations and notes on the development of parasitic species of Isopoda, more specifically *Cymothoa* Fabricius, 1793. The egg Stage 2 therein (his fig. 7), is comparable to the eggs of *A. antarctica*, where an accumulation of cells is visible on the ventral surface. The overall shape of the embryos of *A. antarctica* are very similar to Stage 5 individuals of *Cymothoa* (see Bullar, 1878, fig. 15), where the head and trunk appendages are becoming developed and distinct and antennae are formed and folded ventrally, covering the mouth appendages. No scale was provided for either stage.

Holdich (1968) described some developmental stages of *Dynamene bidentata* (Adams, 1800), including egg (~0.5 mm) and embryonic stages (~0.65 mm; his fig. 1). The examined eggs of *A. antarctica* are similar to that of *D. bidentata* at developmental Stage B2–B3, where only a single membrane surrounds the yolk and a few limb buds are visible. The embryos of *A. antarctica* are similar to that of *D. bidentata* at developmental Stage C2, with distinct trunk and pleon appendages, but with a ventrally folded pleon versus the still dorsally folded pleon of *D. bidentata*.

Wägele (1987) provided a schematic representation of the embryonic stages of *Ceratoserolis trilobitoides* (Eights, 1833) (his fig. 1), in which egg and embryonic stage individuals were illustrated. The eggs herein, are morphologically similar to that of Stage A1 – B2 individuals in Wägele (1987), with embryonal tissue visible and the formation of a germ band. The mean egg sizes of *C. trilobitoides* measured slightly larger than that of *A. antarctica*, at ~2.97 – 3.55 mm. The embryos herein, are similar in developmental morphology to that of stage B3 – C1 in the latter publication.

Johnson (2001) gave detailed descriptions and discussions on the development of marine peracaridan crustaceans and provided some illustrations of developmental stages of *Limnoria lignorum* (Rathke, 1799). The embryos of *A. antarctica* can be compared to the Stage C individuals of *L. lignorum*, which are individuals that have moulted from the egg membranes, but still enclosed by an embryonic membrane (~0.3 mm, Johnson, 2001, fig. 10C).

Bakenhaster (2006) provided illustrations of immature developmental stages of *Glossobius hemiramphi* Williams and Bunkley-Williams, 1985, of which the therein 'marsupiumite Stage 3' (~1.54 mm; Bakenhaster, 2006, fig. 5) is most similar to the embryos examined herein. The eggs therein are unsegmented and seem to be in an unfertilized state at ~1.19 mm.

Wolff (2009) studied the embryonic development of *Porcellio scaber* Latreille, 1804 (Oniscidea), with eggs (Stage 5–6 therein) that similarly show the differentiation between anterior and posterior ends, without segmental differentiation, measuring ~0.5 mm in length. The embryos herein are comparable to Stage 14 individuals in Wolff (2009), with elongated trunk appendages, each with seven articles; with pleopods visible. These embryos are significantly smaller than those of *A. antarctica*, measuring ~0.7 mm.

Milatovic (2010) studied the development and internal anatomy of *P. scaber* (Oniscidea) and provided detailed photographs of various stages. The eggs at Stage 2 therein (0.8 mm; his fig. 1b), are similar to the eggs of *A. antarctica*, mostly comprised of yolk and with the germ disc visible. The embryos of *A. antarctica* are similar to Stage 13–18 of *P .scaber* (~0.86 mm; Milatovic, 2010, fig. 1h–j).

The sizes of eggs and embryos are species specific and largely variable among groups of Isopoda (Wägele, 1987; Kroer, 1989; Clark and Gore, 1992; Johnson, 2001). The correlation between egg size and female size is still unclear. In some cases, there seems to be no correlation (De Geer, 1778; Leonardsson, 1986), in others a correlation has been noted that species with larger adult female individuals, have larger relative eggs (Kroer, 1989; Tsai and Chen, 1997). Usually, egg size ranges between 0.3–0.8 mm for tropical and shallow water inhabitants, with some of the smallest eggs measuring 0.12–0.15mm. Species that inhabit the deep-sea or polar regions (usually the species that are large in size) have larger egg sizes (~2 mm). The exception is of course the eggs of the giant isopod *Bathynomus giganteus* A. Milne-Edwards, 1879, which measure 10–12mm in diameter.

Immature stage 1

The first of three pre-hatch moults occurs when the embryos hatch from the egg and initially remain in the brood pouch (Johnson, 2001). According to Johnson (2001), subsequent pre-hatch moult follows ('post-naupliar' moult). These 'egg hatchlings' are herein referred to as immature stage 1. Within other ingroups of Isopoda, this stage is also called 'pre-manca', 'prehatch II', 'first mancal stage', 'manca-I' or 'pullus I' (Schioedte and Meinert, 1884; Trilles, 1965; Wägele, 1987; Adlard and Lester, 1995; Svavarsson and Davídsdóttir, 1995; Thatcher et al., 2003; Araujo et al., 2004; Bakenhaster, 2004; Bakenhaster et al., 2006; Brum and Araujo, 2007; Aneesh et al., 2018). This ontogenetic stage is characterized by a well-segmented individual, not enclosed by a membrane, still inside the brood pouch. To study these individuals, they must be removed manually from the brood pouch of the female. Immature stage 1 specimens are further characterized by lacking trunk appendage 7; having an underdeveloped anterior trunk segment 1 and coxa 7; and lacking setae on pleon appendages (Segal, 1987; Van der Wal and Haug, 2020, herein).

Specimens *A. antarctica* (NIWA 23664) and *A. nohinohi* (NIWA 24018) are preserved during this stage. These specimens have no external sexual structures developed; therefore, sexes are not yet differentiated.

Even within a 'defined' developmental stage, individuals can be preserved at an earlier or a later phase during a particular developmental stage. For example, even though both *A. antarctica* (NIWA 23664, Fig. 5) and *A. nohinohi* (NIWA 24018, Fig. 7) are immature stage 1 individuals, they represented slightly different phases of this stage. The tergites and coxae of *A. nohinohi* (NIWA 24018, Fig. 7) are not yet fully developed and differentiated; with a soft and fragile body and the ventrally folded 'embryonic' shape. In contrast to this, *A. antarctica* (NIWA 23664, Fig. 5) has a hardened, more elongate body with completely differentiated segments and appendages. This indicates that *A. antarctica* (NIWA 23664, Fig. 5) is of a later immature stage 1 than *A. nohinohi* (NIWA 24018, Fig. 7), possibly having had the second pre-hatch moult ('post-naupliar' moult).

Considering actual body size, *A. antarctica* is approximately twice as large as *A. nohinohi,* during all ontogenetic stages. Females of *A. antarctica* range between 12–30 mm and males between 10–20 mm (Brandt, 1991; Bruce, 2009, this study). The only egg measurements are from this study, at an average of ~2.25 mm. Females of *A. nohinohi* range between 6.4–10.2 mm; males between 4.9–6.7 mm; 'mancas' between 3.4–5.0 mm and eggs between 1.0–1.2 mm (Bruce 2009, this study). *Aegiochus antarctica* (NIWA 23664, Fig. 5) measured at 4.48 mm and *A. nohinohi* 1.6 mm (NIWA 24018, Fig. 7).

In addition to size, other morphological variations between the examined specimens include: the rectangular body shape of *A. nohinohi* (NIWA 24018, Fig. 7) compared to a medially ovoid body of *A. antarctica* (NIWA 23664, Fig. 5); long, ventrally folded rostrum of *A. nohinohi* (NIWA 24018, Fig. 7) versus the triangular, slightly folded rostrum of *A. antarctica* (NIWA 23664, Fig. 5); mouthparts of *A. nohinohi* (NIWA 24018, Fig. 7) all proportionally narrower than that of *A. antarctica* (NIWA 23664, Fig. 5), the former covered in a soft outer layer of chitin.

By the end of immature stage 1, the young are released from the brood pouch of the female. The hatching happens after a final 'pre-hatch' moult ('larval ecdysis' Johnson, 2001) in the brood pouch (Brusca, 1978; Adlard and Lester, 1995; Johnson, 2001; Bakenhaster, 2004), resulting in the next developmental stage.

Immature stage 2

During this ontogenetic stage, individuals have been released from the brood pouch. These individuals are referred to as 'manca', manca-II or 'pullus II' (Schioedte and Meinert, 1884; Trilles, 1965; Sandifer and Kerby, 1983; Brusca and Iverson, 1985; Wägele, 1987; Sartor and Pires, 1988; Adlard and Lester, 1995; Svavarsson and Davídsdóttir, 1995; Thatcher et al., 2003; Araujo et al., 2004; Brum and Araujo, 2007; Aneesh et al., 2018). This stage still lacks the 7th pair of trunk appendages (Segal, 1987) characterized by the initial development of trunk appendage 7 at the end of this stage, where it is still highly underdeveloped and small, if at all developed.

Specimens *A. antarctica* (NIWA 23671, Fig. 4) and *A. nohinohi* (NIWA 24018, Fig. 8) are preserved during this stage, characterized by the initial development of trunk appendage 7 at the end of this stage, where it is still highly underdeveloped and small, if at all developed. This stage can further be distinguished by a large number of setae on pleon appendages, aiding in swimming. This seems to also be the case for Aegidae, to a lesser degree, as the examined immature stage 2 specimens have long setae on pleon appendages.

In the examined specimens from this stage, trunk appendage 7 is still lacking. Furthermore, it seems that the external sexual structures also start to develop at some point during this stage, indicating either an immature male specimen, where penes and appendix masculina are visible (as in specimen *A. nohinohi*), or an immature female specimen, where no such structures are developed (as in specimen *A. antarctica*). Wägele (1990) showed similar results, where no intermediate gonads were present in specimens of *A. antarctica*, but either male gonads or immature female ovaries. This further substantiates that species of Aegidae are not hermaphroditic and are not all released from the brood pouch as males, as seen in some parasitic groups of Isopoda.

Aegiochus antarctica (NIWA 23671, Fig .4) and *A. nohinohi* (NIWA 24018, Fig. 8) are both immature stage 2 hatchlings, lacking trunk appendage 7 and with an underdeveloped coxa 7. Both specimens are similar in length, but *A. antarctica* (NIWA 23671, Fig. 4) has a larger length to width ratio than *A. nohinohi* (NIWA 24018, Fig. 8), resulting in the former having a more ovoid body shape compared to the latter. *Aegiochus nohinohi* (NIWA 24018, Fig. 8) have underdeveloped penial lobes visible (Fig. 8D), comparable to the fully developed penes of an adult male specimen (Fig. 8H). This indicates that external male structures start to develop during this stage of ontogeny. In contrast, *A. antarctica* (NIWA 23671, Fig. 4) has no developed external sexual structures visible (Fig. 4J, K), compared to the well-developed penes of an adult male specimen. This either indicates that these structures have not yet developed at this stage, or, more likely, that this specimen will develop as a female. Other interspecific variations among these specimens include: the shape and size of the eyes, with *A. antarctica* (NIWA 23671, Fig. 4) having much smaller, less-defined eyes than *A. nohinohi* (NIWA 24018, Fig. 8); anterior trunk segments of *A. antarctica* (NIWA 23671, Fig. 4) decreasing in length from anterior to posterior, with a short, underdeveloped trunk segment 7 and those of *A. nohinohi* (NIWA 24018, Fig. 8) subequal in length, with a longer, more developed trunk segment 7; the shape of the pleotelson, with *A. antarctica* (NIWA 23671, Fig. 4) having a triangular pleotelson with converging to a medial point and *A. nohinohi* (NIWA 24018, Fig. 8) with a broadly rounded pleotelson posterior margin.

Immature stage 3

Four specimens from the examined material represent the 3rd immature stage, in other groups referred to as the 'natatory-stage' (Jones et al., 2008), 'juvenile' (Kroer, 1989; Aneesh et al., 2015), 'aegathoid' (Brusca, 1978) or manca III (Araujo et al., 2004; Brum and Araujo, 2007). This stage is usually characterized by a fully developed pair of trunk appendage 7 and external male structures. In the examined specimens, three of the four specimens have near fully developed external male sexual structures, but the trunk appendage 7 is still largely or slightly underdeveloped and smaller than the remaining trunk appendages [*A. monophthalma* (NIWA 23759, Fig. 1); *A. mahana* (NIWA 17943, Fig. 2); *A. kanohi* (NIWA 24023, Fig. 6)]. This observation leads to the interpretation that, at least in species of Aegidae, the external male sexual structures develop before the trunk appendage 7 pair is fully developed. One specimen *A. vigilans* [(NIWA 23779, Fig. 9)] has an underdeveloped trunk appendage 7, without any external male structures, which should have at least started to develop at this stage, leading to the interpretation that this specimen will develop as a female.

In other ingroups of Isopoda, individuals with this developmental stage have large numbers of setae on the swimming appendages (uropods and pleon appendages), which is also seen in the examined specimens, especially with regards to the uropodal setae. Similar to the examined specimens, this stage seems to lack any traces of yolk (Segal, 1987; Jones et al., 2008). In the brightfield photograph of *A. kanohi* (NIWA 24023, Fig. 6B), the gut content is seen as a dark mass in the mid region of the body, indicating that this specimen likely fed recently before being preserved.

A wide range in size is noted among the examined immature stage 3 specimens, correlating to the size variations seen in adults of species of Aegidae. *Aegapheles monophthalma* (NIWA 23759, Fig. 1) and *A. mahana* (NIWA 17943, Fig. 2) are the largest of the immature stage individuals examined, at 26.5 mm and 21.0 mm in length respectively. *Aegapheles vigilans* (NIWA 23779, Fig. 9) is approximately half of this size, at 12.8 mm in length and *A. kanohi* (NIWA 24023, Fig. 6) the smallest of this developmental stage, at 6.9 mm. Besides the range in size, other interspecies variations were noted, including: the shape of the body, from rectangular to ovoid; the shape of the frontal lamina, the number of ommatidia (ranging between 117 and 828 ommatidia per eye); the number of articles on antennulae and antennae; the width of pleon segments and shape of the corresponding pleon segment lateral margins; the shape of the pleotelson and pleotelson posterior margin; shape of the uropods and the length of uropodal setae.

Life cycle and development

One of the most prominent developmental variations among the collection of examined specimens (immature and adult stages) is the overall body size, which is highly variable among species. Similar to other ingroups of Isopoda, such as the obligatory parasitic representatives of Cymothoidae, species of Aegidae are known to be sexual dimorphic. Adult males are generally smaller in overall body size than adult females and with ovigerous and gravid females usually being the largest in size. This trend is also noted in the herein examined material (Fig. 10). The differentiation of developmental stages noted and described from the examined specimens, is comparable to what is known for representatives of Cymothoidae (Van der Wal and Haug, 2020).

Further, unlike representatives of Cymothoidae, representatives of Aegidae develop as separate sexes and show no indication of hermaphroditism. The phenomenon of protandric hermaphroditism is possibly the evolutionary result of an increasingly parasitic lifestyle as a means of ensuring reproduction and the survival of sedentary adults in more isolated environments. Since representatives of Aegidae have no restriction of movement or space, copulation and reproduction are less of a challenge, allowing individuals to develop as separate sexes.

Due to the lack of immature stage individuals described in the literature, no life cycle, or indication of the morphological development of species of Aegidae, has been reconstructed. The results from this study are used to generate a tentative restoration of the general life cycle of Aegidae (Fig. 11), based on the various immature stages examined herein, with the inclusion of some examined adult stage specimens from various species. The embryonic development of specimens of Aegidae is similar to that of the parasitic individuals of Cymothoidae. Eggs (Fig. 11A) develop into embryos (Fig. 11B) with segmentation and limb bud formation as the main differentiation between these stages. Eggs and embryos of *A. antarctica* are larger than any recorded egg or embryo of Cymothoidae.

The staging of immature stages follows the same as Van der Wal and Haug (2020) for specimens of Cymothoidae. The three immature stages (stage 1, Fig. 11C; stage 2, Fig. 11D, J; stage 3, Fig. 11E, F, K), discussed above, are differentiated by the same morphological characters as those of Cymothoidae. This infers that the development of immature individuals of these two groups is initially independent of the eventual feeding habit (plesiomorphic conditions). Up to this point in the development, the differentiation of developmental stages between Cymothoidae and

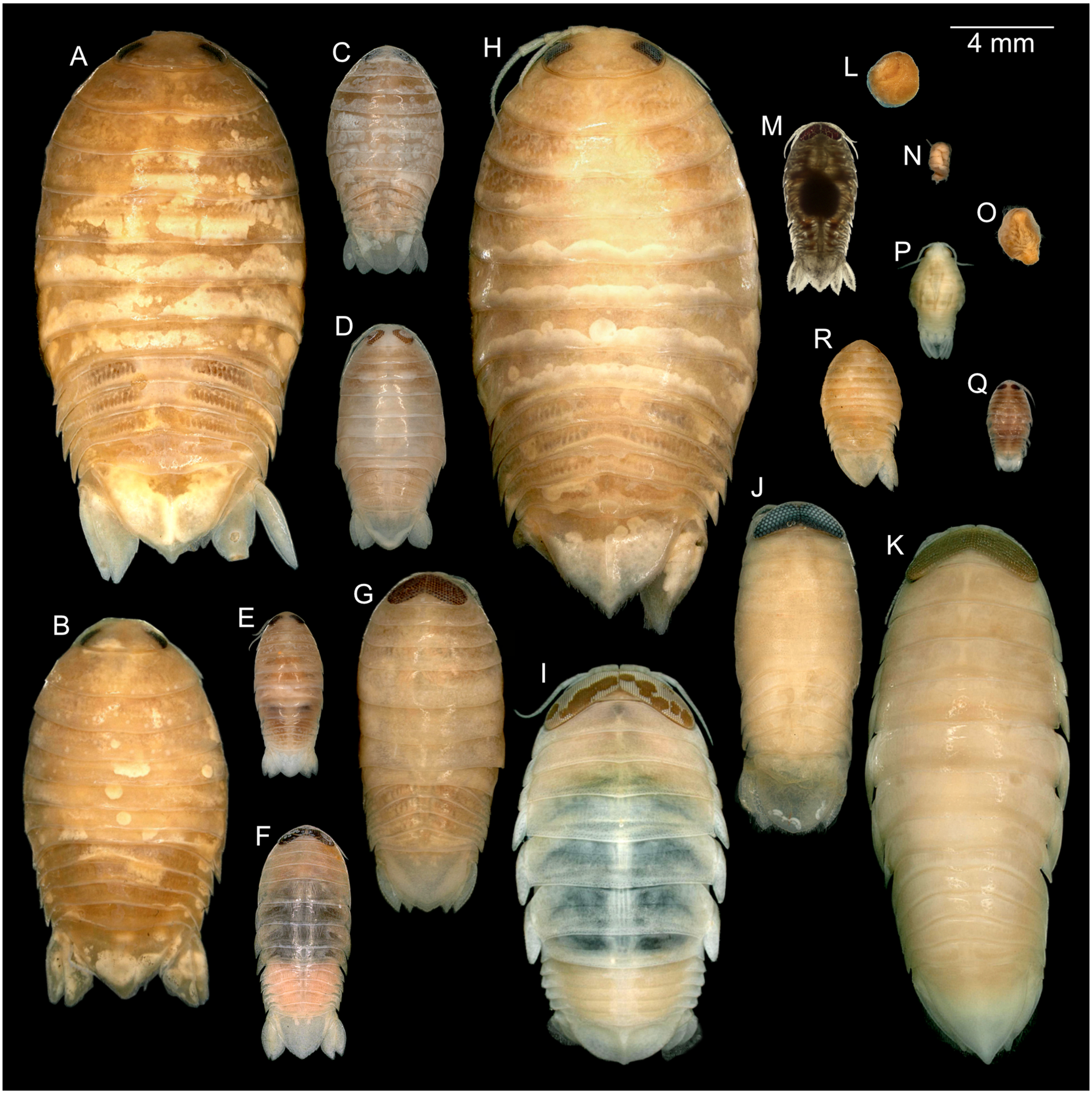

Figure 10. All examined specimens to scale for size comparison. **A**, *Aegiochus antarctica* (Hodgson, 1910) ovigerous female (NIWA 23671). **B**, *Aegiochus antarctica* (Hodgson, 1910) male (NIWA 23671). **C**, *Aegiochus nohinohi* Bruce, 2009 ovigerous female (NIWA 24018). **D**, *Aegiochus nohinohi* Bruce, 2009 non-ovigerous female (NIWA 24018). **E**, *Aegiochus nohinohi* Bruce, 2009 male (NIWA 24018). **F**, *Aegiochus kanohi* Bruce, 2009 male (NIWA 24023). **G**, *Aegiochus kanohi* Bruce, 2009 non-ovigerous female (NIWA 24023). **H**, *Aegiochus antarctica* (Hodgson, 1910) gravid female (NIWA 23671). **I**, *Aega monophthalma* Johnston, 1834 immature male stage 3 (NIWA 23759). **J**, *Aegiochus vigilans* (Haswell, 1881) immature female stage 3 (NIWA 23779). **K**, *Aegapheles mahana* Bruce, 2009 immature male stage 3 (NIWA 17943). **L**, *Aegiochus antarctica* (Hodgson, 1910) eggs (NIWA 23671). **M**, *Aegiochus kanohi* Bruce, 2009 immature male stage 3 (NIWA 24023). **N**, *Aegiochus nohinohi* Bruce, 2009 immature stage 1 (NIWA 24018). **O**, *Aegiochus antarctica* (Hodgson, 1910) embryos (NIWA 23671). **P**, *Aegiochus antarctica* (Hodgson, 1910) immature stage 1 (NIWA 23664). **Q**, *Aegiochus nohinohi* Bruce, 2009 immature male stage 3 (NIWA 24018). **R**, *Aegiochus antarctica* (Hodgson, 1910) immature female stage 2 (NIWA 23671).

Aegidae are based on whether the individual has been released from the brood pouch; the presence or absence of trunk appendage 7 (8th pair of thoracopods); the development of anterior trunk segment 7; and the presence or absence of setae on pleon appendages. Differentiation in developmental stages between the two groups becomes visible with the development of external sexual structures. Since representatives of Cymothoidae are hermaphroditic, they all have penes and appendix masculina, which develop at the end of immature stage 2. As representatives of Aegidae are not hermaphroditic, some immature stage 2 individuals do not have penes or appendix masculina, indicating an immature female specimen.

During the next stage of ontogeny, the external male sexual structures and the 7th pair of trunk appendages are fully developed (Fig. 11G–I). In Cymothoidae, all individuals of this stage will have male sexual structures. The lack of male sexual structures in certain individuals of Aegidae with fully

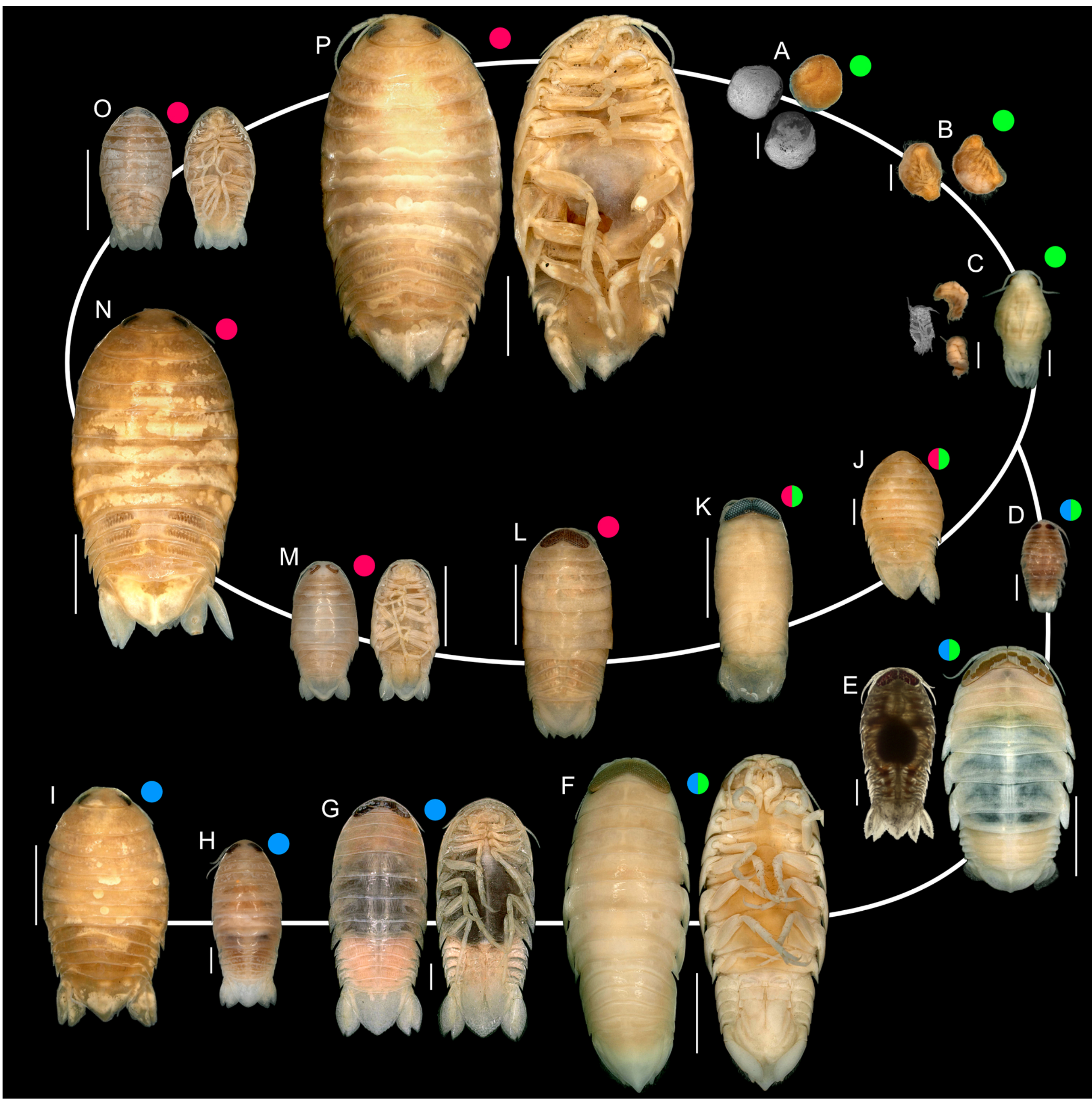

Figure 11. A tentative restoration of the life cycle of Aegidae, based on the material examined. **A**, Eggs **B**, Embryos **C**, Immature stage 1 **D**, Immature male stage 2 **E–F**, Immature male stage 3. **G–I**, Adult male. **J–K**, Immature female stage 3. **L–M**, Non-ovigerous female. **N–O**, Ovigerous female. **P**, gravid female. Short scale bar, 1 mm; long scale bar, 5 mm.

developed thoracopods, indicates a non-ovigerous female specimen (Fig. 11L–M). This differentiation provides the first indication of correlation between development and feeding habit between these two groups. Female specimens without developed brood pouches ('immature females' or non-ovigerous females) are here considered as adult females, able to develop a brood pouch and release eggs upon copulation and likely with fully developed internal ovaries. In contrast, species of Cymothoidae have an additional developmental stage as a result of hermaphroditism, namely the 'transitional stage'. During this stage, an individual (male) starts to develop female characters (oostegites) upon chemical signalling from the presence of another male. In these individuals, both male and female characters are present, with male characters becoming more reduced with further development into an ovigerous female.

The development of oostegites marks the next ontogenetic stage, an ovigerous female (Fig. 11N–O). In these individuals, the brood pouch becomes fully developed, but eggs have not yet been released. Ovigerous female specimens of Aegidae do not seem to have any indication of reduced male structures. Once copulation has occurred and eggs are released into the brood pouch, the specimen becomes a gravid female (Fig. 11P) and will remain a gravid female until the young (immature stage 2 individuals) are released from the brood pouch. If the female survives the ordeal, she will undergo a successive moult of the oostegites, enabling the development of a new brood.

CONCLUSION

The morphological differences observed among the examined early developmental stages of Aegidae substantiate the importance of examining, describing, and illustrating immature stage specimens. The inter- and intra-specific variations noted in the examined developmental stages provide support that immature stage individuals can be distinguished from adult stages of the corresponding species and therefore should not be disregarded. Immature stage specimens might be useful in species determination and distinction, based on inter-specific variations and developmental differentiation among immature stage individuals. Distinct immature developmental stages can be distinguished and determined, based on the presence or absence of certain characters that develop during specific stages in ontogeny.

The described variations among developmental stages of the permanently parasitic representatives of Cymothoidae and the more generalist, opportunistic representatives of Aegidae, support the hypothesis that differentiation in ontogenetic stages of two closely related groups, correlate to a difference in lifestyle and feeding habit of the two groups. Further comparison between the development of Aegidae and other ingroups of Cymothoida, are expected to be useful to provide more comprehensive insight into the evolution of developmental stage differentiation among groups of animals that exhibit such an array of feeding habits and ecological roles.

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Conceptualization and Design: SvdW, JTH. Performed research: SvdW.

Acquisition of data: SvdW. Analysis and interpretation of data: SvdW, JTH.

Preparation of figures/tables/maps: SvdW. Writing – original draft: SvdW. Writing - critical review and editing: SvdW, JTH.

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All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

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The authors declare no competing interest.

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