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First Description of Life Stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 (Isopoda: Cymothoidae) and Growth-associated Morphological Changes

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Cymothoidae are mainly described based on the morphology of adult females, making species identification difficult because of the limited morphological information on male, juvenile, and manca life stages. In particular, most species in the genus *Anilocra* Leach, 1818 lack morphological information beyond that of females, highlighting the need to accumulate such data. In the present study, we described the aegathoid stage, male, and transitional morphology of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from Japanese waters and documented changes in morphology with growth for the first time. With growth, the morphology of *A. prionuri* changed: 1) body shape becomes rounder, 2) eye length becomes shorter, 3) shortest pereonite changes from 7 to 2, 4) antennular article 3 enlarged, 5) length of dactylus relative to propodus in pereopod 1 becomes longer, 6) pleopod peduncle becomes shorter, 7) decrease robust setae of pereopods, coupling hooks and plumose setae of pleopods, swimming setae of pleotelson, pleopod, and uropod, 8) appendix masculina on the pleopod 2 endopod shortens and disappears, 9) rami of pleopods and uropods become rounded, and 10) endopods of uropods become elongated. The aegathoid stage of *A. prionuri* was distinguished from that of *Anilocra clupei* Williams and Bunkley-Williams, 1986, also distributed in Japan by 1) 3–5 and 0–5 plumose setae of pleopods 1 and 2, (5 and 8 plumose setae in *A. clupei*), 2) uropodal exopod longer than endopod (same length in *A. clupei*), and 3) triangular uropodal exopod (oval in *A. clupei*).

Keywords: Aegathoid stage, Fish parasite, Male, Manca, Transitional

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BACKGROUND

Cymothoidae Leach, 1818 (Crustacea: Isopoda) includes more than 360 species from 42 genera of cosmopolitan fish parasites (Boyko et al. 2024b). It is one of the largest families of isopods, inhabiting all seas except polar regions (Ahyong et al. 2011, Smit et al. 2014). Their hosts include diverse fish taxa that inhabit marine, brackish, and freshwater environments (Smit et al. 2014, Yamauchi 2016). These parasites attach to their hosts at four sites: the branchial cavity, buccal cavity, abdominal cavity, and the body surface (Smit et al. 2014). Cymothoids have five life stages: manca, juvenile, male, transitional, and female. In addition, juveniles with elongated body shapes, such as *Anilocra* Leach, 1818 and *Nerocila* Leach, 1818, are known to be at the aegathoid stage (Saito et al. 2014, Fujita 2022). Free-swimming mancae grow into juveniles and mature into adult males on their hosts. Afterward, adult cymothoids change sex from male to female (Brusca 1978a, b, 1981, Kottarathil and Kappalli 2019, Aneesh and Kappalli 2020). Cymothoids are primarily identified based on the morphological characteristics of adult females. Thus, species identification using traditional morphometrics is difficult, making molecular analysis the only reliable method to identify non-female specimens (Fujita et al. 2021). To resolve this limitation of species identification, it is necessary to accumulate more morphological information on cymothoid juveniles and mancae. In addition, for species identification, it is important to accumulate DNA sequences linked to morphological information of adult females as Helna et al. (2023).

The genus *Anilocra* is an external attaching cymothoid, comprising 60 valid species (Boyko et al. 2024a), which often lack morphological data on other life stages, except for females (Table 1). Three species of *Anilocra* have been reported in Japan: *Anilocra clupei* Williams and Bunkley-Williams, 1986; *Anilocra prionuri* Williams and Bunkley-Williams, 1986; and *Anilocra harazakii* Uyeno and Tosuji, 2023 (Williams and Bunkley-Williams 1986, Uyeno and Tosuji 2023). Of the three species, morphological descriptions of aegathoid stages of *A. clupei* (Saito et al. 2018, Fujita et al. 2021, Fujita 2022), and manca of *A. harazakii* (Uyeno and Tosuji 2023) were reported. However, morphological information on *A. prionuri*, excluding adult females, has not yet been provided.

In this study, we examined the morphology of *A. prionuri* from the aegathoid stage to the ovigerous female life stages, and documented changes in morphology with growth.

Table 1. resence or absence of morphological information on the genus *Anilocra*

	Manca	Juvenile	Male	References
Anilocra abudefdufi Bunkley-Williams and Williams, 1981	-	-	-	
Anilocra acanthuri Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra acuminata Haller, 1880	-	-	-	
Anilocra acuta Richardson, 1910	-	-	-	
Anilocra alloceraea Koelbel, 1879	-	-	-	
Anilocra amboinensis Schioedte and Meinert, 1881	-	-	-	
Anilocra angeladaviesae Welicky and Smit, 2019	-	-	○	Welicky and Smit (2019)
Anilocra ankistra Bruce, 1987	-	-	○	Bruce (1987)
Anilocra apogonae Bruce, 1987	-	○**	○	Jones et al. (2008)
Anilocra atlantica Schioedte and Meinert, 1881	-	-	-	
Anilocra australis Schioedte and Meinert, 1881	-	-	-	

Anilocra boucheti Uyeno and Tosuji, 2023	-	-	-	
Anilocra brillae Welicky, Hadfield, Sikkel and Smit, 2017	-	-	-	
Anilocra bunkleywilliamsae Welicky and Smit, 2019	-	-	-	
Anilocra capensis Leach, 1818	-	-	○	Welicky and Smit (2019)
Anilocra caudata Bovallius, 1887	-	-	-	
Anilocra cavicauda Richardson, 1910	-	-	-	
Anilocra chaetodontis Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra chromis Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra clupei Williams and Bunkley-Williams, 1986	-	○	-	Saito et al. (2018), Fujita et al. (2021), Fujita (2022)
Anilocra coxalis Schioedte and Meinert, 1881	-	-	-	
Anilocra dimidiata Bleeker, 1857	-	-	-	
Anilocra elviae Winfield, Alvarez and Ortiz, 2002	-	-	-	
Anilocra frontalis H. Milne Edwards, 1840	-	-	-	
Anilocra gigantea (Herklots, 1870)	-	-	-	
Anilocra grandmaae Aneesh, Hadfield, Smit and Kumar, 2021	-	-	-	
Anilocra guinensis Bovallius, 1887	-	-	-	
Anilocra hadfieldae Welicky and Smit, 2019	-	-	○	Welicky and Smit (2019)
Anilocra haemuli Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra harazakii Uyeno and Tosuji, 2023	○	-	-	Uyeno and Tosuji (2023)
Anilocra hedenborgi Bovallius, 1887	-	-	-	
Anilocra holacanthi Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra holocentri Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra huacho Rokicki, 1984	-	-	-	
Anilocra ianhudsoni Welicky and Smit, 2019	-	-	○	Welicky and Smit (2019)
Anilocra jovanasi Welicky and Smit, 2019	-	-	-	
Anilocra koolanae Bruce, 1987	-	-	-	
Anilocra laevis Miers, 1878	-	-	-	
Anilocra leptosoma Bleeker, 1857	-	-	-	
Anilocra longicauda Schioedte and Meinert, 1881	-	○	-	Jones et al. (2008)
Anilocra marginata (Bleeker, 1857)	-	-	-	
Anilocra meridionalis Searle, 1914	-	-	-	
Anilocra monoma Bowman and Tareen, 1983	-	-	-	
Anilocra montti Thatcher and Blumenfeldt, 2001	-	-	○***	Thatcher and Blumenfeldt (2001)
Anilocra morsicata Bruce, 1987	-	-	-	
Anilocra myripristis Bunkley-Williams and Williams, 1981	-	-	○*	Bunkley-Williams and Williams (1981)
Anilocra nemipteri Bruce, 1987	-	○	○	Jones et al. (2008)
Anilocra occidentalis Richardson, 1899	-	-	-	
Anilocra partiti Bunkley-Williams and Williams, 1981	-	-	-	
Anilocra paulsikkeli Welicky and Smit, 2019	-	-	○	Welicky and Smit (2019)
Anilocra physodes (Linnaeus, 1758)	-	○	○	van der Wal and Haug (2020)
Anilocra pilchardi Bariche and Trilles, 2006	○	-	○*	Bariche and Trilles (2006)
Anilocra plebeia Schioedte and Meinert, 1881	-	-	-	
Anilocra pomacentri Bruce, 1987	○****	-	○	Adlard and Lester (1994, 1995)
Anilocra prionuri Williams and Bunkley-Williams, 1986	-	○	○	This study
Anilocra recta Nierstrasz, 1915	-	-	-	
Anilocra rhodotaenia Bleeker, 1857	-	-	-	
Anilocra rissoniana (Leach, 1818)	-	-	-	
Anilocra soelae Bruce, 1987	-	-	-	
Anilocra tropica Avdeev, 1977	-	-	-	

*, these individuals were labeled male, but have the characteristics of aegathoid stage. **, *Anilocra* cf. *apogonae*. ***, no female individuals have been found. ****, only overall views were shown.

MATERIALS AND METHODS

Sampling

Eleven cymothoid individuals were collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835, by line angling on January 2, 2024, at the Okino-se, off Oshima, Ushibuka-cho, Amakusa, Kumamoto Prefecture, Japan (32°10'30.6"N 129°56'25.1"E). The host fish and cymothoids were frozen, transported to the laboratory, and fixed in 99.5% ethanol. These samples were deposited at the Seto Marine Biological Laboratory (SMBL), Field Science Education and Research Center, Kyoto University (registration number: SMBL-V0772–V0783).

Morphological examination

Cymothoid photographs were captured under a stereomicroscope SMZ18 (Nikon, Tokyo, Japan) using the real-time EDF function in NIS-Elements Documentation (version 5.30.00) (Nikon), and the photographs were combined using Photoshop 2024 (version 25.11.0) (Adobe, San Jose, CA, USA). Morphological descriptions were made with the aid of an SMZ800 stereomicroscope with a P-IDT drawing tube (Nikon). The drawings were digitally inked using Illustrator 2024 (version 28.4.1) (Adobe) and a DTC133 pen display (Wacom, Saitama, Japan). The measurements and terminologies followed those described by Aneesh et al. (2019). The life stages of the cymothoids were determined as described by Aneesh et al. (2016). Species descriptions were prepared in the DEscription Language for TAxonomy (DELTA) according to Coleman et al. (2010) (Supplementary File S1).

DNA sequencing

The cytochrome *c* oxidase subunit I (*COI*) and 16S rRNA sequences of the four individuals were determined to accumulate DNA information related to their morphology. The *COI* and 16S rRNA sequences of an aegathoid stage (SMBL-V0772), a male (SMBL-V0778), a transitional (SMBL-V0780), and an ovigerous female (SMBL-V0781) were sequenced. DNA extraction and PCR amplification were performed according to Fujita et al. (2023b). PCR products were sent to Eurofins Genomics (Tokyo, Japan) for sequencing using the dye terminator method. The sequences were deposited in GenBank (accession numbers: LC860811–LC860816).

RESULTS

TAXONOMY

Taxonomic descriptions are also shown in DELTA format (Supplementary File S1).

Order: Isopoda Latreille, 1816

Superfamily: Cymothooidea Leach, 1814

Family: Cymothoidae Leach, 1814

Genus: *Anilocra* Leach, 1818

***Anilocra prionuri* Williams and Bunkley-Williams, 1986**

[Japanese name: Nizadai-no-ginka]

(Figs. 1–19, SM1)

Material examined: six aegathoid stages, SMBL-V0772–0777, BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm; two males, SMBL-V0778 and V0779. BL20.0 and 20.1 mm; 1 transitional, SMBL-V0780, BL24.7 mm; 2 ovigerous female, SMBL-V0781 and V0782, BL34.0 and 34.2 mm. All specimens from Okino-se, the East China Sea, off Oshima, Ushibuka-cho, Amakusa City, Kumamoto Prefecture, Japan (32°10'30.6"N 129°56'25.1"E), body surface of *Prionurus scalprum* Valenciennes, 1835 (SL: 304.5 mm, SMBL-V0783), 2 January 2024, coll. T. Ohnaka.

Fig. 1. scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835 infested by 11 individuals of *Anilocra prionuri* Williams and Bunkley-Williams, 1986, SMBL-V0783. Scale bar: 50 mm.

Fig. 2. orsal views of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986

collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 5 mm.

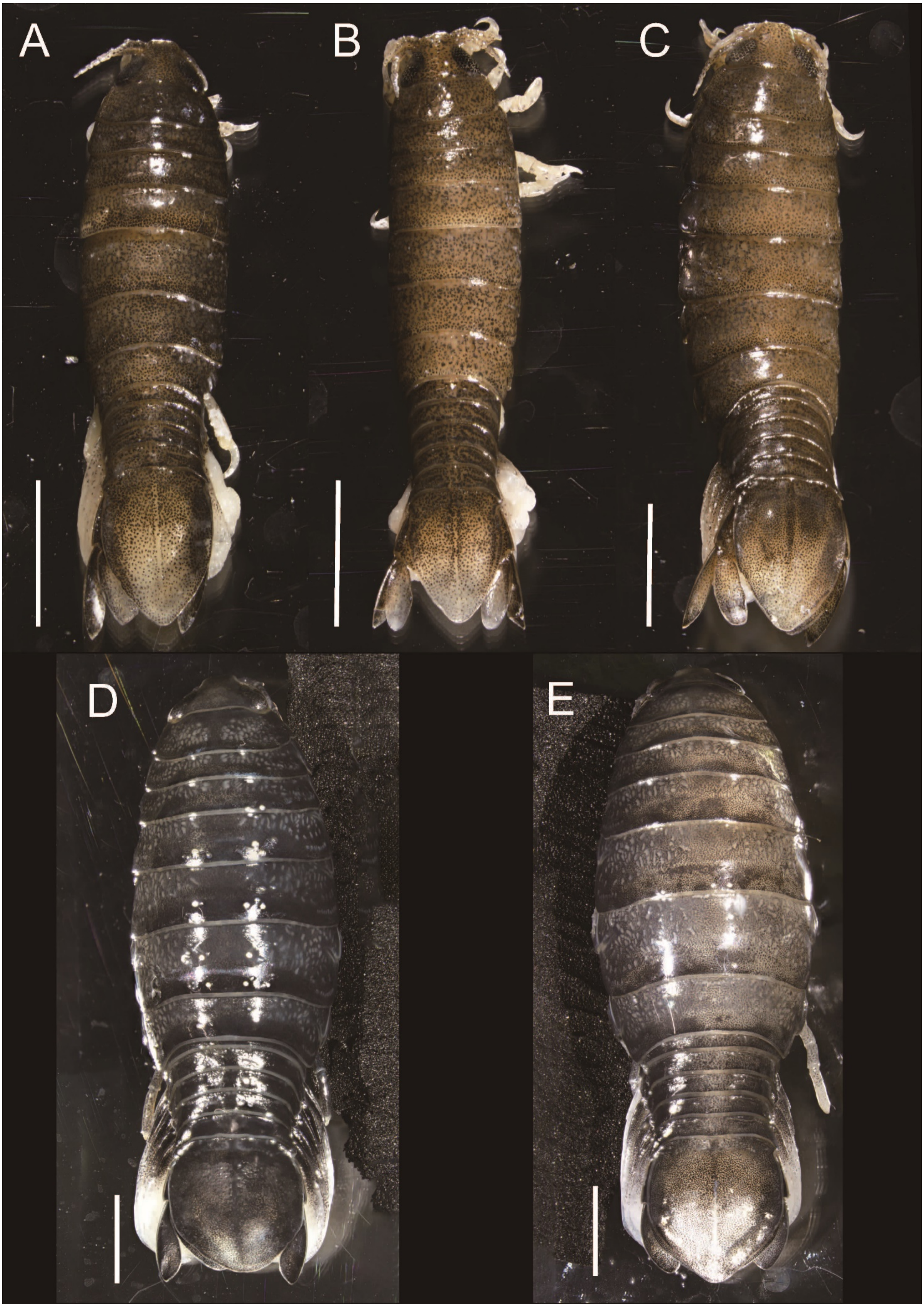

Fig. 3. orsal views of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a

scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: 5 mm.

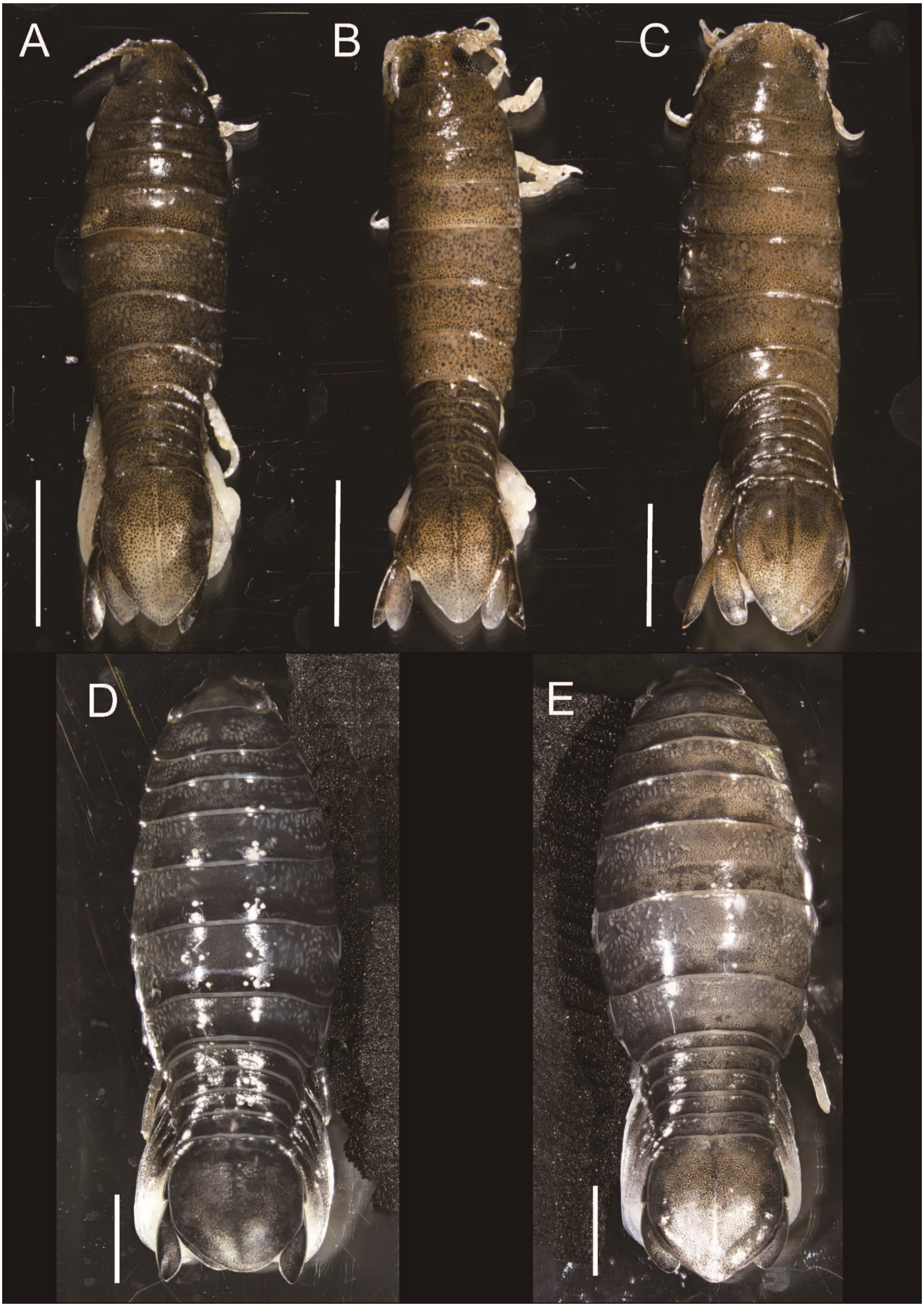

Fig. 4. entral views of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams,

1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 5 mm.

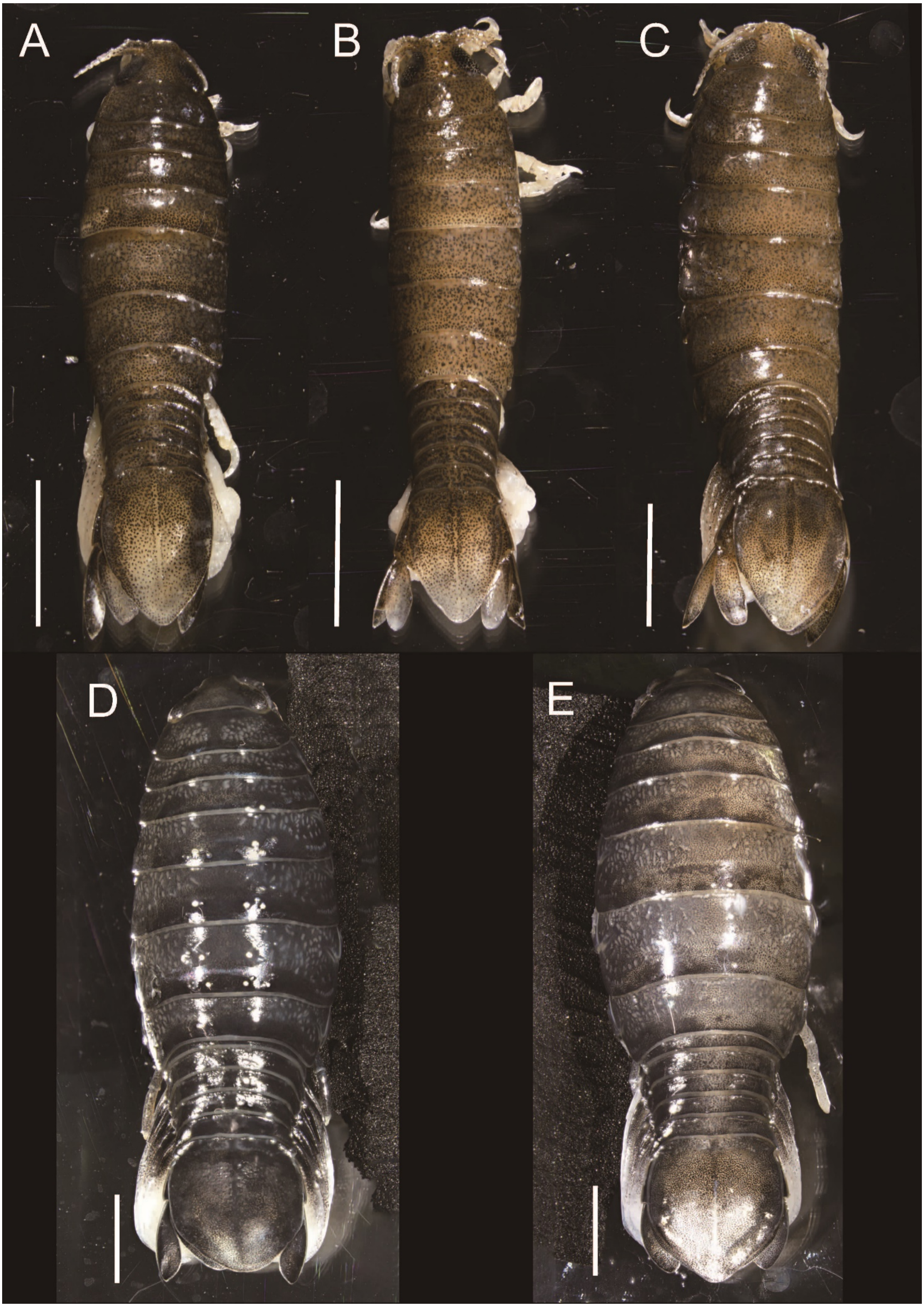

Fig. 5. entral views of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a

scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, SMBL-V0778, V0779, males, (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: 5 mm.

Description of aegathoid stage (Figs. 2, 6, 8, 10, 12, 14, 16, 18): Body narrow, 4.0–5.1 times as long as greatest width, widest at pereonite 5 or pereonite 6, with smooth dorsal surfaces.

Cephalon 1.3–2.1 times wider than long, semi-oval, with well developed rostrum, not immersed in pereonite 1. Eyes oval, with distinct margins, with long axis of each eye 0.7–1.0 times length of cephalon, and short axis 0.1–0.3 times maximum width of cephalon. Anterior border of pereonite 1 straight. Coxae almost invisible in dorsal view, of pereonites 2–4 roundly, of pereonites 5–7 concave; pereon longest at pereonite 5 or pereonite 6, shortest at pereonite 7; posterior margins of pereonites 1–5 smooth and slightly curved laterally, that of pereonites 6 and 7 slightly recessed. Pleonites 1–5 0.2–0.3 times as long as total length, 0.7–0.8 times as wide as greatest body width, with all pleonites visible in dorsal view. Pleotelson 1.4–1.5 times as long as wide, 0.8–1.3 times as long as pleonites 1–5, with usually swimming setae posterior margins.

Antennula 8 articles, extending beyond mid-length of cephalon, article 3 enlargement or no enlargement. Antenna 10–11 articles, extending beyond anterior border of pereonite 1.

Pereopod 1 basis 1.7–2.0 times as long as greatest width; ischium 0.5–0.6 times as long as basis; merus 0.3–0.6 times as long as ischium, with 1 robust seta on superior distal angle; carpus 0.5–1.3 times as long as merus; propodus 2.8–4.5 times as long as carpus; dactylus 0.7–0.8 times as long as propodus. Pereopod 7 basis 2.4–2.7 times as long as greatest width; ischium 0.8 times as long as basis; merus 0.5–0.6 times as long as ischium, with 1–2 robust setae on superior distal angle, 0–1 robust seta on inferior margin; carpus 0.9–1.2 times as long as merus, with 0–3 robust setae on inferior margin; propodus 1.5–1.8 times as long as carpus, with 2–7 robust setae on inferior margin; dactylus 0.7–0.8 times as long as propodus.

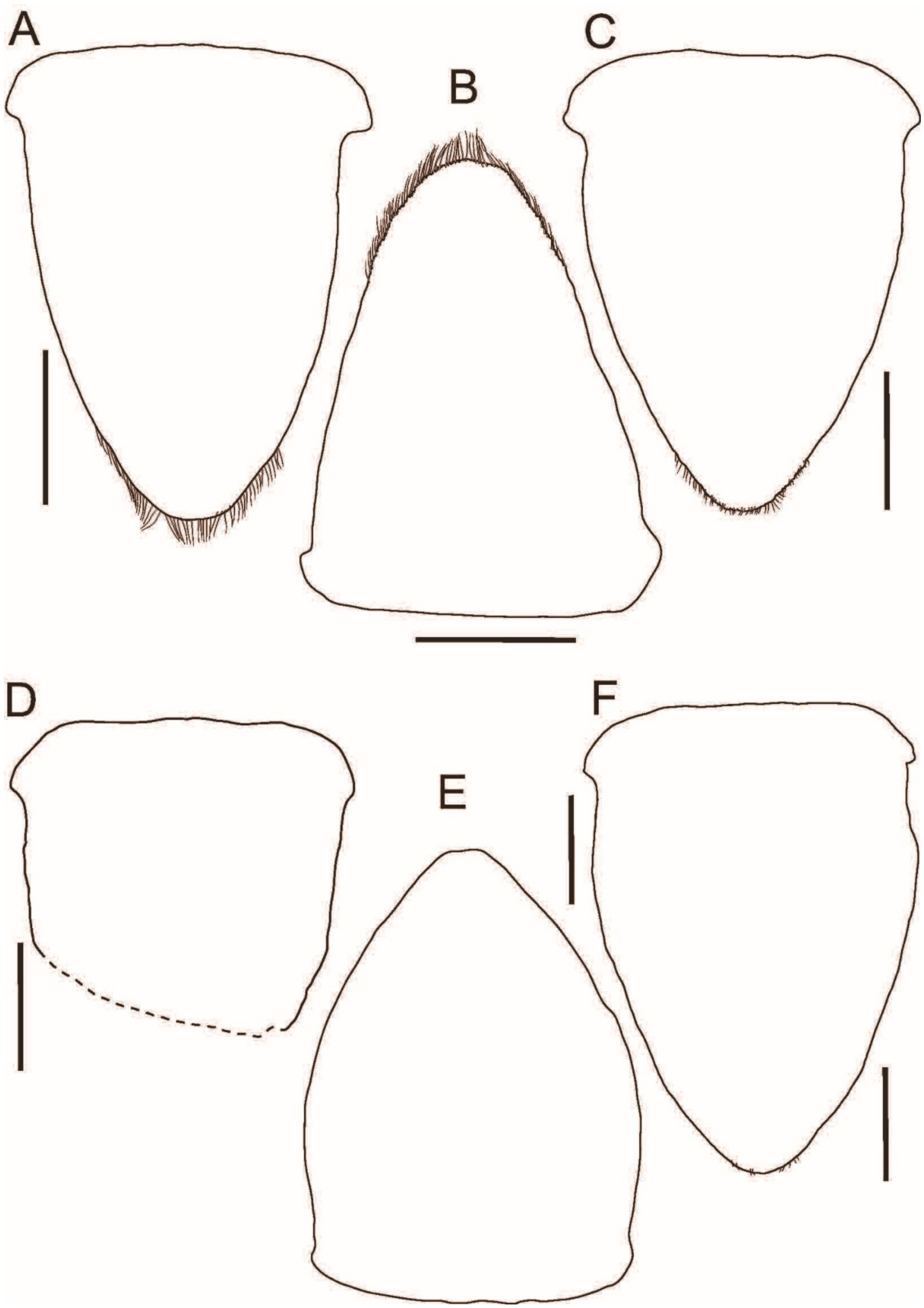

Fig. 6. leotelsons of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 1 mm.

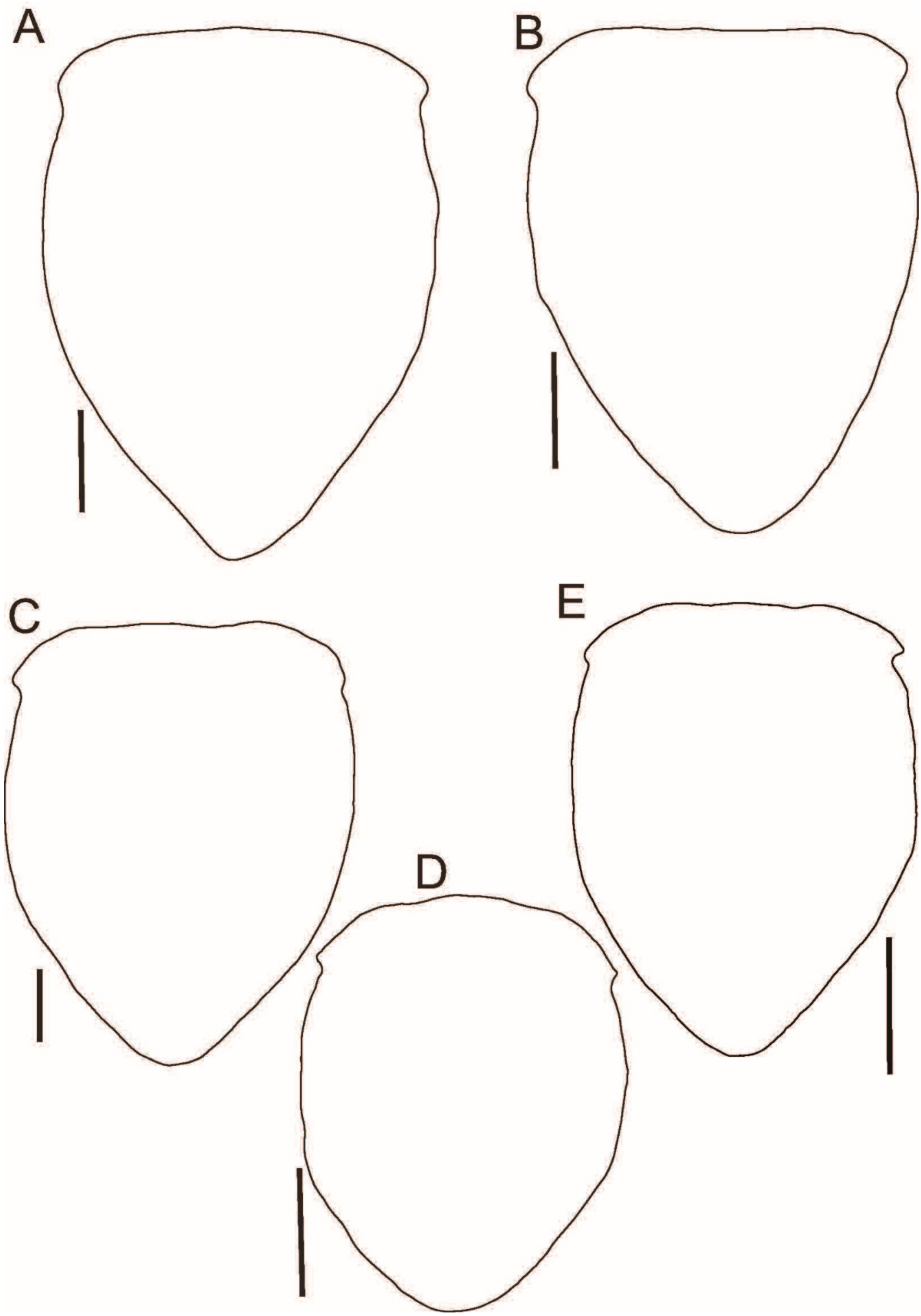

Fig. 7. leotelsons of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: A–C, 1 mm; D, E, 3 mm.

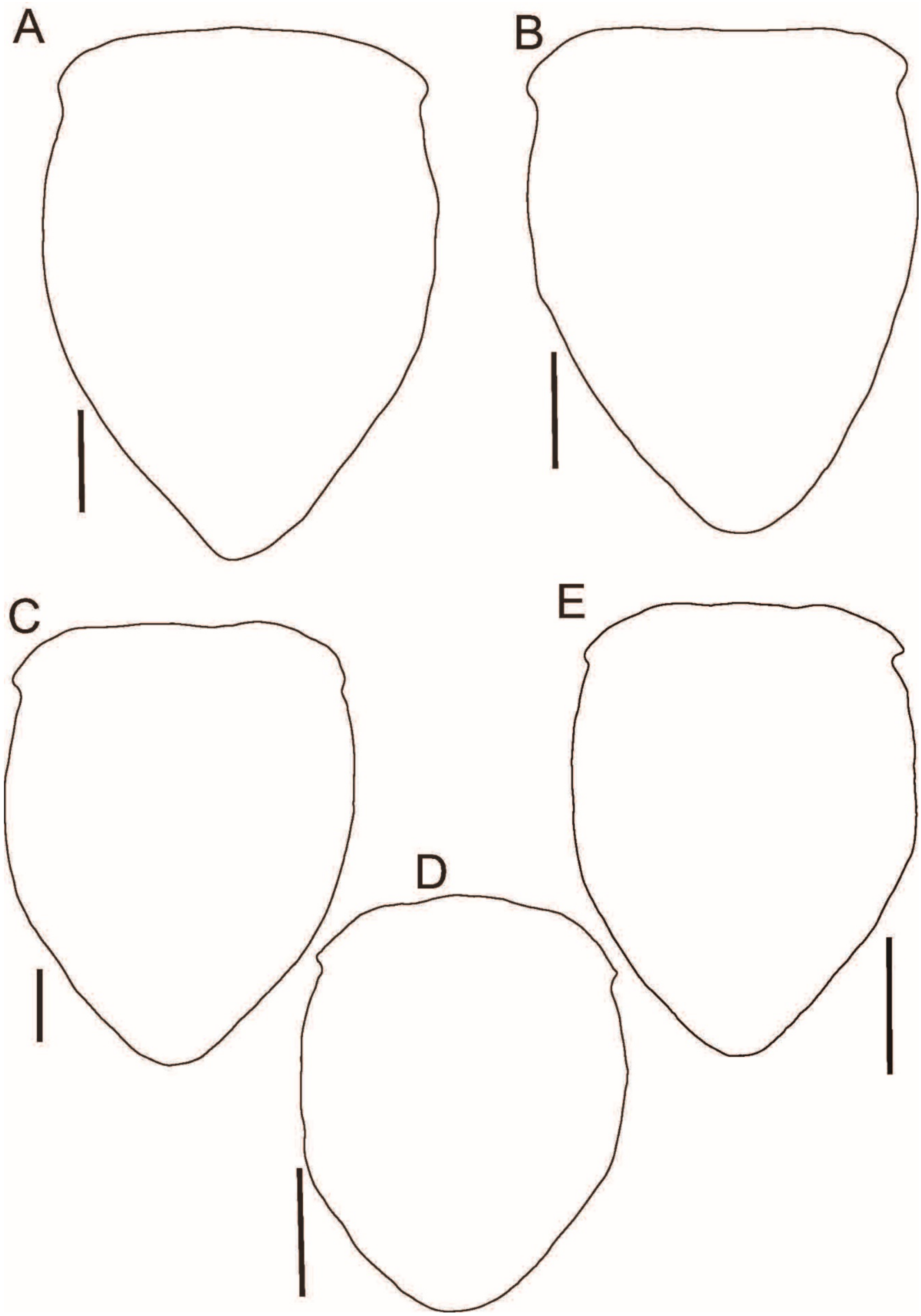

Fig. 8. nntenules of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.3 mm.

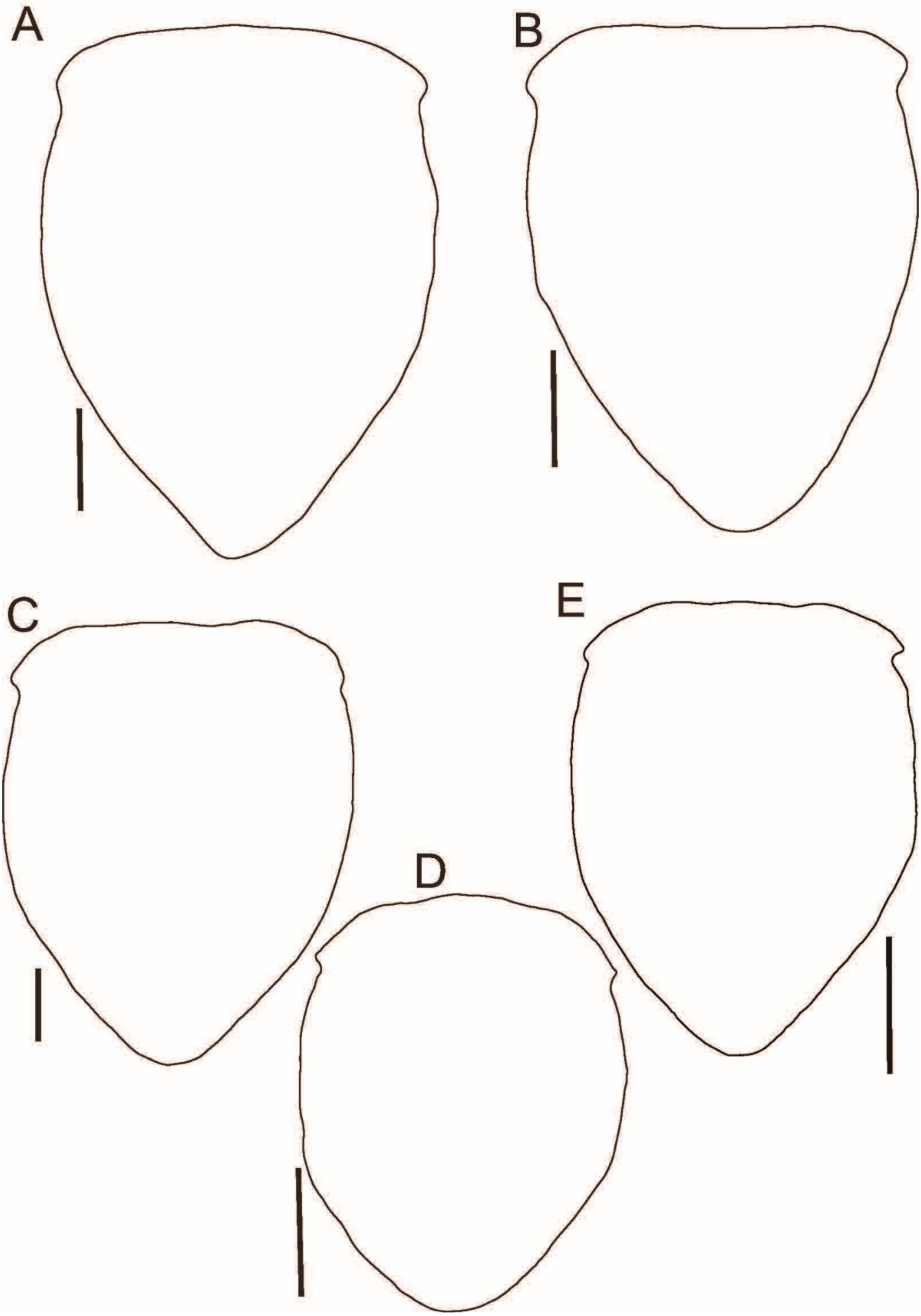

Fig. 9. nntenules of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: 0.5 mm.

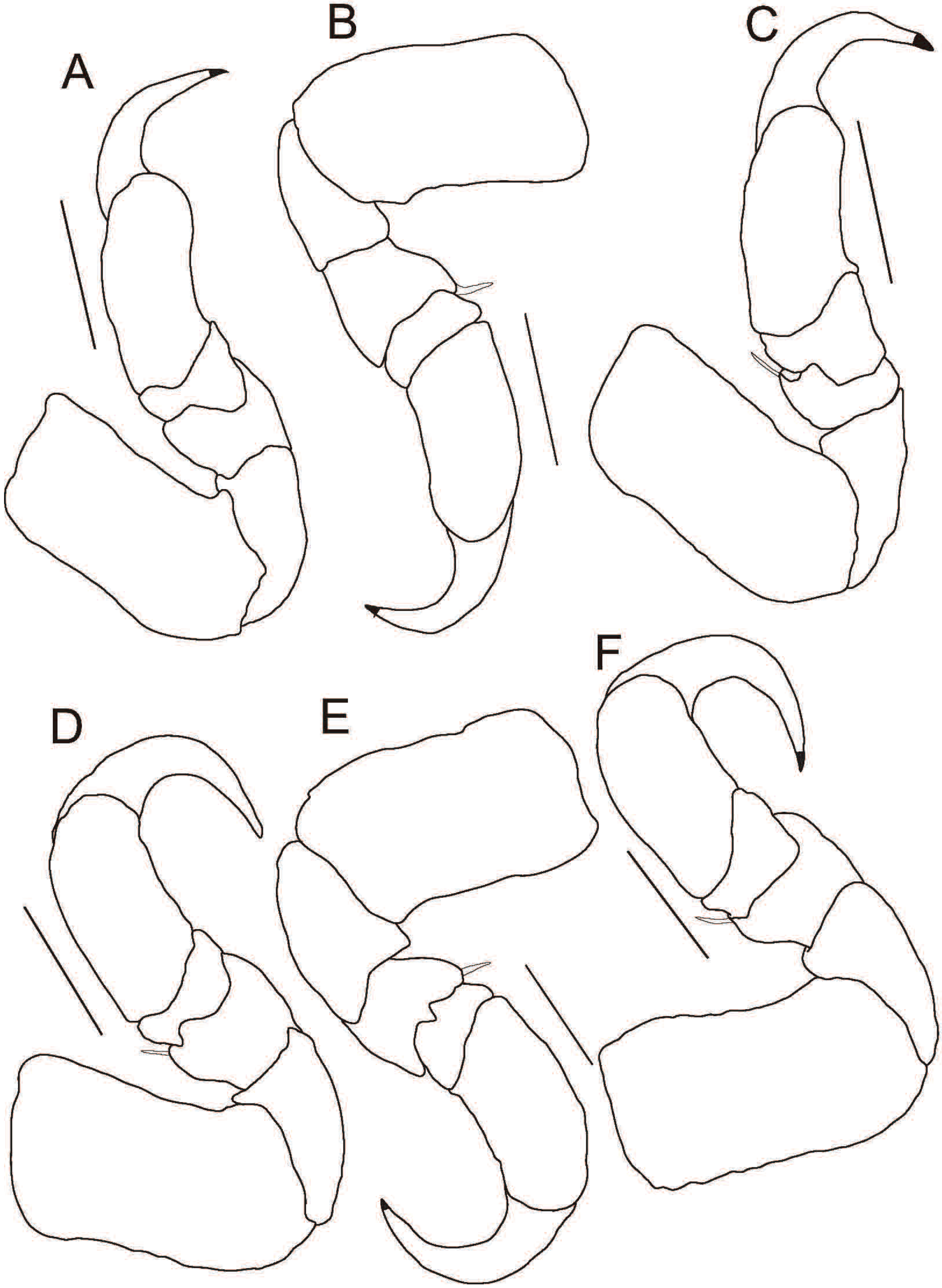

Fig. 10. ereopods 1 of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.5 mm.

Pleopods all lamellar with smooth surfaces. Pleopod 1 penduncle 0.6–1.0 times as wide as long, medial margin with 4–5 coupling hooks and 3–5 plumose setae; endopod rectangular, 1.6–1.9 times as long as wide; exopod elliptical, 1.7–2.2 times as long as wide, 0.9–1.1 times as long as endopod. Pleopod 2 peduncle 0.5–0.6 times as wide as long, medial margin with 4 coupling hooks and 0–5 plumose setae; endopod rectangular, 1.8–2.2 times as long as wide, with appendix masculina, without swimming seta; exopod elliptical, 1.7–1.9 times as long as endopod, 1.0–1.2 times as long as wide, lateral margin with or without swimming seta.

Uropodal peduncle triangular, 1.9–2.4 times as long as wide, 0.7–1.0 times as long as exopod, with distal corner with 2–26 setae; endopod rami 0.7–0.9 times as long as that of exopod; extending beyond posterior margin of pleotelson; endopod oval, 2.1–2.6 times as long as greatest width, with apical and distal half or less of medial and lateral margins with swimming setae; exopod triangular, 2.9–4.0 times as long as greatest width, with apical margins bearing swimming setae.

Description of male (Figs. 3AB, 7AB, 9AB, 11AB, 13AB, 15AB, 17AB, 19AB): Body narrow, 3.5–4.4 times as long as greatest width, widest at pereonite 5, with smooth dorsal surfaces.

Cephalon 1.6–2.1 times wider than long, semi-oval, with well-developed rostrum, not immersed in pereonite 1. Eyes oval, with distinct margins, with long axis of each eye 0.8–0.9 times length of cephalon, and short axis 0.2 times maximum width of cephalon. Anterior border of pereonite 1 straight. Coxae almost invisible in dorsal view, of pereonites 2–4 roundly, of pereonites 5–7 concave; pereon longest at pereonite 4 or pereonite 5, shortest at pereonite 2; posterior margins of pereonites 1–5 smooth and slightly curved laterally, that of pereonite 6 and 7 slightly recessed. Pleonites 1–5 0.1–0.2 times as long as total length, 0.7 times as wide as greatest body width, with all pleonites visible in dorsal view. Pleotelson 1.4–1.5 times as long as wide, 1.7–1.9 times as long as pleonites 1–5, with no seta.

Antennula 8 articles, extending beyond mid-length of cephalon, article 3 enlargement. Antenna 10 articles, extending beyond anterior border of pereonite 1.

Pereopod 1 basis 1.7–1.8 times as long as greatest width; ischium 0.5–0.7 times as long as basis; merus 0.5 times as long as ischium, with 1 robust seta on superior distal angle; carpus 0.7–0.8 times as long as merus; propodus 2.4–4.0 times as long as carpus; dactylus 0.8–1.0 times as long as propodus. Pereopod 7 basis 3.1–3.5 times as long as greatest width; ischium 0.7–0.8 times as long as basis; merus 0.5 times as long as ischium, with 1 robust seta on superior distal angle, no robust seta on inferior margin; carpus 1.1 times as long as merus, with 1–2 robust setae on inferior margin; propodus 1.7–1.8 times as long as carpus, with 3–5 robust setae on inferior margin; dactylus 0.8 times as long as propodus.

Pleopods all lamellar with smooth surfaces. Pleopod 1 penduncle 0.6–0.7 times as wide as long, medial margin with 4 coupling hooks and 0–3 plumose setae; endopod elliptical, 1.6–1.8 times as long as wide; exopod elliptical, 1.8–1.9 times as long as wide, 1.1 times as long as endopod. Pleopod 2 peduncle 0.4–0.5 times as wide as long, medial margin with no coupling hook and no plumose seta; endopod rectangular, 1.9–2.0 times as long as wide, with appendix masculina, without swimming seta; exopod elliptical, 1.7 times as long as endopod, 1.1–1.2 times as long as wide, without swimming seta.

Uropodal peduncle triangular, 1.9–2.1 times as long as wide, 0.7 times as long as exopod, with distal corner with 9–11 setae; endopod rami 0.9–1.0 times as long as that of exopod; extending beyond posterior margin of pleotelson; endopod oval, 2.6–2.7 times as long as greatest width, without swimming seta; exopod triangular, 3.7–3.9 times as long as greatest width, without swimming seta.

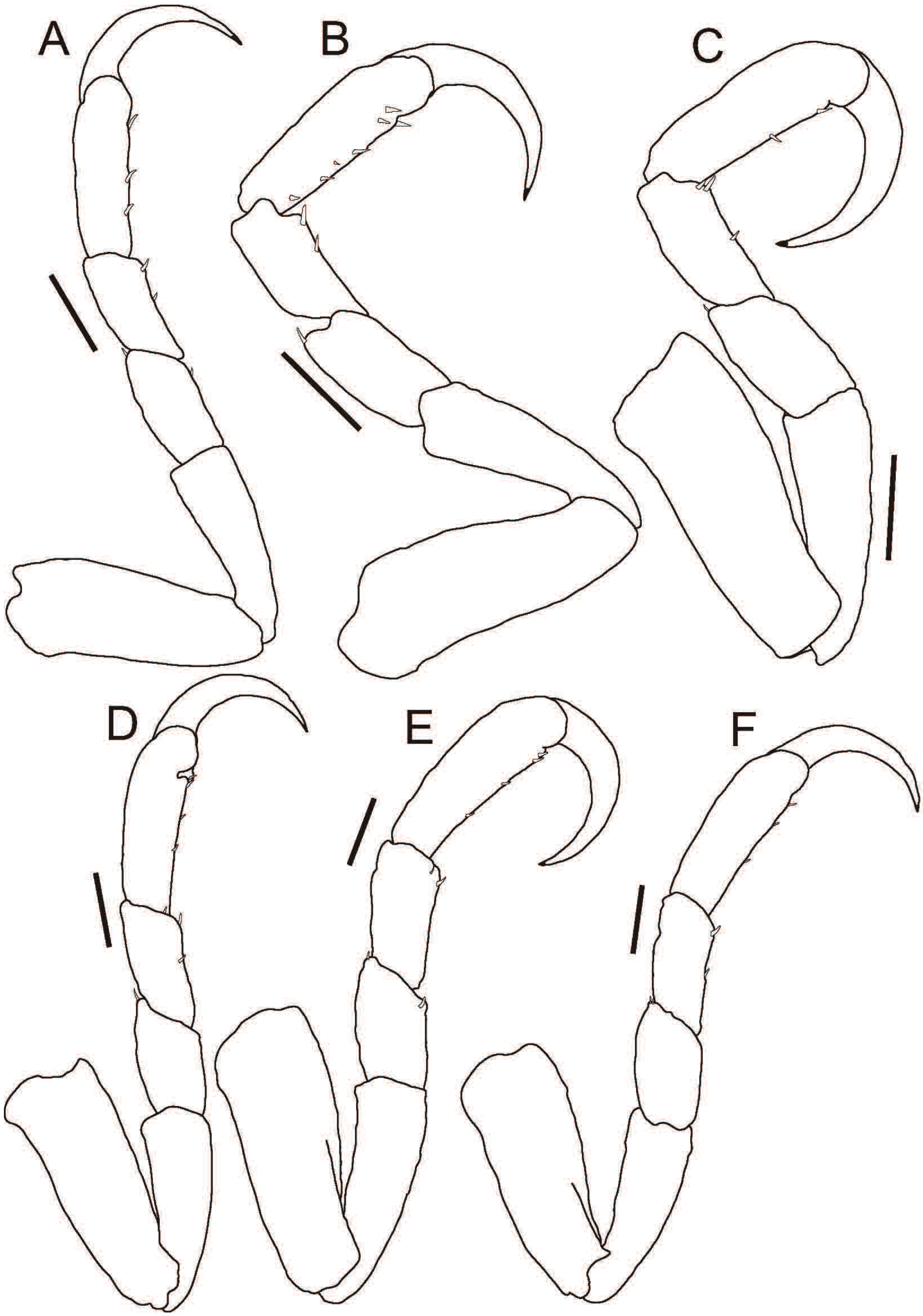

Fig. 11. ereopods 1 of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: 0.5 mm.

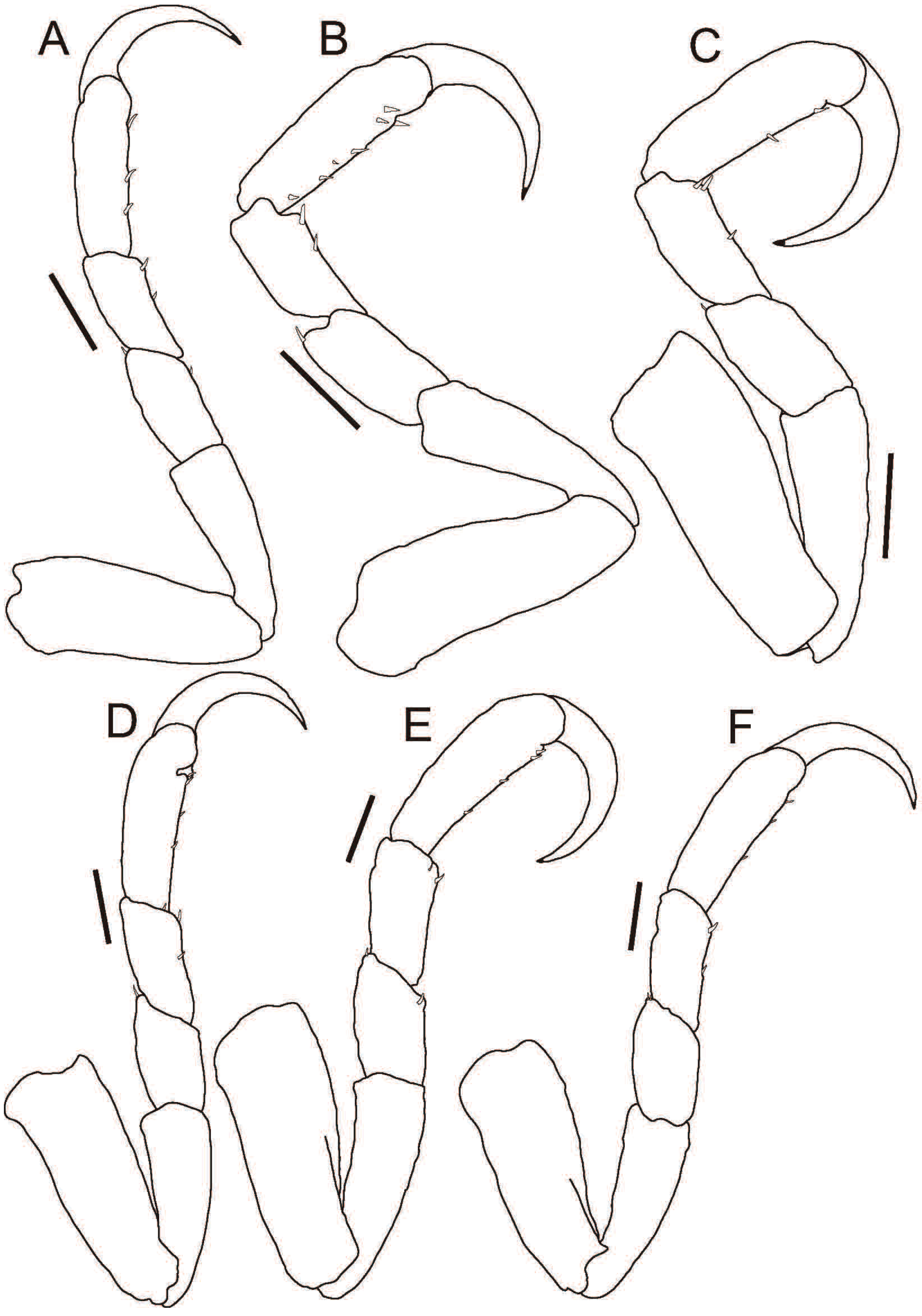

Fig. 12. ereopods 7 of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.5 mm.

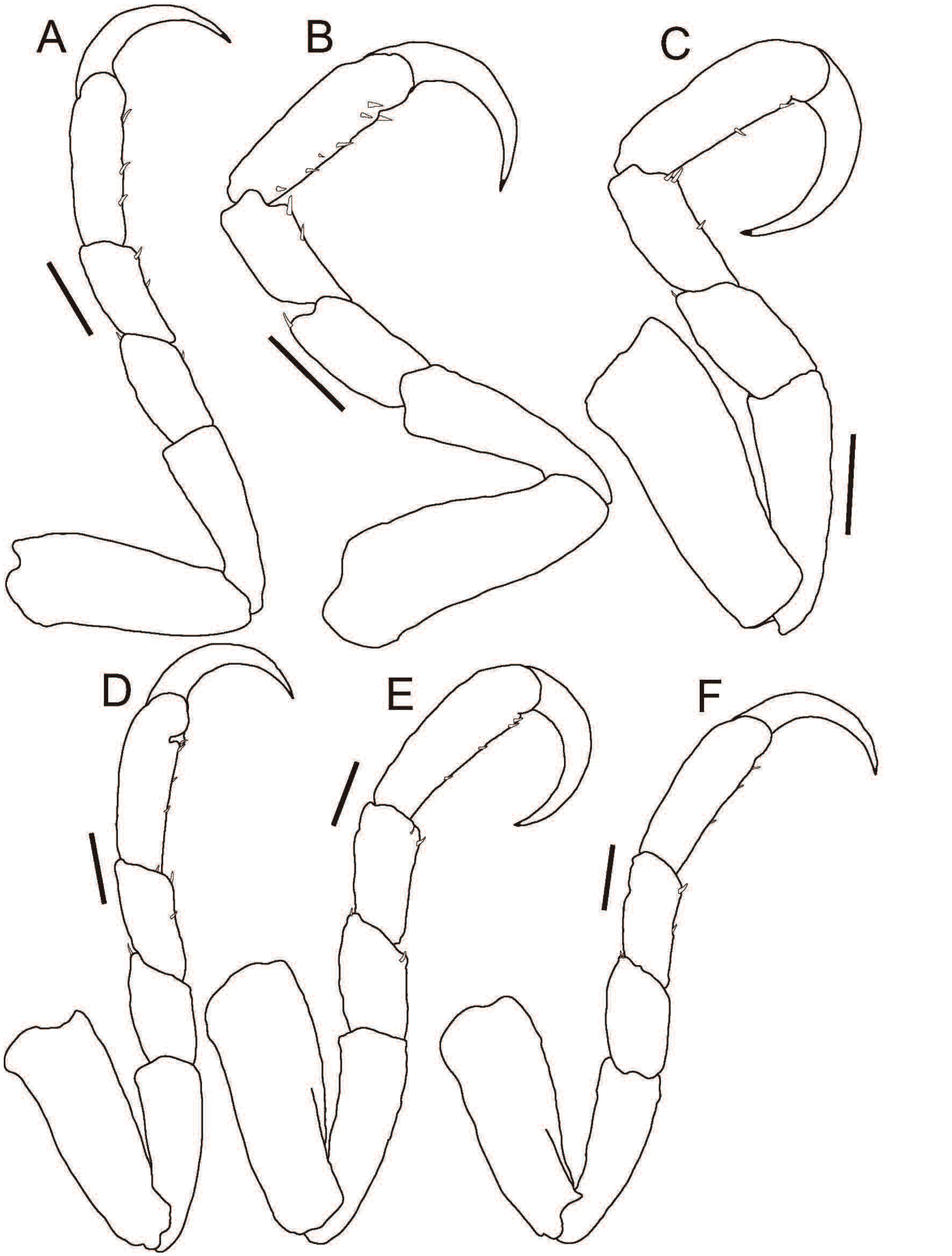

Fig. 13. ereopods 7 of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: 1 mm.

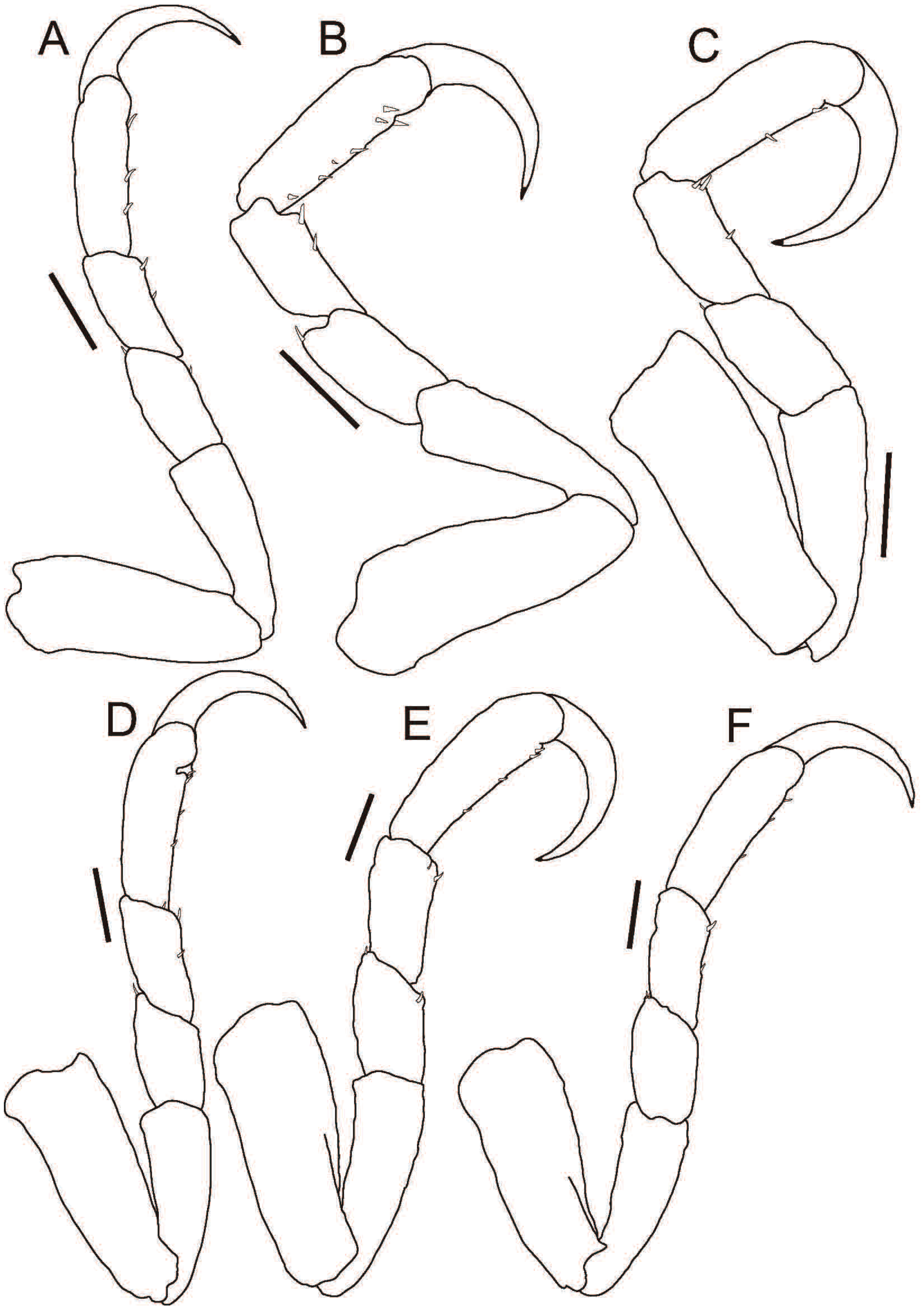

Fig. 14. leopods 1 of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.5 mm.

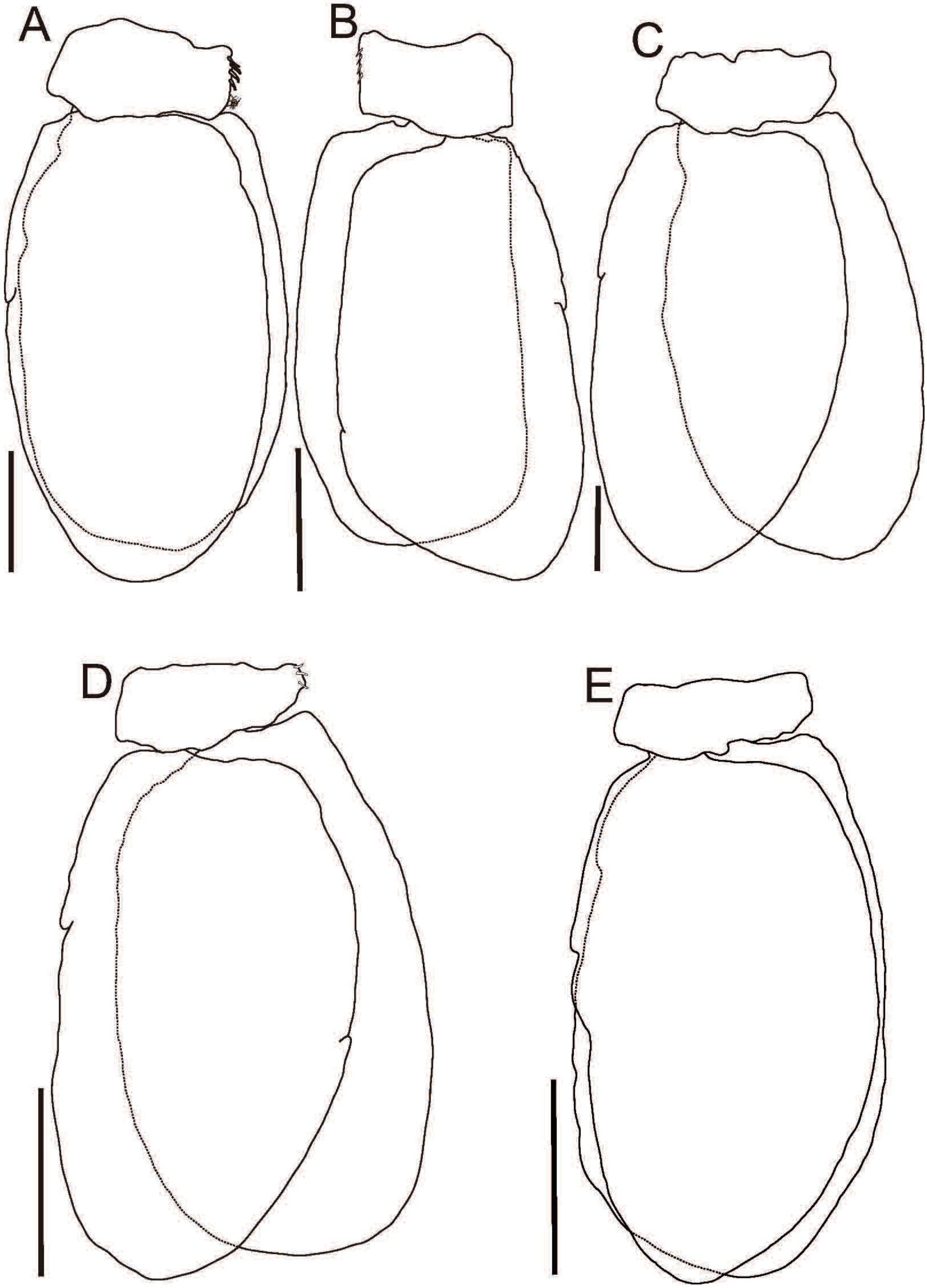

Fig. 15. Pleopods 1 of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: A–C, 1 mm; D, E, 3 mm.

Description of transitional (Figs. 3C, 7C, 9C, 11C, 13C, 15C, 17C, 19C): Body narrow, 3.7 times as long as greatest width, widest at pereonite 5, with smooth dorsal surfaces.

Cephalon 2.0 times wider than long, semi-oval, with well-developed rostrum, not immersed in pereonite 1. Eyes oval, with distinct margins, with long axis of each eye 0.8 times length of cephalon, and short axis 0.2 times maximum width of cephalon. Anterior border of pereonite 1 straight. Coxae almost invisible in dorsal view, of pereonites 2–4 roundly, of pereonite 5–7 concave; pereon longest at pereonite 5, shortest at pereonite 2; posterior margins of pereonites 1–5 smooth and slightly curved laterally, that of pereonite 6 and 7 slightly recessed. Pleonites 1–5 0.18 times as long as total length, 0.7 times as wide as greatest body width, with all pleonites visible in dorsal view. Pleotelson 1.4 times as long as wide, 1.2 times as long as pleonites 1–5, with no seta.

Antennula 8 articles, extending beyond mid-length of cephalon, article 3 enlargement. Antenna 10 articles, extending beyond anterior border of pereonite 1.

Pereopod 1 basis 1.8 times as long as greatest width; ischium 0.7 times as long as basis; merus 0.3 times as long as ischium, with 1 robust seta on superior distal angle; carpus 0.9 times as long as merus; propodus 3.3 times as long as carpus; dactylus 0.8 times as long as propodus. Pereopod 7 basis 3.3 times as long as greatest width; ischium 0.7 times as long as basis; merus 0.4 times as long as ischium, with 1 robust seta on superior distal angle, no robust seta on inferior margin; carpus 1.2 times as long as merus, with no robust seta on inferior margin; propodus 1.7 times as long as carpus, with 3 robust setae on inferior margin; dactylus 0.7 times as long as propodus.

Pleopods all lamellar with smooth surfaces. Pleopod 1 penduncle 0.4 times as wide as long, medial margin with no coupling hook and no plumose seta; endopod elliptical, 1.8 times as long as wide; exopod elliptical, 1.8 times as long as wide, as long as endopod. Pleopod 2 peduncle 0.4 times as wide as long, medial margin with no coupling hook and no plumose seta; endopod rectangular, 2 times as long as wide, without appendix masculina, without swimming seta; exopod elliptical, 1.8 times as long as endopod, as long as wide, without swimming seta.

Uropodal peduncle triangular, 1.9 times as long as wide, 0.7 times as long as exopod, with distal corner with 3 setae; endopod rami 0.9 times as long as that of exopod; extending beyond posterior margin of pleotelson; endopod oval, 2.8 times as long as greatest width, without swimming seta; exopod triangular, 4.2 times as long as greatest width, without swimming seta.

Description of ovigerous female (Figs. 3DE, 7DE, 9DE, 11DE, 13DE, 15DE, 17DE, 19DE): Body elliptical, 2.8–2.9 times as long as greatest width, widest at pereonite 6, with smooth dorsal surfaces.

Cephalon 1.3–1.4 times wider than long, semi-oval, with wide rostrum, not immersed in pereonite 1. Eyes oval, with distinct margins, with long axis of each eye 0.5 times length of cephalon, and short axis 0.2–0.3 times maximum width of cephalon. Anterior border of pereonite 1 medially protrudes forward. Coxae almost invisible in dorsal view, of pereonites 2–4 roundly, of pereonites 5–7 concave; pereon longest at pereonite 5 or pereonite 6, shortest at pereonite 2; posterior margins of pereonites 1–5 smooth and slightly curved laterally, that of pereonites 6 and 7 slightly recessed. Pleonites 1–5 0.2 times as long as total length, 0.6–0.7 times as wide as greatest body width, with all pleonites visible in dorsal view. Pleotelson 1.0–1.1 times as long as wide, 1.4 times as long as pleonites 1–5, with no seta.

Antennula 8 articles, extending beyond mid-length of cephalon, article 3 enlargement. Antenna 10 articles, extending beyond anterior border of pereonite 1.

Pereopod 1 basis 1.7–2.0 times as long as greatest width; ischium 0.5–0.6 times as long as basis; merus 0.3 times as long as ischium, with 1 robust seta on superior distal angle; carpus 0.9–1.2 times as long as merus; propodus 2.5–2.9 times as long as carpus; dactylus 1.0–1.1 times as long as propodus. Pereopod 7 basis 3.0–3.3 times as long as greatest width; ischium 0.8 times as long as basis; merus 0.4–0.5 times as long as ischium, without robust seta; carpus 1.0–1.1 times as long as merus, with 2–4 robust setae on inferior margin; propodus 1.7–1.8 times as long as carpus, with 3–4 robust setae on inferior margin; dactylus 0.8 times as long as propodus.

Pleopods all lamellar with smooth surfaces. Pleopod 1 penduncle 0.4–0.5 times as wide as long, medial margin with 0–3 coupling hooks and no plumose seta; endopod elliptical, 1.7 times as long as wide; exopod elliptical, 1.7–1.8 times as long as wide, as long as endopod. Pleopod 2 peduncle 0.4–0.5 times as wide as long, medial margin with no coupling hook and no plumose seta; endopod elliptical, 1.8 times as long as wide, without appendix masculina, without swimming seta; exopod elliptical, 1.7–1.8 times as long as endopod, as long as wide, without swimming seta.

Uropodal peduncle triangular, 1.7–2.0 times as long as wide, 0.6 times as long as exopod, with distal corner with 0–1 seta; endopod rami 1.0–1.1 times as long as that of exopod; extending beyond posterior margin of pleotelson; endopod oval, 3.0–3.2 times as long as greatest width, without swimming seta; exopod oval, 3.4–3.6 times as long as greatest width, without swimming seta.

Manca: Unknown.

Coloration: The color changed from pearl yellow to dark brown as the individual grew (in preserved ethanol).

Hosts: *Anilocra prionuri* had the highest record from *P. scalprum* (Hata et al. 2017, Nagasawa 2018). *Anilocra prionuri* was also recorded from the large-scale blackfish *Girella punctata* Gray, 1835, and threadsail filefish *Stephanolepis cirrhifer* (Temminck and Schlegel, 1850) (Williams and Bunkley-Williams 1986).

Distribution: *Anilocra prionuri* has been reported on the Pacific Ocean and East China Sea coasts of southern Japan (Williams and Bunkley-Williams 1986, Hata et al. 2017, Nagasawa 2018). See Nagasawa (2018).

DNA sequences accession numbers: SMBL-V0772 (COI: LC860812), SMBL-V0778 (*COI*: LC860813, 16S rRNA: LC860815), SMBL-V0780 (16S rRNA: LC860816), SMBL-V0781 (*COI*: LC860811, 16S rRNA: LC860814).

Remarks: Females of *A. prionuri* are distinguished from the other two species recorded in Japan by having swelling-free pereopod 1–4 dactyls and a uropod slightly extending the posterior margin of the pleotelson. Of the three *Anilocra* species found in Japan, aegathoid stages have been described only for *A. clupei* (Table 1). In the aegathoid stage of *A. clupei* and the smaller aegathoid stage of *A. prionuri*, antennular characteristics were underdeveloped. The swelling of dactyls in *A. clupei* is also underdeveloped in the aegathoid stage; therefore, these characteristics cannot be used for species identification of the aegathoid stages. The aegathoid stage of *A. prionuri* is distinguished from that of *A. clupei* by 1) 3–5 and 0–5 plumose setae of pleopod 1 and 2 (5 and 8 plumose setae in *A. clupei*), 2) uropodal exopod longer than endopod (same length in *A. clupei*), and 3) triangular uropodal exopod (oval in *A. clupei*).

With growth, the morphology of *A. prionuri* changed: 1) body shape becomes rounder, 2) eye length becomes shorter, 3) shortest pereonite changes from 7 to 2, 4) antennula article 3 enlarged, 5) length of dactylus relative to propodus in pereopod 1 becomes longer, 6) pleopod penduncle becomes shorter, 7) decrease robust setae of pereopods, coupling hooks and plumose setae of pleopods, swimming setae of pleotelson, pleopod, and uropod, 8) appendix masculina on the pleopod 2 endopod shortens and disappears, 9) rami of pleopods and uropods become rounded, and 10) endopods of uropods become elongated.

The aegathoid stage was distinguished from the male by 1) pereon shortest at pereonite 7 (pereonite 2 in male), 2) longer pleotelson, 3) antennula article 3 enlargement or no enlargement (enlargement in male), 4) Pleopod 1 endopod rectangular (elliptical in male), 5) pleopod 2 peduncle with 4 coupling hooks (no coupling hook in male), 6) posterior margins of pleotelson, pleopods, and uropods having swimming setae. The male is distinguished from the traditional by 1) pleopod 1 penduncle with coupling hooks (no coupling hook in traditional), 2) pleopod 2 endopod with appendix masculina (without it in traditional), 3) uropodal peduncle distal corner with 9–11 setae (3 setae in traditional). The traditional is distinguished from the female by 1) body narrow (elliptical in the female), 2) widest at pereonite 5 (pereonite 6 in the female), 3) cephalon having narrower rostrum (wide rostrum in the female), 4) bigger eyes, 5) anterior border of pereonite 1 straight (medially protrudes forward in the female), 6) pereopod 7 merus with a robust seta on superior distal angle (without it in the female), 7) pleopod 2 endopod rectangular (elliptical in the female), 8) uropodal peduncle distal corner 3 setae (0–1 seta in the female), 9) uropodal exopod triangular (oval in the female).

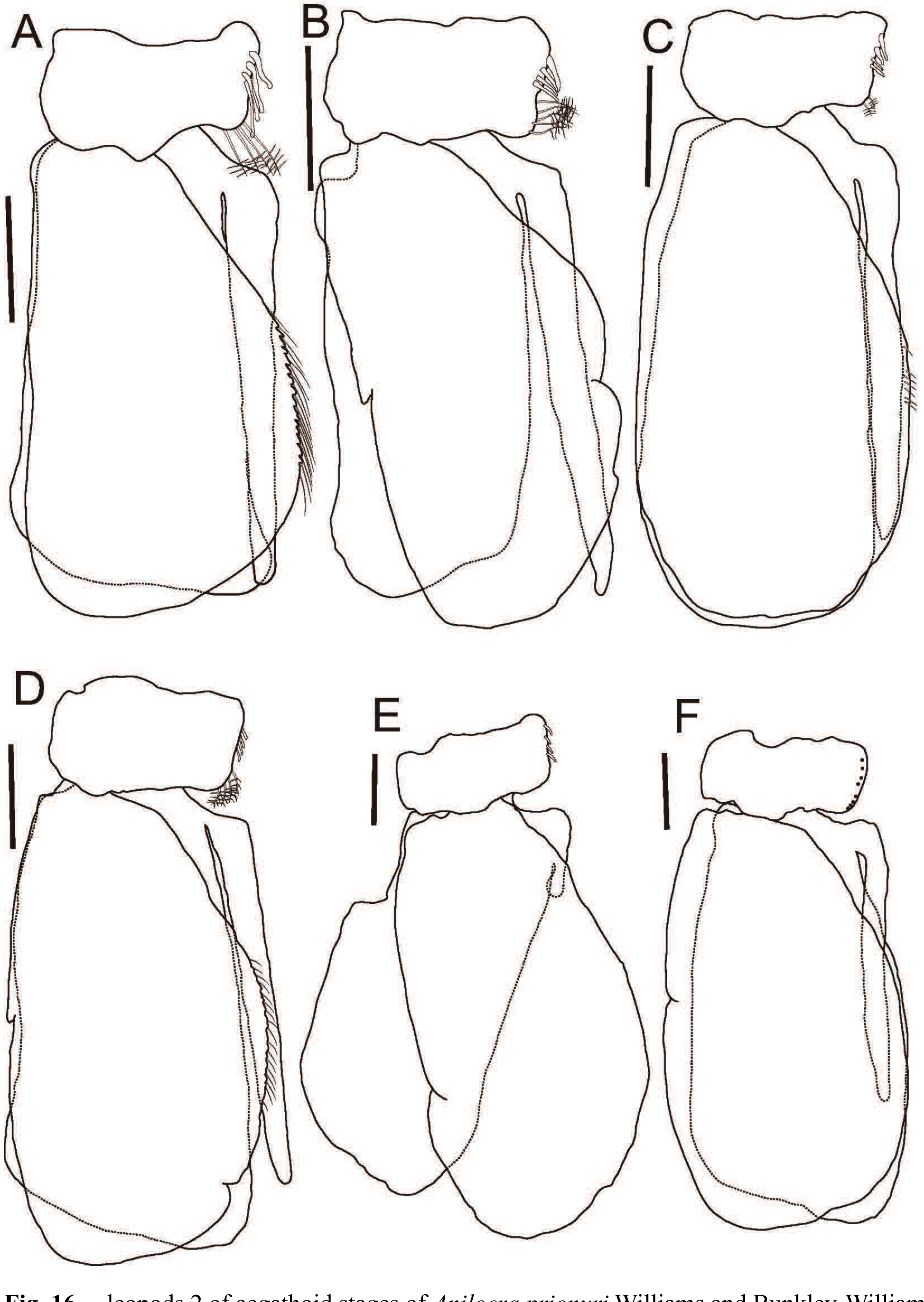

Fig. 16. leopods 2 of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.5 mm.

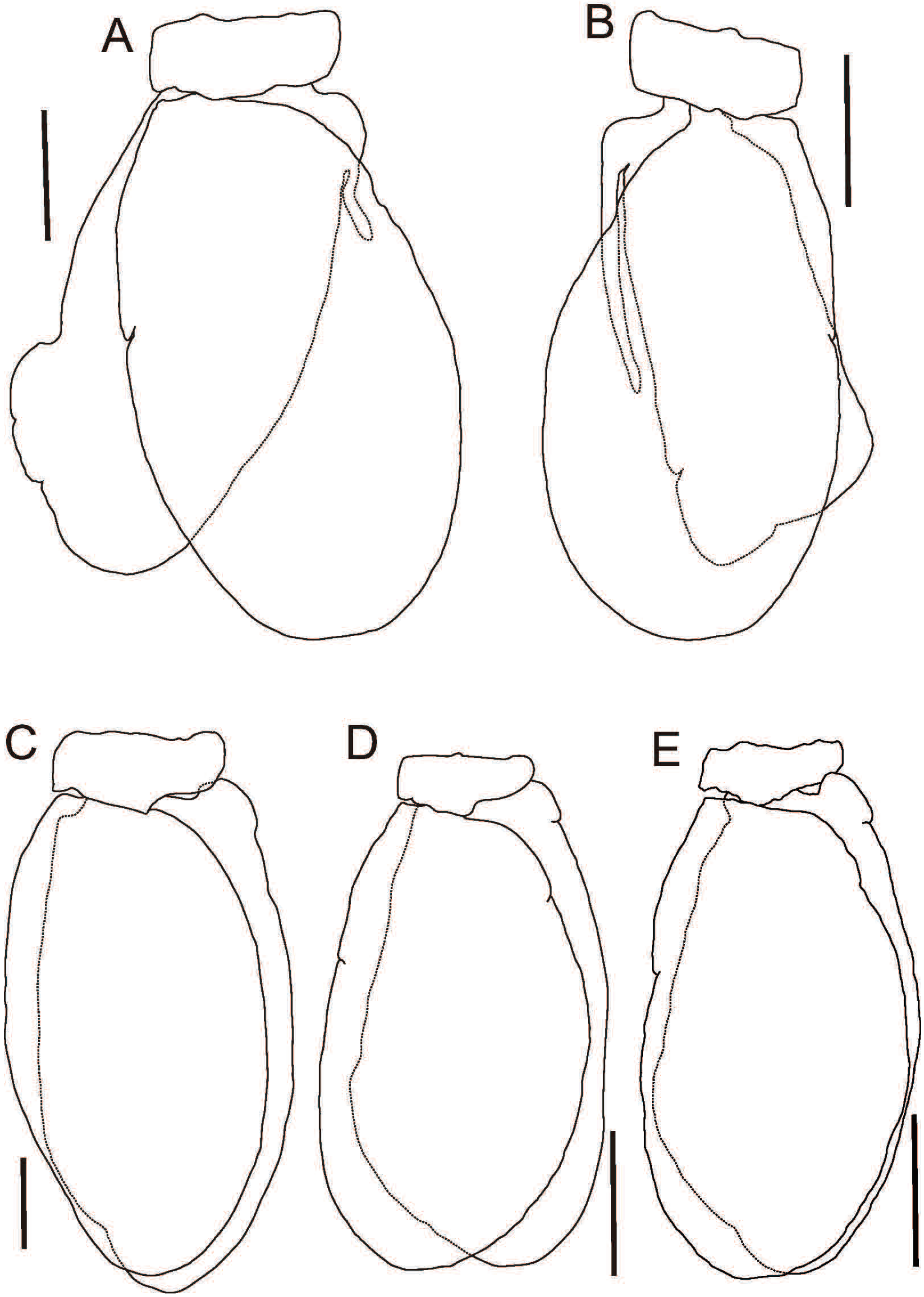

Fig. 17. leopods 2 of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: A–C, 1 mm; D, E, 3 mm.

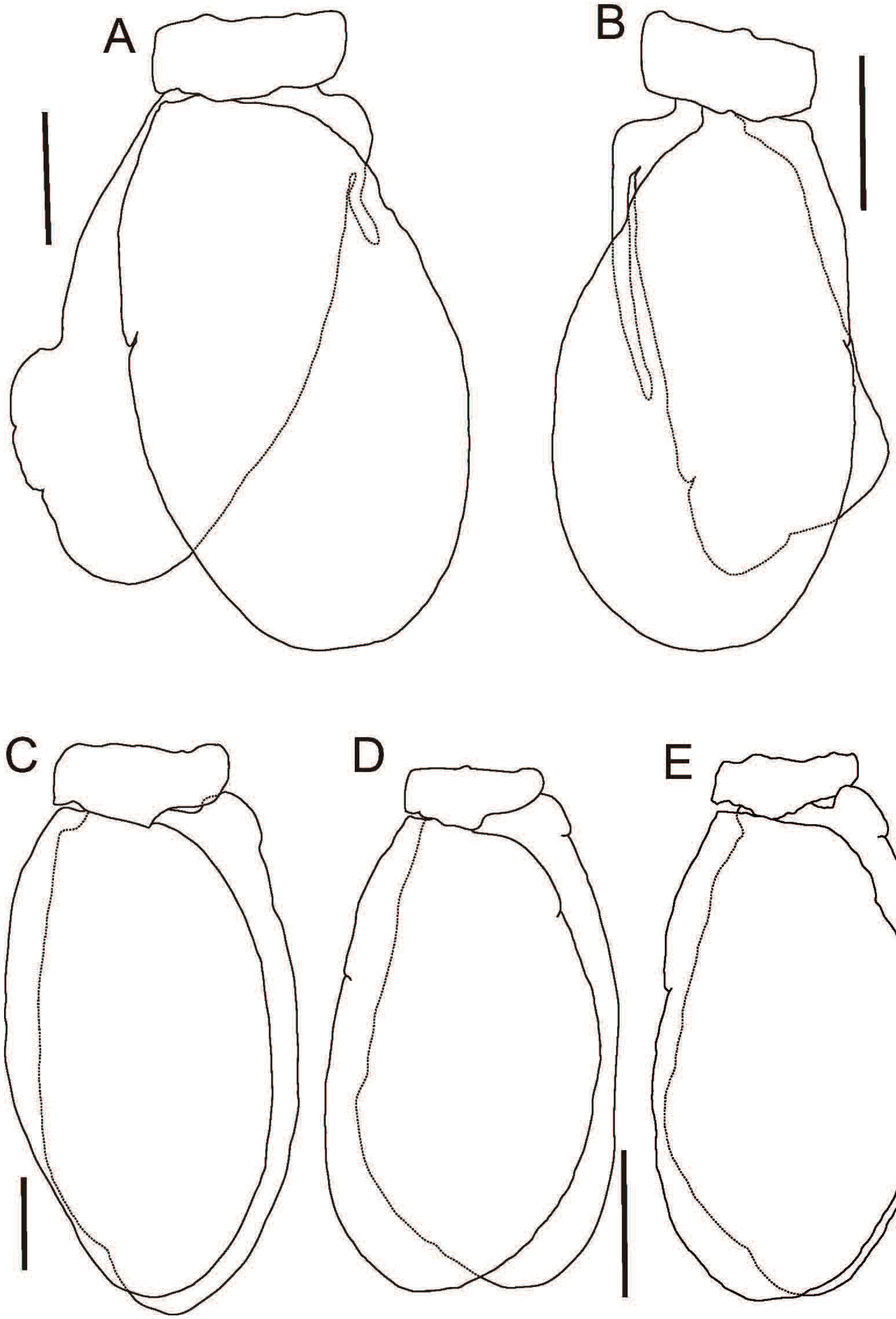

Fig. 18. Uropods of aegathoid stages of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A–F, SMBL-V0772–V0777 (BL14.2, 14.4, 14.8, 15.5, 17.6, and 18.0 mm). Scale bar: 0.5 mm.

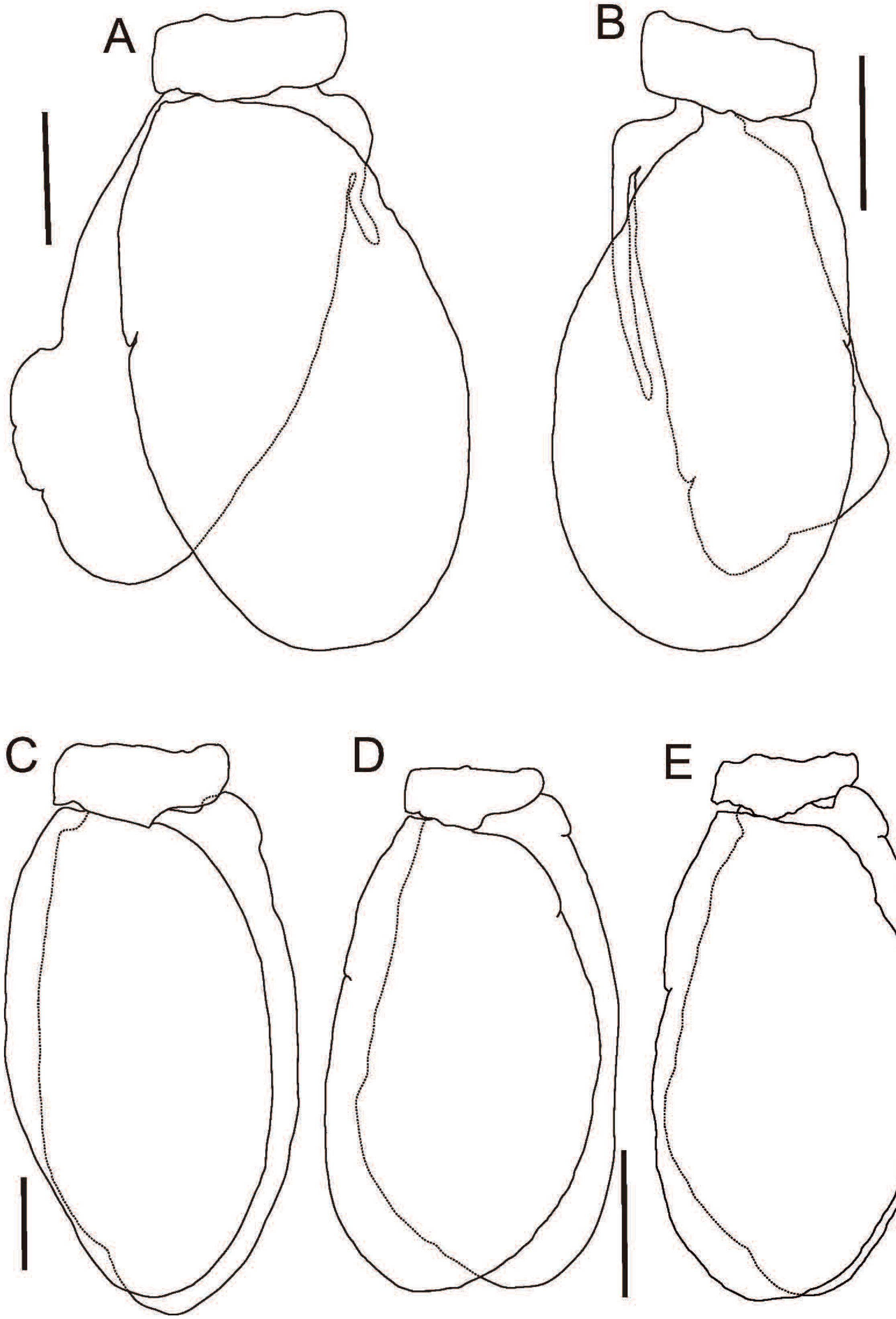

Fig. 19. Uropods of *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. A, B, males SMBL-V0778, V0779 (BL20.0 and 20.1 mm); C, SMBL-V0780*,* transitional (BL24.7 mm); D, E, SMBL-V0781, V0782, ovigerous females (BL34.0 and 34.2 mm). Scale bar: A–C, 1 mm; D, E, 3 mm.

DISCUSSION

Williams and Bunkley-Williams (1986) described aegathoid *Anilocra* spp. parasitizing the Japanese anchovy, *Engraulis japonicus* Temminck and Schlegel, 1846, and silver-stripe round herring, *Spratelloides gracilis* (Temminck and Schlegel, 1846) respectively, as well as *A. clupei* and *A. prionuri*. They considered these two types of aegathoid stages to be distinct species and speculated that they might be either *A. clupei* or *A. prionuri*. The number of plumose setae on the medial margin of the pleopod peduncle in these individuals remains unclear. Nevertheless, the morphology of the uropods is similar to that of *A. clupei* because the exopod is oval, and the endopod and exopod are almost the same length in *Anilocra* sp. (infecting *E. japonicus*). In *Anilocra* sp. (infecting *S. gracilis*), the uropodal exopod is triangular and longer than the endopod, making it similar to *A. prionuri*. Saito et al. (2014) collected six free-swimming aegathoid stages of *Anilocra* sp. from Osaka Bay on the Pacific coast of central Honshu, Japan. These individuals have 6 and 8 plumose setae on the medial margins of pleopods 1 and 2 peduncle, uropodal exopod as long as endopod, and oval uropodal exopod, respectively; therefore, we identified them as *A. clupei.*

In *A. clupei*, the aegathoid stage shows lower host specificity than females (Fujita 2022). Adlard and Lester (1995) and Williams and Bunkley-Williams (2019) stated that, in *Anilocra*, the aegathoid stages function as males. The aegathoid stages (males) migrate between multiple hosts (intermediate hosts) and mate with females on intermediate hosts. However, no direct data have been presented to support this hypothesis. To test this hypothesis, it is necessary to confirm the maturity of the gonads at each life stage, and depending on its results, the classification of life stages also established in the present study may be revised in the future. The hypothesis that aegathoid stages migrate between hosts also needs to be tested. Among the cymothoids of other genera, juveniles of *Mothocya parvostis* Bruce, 1986 and *Ceratothoa verrucosa* (Schioedte and

Meinert, 1883) are presumed to use fish other than the final host as optional intermediate hosts (Fujita et al. 2020, 2023a, b), and differences in host use among these species should also be considered.

Morphological information on the life stages of non-females of Cymothoidae is scarce; however, taxonomic keys based on the morphology of four species of Cymothoid mancae in the Northern Gulf of Mexico have been provided (Bakenhaster 2004). In Japanese cymothoids, the aegathoid stages of *Nerocila japonica* (Schioedte and Meinert 1881) and *Nerocila phaiopleura* (Bleeker 1857) can also be distinguished by morphology (Saito and Ogawa 2019). To increase the number of cymothoids that can be identified by morphology, it is important to acquire the morphological data of each species' life stages.

CONCLUSIONS

In this study, we describe the morphology of the *A. prionuri* aegathoid, male, and transitional stages. This made it possible to distinguish between the aegathoid stages of *A. clupei* and *A. prionuri* based on their morphology. In addition, COI and 16S rRNA sequences linked to the morphological information were sequenced for future molecular species identification. Clarifying the morphology of the mancae and the maturity of the gonads at each life stage is necessary to further understand the life cycle of *A. prionuri*.

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Authors' contributions: F: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - Original Draft. TO: Resources, Writing - Review & Editing.

Competing interests: We have no competing interest to declare.

Availability of data and materials: The specimens were deposited in the Seto Marine Biological Laboratory (SMBL), Field Science Education and Research Center, Kyoto University (SMBL-V0772–V0783). Taxonomic data was contained in supplementally file S1. Molecular data were deposited in GenBank (accession numbers: LC860811–LC860816).

Consent for publication: Not applicable.

Ethics approval consent to participate: The authors confirm that the ethical policies of the journal were followed.

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Supplementary materials

SM1. DELTA format file of describing *Anilocra prionuri* Williams and Bunkley-Williams, 1986 collected from a scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835. (downlaod)