Freshwater copepods from the Gnangara Mound Region of Western Australia

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ABSTRACT

The Gnangara Mound is a 2,200 km^2 unconfined aquifer located in the Swan Coastal Plain of Western Australia. This aquifer is the most important groundwater resource for the Perth Region and supports a number of groundwater-dependent ecosystems such as the springs of the Ellen Brook Valley and root mat communities of the Yanchep Caves. Although freshwater copepods have been documented previously from those caves and springs, their specific identity were hitherto unknown. The current work identifies formally copepod samples collected from 23 sites (12 cave, 5 spring, 3 bore and 3 surface water localities) within the Gnangara Mound Region. Fifteen species were documented in this study: the cyclopoids *Australoeucyclops* sp., *Eucyclops edytae* **n. sp.**, *Macrocyclops albidus* (Jurine, 1820), *Mesocyclops brooksi* Pesce, De Laurentiis & Humphreys, 1996, *Metacyclops arnaudi* (Sars, 1908), *Mixocyclops mortoni* **n. sp.**, *Paracyclops chiltoni* (Thomson, 1882), *Paracyclops intermedius* **n. sp.** and *Tropocyclops confinis* (Kiefer, 1930), and the harpacticoids *Attheyella* (*Chappuisiella*) *hirsuta* Chappuis, 1951, *Australocamptus hamondi* Karanovic, 2004, *Elaphoidella bidens* (Schmeil, 1894), *Nitocra lacustris pacifica* Yeatman, 1983, *Paranitocrella bastiani* **n. gen. et n. sp.** and *Parastenocaris eberhardi* Karanovic, 2005. *Tropocyclops confinis* is recorded from Australia for the first time and *A.* (*Ch.*) *hirsuta* and *E. bidens* are newly recorded for Western Australia. The only species endemic to the Gnangara Mound Region are *E. edytae* **n. sp.** (occurs primarily in springs and rarely in the Yanchep Caves), *P. bastiani* **n. gen. et n. sp.** (confined to the Yanchep Caves) and *P. intermedius* **n. sp.** (found in springs). *Paracyclops chiltoni* was the most common species, whilst *T. confinis* and *N. l. pacifica* were rarely encountered. *Metacyclops arnaudi* was the only taxon absent from groundwaters. The copepod fauna recorded in the caves and springs of the Gnangara Mound Region are comparable, with respect to species richness, endemicity and the varying degrees of dependency on the subterranean environment, to those reported from similar habitats in South Australia and Western Australia. Restoring the root mats and maintaining permanent water flow within the Yanchep Caves as well as minimising urban development near the Ellen Brook springs are essential to protect the copepod species, particularly the endemic *P. bastiani* **n. gen. et n. sp.** and *E. edytae* **n. sp.**, inhabiting these unique hypogean environments.

Keywords: Copepoda, Cyclopoida, Harpacticoida, Subterranean, Australia

INTRODUCTION

The Gnangara Mound is a shallow, unconfined aquifer underlying the Quaternary dune deposits of the Swan Coastal Plain in Western Australia (Davidson 1995). This aquifer reaches a maximum elevation of 70 m above sea level and covers an area of about 2,200 km^2, bounded by Gingin Brook to the north, the Gingin Scarp to the east, the Swan River to the south and the Indian Ocean to the west. The Gnangara Mound is the primary groundwater resource for public, agricultural and commercial needs of the Perth Region and also supports a number of groundwater-dependent ecosystems (Western Australian Planning Commission 1999a, b).

The groundwater-dependent cave and spring communities on the western and eastern side, respectively, of the Gnangara Mound Region are of particular scientific interest. The caves occur in Yanchep National Park, which is located about 5 km from the coastline and lies in an area consisting of an aeolian calcarenite layer (*ca.* 3–20 m thick) overlying quartz sands of mid-Pleistocene age (Kendrick et al. 1991). Further, most caves are relatively small, having a vertical range of less than 20 m (Jasinska & Knott 2000). At the calcarenite-sand boundary, groundwater from the Gnangara Mound seeps through the overlying sediment forming shallow, and often permanent, epiphreatic streams which flow through the caves. Some of the shallower caves also contain an extensive root mat system produced by the native tuart tree, *Eucalyptus gomphocephala* DC, growing above the caves. These root mats, which develop in association with mycorrhizal fungi along the periphery of the epiphreatic streams, provide an abundant and constant primary food source for a diverse assemblage of aquatic invertebrates (Jasinska et al. 1996; Jasinska & Knott 2000).

The springs in the Gnangara Mound Region occur at elevations between 40–60 m above sea level along the Ellen Brook Valley and are known to support a diverse flora and invertebrate fauna (Ahmat 1993; Jasinska & Knott 1994). These springs, which are composed of helocrene, rheocrene, limnocrene and tumulus types, form at the boundary between the fluvial Guildord clays and the overlying aeolian Bassendean Sands (Knott & Jasinska 1998). The Gnangara Mound springs are, as with other springs scattered throughout the Great Artesian Basin of central Australia, ecologically important formations. They collectively provide a stable habitat and refuge for both endemic and disjunct populations of plants and animals living in an essentially xeric environment. For instance, the bog clubmoss *Lycopodium serpentium* Kunze and the pretty sundew *Drosera pulchella* Lehm. occur typically in permanent swamps of the southwest corner of Western Australia but persist further north in the permanently moist conditions provided by the Gnangara Mound springs (Knott & Jasinska 1998).

Crustaceans are, as is typical for the stygofauna of Australia (Humphreys 2006), well represented in the caves and springs of the Gnangara Mound Region. Among the crustaceans occurring in five caves and four springs, respectively, 30–55% and 66–78% belong to the Copepoda (Jasinska & Knott 1994; Jasinka 1997). The specific identity of these copepods, along with many of the other invertebrate taxa reported from the caves and springs, are nonetheless unknown. This is rather unfortunate as these ecologically significant cave and spring habitats are currently at risk of destruction mainly by human activities such as groundwater abstraction and suburban development. Clearly, knowledge of copepod biodiversity in these caves and springs is valuable not only from a zoological standpoint, but more importantly with regards to the threatened Yanchep Caves and Ellen Brook Valley springs, for identifying species of high conservation value. The current work, which identifies formally the species of copepod crustaceans from the Gnangara Mound Region, is the first step in resolving this issue.

MATERIALS AND METHODS

Copepods were obtained intermittently from 1990–2008 from a total of 23 sites within the Gnangara Mound Region of Western Australia (Fig. 1; Table 1). Twenty sites are categorised as subterranean: five from springs situated along the eastern flank of the Gnangara Mound, one from a cave (Lot 51 Cave) located about 0.5 km beyond the Yanchep National Park boundary, and the remaining 14, comprised of 11 cave and and three groundwater monitoring bore sites, were confined within Yanchep National Park. An additional three surface water sites within Yanchep National Park were included for comparative purposes. Supplemental copepod material was also kindly provided by the Department of Environment and Conservation (DEC).

Samples were obtained from these sites as follows: a) in each cave by sweeping a 70 µm mesh net across submerged root mats; b) at each spring by sweeping a 500 µm mesh sieve along the sediment surface close to the point of the spring discharge, but if not possible due to dense cover of vegetation, along narrow water channels radiating away from the discharge point; c) from each bore by retreiving a bailer lowered to the sediment bottom; and d) from surface water by sweeping a 500 µm mesh sieve through rooted aquatic vegetation. All samples were each placed in a plastic bag, covered with water from the site, labelled and sealed tightly, and transported alive to the laboratory under cool, dark conditions. In the laboratory, copepods were sorted from debris under a dissecting microscope and preserved in 70–100% ethanol.

Preserved specimens were soaked in lactic acid prior to examination using an Olympus BX51 compound microscope equipped with differential interference contrast. Selected specimens were measured using an ocular micrometer, dissected, and examined using the wooden slide procedure of Humes & Gooding (1964). Selected whole specimens and dissected appendages were also drawn with the aid of a camera lucida. Morphological terminology follows Huys & Boxshall (1991) and Karaytug (1999). The classification scheme provided in Dussart & Defaye (2006) and Wells (2007) for the Cyclopoida and Harpacticoida, respectively, were adopted in this study. Keys to the Australian species of *Eucyclops* and *Metacyclops* were modified, respectively, from Morton (1990) and Karanovic (2004b).

RESULTS

Order Cyclopoida Rafinesque, 1815

Family Cyclopidae Rafinesque, 1815

Subfamily Eucyclopinae Kiefer, 1927

Genus *Australoeucyclops* Karanovic, 2006

Australoeucyclops sp.

Material examined. Cabaret Cave (YN30), Yanchep National Park, Western Australia (31°32'31"S, 115°41'24"E): 11 ♀♀ (2 dissected and mounted on one slide each), 3 ♂♂, and 1 copepodite, 1 June, 1990; 7 ♀♀, 5 ♂♂, and 4 copepodites, 27 January, 1991; 6 ♀♀, 2 ♂♂, and 2 copepodites, 5 February, 1992; 1 ♂, 29 July, 1993; 5 ♀♀, 5 ♂♂, and 5 copepodites, collection date unknown; Carpark Cave (YN18), Yanchep National Park, Western Australia (31°33'08"S, 115°41'08"E): 2 ♀♀ and 2 copepodites, collection date unknown; Lot 51 Cave (YN555), Yanchep, Western Australia (31°34'31"S, 115°42'10"E): 1 ♀, 18 September, 2003; 7 ♀♀ and 2 ♂♂, 22 September, 2003; 4 ♀♀ and 1 ♂, 6 October, 2004; 100 ♀♀ and 14 ♂♂, 8 November, 2005; 9 ♀♀, 8 ♂♂, and 2 copepodites, 10 October, 2007; Fridge Grotto Cave (YN81), Yanchep National Park, Western Australia (31°31'21"S, 115°40'17"E): 3 ♀♀, 17 July, 1992; Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E): 1 ♀, 1 ♂, and 6 copepodites, 17 March, 1993; 7 ♀♀ and 4 copepodites, 28

August, 1994; Yellagonga Cave (YN438), Yanchep National Park, Western Australia (31°33'04"S, 115°40'58"E): 123 ♀♀ (2 dissected and mounted on one slide each), 83 ♂♂, and 205 copepodites, 4 October, 2003; Mire Bowl Cave (YN61), Yanchep National Park, Western Australia (31°31'32"S, 115°40'32"E): 1 ♂, and 1 copepodite, 17 July, 1992; 1 ♀, 18 September, 2002; 1 ♀ and 1 ♂, 22 September, 2003; 4 ♀♀ (1 dissected and mounted on slide), 8 November, 2005; Orpheus Cave (YN256), Yanchep National Park, Western Australia (31°31'00"S, 115°40'10"E): 1 ♂, 17 July, 1992; Spillway Cave (YN565), Yanchep National Park, Western Australia (31°32'41"S, 115°40'37"E): 2 ♀♀, 8 November, 2005; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 1 ♀, 2 June, 1996; 3 ♀♀ and 2 copepodites, 27 November, 1996; Water Cave (YN11), Yanchep National Park, Western Australia (31°33'02"S, 115°40'59"E): 5 ♀♀, 1 ♂, and 8 copepodites, 19 September, 2003; Mrs. King's tumulus spring, Bullsbrook, Western Australia (31°39'04"S, 115°57'11"E): 1 ♀ and 1 copepodite, 8 May, 1996.

Remarks. The genus *Australoeucyclops* was established by Karanovic (2006) to accommodate a new species, *A. karaytugi* Karanovic, 2006, collected from a spring in the Pilbara Region of Western Australia. He also formally transferred *Paracyclops linderi* (Lindberg, 1948), *P. eucyclopoides* Kiefer, 1929, *P. timmsi* Kiefer, 1969 and *P. waiariki* Lewis, 1974 into *Australoeucyclops*, and stated that an as yet undescribed member of this genus existed in the Margaret River Region of Western Australia. Our specimens resemble members of this genus in having a slender habitus, 12-segmented female antennule, the inner corner of the basis of legs 2 to 4 produced into a large acute process, absence of an inner seta on the proximal exopodal segment of leg 4 and 1-segmented leg 5 armed with 3 apical elements on the free exopodal segment. Indeed, the specimens from Cabaret Cave were identified previously as *Eucyclops linderi* by Jasinska & Knott (2000). Recent comparisons between those cave specimens and Lindberg's (1948) original description of *E. linderi* (=

Australoeucyclops linderi) indicated that the former is not conspecific with the latter. Further comparisons between our specimens and a set of detailed illustrations kindly provided by Dr. Tomislav Karanovic (University of Tasmania) of the undescribed *Australoeucyclops* species from a dam and springs in the Margaret River area (see Eberhard 2004) revealed that these disjunct copepod populations contain individuals of the same species. We have also examined specimens collected from Beekeepers Cave, located west of Eneabba, Western Australia (*ca*. 200 km north of Yanchep National Park), that are conspecific with those from the southern populations. As Dr. Karanovic (*in litt.*) is currently describing this new *Australoeucyclops* taxon, we have in this study, for reasons related to ICZN rules, deliberately refrained from using his proposed binomen and excluded descriptions and illustrations of this as yet undescribed taxon.

Genus *Eucyclops* Claus, 1893

Eucyclops edytae n. sp.

(Figs)

Type material. Holotype ♀, allotype ♂ and 32 paratypes (3 ♀♀, 3 ♂♂, and 22 copepodites in alcohol; 2 ♀♀ and 2 ♂♂ dissected and mounted on one slide each), Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E), 20 December, 1994.

Other material examined. Cabaret Cave (YN30), Yanchep National Park, Western Australia (31°32'31"S, 115°41'24"E): 1 ♀, 9 October, 2007; Bevan Peters' spring, Ellenbrook, Western Australia (31°35'14"S, 115°57'47"E): 1 ♀, 2 August, 1992; 4 ♀♀, 4 ♂♂, and 10 copepodites, 21 December, 1992; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 2 ♀♀, 1995; 1 ♀, 2 ♂♂, and 12 copepodites, 7 November, 2005; 5 ♀♀ (1 dissected and mounted on slide) and 1 ♂, 9 October, 2006; 31 ♀♀ and 17 ♂♂, 9 October, 2007; Mrs. King's tumulus spring, Bullsbrook, Western Australia (31°39'04"S, 115°57'11"E): 2 ♀♀, 8 May, 1996; 1 ♀ dissected and mounted on slide (DEC collection), 5

December, 2002; Sue's spring (South), Bullsbrook, Western Australia (31°38'42"S, 115°58'17"E): 1 damaged ♀, 1 February, 2008.

Description of female. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami), based on 10 specimens, 610–760 µm, mean 690.5 µm; body width 220–270 µm, mean 243 µm. Prosome (Fig. 2A) composed of cephalothorax and 3 free pedigerous somites. Urosome (Fig. 2A) comprised of fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Fourth and fifth pedigerous somites each furnished with setules along posterolateral corners. Genital double-somite subequal in length, mean 88.5 × 88 µm; seminal receptacle not observed. Posterior margin of urosomites 2–4 slightly uneven dorsally and serrate ventrally. Anal somite (Figs 2B–C) with spinular row dorsally and ventrally; anal cleft with longitudinal rows of setules.

Caudal ramus (Figs 2C–D) longer (35–45 µm; mean 42.5 µm) than wide (20–25 µm; mean 23 µm); bears 6 setae (seta I absent), spinular row at base of setae II and III, and 4 groups of spinules on ventral surface. Setae II and VII inserted at posterior ⅔ of ramus. Seta VII setulate; seta II with few spinules apically; remaining setae spinulate. Seta VI twice as long as seta III. Setae IV and V with proximal breaking plane.

Antennule (Fig. 3A) 12-segmented, with armature and ancestral segmentation pattern in brackets as follows: 8 (I–V), 4 (VI–VII), 2 (VIII), 6 (IX–XI), 4 (XII–XIII), 1+spine (XIV), 2 (XV–XVI), 3 (XVII–XX), 2+ae (XXI–XXIII), 2 (XXIV), 2+ae (XXV), and 7+ae (XXVI–XXVIII). First segment with proximoventral spinular rows. Finely serrate hyaline membrane present on segments 10 and 12.

Antenna (Figs 3B–C) 4-segmented, comprising coxobasis and 3-segmented endopod. Coxobasis with long distolateral exopodal seta, 2 distomedial barbed setae, and complex ornamentation on frontal and caudal surfaces as figured. Proximal endopodal segment with inner naked seta and lateral spinular patch. Middle endopodal segment bears 9 inner setae and spinules along outer margin. Terminal endopodal segment with usual proximal and distal spinules and 7 distal setae.

Labrum (Fig. 3D) with 2 teeth on each lateral corner, 15 teeth along medial margin, and long setules on anterior surface.

Mandible (Fig. 3E) composed of coxa and reduced palp. Distal end of coxal gnathobase with outer quadridentate tooth, 2 central bicuspidate teeth, 2 inner unicuspidate teeth, spinulate seta, and row of strong spinules. Palp with row of spinules near base and 3 distal setae (2 long and plumose, 1 short and naked).

Maxillule (Fig. 4A) comprising praecoxa and 2-segmented palp. Praecoxal arthrite bears 7 elements (of which 4 are unornamented) along medial margin and spinulate seta and 3 large unicuspidate teeth distally. Coxobasis with proximal seta and 3 terminal setae. Endopod 1-segmented, armed with 3 setae.

Maxilla (Fig. 4B) 5-segmented, composed of praecoxa, coxa, basis and 2-segmented endopod. Praecoxal endite armed with 2 spinulate setae. Proximal and distal coxal endites with 1 and 2 spinulate setae, respectively; few spinules present proximally on outer margin of coxa. Basis drawn out into large claw furnished with large teeth along middle part of inner margin; accessory armature composed of spinulate spine and seta. Proximal endopodal segment with 2 setae; distal endopodal segment with 3 setae.

Maxilliped (Fig. 4C) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa with 3 medial spinulate setae and row of stout spinules. Basis with 2 large patches of spinules along outer margin, several long spinules on antero-medial surface, and 2 medial spinulate setae. Proximal endopodal segment with long spinules on anterior surface and long, inner spinulate seta. Terminal endopodal segment with largest element fused to segment, claw-like, and furnished with long spinules; middle and lateral setae unilaterally spinulate.

Legs 1–4 biramous (Figs 4D, 5A–D), with 3-segmented rami. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III,5	0-1; 0-2; 1,I,4
Leg 2	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I+1,3
Leg 3	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I+1,3
Leg 4	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 1,II,2

Leg 1 (Fig. 4D) intercoxal sclerite with spinular row on anterior surface; posterior surface with 2 spinular rows. Coxa with fine spinules along distal margin of anterior surface and well developed spinules laterally and medially on posterior surface. Basis with small, mediodistal triangular process, setules along inner margin, and spinules at insertion point of rami and inner spine. Outer seta setulate; inner spinulate spine reaches to proximal ½ of terminal endopodal segment. Anterior surface of endopodal segments and posterior surface of first two exopodal segments and middle endopodal segment with distal spinular row. Inner margin of exopodal segments and outer margin of endopodal segments with setules; outer margin of middle exopodal segment also with setules. Outermost seta on terminal exopodal segment heterogeneously ornamented, with lateral row of denticles and inner row of setules; all other setae on rami plumose. All spines on rami denticulate; small spinules present at insertion point of each spine.

Leg 2 (Fig. 5A) intercoxal sclerite and coxa similar to those of leg 1, except coxa with additional row of setules along lateral margin and more prominent spinular row along distal margin. Basis with mediodistal triangular process, inner corner produced into large acute process, and spinules at insertion point of endopod and along outer and inner margins. Exopod ornamented as in leg 1, except with additional distal spinular row on anterior surface of proximal segment and 1–2 minute denticles on proximolateral margin of middle and terminal segments. Proximal outer spine on terminal exopodal segment ⅔ length of other outer spines. All setae on rami plumose. Endopod ornamented as in leg 1, except with more developed spinules on anterior surface and additional spinular row on posterior surface of first segment and few proximomedial setules on distal segment.

Leg 3 (Fig. 5B) similar to leg 2, except for additional spinular row along posterior margin of intercoxal sclerite, relatively shorter outer seta on basis, absence of mediodistal triangular process on basis, naked outer margin of middle exopodal segment, and naked inner margin on distal endopodal segment.

Leg 4 (Figs 5C–D) intercoxal sclerite with fewer spinules than those of preceding legs. Coxa with highly complex ornamentation on posterior surface as figured. Basis structured as in leg 2. Rami ornamented as in leg 3. Inner apical spine two times longer than outer apical spine on terminal endopodal segment.

Leg 5 (Figs 2B, 6A) 1-segmented, armed with 3 elements; outer and middle setae setulate; base of middle seta strongly produced. Inner spine longest of 3 elements, curves slightly inward at distal half, reaches to proximal ⅔ of genital double-somite, and furnished with spinules at base.

Leg 6 (Fig. 6B) rudimentary, represented by long, weakly spinulate seta and 2 short naked spines on genital operculum.

Male. Mean body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami), based on 10 specimens, 569 µm (480–620 µm); mean body width 181 µm (170–190 µm) at posterior margin of cephalothorax. Prosome (Fig. 6C) composed of cephalothorax and 3 free pedigerous somites; posterior margin of prosomites smooth. Urosome (Fig. 6C) comprised of fifth pedigerous somite, genital somite and 4 free abdominal somites. Fourth and fifth pedigerous somites without setules on posterolateral corners. Posterior margin of urosomites 2–5 uneven dorsally and serrate ventrally. Genital somite (Figs 6C, F) wider than long (mean 50 × 62 µm). Caudal ramus (Fig. 6C) longer than wide (mean 34 × 19 µm), armed and ornamented as in female.

Antennule (Fig. 6D) 15-segmented, digeniculate, with armature and ancestral segmentation pattern as follows: 8+ae (I–V), 4 (VI–VII), 2 (VIII), 2+ae (IX), 2 (X), 2 (XI), 2 (XII), 2 (XIII), 2+ae (XIV), 2 (XV), 2 (XVI), 2 (XVII), 6 (XVIII-XX), 4 (XXI-XXIII), and 11+ae (XXIV–XXVIII). Apically blunt, setulose seta(e) present on segments 1–5. Short, spinulate seta present on segments 11 and 13. Short, highly chitinized spine present on segment 12. Two very short, blunt setae present on segment 13; similar element on segment 14. Modified ridged element(s) present on segments 13 and 14.

Leg 3 basis (Fig. 6E) with small acute process between rami.

Leg 5 (Fig. 6F) with inner spine extending to proximal margin of leg 6.

Leg 6 (Fig. 6F) represented by 3 elements on genital operculum; outer seta with sparse setules; middle seta unilaterally spinulate; inner spine slightly shorter than outer and middle setae, with spinules at base.

Etymology. This species is named in honour of Dr. Edyta J. Jasinska, for her pioneering studies on the root mat communities of the Yanchep National Park Caves in Western Australia.

Remarks. Among the 11 eucyclopine genera, the new species conforms to the genus *Eucyclops* sens. lat. by having setules on the distolateral margins of the fifth pedigerous somite, a 12-segmented antennule that bears a hyaline membrane on the distal segments, maxilliped with the innermost element on the terminal endopodal segment fused basally to the segment, the inner corner of the basis of legs 2 to 4 produced into a large acute process, and a 1-segmented leg 5 armed with two setae and one spine (Morton 1990; Dussart & Defaye 1995).

Most *Eucyclops* species possess spinules along either a small portion or almost the entire length of the lateral margin of each caudal ramus. The absence of this feature, as exhibited by the new species, is shared with 13 species: *E. teras* (Graeter, 1907), *E. angustus* (G. O. Sars, 1909), *E. dubius* (G. O. Sars, 1909), *E. laevimargo* (G. O. Sars, 1909), *E. indicus* (Kiefer, 1927), *E. glaber* Kiefer, 1935, *E. nudus* Kiefer, 1935, *E. caparti* Lindberg, 1951, *E. congolensis* Lindberg, 1951, *E. orthostylis* Lindberg, 1952, *E. miurai* Itô, 1952, *E. persistens* Monchenko, 1978, *E. puteincola* Kiefer, 1981, *E. neocaledoniensis* Dussart, 1984 and *E. bathanalicola* Boxshall & Strong, 2004. Of these, *E. edytae* **n. sp.** is most similar to *E. puteincola* in having caudal rami that are less than three times as long as wide, caudal seta VI at least two times longer than seta III and the inner spine on leg 5 that is at least two times as long as the free exopodal segment.

Eucyclops edytae **n. sp.** can be easily distinguished from *E. puteincola*, and all other congeners, by the unique spinulation pattern on the mid-ventral surface of the caudal rami. In other *Eucyclops* species, the mid-ventral surface of each caudal ramus is devoid of integumental structures. The new species differs further from *E. puteincola* with respect to the relative length of the inner spine on leg 1 basis, relative lengths of the apical spines on the terminal endopodal segment of leg 4, and insertion point of the outer seta and the relative length of the middle seta on leg 5. The inner spine on leg 1 basis extends to the proximal half of the terminal endopodal segment in the new species, whereas it reaches to the distal margin of same limb segment in *E. puteincola*. The outer apical spine on the terminal endopodal segment of leg 4 is half as long as the inner apical spine in the new species. In *E. puteincola* this outer apical spine is about two-thirds as long as the adjacent spine. The outer seta and inner spine on leg 5 are inserted at the same level in the new species, but these elements are each inserted at a different level in *E. puteincola*. The middle seta on leg 5 is shorter than the inner spine in the new species, but longer than the inner spine in *E. puteincola*.

Eucyclops edytae **n. sp.** is the sixth member of the genus to be reported from Australia. The other five species recorded previously from this continent are: *E. rutterni* Kiefer, 1933, *E. nichollsi* Brehm, 1950, *E. australiensis* Morton, 1990, *E. baylyi* Morton, 1990 and *E. spatulatus* Morton, 1990 [see Morton (1990)]. Of these, *E. spatulatus* and *E. australiensis* are also known to occur in Western Australia. These two taxa are, unlike *E. edytae* **n. sp.**, stricly lacustrine species and distributed in other states such as South Australia, Victoria, Tasmania and New South Wales (Morton 1990). Although *E. edytae* **n. sp.** is currently known to exist exclusively in the hypogean environment, extensive sampling of surface water habitats in Western Australia is required to determine whether it is a truly stygobitic or stygophilic species.

Key to females of Australian species of *Eucyclops*

1 Caudal rami with short longitudinal row of spinules along lateral margin, or longitudinal row of spinules entirely absent … 2

- Caudal rami with spinules along almost the entire length of lateral margin … 3

2 Caudal rami with 6–8 small spinules (these spinules rarely absent) along lateral margin; leg 5 with inner spine about half as long as middle seta … *E. rutterni* Kiefer, 1933

- Caudal rami without longitudinal row of spinules along lateral margin; leg 5 with inner spine slightly longer than middle seta … *E. edytae* **n. sp.**

3 Leg 5 with setiform inner spine, equal in width to middle and outer setae … 4

- Leg 5 with broad inner spine, about twice as wide as middle and outer setae … 5

4 Legs 3 and 4 with spatulate distal seta on the terminal exopodal segment … *E. nichollsi* Brehm, 1950

- Legs 3 and 4 with unmodified distal seta on the terminal exopodal segment … *E. baylyi* Morton, 1990

5 Leg 4 rami with spatulate setae on the terminal segments … *E. spatulatus* Morton, 1990

- Leg 4 rami with unmodified setae on the terminal segments … *E. australiensis* Morton, 1990

Genus *Macrocyclops* Claus, 1893

Macrocyclops albidus (Jurine, 1820)

Material examined. Spillway Cave (YN565), Yanchep National Park, Western Australia (31°32'41"S, 115°40'37"E): 20 ♀♀ (1 dissected and mounted on slide) and 4 copepodites, 8 November, 2005; Mrs. King's tumulus spring, Bullsbrook, Western Australia (31°39'04"S, 115°57'11"E): 5 ♀♀ and 6 copepodites, 8 May, 1996; Sue's spring (South), Bullsbrook, Western Australia (31°38'42"S, 115°58'17"E): 3 copepodites, 1 February, 2008.

Remarks. Our material agrees favourably with the redescription of *Macrocyclops albidus* (Jurine, 1820) provided by Ueda et al. (1996). This cosmopolitan species is the only representative of *Macrocyclops* known to occur in Australia (Dussart & Defaye 2006). It has been recorded previously from epigean habitats in New South Wales (Sars 1908; Bayly 1964), Queensland (Bayly *loc. cit.*; Timms 1967), South Australia (Cooling & Boulton 1993), Victoria (Timms 1981) and Western Australia (Pusey & Edward 1990; Bayly 1992; Cale et al. 2004; Pinder et al 2004). Although *M. albidus* typically inhabits lakes and streams (Fernando & Ponyi 1981), it is known to occur, as observed in the present study, in groundwaters as well (Itô 1957; Pospisil 1999; Reeves et al. 2000; Bruno & Perry 2004; Lewis & Reid 2007; Moseley 2007).

Genus *Paracyclops* Claus, 1893

Paracyclops chiltoni (Thomson, 1882)

Material examined. Boomerang Cave (YN99), Yanchep National Park, Western Australia (31°32'33"S, 115°41'24"E): 1 ♂, 14 November, 1996; Cabaret Cave (YN30), Yanchep National Park, Western Australia (31°32'31"S, 115°41'24"E): 1 ♀, 1 June, 1990; 2 ♀♀ and 1 ♂, 19 June, 1990; Spillway Cave (YN565), Yanchep National Park, Western Australia (31°32'41"S, 115°40'37"E): 2 ♀♀ (1 dissected and mounted on slide), 8 November, 2005; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 1 ♀ and 4 ♂♂, 27 November, 1996; Water Cave, Yanchep National Park, Western Australia (31°33'02"S, 115°40'59"E): 1 ♀ and 1 copepodite, 9 October, 2007; YN3 bore, Yanchep National Park, Western Australia (31°32'28"S, 115°41'30"E): 1 ♀, 28 August, 1994; YN5 bore, Yanchep National Park, Western Australia (31°32'35"S, 115°41'07"E): 4 ♀♀ and 1 ♂, 28 August, 1994; Bevan Peters' spring, Muchea, Western Australia (31°35'14"S, 115°57'47"E): 1 ♂, 21 December, 1992; 5 ♀♀, 4 ♂♂, and 16 copepodites, 11 September, 1993; Edgecombe spring, Ellenbrook, Western Australia (31°47'39"S, 115°59'43"E): 18 ♀♀, 10 ♂♂, and 24 copepodites, 4 November, 1995; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 1 ♂, 1995; Sue's spring (South), Bullsbrook, Western Australia (31°38'42"S, 115°58'17"E): 1 ♀ and 3 ♂♂, 1 February, 2008.

Remarks. Although *Paracyclops chiltoni* (Thomson, 1882) was recorded previously from temporary freshwater pools in Victoria (Morton & Bayly 1977), springs in South Australia (Zeidler 1989) and rivers and swamps in Western Australia (Storey et al. 1993; Pinder et al. 2004), these records were not included in Karaytug's (1999) treatise of the genus *Paracyclops* Claus, 1893 nor in Dussart & Defaye's (2006) world directory of the inland cyclopoids. The occurrence of *P. chiltoni* in Australia is confirmed herein as our material agrees in every detail with the excellent redescription of this species given in Karaytug

(1999). *Paracyclops chiltoni* is indeed widespread in Australia as evidenced by Morton's (1977) accurate account in his unpublished M.Sc. Thesis of this species obtained from numerous freshwater bodies in Tasmania, South Australia, New South Wales, Queensland and Victoria. This distribution pattern is not unexpected given that this species is a cosmopolitan taxon, with populations occurring in extremely isolated places such as New Zealand, Easter Island, Hawaii and Crozet Island (Karaytug 1999).

Paracyclops intermedius **n. sp.**
(Figs)

Type material. Holotype ♀, allotype ♂ and 4 paratypes (1 ♀ and 2 ♂♂ dissected and mounted on one slide each; 1 copepodite in alcohol), Mrs. King's tumulus spring, Bullsbrook, Western Australia (31°39'04"S, 115°57'11"E), 8 May, 1996.

Other material examined. Bevan Peters' spring, Muchea, Western Australia (31°35'14"S, 115°57'47"E): 9 ♀♀ (1 dissected and mounted on slide), 1 ♂, and 5 copepodites, 21 December, 1992; 13 ♀♀, 16 ♂♂, and 32 copepodites, 28 August, 1995; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 1 ♂, 20 December, 1994; 1 ♀ dissected and mounted on slide, 9 October, 2006; 6 ♀♀, 9 October, 2007.

Description of female. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami) of holotype (Fig. 7A) and specimen without telescoped somites ('non-contracted') from Bevan Peters' spring August 1995 collection, 730 and 740 µm, respectively; body width 315 and 240 µm, respectively. Mean body length and width of 5 specimens with telescoped somites from Bevan Peters' spring December 1992 collection, 536 and 218 µm, respectively (Fig. 7B). Prosome composed of cephalothorax and 3 free pedigerous somites; posterior margin of prosomites smooth.

Urosome comprised of fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Dorsal surface of fifth pedigerous somite with uneven posterior margin and setules along posterolateral corners. Urosomites 2–4 (Fig. 7C) furnished with transverse surface ridges and serrate frill along posterior margin. Genital double-somite slightly longer than wide (105 × 100 µm and 110 × 100 µm) in non-contracted specimens, but wider than long (mean 77.5 × 93 µm) in telescoped specimens. Seminal receptacle comprised of narrow anterior lobe and broad posterior lobe. Anal somite (Figs 7C, 8A) with posteroventral spinular row extending around to dorsal surface; anal cleft with dense patch of spinules.

Caudal ramus (Figs 7C, 8A) longer than wide (50 × 27.5 µm in both non-contracted specimens; mean 48.5 × 26 µm in contracted specimens); bears 6 setae (seta I absent). Base of seta II flanked by lateral transverse spinular row and medial oblique spinular row; lateral transverse spinular row extends along ventral surface beyond midline of ramus in paratype only. Spinular row at base of seta III extends ventromedially to seta V. Setae II and VII pinnate; other setae spinulate. Seta VI twice as long as seta III. Setae IV and V with proximal breaking plane.

Antennule (Fig. 8B) 11-segmented, with armature and ancestral segmentation pattern in brackets as follows: 8 (I–V), 4 (VI–VII), 2 (VIII), 6 (IX–XI), 4 (XII–XIII), 1+spine (XIV), 2 (XV–XVI), 3 (XVII–XX), 4+ae (XXI–XXIV), 2+ae (XXV), and 7+ae (XXVI–XXVIII). First segment with 2 proximal groups of spinules; remaining segments unornamented.

Antenna (Figs 8C–D) 4-segmented, composed of coxobasis and 3-segmented endopod. Coxobasis with 2 distomedial setae, long distolateral exopodal seta, and complex ornamentation on frontal and caudal surfaces as figured; spinular row present near bases of distomedial setae; all setae ornamented with spinules. Proximal endopodal segment armed with inner barbed seta and furnished with outer spinular row and inner oblique row of spinules on caudal surface. Middle endopodal segment bears 9 inner setae and spinular patch along outer margin. Terminal endopodal segment with proximal and distal spinular rows and 7 apical setae.

Labrum (Fig. 8E) with 2 teeth on each lateral corner, 12 teeth along medial margin, and long setules on anterior surface.

Mandible (Fig. 8F) composed of coxa and reduced palp. Cutting edge of coxal gnathobase with quadridentate tooth, 2 bicuspidate teeth, 4 unicuspidate teeth, barbed seta, and spinular row. Palp furnished with small and large spinular rows near its base and armed with 1 short and 2 long setae.

Maxillule (Fig. 9A) composed of praecoxa, coxobasis and endopod. Praecoxal arthrite bears 7 medial elements, 3 distal unicuspidate teeth, and distal spinulate seta; both proximalmost elements ornamented with spinules; distalmost element with large proximal spinule. Coxobasis with proximal seta and 3 terminal setae. Endopod 1-segmented, armed with 3 setae.

Maxilla (Fig. 9B) 5-segmented, composed of praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with outer spinular rows and 2 spinulate setae on endite. Coxa with spinules along outer margin and 1 and 2 spinulate setae, respectively, on proximal and distal endites. Basis drawn out into large claw furnished with large teeth along middle part of inner margin; accessory armature composed of strong spinulate spine and naked seta. Proximal endopodal segment with 2 spinulate setae; distal endopodal segment with 3 setae.

Maxilliped (Fig. 9C) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa unornamented; armed with 3 medial spinulate setae. Basis with 2 spinular patches along outer margin, proximomedial spinular row, and 2 medial spinulate setae. Proximal endopodal segment with single spinule on anterior surface and inner spinulate seta. Terminal endopodal segment with 3 elements; innermost element fused to segment, furnished with long spinules and minute teeth.

Legs 1–4 biramous (Figs 9D–E, 10A–D, 11A–B), with 3-segmented rami. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III,5	0-1; 0-1; 1,I,4
Leg 2	0-I	1-0	I-1; I-1; III,I,5	0-1; 0-1; 1,I,4
Leg 3	0-I	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I,4
Leg 4	0-I	1-0	I-1; I-1; II,I,5	0-1; 0-1; 1,II,2

Leg 1 (Figs 9D–E) intercoxal sclerite with single spinular row on anterior surface and 2 spinular rows on posterior surface. Coxa ornamented with minute spinules on anterior surface and 2 well developed spinular rows on posterior surface; inner element semispinulose (proximolateral spinule in Fig. present on right leg of paratype only). Basis with large mediodistal protrusion extending between insertion point of rami, inner row of setules, and spinules on anterior surface. Outer seta setulate; inner spinulate spine extends to proximal ⅓ of terminal endopodal segment. Exopod with large spinules along outer margin of first segment and distal spinules on posterior surface and setules along inner margin of proximal and middle segments. Endopodal segments with distal spinular rows on anterior surface; outer margin setules on proximal and middle segments relatively stiffer than those on apical segment; middle segment with spinular row on posterior surface; terminal segment with large distolateral spiniform process. Outermost seta on terminal exopodal segment with lateral row of denticles and inner row of setules; all other setae on rami plumose. All spines denticulate; spinules present at insertion point of all spines.

Leg 2 (Figs 10A–B) intercoxal sclerite with 2 spinular rows on anterior and posterior surfaces. Coxa ornamented as in leg 1, except with additional spinular row proximolaterally, 2 median spinular rows on anterior surface (position of missing spinules indicated by sockets (arrowed) in Fig. 10A; these spinules are intact in dissected non-type material), and lateral spinular row on posterior surface; inner spinulate spine bears single proximolateral spinule. Basis with lateral spinules, 2 middle spinular rows, minute spinules at insertion point of endopod, and row of setules along inner margin. Rami ornamented as in leg 1, except for naked inner margin on middle exopodal segment and additional distal spinular row on anterior surface of proximal and middle exopodal segments and minute spinule at insertion point of most setae. All setae on rami plumose.

Leg 3 (Figs 10C–D) similar to leg 2, except with relatively shorter outer seta on basis, additional inner seta on middle endopodal segment and setules along inner margin of last 2 endopodal segments, relatively finer spinules on outer margin of proximal and middle endopodal segments, and relatively less developed distolateral spiniform process and shorter apical spine on terminal endopodal segment.

Leg 4 (Figs 11A–B) intercoxal sclerite with few spinules on anterior surface, thin spinules along posterior margin, and 2 spinular rows (1 row incomplete) on posterior surface. Coxa with more complex ornamentation pattern on posterior surface than observed for preceding legs. Outer seta on basis longer than that of leg 3. Rami ornamented as in leg 3, except with additional setules along inner margin of middle exopodal segment, naked medial margin on middle endopodal segment, and relatively less developed distal spinules on anterior surface of proximal and middle endopodal segments. Terminal endopodal segment lacks distolateral spiniform process; inner apical spine 2 times longer than outer apical spine.

Leg 5 (Fig 11C) 1-segmented, armed with lateral and middle pinnate setae and inner spinulate spine; outer seta longer than other 2 elements. Base of outer seta produced, lacking spinular row; inner spine with spinules at base.

Leg 6 (Fig. 11D) represented by spinulate seta and 2 short naked spines (only outermost spine articulates at base) on genital operculum.

Male. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami) of allotype (Fig. 11E) and non-contracted specimen from Egerton spring, 610 and 670 µm, respectively; body width 185 µm in both specimens. Mean body length and width of 3 specimens with telescoped somites from Sawpit spring, 485 and 185 µm, respectively. Prosome composed of cephalothorax and 3 free pedigerous somites; posterior margin of prosomites smooth. Urosome comprised of fifth pedigerous somite, genital somite and 4 free abdominal somites. Fifth pedigerous somite lacks setules along posterolateral corners. Urosomites 2–5 furnished with transverse surface ridges (not figured) and serrate frill along posterior margin. Genital somite wider than long (55 × 85 µm and 60 × 85 µm in non-contracted specimens; mean 50 × 84 µm in contracted specimens). Caudal ramus longer than wide (35 × 25 µm in allotype, 40 × 25 µm in other non-contracted specimen, and mean 37 × 22.5 µm in contracted specimens), armed and ornamented as in female.

Antennule (Fig. 12A) 16-segmented, digeniculate, with armature and ancestral segmentation pattern in brackets as follows: 8+ae (I–V), 4 (VI–VII), 2 (VIII), 2+ae (IX), 2 (X), 2 (XI), 2 (XII), 2 (XIII), 2+ae (XIV), 2 (XV), 2 (XVI), 2 (XVII), 2 (XVIII), 4 (XIX–XX), 4 (XXI-XXIII), and 11+ae (XXIV–XXVIII). Seta A on proximal segment simple, unmodified. Setae D and F on proximal segment with blunt, setulose apex; similar elements present on segments 2–5. One element on segment 10 modified into long, massive spine with recurved base and acuminate tip. One of two elements on segment 13 digitiform; similar element present on segment 14. Short, blunt element and modified ridged element(s) present on segments 14 and 15.

Leg 6 (Fig. 12B) represented by 3 subequal elements on genital operculum; outer seta with sparse setules; middle seta spinulate; inner spine with spinules at base.

Etymology. The specific name alludes to the new species' morphological similarity to *P. affinis* and *P. canadensis*.

Remarks. *Paracyclops intermedius* **n. sp.** shares several features, such as urosomal surface ridges, 11-segmented antennule and one inner seta on the middle endopodal segment of leg 4, in common with the *P. affinis*-lineage, a natural group recognised formally by Karaytug (1998, 1999) that includes *P. affinis* (G. O. Sars, 1863), *P. canadensis* (Willey, 1934) and *P. uenoi* Itô, 1962. *Paracyclops affinis* is distributed in the Ethiopian and Palaearctic regions, whilst *P. canadensis* is restricted to North America and *P. uenoi* is endemic to the Ryukyu Islands (Karaytug 1999). It is worth noting, however, that Ishida (2006) recently attributed four female cyclopoid specimens collected from Kyoto, Japan, to *P. canadensis*, which significantly extends the distribution of this species from the Nearctic to the Palaearctic. Although Ishida's relatively detailed illustrations of his Japanese specimens clearly depict that the caudal rami, antennal coxobasis, natatory legs and leg 5 are structurally similar to those of *P. canadensis*, it is conceivable that Ishida's specimens are not conspecific with *P. canadensis* as they contain some disparate features, such as a naked anal cleft (highly spinulose in *P. canadensis*), 10-segmented antennule (11-segmented in *P. canadensis*) and different spinulation pattern on the posterior surface of leg 4 coxa. It is unfortunate that Ishida did not include the mouthparts in his description, as these appendages often contain species-specific characters (we currently must assume that these appendages are identical to those of *P. canadensis*). A detailed examination of Ishida's specimens is needed in order to resolve the taxonomic status of the Japanese *P. canadensis*.

Paracyclops uenoi differs from the other three related taxa by having two setae, as opposed to one seta, on the middle endopodal segments of legs 1 and 2. *Paracyclops intermedius* **n. sp.** and *P. canadensis* differ from *P. affinis* by having caudal seta III shorter than seta VI, spinules along the outer margin of the maxillary coxa, one spinule on the anterior surface of the proximal endopodal segment of the maxilliped, two median spinular rows on the anterior surface of the coxae of legs 2–4, four spines on the terminal exopodal segment of leg 3, an unornamented base on the outer seta of leg 5, an aesthetasc on the male antennulary segment 1, and male leg 6 with the outer seta as long as the middle seta.

Paracyclops intermedius **n. sp.** can be readily distinguished from *P. canadensis* by the: 1) absence of spinules on the lateral borders of the anal cleft; 2) presence of spinules near the insertion of the inner setae on the caudal surface of the antennal coxobasis (a characteristic of *P. affinis*); 3) relatively more developed spinular rows on the frontal surface of the antennal coxobasis; 4) fused innermost element on the terminal endopodal segment of the maxilliped (a characteristic of *P. affinis*); 5) large distolateral spiniform process on the terminal endopodal segment of leg 1; 6) presence of one spinule on the proximolateral margin of the inner coxal spines of legs 2–4 (a characteristic of *P. affinis*); 7) relatively less developed spinules along the posterior margin of leg 4 intercoxal sclerite (a characteristic of *P. affinis*); 8) different spinulation pattern on the posterior surface of leg 4 coxa; 9) relatively longer setae on leg 5 (the two setae are as long as the inner spine); and 10) presence of a modified element on male antennulary segment 10 (a characteristic of *P. affinis*).

Paracyclops intermedius **n. sp.**, together with *P. chiltoni* and *P. affinis*, are the only representatives of the genus known to exist in Australia thus far. The last species was reported by Sars (1914) from New South Wales, Morton (1977) from one locality in New South Wales and Timms & Morton (1988) from Queensland's Cape York area. Presently, there is no reason to doubt Morton's (*loc. cit.*) unpublished record, as his relatively detailed description precisely matches Karaytug's (1999) excellent redescription of *P. affinis*. *Paracyclops intermedius* **n. sp.** is most likely not a stygophile, particularly considering that other members of this genus occur in epigean habitats (Karaytug 1999). This species may also occur in other Australian States, as Morton (*loc. cit.*) also described a species, named

Paracyclops myallensis, from a swamp near Newcastle, New South Wales, that is similar to the material upon which our description is based. Morton's record, however, must be confirmed as his description was based on only two female specimens and was not supported by a complete set of illustrations.

Key to females of Australian species of *Paracyclops*

1 Urosomal somites 2–4 with numerous cuticular pits; caudal rami with cuticular depressions on ventral surface; legs 2 and 4 with 2 inner setae on middle endopodal segment … *P. chiltoni* (Thomson, 1882)

- Urosomal somites 2–4 with surface ridges; caudal rami without cuticular depressions on ventral surface; legs 2 and 4 with 1 inner seta on middle endopodal segment … 2

2 Caudal seta III longer than seta VI; leg 3 with 3 spines on terminal exopodal segment … *P. affinis* (G. O. Sars, 1863)

- Caudal seta III shorter than seta VI; leg 3 with 4 spines on terminal exopodal segment … *P. intermedius* **n. sp.**

Genus *Tropocyclops* Kiefer, 1927

Tropocyclops confinis (Kiefer, 1930)

Material examined. Lot 51 Cave (YN555), Yanchep, Western Australia (31°34'31"S, 115°42'10"E): 2 ♀♀ dissected and mounted on one slide each, 22 September, 2003.

Redescription of female. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami) 660 µm, based on digital image of 1 specimen (Fig. 13A). Prosome composed of cephalothorax and 3 free pedigerous somites. Urosome comprised of fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Genital double-somite (Fig.13B) longer (85–90 µm) than wide (60–70 µm); seminal receptacle not observed. Posterior margin of urosomites smooth. Anal somite (Fig.) with spinular row along posterior margin.

Caudal ramus (Fig. 13C) more than two times longer (40 µm) than wide (17.5 µm), with 6 spinulate setae (seta I absent) and spinular row at base of seta III. Seta III 1.25 times as long as seta VI. Seta VII about 1.7 times as long as seta VI. Setae IV and V with proximal breaking plane.

Antennule (Fig. 13D) 12-segmented; armature formula not recorded as many setae were missing or broken off. First segment with 2 ventral groups of spinules; finely serrate hyaline membrane present on segments 10–12.

Antenna (Figs 13E–F) 4-segmented, comprising coxobasis and 3-segmented endopod. Coxobasis with 2 distomedial naked setae, long distolateral exopodal seta, proximal spinular row on frontal surface, and 2 lateral and 2 median groups of spinules on caudal surface. Proximal endopodal segment with inner naked seta and small patch of spinules along lateral margin. Middle endopodal segment with 8 inner setae (position of 1 missing seta indicated by arrow in Fig. 13E) and spinules along outer margin. Terminal endopodal segment armed with 7 setae.

Labrum (Fig. 13G) with 15 teeth between lateral corners and long setules on anterior surface.

Mandible (Fig. 14A) composed of coxa and reduced palp. Gnathobase with 6 unicuspidate teeth, bifurcate tooth (each branch with rounded tip), barbed seta, and fine spinular row. Palp with few spinules near base and usual 3 setae (1 short and 2 long).

Maxillule (Fig. 14B) comprising praecoxa and 2-segmented palp. Praecoxal arthrite bears 7 medial elements (3 spinulate, 4 naked), 3 distal chitinized teeth, and distal spinulate seta. Coxobasis with proximal seta and 3 terminal setae. Endopod 1-segmented, armed with 3 setae.

Maxilla (Fig. 14C) 5-segmented, comprising praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with outer patch of fine spinules and endite armed with 2 spinulate setae. Proximal and distal coxal endites with 1 and 2 spinulate setae, respectively. Basis drawn out into powerful claw furnished with large spinules along middle part of both margins; accessory armature composed of large spinulate spine and naked seta. Proximal endopodal segment with 2 strong setae; frontal seta with large teeth along upper margin. Distal endopodal segment with 3 setae.

Maxilliped (Fig. 14D) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa bears 3 spinulate setae. Basis with 2 large patches of spinules along outer margin, large patch of spinules on antero-medial surface, and 2 medial setae. Proximal endopodal segment bears long spinules on antero-medial surface and inner spinulate seta. Terminal endopodal segment with 3 elements; longest element with fine spinules scattered along both margins and row of teeth along distal half of upper margin.

Legs 1–4 biramous (Figs 14E, 15A–E, 16A–B), with 3-segmented rami. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1*-0	I-1; I-1; II,I, 5	0-1; 0-2; 1,I+1,3
Leg 2	0-I	1*-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I+1,3
Leg 3	0-I	1*-0	I-1; I-1; II,I,5	0-1; 0-2; 1,I+1,3
Leg 4	0-I	1*-0	I-1; I-1; II,I,5	0-1; 0-2; 1,II,2

*Position of missing seta indicated by socket (arrowed in Figs 14E, 15B, 16A)

Leg 1 (Figs 14E, 15A) intercoxal sclerite unornamented and bilobed distally. Coxa unornamented on anterior surface; posterior surface with 2 groups of spinules laterally. Basis with spinules at insertion point of endopod. First 2 segments of each ramus with distal spinular row on anterior and posterior surfaces; outer margin of endopodal segments with fine setules. Outermost seta on terminal exopodal segment with denticles along outer margin and setules along inner margin; all other setae plumose. All spines denticulate; spine on terminal endopodal segment long and slim, about 1.8 times longer than segment.

Leg 2 (Figs 15B–C) ornamented as in leg 1, except for additional spinular rows on posterior surface of intercoxal sclerite and medial spinular row on posterior surface of coxa. Inner coxal spine with long spinules proximally and minute spinules distally. All setae on rami plumose.

Leg 3 (Fig. 15D–E) identical to leg 2, except proximal exopodal segment with longer outer spine that is adpressed against outer margin of middle exopodal segment and terminal exopodal segment bears only 3 spines.

Leg 4 (Fig. 16A–B) intercoxal sclerite and coxa ornamented as those of leg 3, except for posterior surface of coxa with additional spinular rows along midline. Rami (Fig.) ornamented as those of leg 1. Terminal endopodal segment with inner spine 2.5 times as long as outer spine.

Leg 5 (Fig 16C) 1-segmented, armed with spine and 2 setae; middle seta about 2.2 times longer than inner spine; unilaterally spinulate spine with spinular row at insertion point.

Leg 6 not observed.

Remarks. Our material agrees favourably with the illustrations of *Tropocyclops confinis* (Kiefer, 1930) provided in Dumont (1981), Yeatman (1983) and Boxshall & Braide (1991). Moreover, careful comparisons between our material and two female *T. confinis* specimens from Madagascar, which were kindly provided by Professor Henri Dumont (Ghent University), revealed that we are almost certainly dealing with the same species. Several morphological differences were detected between our samples and those from Madagascar as follows (features of our material given first followed by Dumont's specimens): 1) the second endopodal segment of the antenna bears eight rather than nine inner setae; 2) the anterior surface of the intercoxal sclerites of legs 1 to 4 are naked instead of ornamented with an incomplete spinular row; 3) the posterior surface of leg 1 intercoxal sclerite is naked rather than furnished with two spinular rows; 4) the inner margin of leg 1 basis is naked rather than ornamented with setules; and 5) the inner margin of leg 5 is naked as opposed to furnished with spinules. Due to the lack of material from the Yanchep Caves, we are uncertain at this time whether these subtle differences represent either geographical or interspecific variation. Examination of additional material from Western Australia is required to resolve this issue. Nevertheless, we believe it is appropriate to treat our specimens as *T. confinis* until there is evidence to the contrary.

With a spine formula of 3.4.3.3 on the terminal exopodal segment of legs 1 to 4, *T. confinis*, along with *T. prasinus* (Fischer, 1860), *T. tenellus* (G. O. Sars, 1909), *T. brevispinus* Shen & Tai, 1962, *T. longiabdominalis* Shen & Tai, 1962, *T. polkianus* Einsle, 1971, *T. brevis* Dussart, 1972, *T. rarus* Dussart, 1983, *T. nananae* Reid, 1991, *T. jamaicensis* Reid & Janetzky, 1996 and *T. bopingi* Dumont, 2006, belong to the "*terni*"-group [*sensu* Kiefer (1931)]. Among this group, *T. confinis* shares an unusual configuration with respect to the outer spine on the proximal exopodal segment of leg 3 (i.e., this spine is held parallel to the segment – Fig. 15D) with *T. bopingi*. The former taxon can be readily distinguished from the latter by the larger body size (660 µm vs. 380–420 µm), presence of spinules on the antennal coxobasis, absence of an inner seta on leg 1 basis, absence of a mediodistal triangular process on the basis of legs 2 to 4, and considerably shorter outer seta on leg 5.

Tropocyclops confinis has been reported previously in the Ethiopian, Palaearctic, Oriental, Neotropical and South Pacific Regions (Dussart & Defaye 2006). The discovery of *T. confinis* from Lot 51 Cave in Western Australia, therefore, constitutes the first record of this species from the Australian continent. In fact, this species may be widespread in

Australia, as Morton (1977) described a species, designated *Tropocyclops* sp. A, from surface waters in Victoria, Tasmania, New South Wales and Queensland that resembles the material upon which our description is based. This would not be unexpected considering *T. confinis* has a relatively broad distribution pattern as discussed above. Nonetheless, Morton's record must be verified as his taxonomic account was brief and lacked illustrations. It must be noted that Timms & Morton (1988) recorded two *Tropocyclops* species (listed as *Tropocyclops* sp. 1 and 2) from several fresh water sites in tropical Australia, but the specific identity of both taxa remains unknown.

The collection of *T. confinis* from the hypogean environment is highly unusual as this species typically inhabits rivers, lakes and ponds (Defaye 1988). The occurrence of this species in the Yanchep Caves is interpreted to be merely artificial as evidenced by the collection of only two individuals concurrently from a single cave during the entire sampling campaign. The source of these individuals remains unknown. Clearly extensive sampling of surface waters within Australia is needed to determine the distribution pattern and preferred habitat(s) of this species on this continent.

Subfamily Cyclopinae Kiefer, 1927

Genus *Mesocyclops* G. O. Sars, 1914

Mesocyclops brooksi Pesce, De Laurentiis & Humphreys, 1996

Material examined. Lot 51 Cave (YN555), Yanchep, Western Australia (31°34'31"S, 115°42'10"E): 1 ♀, 22 September, 2003; 4 ♀♀, 6 October, 2004; 22 ♀♀ (1 dissected and mounted on slide), 7 ♂♂, and 2 copepodites, 8 November, 2005; Spillway Cave (YN565), Yanchep National Park, Western Australia (31°32'41"S, 115°40'37"E): 1 ♀, 8 November, 2005; pool at Loch M^{c}Ness, Yanchep National Park, Western Australia (31°32'57"S, 115°40'49"E): 6 ♀♀, 1 August, 2007; 9 ♀♀, 4 ♂♂, and 3 copepodites, 22 August, 2007.

Remarks. *Mesocyclops brooksi* was established by Pesce et al. (1996) to accommodate several specimens collected from Bobs Well in the Pilbara Region of Western Australia. This species was subsequently reported from additional well sites in the Pilbara (De Laurentiis et al. 1999; Hołyńska & Brown 2003; Karanovic 2006) and Murchison Regions (Karanovic 2004a), as well as from many epigean localities in the south-west of Western Australia (Halse et al. 2000a, 2002a; Hołyńska & Brown *loc. cit.*; Cale et al. 2004; Pinder et al. 2004) and from one site in Queensland (Hołyńska & Brown *loc. cit.*).

Genus *Metacyclops* Kiefer, 1927

Metacyclops arnaudi (Sars, 1908)

(Figs)

Material examined. Lake Yonderup, Yanchep National Park, Western Australia (31°33'23"S, 115°41'09"E): 16 ♀♀ (1 dissected and mounted on slide) and 1 copepodite, 22 August, 2007; pool at Loch M^{c}Ness, Yanchep National Park, Western Australia (31°32'57"S, 115°40'49"E): 2 ♀♀, 22 August, 2007; swamp near Carpark Cave, Yanchep National Park, Western Australia (31°33'11"S, 115°41'08"E): 49 ♀♀ (18 damaged; 5 dissected and mounted on one slide each), 7 ♂♂ (1 damaged; 2 dissected and mounted on one slide each), and 19 copepodites, 1 August, 2007.

Redescription of female. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami), based on 7 specimens, 890–990 µm, mean 936 µm; body width 290–320 µm, mean 307 µm. Prosome (Fig. 17A) composed of cephalothorax and 3 free pedigerous somites; all prosomites densely ornamented with cuticular pits (not figured); posterior margin of prosomites smooth. Urosome (Figs 17A–B) comprised of fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Genital double-somite longer (150–160 µm; mean 156 µm) than wide (120–130 µm; mean

124 µm), with numerous cuticular pits (not figured); posterior margin smooth dorsally and serrate ventrally; seminal receptacle not observed. Postgenital somites 1–2 (Figs 17B, 18A) with few cuticular pits (not figured); posterior margin uneven dorsally and smooth ventrally. Anal somite (Figs 17B, 18A) with numerous cuticular pits (not figured) and spinular row along posterior margin of ventral surface extending to dorsal surface; anal cleft with 3 transverse spinular rows.

Caudal ramus (Fig. 17B) longer (80–90 µm; mean 83 µm) than wide (22.5–25 µm; mean 24.6 µm), with 6 setae (seta I absent) and numerous cuticular pits (not figured). Spinules present at insertion point of setae II and III. Seta II unilaterally spinulate; seta VII with few setules apically; remaining setae spinulate. Seta III and VI subequal; seta VII longer than setae III and VI. Middle terminal setae with proximal breaking plane.

Antennule (Fig. 18B) 11-segmented, with armature and ancestral segmentation pattern in brackets as follows: 7+ae (I–V), 4 (VI–VII), 6 (VIII–XI), 2 (XII–XIII), 1+spine (XIV), 2 (XV–XVI), 3 (XVII–XX), 2+ae (XXI–XXIII), 2 (XXIV), 2+ae (XXV), and 7+ae (XXVI–XXVIII). First segment with proximoventral spinular row; segments 1–8 with cuticular pits (not figured). Some specimens from swamp near Carpark Cave with partial articulation(s) on posterior margin of antennule as follows: on segment 2 in 3 specimens, segment 4 in 1 specimen, segment 6 (arrowed in Fig.) in 3 specimens, and segments 3 and 6 in 1 specimen.

Antenna (Figs 18C–D) 4-segmented, comprising coxobasis and 3-segmented endopod; all endopodal segments with cuticular pits on frontal surface (not figured). Coxobasis armed with 2 distomedial barbed setae and long distolateral exopodal seta; frontal surface with proximal row of minute spinules and short spinular row on lateral margin; caudal surface with several groups of spinules as figured. Proximal endopodal segment with inner spinulate seta and large patch of spinules along lateral margin. Middle endopodal segment bears 9 medial setae and 2 spinular rows on lateral margin. Terminal endopodal segment with proximal and distal spinules and 7 setae.

Labrum (Fig. 18E) with long setules on anterior surface, central toothed process, and 11 teeth between 2 blunt protrusions on distal margin.

Mandible (Fig. 18F) composed of coxa and reduced palp. Coxal gnathobase with large quadridentate tooth, 3 bicuspidate teeth, 2 unicuspidate teeth, long unicuspidate tooth with proximal accessory process, barbed seta, and row of strong spinules. Palp with 3 apical setae (2 long and plumose, 1 short and unilaterally barbed).

Maxillule (Fig. 18G) composed of praecoxa and 2-segmented palp. Praecoxal arthrite bears 7 medial elements (1 spinulate, 1 with large proximal spinule, 5 naked), 3 distal unicuspidate teeth, and distal spinulate seta. Coxobasis with proximal seta and 3 terminal setae. Endopod 1-segmented, armed with 3 distal setae.

Maxilla (Fig. 19A) indistinctly 5-segmented, composed of praecoxa, coxa, basis and 2-segmented endopod. Praecoxa unornamented, with 2 spinulate setae on endite. Coxa with cuticular pits along lateral margin and longitudinal spinular row on anterior surface; proximal and distal endites with 1 and 2 spinulate setae, respectively. Basis drawn out into large claw furnished with large spinules along middle part of inner margin and cuticular pits on distal end; accessory armature composed of naked seta and large spinulate spine; few cuticular pits present on outer margin. Proximal endopodal segment partially fused to basis, armed with 2 strong setae. Distal endopodal segment bears 3 setae.

Maxilliped (Fig. 19B) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa with 3 medial spinulate setae and outer row of stout spinules. Basis with patch of large spinules along outer margin, row of long spinules on anteromedial surface, and 2 medial spinulate setae. Proximal endopodal segment with long spinules on anterior surface and long inner spinulate seta. Terminal endopodal segment unornamented, bears 3 long setae.

Legs 1–4 biramous (Figs 19C–D, 20A–E), with 2-segmented rami. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; III,5	0-1; 1,I,4
Leg 2	0-1	1-0	I-1; II,I,5	0-1; 1,I+1,4
Leg 3	0-1	1-0	I-1; II,I,5	0-1; 1,II,4
Leg 4	0-1	1-0	I-0; II,I,5	0-1; I,I,I+2

Leg 1 (Fig. 19C) intercoxal sclerite naked. Coxa highly ornamented with spinules and pores on anterior surface and lateral spinular row on posterior surface. Basis with mediodistal triangular process, setules along inner margin, few pores near insertion point of endopod, and spinules on anterior surface and at insertion point of endopod and inner spine. Outer seta setulate; inner spinulate spine extends to distal margin of terminal endopodal segment. Proximal exopodal segment with pores and distal spinular row on posterior surface; outermost seta on terminal segment with lateral row of spinules and inner row of setules; insertion point of all spines with small spinules; both segments with setules along inner margin. Proximal endopodal segment with setules along lateral margin and proximal group of pores and distal spinular row on anterior surface; distal endopodal segment with setules along outer and proximomedial margins and long, thin spinules at insertion point of outer seta and apical serrate spine. All spines serrate.

Leg 2 (Fig. 19D) similar to leg 1, except as follows: (1) coxa with additional distolateral spinular row and considerably less developed spinular row on distal margin; (2) basis lacks inner spine and bears additional lateral spinular row and triangular process near rounded inner distal angle; (3) terminal exopodal segment with pores on posterior surface and homogeneously ornamented outermost seta; (4) terminal endopodal segment with additional seta, relatively smaller spinules at insertion point of outer seta and apical spine, and indentation on mid-lateral margin; and (5) rami with minute spinule(s) at insertion point of most setae.

Leg 3 (Fig. 20A) identical to leg 2, except terminal endopodal segment with pores on posterior surface and 2 apical, subequal spines. Two specimens collected from swamp near Carpark Cave with formula 1,I+1,4 on terminal endopodal segment (Fig. 20B).

Leg 4 (Figs 20C–D) ornamented as in leg 3, except posterior surface of coxa with more complex ornamentation and proximal endopodal segment with pores and distal spinular row on posterior surface. Outer spine on terminal endopodal segment about 0.84 times as long as apical and inner spine. Same two specimens mentioned above with formula 1,I,3 on terminal endopodal segment (Fig. 20E).

Leg 5 (Figs 17A, 20F) held laterally, visible in dorsal view; composed of protopod completely fused to somite and free exopod segment. Protopodal seta long, with few setules apically. Exopod subquadrate, bears 2 apical elements; spine about 0.33 times as long as adjacent seta and 1.3 times as long as exopodal segment.

Leg 6 (Fig. 20G) rudimentary, represented by weakly spinulate seta and 2 short naked spines on genital operculum.

Male. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami), based on 3 specimens, 700–730 µm, mean 720 µm; body width 200–210 µm, mean 203 µm. Prosome (Fig. 21A)composed of cephalothorax and 3 free pedigerous somites. Urosome (Fig. 21A) comprised of fifth pedigerous somite, genital somite and 4 free abdominal somites. All somites ornamented with cuticular pits (not figured). Genital somite wider than long (mean 83 × 93 µm). Caudal ramus longer than wide (mean 57 × 20 µm), armed and ornamented as in female.

Antennule (Fig. 21B) 17-segmented, digeniculate, with armature and ancestral segmentation pattern as follows: 7+3ae (I–V), 4 (VI–VII), 1 (VIII), 2+ae (IX), 1 (X), 2 (XI), 2 (XII), 2 (XIII), 2+ae (XIV), 2 (XV), 2 (XVI), 2 (XVII), 2+ae (XVIII), 3 (XIX–XX), 3 (XXI-XXIII), 3 (XXIV-XXV), and 6+ae (XXVI–XXVIII). Cuticular pits present on segments 1–3 and 11–15. Short, highly chitinized spine present on segments 9 and 12. Short, spinulate seta present on segments 11–14. Short, blunt element present on segment 14. Modified anvil-shaped element(s) present on segments 14 and 15.

Free exopod segment of leg 5 (Fig. 21C) with inner spine slightly shorter than segment and 0.25 times as long as adjacent seta.

Leg 6 (Fig. 21D) represented by 3 elements on genital operculum; outer setulate seta longest of 3 elements; middle seta unilaterally spinulate; inner spine ½ length of middle seta.

Remarks. We attribute our specimens to *Metacyclops arnaudi* (Sars, 1908) as they conform, in general, to Sars' original description of two adult females collected from a swamp at St Arnaud in Victoria, Australia. Admittedly, there are a number of differences between our specimens and Sars' description as follows (with features of Sars' material given first followed by our material): the length/width ratio of the caudal rami is 6.2 versus 3.4; the second endopodal segment of the antenna bears eight as opposed to nine inner setae; the inner spine on the basis of leg 1 extends to the middle rather than to the distal end of the second endopodal segment; and the armature formula on the second endopodal segment of legs 3 and 4 is 1,I+1,4 and 1,I,3, respectively, as opposed to 1,II,4 and I,I,I+2. Although the last set of differences is taxonomically significant, it is premature, in this case, to attribute a new specific status to the Yanchep specimens based entirely on the leg dissimilarities described above given that the armature pattern on the endopods of legs 3 and 4 of those specimens was variable. As depicted in Figures 20B & E, legs 3 and 4 in two individuals from our samples are structurally identical to those of Sars' specimens. Regrettably, the type material of *M.*

arnaudi is no longer extant (see Hamond 1987) so the discrepancies highlighted above between our specimens and Sars' material remain unresolved. Nonetheless, we are confident that our specimens are conspecific with *M. arnaudi*, particularly considering that: a) the Western Australian population matches Sars' material with respect to the proportions of the urosomal somites, segmentation of the antennule, structure of the bases of legs 1 to 4, armature pattern on the exopod of legs 1 to 4, and most importantly, the position and structure of leg 5; and b) variations in the proportion of the caudal rami and armature of the natatory legs are known to occur in the Cyclopidae (Reid 1992; Dumont 2006).

Although *M. arnaudi* was redescribed by Kiefer (1967) based on specimens collected by Dr. Ian A. E. Bayly from salt lakes in Victoria, this material was later revealed by Fiers (2001) to represent a new genus and species, *Meridiecyclops baylyi*. The latter author also noted that the taxonomic affinities between *M. arnaudi* and his newly established genus *Meridiecyclops* were difficult to establish as the male of *M. arnaudi* has never been described and the only illustrations available for comparison were those of Sars (1908). For these reasons, Fiers decided to retain *M. arnaudi* in the genus *Metacyclops* Kiefer, 1927, which was adopted by Karanovic (2004a, b). Our description of both sexes of this enigmatic species revealed that it is indeed a member of *Metacyclops*; it cannot be included in *Meridiecyclops* given that the male maxilla, as well as the female genital double-somite and basis and proximal endopodal segment of leg 4, are not modified.

Metacyclops arnaudi has been recorded previously, often as *Microcyclops arnaudi*, in aquatic faunal investigations in Victoria (Geddes 1976; Morton & Bayly 1977) and Western Australia (Geddes et al. 1981; Bayly 1982; Halse et al. 2000b, 2002a). We must also add that this cyclopoid species was also reported, as *Microcyclops arnaudi*, from freshwater pools in Victoria, South Australia and Tasmania by Morton (1977). We strongly believe the specimens reported in Morton (1977), Morton & Bayly (1977), Geddes et al. (1981) and

Bayly (1982) are conspecific with our material for the following reasons. Firstly, Morton's (*loc. cit.*) relatively detailed description of *M. arnaudi* is congruent, particularly regarding the relative proportions of the caudal rami and structure of leg 5, with our taxonomic account. Even though the armature of legs 1 to 4 given in Morton's account was identical to that of Sars' (1908) material, Morton also noted, with respect to leg 4, that "the outer seta and distalmost inner seta may sometimes (not uncommonly) be transformed into spines". Secondly, the cyclopoid specimens collected by Geddes et al. (1981) and Bayly (1982), which included *M. arnaudi* (listed as *Microcyclops arnaudi*) among others, were identified by Mr. David Morton [see Methods section in Geddes et al. (*loc. cit.*) and Acknowledgement section in Bayly (*loc. cit.*)]. Lastly, we have examined three adult female *M. arnaudi* specimens lodged in the Crustacea collection of Museum Victoria (Reg. No. J12213 – *Microcyclops arnaudi* collected on July, 1979, from a semi-permanent pond in South Portland, Victoria) that: a) were identified by Mr. David Morton; and b) are morphologically similar to our Western Australian material. The Museum Victoria specimens vary slightly from our samples, however, by having relatively more cuticular pits on postgenital somites 1 and 2 and a relatively longer inner apical spine on the terminal endopodal segment of leg 4. It is now apparent that *M. arnaudi*, as currently recognised by us, is a somewhat variable species that occurs throughout the southern half of Australia.

The presence of three spines on the distal exopodal segment of legs 1 to 4 is, as previously noted by Karanovic (2004a), a synapomorphy of *M. arnaudi*, *M. monacanthus* (Kiefer, 1928), *M. margaretae* (Lindberg, 1938), *M. trispinosus* Dumont, 1981, *M. pilanus* Karanovic, 2004, *M. laurentiisae* Karanovic, 2004, *M. kimberleyi* Karanovic, 2004 and *M. pilbaricus* Karanovic, 2004. This small assemblage of species, termed the "*trispinosus*"-group by Karanovic (2004a), exhibit a Gondwana distribution: *M. monacanthus* was described from New Zealand, *M. margaretae* from India, *M. trispinosus* from Africa, and the remaining five species from Australia (Sars 1908; Kiefer 1928; Lindberg 1938; Dumont 1981; Karanovic 2004a, b). Among members of the "*trispinosus*"-group, *M. arnaudi* has cuticular pits on the surface of the body somites, caudal rami and certain appendages, an exopodal seta on the antenna, nine inner elements on the middle endopodal segment of the antenna and one apical spine on the distal endopodal segment of leg 4 in common with *M. pilanus* and *M. laurentiisae*. *Metacyclops arnaudi* can be easily distinguished from these two closely related taxa by having an aesthetasc on the first antennulary segment and leg 5 armed with a spine that is longer than the free exopodal segment in the adult female. It is worth noting here that this characteristic aesthetasc is present on all three Museum Victoria specimens. It is unclear whether this element is present or absent in Sars' (1908) and Morton's (1977) specimens, as it was not depicted (nor the other aesthetascs invariably present on the distal antennulary segments of cyclopid species) in Sars' illustration of the antennule and the antennulary armature pattern was not given in Morton's description.

Key to females of Australian species of *Metacyclops*

1 Legs 1–4 with spine formula 3.4.4.3 on the distal exopodal segment … *M. superincidentis* Karanovic, 2004

- Not as above ... 2

2 Legs 1–4 with spine formula 3.4.4.2 on the distal exopodal segment … *M. mortoni* Pesce, De Laurentiis & Humphreys, 1996

- Legs 1–4 with spine formula 3.3.3.3 on the distal exopodal segment … 3

3 Antenna with exopodal seta; body somites furnished with cuticular pits … 4

- Antenna without exopodal seta; body somites lacking cuticular pits … 6

4 First antennulary segment with proximal aesthetasc; spine on free exopodal segment of leg 5 longer than segment ... *M. arnaudi* (G. O. Sars, 1908)

- First antennulary segment without proximal aesthetasc; spine on free exopodal segment of leg 5 considerably shorter than segment ... 5

5 Genital double-somite wider than long; antennule relatively long, reaches to posterior margin of cephalothorax ... *M. laurentiisae* Karanovic, 2004

- Genital double-somite longer than wide; antennule relatively short and compact, reaches to proximal half of cephalothorax ... *M. pilanus* Karanovic, 2004

6 Seta VII on caudal ramus about as long as ramus; maxilliped with 3 elements on syncoxa and distal endopodal segment ... *M. pilbaricus* Karanovic, 2004

- Seta VII on caudal ramus about twice as long as ramus; maxilliped with 2 elements on syncoxa and distal endopodal segment ... *M. kimberleyi* Karanovic, 2004

Genus *Mixocyclops* Kiefer, 1944

Mixocyclops mortoni n. sp.

(Figs)

Type material. Holotype ♀ and paratype ♀ (dissected and mounted on slide), YN7 bore, Yanchep National Park, Western Australia (31°33'17"S, 115°41'13"E), 17 July, 1992.

Other material examined. Lot 51 Cave (YN555), Yanchep, Western Australia (31°34'31"S, 115°42'10"E): 1 copepodite, 7 November, 2006; Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E): 1 damaged ♂ (dissected and mounted on slide), 17 March, 1993; Edgecombe spring, Ellenbrook, Western Australia (31°47'39"S, 115°59'43"E): 1 ♀, 9 October, 2006; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 1 ♀ dissected and mounted on slide, 9 October, 2006.

Description of female. Total body length (measured from anterior margin of cephalothorax to posterior margin of caudal rami), based on 2 specimens, 375–380 µm; body width 142.5–150 µm. Prosome (Fig. 22A) composed of cephalothorax and 3 free pedigerous somites. Urosome (Figs 22A–B) comprising fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Genital double-somite wider (75–90 µm) than long (55–65 µm); seminal receptacle unilobate, situated in proximal ½ of genital double-somite. Anal somite (Figs 22A–B) with spinular row along posterior margin, and patch of spinules on anal cleft; anal operculum large, semi-circular, extends to proximal margin of caudal rami. Posterior margin of all somites smooth.

Caudal ramus (Figs 22B–C) longer (22.5–25 µm) than wide (15–16.5 µm), bears 6 setae (seta I absent), 2 proximomedial spinules on dorsal surface, and spinular row at insertion point of all elements except for setae IV and V. Seta II pinnate, seta VII setulate, all others spinulate. Setae II and VI subequal in length. Seta III 2.9 times as long as seta VI. Seta VII about 2 times longer than ramus. Setae IV and V with proximal breaking plane.

Antennule (Fig. 22D) 11-segmented, with armature and ancestral segmentation pattern in brackets as follows: 7 (I–V), 4 (VI–VII), 7 (VIII–XI), 2 (XII–XIII), 1+spine (XIV), 2 (XV–XVI), 3 (XVII–XX), 2+ae (XXI–XXIII), 2 (XXIV), 2+ae (XXV), and 7+ae (XXVI–XXVIII). First segment with proximal spinular row. Short spine on segment 5 blunt.

Antenna (Fig. 23A) 4-segmented, comprising coxa, basis and 3-segmented endopod. Coxa naked and unarmed. Basis unornamented and armed with distomedial barbed seta; exopodal seta absent. Proximal endopodal segment with inner barbed seta and outer spinular row. Middle endopodal segment bears 5 medial setae and distolateral spinular row. Terminal endopodal segment with usual 7 apical setae and 2 groups of lateral spinules.

Labrum (Fig. 23B) with 10 teeth along posterior margin and setules on anterior surface.

Mandible (Fig. 23C) composed of coxa and highly reduced palp. Coxal gnathobase with tricuspidate tooth, bicuspidate tooth, 4 unicuspidate teeth, barbed seta, and fine spinular row. Palp represented by sparsely pinnate seta.

Maxillule (Fig. 23D) comprising praecoxa and 2-segmented palp. Praecoxal arthrite bears 6 medial elements, 3 distal unicuspidate teeth, and distal seta. Coxobasis with proximal seta and 3 terminal setae. Endopod 1-segmented, armed with 3 setae.

Maxilla (Fig. 23E) 5-segmented, composed of praecoxa, coxa basis and 2-segmented endopod; all segments naked. Praecoxal endite with 2 spinulate setae. Proximal and distal coxal endites with 1 and 2 spinulate setae, respectively. Basis drawn out into large naked claw; accessory armature consists of weakly spinulate spine and naked seta. Proximal and distal endopodal segments each armed with 2 setae.

Maxilliped (Fig. 23F) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa with inner spinulate seta. Basis with medial spinulate seta and spinular row on lateral and anteromedial margins. Proximal endopodal segment with medial spinulate seta and spinular row. Distal endopodal segment unornamented and bears 2 unequal setae.

Legs 1–4 biramous (Figs 24A–D), with 2-segmented rami. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-0	I-0; II,4	0-1; 1,I,3
Leg 2	0-1	1-0	I-0; III,3	0-1; 1,I,2
Leg 3	0-1	1-0	I-0; III,I,3	0-1; 1,I+1,2
Leg 4	0-1	1-0	I-0; III,I,3	0-1; 1,II,2

Leg 1 (Fig. 24A) intercoxal sclerite naked and bilobed distally. Anterior surface of coxa with minute spinules along distal margin; posterior surface naked. Basis with small, mediodistal acute process, spinular rows at insertion point of endopod, and inner distal angle pointed; outer plumose seta long, extends to terminal exopodal segment. Inner and outer

margin of exopod and endopod, respectively, with setules. Proximal exopodal segment with distal spinular row on anterior and posterior surfaces. Proximal endopodal segment with distal spinular row on anterior surface. All spines denticulate, with small spinules at insertion point of each spine.

Leg 2 (Fig. 24B) similar to leg 1, except basis with relatively shorter outer seta, spinules at insertion of outer seta and setules along inner margin, proximal exopodal segment without distal spinular row on anterior surface, terminal exopodal segment is relatively larger and bears an additional spine, and terminal endopodal segment bears 1 less inner seta.

Leg 3 (Fig. 24C) similar to leg 2, except distal endopodal segment bears extra seta and distal exopodal segment bears indentation on mid-lateral margin, median transverse ridge on anterior surface (representing ancestral division between middle and terminal segments), spinular row on posterior surface and extra spine. Specimen from Egerton spring with discontinuous inner cuticle layer on medial margin of distal exopodal segment (arrowed in Fig. 25A).

Leg 4 (Fig. 24D) identical to leg 3, except exopodal segments without spinular row on posterior surface and terminal endopodal segment bears 2 apical spines (outer spine ½ length of inner spine). Specimen from Egerton spring with lateral transverse suture and discontinuous inner cuticle layer on medial margin of distal exopodal segment (arrowed in Fig. 25B). Specimens from Egerton and Three Springs tumulus spring with outer apical spine ⅔ length of inner apical spine on terminal endopodal segment (Fig. 25C).

Leg 5 (Figs 22B, 24E) small, 2-segmented. Protopodal segment naked, expanded laterally, and armed with long outer seta. Free exopodal segment 2 times longer than wide, bears long setulate seta and tiny medial spine.

Leg 6 (Fig. 24F), represented by sparsely setulate seta, naked spiniform seta and spiniform process on genital operculum.

Male. Body measurements were not recorded as the single male specimen was damaged. The antennulary structure could not be described as the pair of antennules was damaged during dissection. Exopod of legs 3 (Fig. 25D) and 4 (Fig. 25E) 3-segmented, both with armature formula I-0; I-0; II,I,3. Leg 6 (Fig. 25F) represented by naked seta and 2 unequal spinulate setae on genital operculum.

Etymology. This species is named after David W. Morton for his outstanding contribution to the knowledge of the Australian freshwater Cyclopidae.

Remarks. The genus *Mixocyclops* presently contains two representatives: *M. crozetensis* Kiefer, 1944 and *M. minutus* Chappuis, 1951. The former taxon was established to accommodate three females and a male collected from a stream on Crozet Island (Kiefer 1944), whilst the latter was described from a female specimen recovered after rehydration of a moss sample that was obtained originally by a waterfall along Guide River in Tasmania (Chappuis 1951). Important features such as the antenna and mouthparts of both species and the male natatory legs of *M. crozetensis* were omitted from these descriptions. The structure of these appendages remains unknown as both species have not been reported since their original discovery.

Judging from the cursory drawings of *M. crozetensis* and *M. minutus*, the former taxon differs from the latter by having a relatively longer caudal seta III, an additional element on the distal endopodal segment of leg 1 and the distal exopodal segment of legs 3 and 4, a relatively longer inner apical spine on the distal endopodal segment of leg 4, and apparently only one element on the distal segment of leg 5. Given that the structure and armature pattern of leg 5 has traditionally been used as a diagnostic feature of most cyclopid genera (Kiefer 1927; Pesce 1996; Reid & Janetsky 1996), Lindberg (1954) argued that *M. minutus* should not be classified in the genus *Mixocyclops* as it bears an apical seta and inner spine on the distal segment of leg 5 as opposed to just a seta on the same segment as in *M.*

crozetensis. Lindberg (*loc. cit.*), however, failed to recognise that Kiefer (*loc. cit.*) admitted he could not determine with absolute certainty whether a tiny spine was present or not on the inner margin of the distal segment of leg 5. A minute inner spine was recently confirmed to be present on the distal segment of leg 5 in the type material of *M. crozetensis* by Dr. Frank Fiers (Royal Belgian Institute of Natural Sciences; *in litt.*). Based on this new information, *M. crozetensis* and *M. minutus* are undoubtedly members of the same genus.

The new species is included in *Mixocyclops* as it shares a relatively broad genital double-somite, short caudal rami with seta VI shorter than seta III, 11-segmented antennule, legs 1 to 4 with 2-segmented rami, leg 1 basis without an inner seta and distal segment of leg 5 armed with an apical seta and small inner spine in common with *M. crozetensis* and *M. minutus* (see Dussart & Defaye 1995). Among these three species, the presence of four spines on the terminal exopodal segment of legs 3 and 4 is shared by *Mixocyclops mortoni* **n. sp.** and *M. crozetensis*. Nevertheless, *Mixocyclops mortoni* **n. sp.** can be easily distinguished from *M. crozetensis* by having two inner setae instead of one on the distal endopodal segment of legs 3 and 4. The suite of apomorphic characters present in *M. minutus*, such as two inner setae on the distal endopodal segment of leg 1 and three outer spines on the terminal exopodal segment of legs 3 and 4, suggest that this species diverged later from the common ancestor of *Mixocyclops* than *M. mortoni* **n. sp.** and *M. crozetensis*.

Mixocyclops mortoni **n. sp.** is not restricted to the hypogean environment within the Gnangara Mound area, as we have in our personal collection several specimens of this species from Boranup Creek located in the Margaret River Region of Western Australia (Tang & Knott, unpublished data) and examined conspecific material in the DEC collection that were obtained from Three Springs tumulus spring and Melaleuca Swamp in the northern and central section, respectively, of the Wheatbelt Region in Western Australia. Indeed, this species may be widespread in the southern half of Australia, as Morton (1977) also described a species, named *Mixocyclops macaulae*, collected from *Sphagnum* bogs on Mt. Baw Baw and Mt. Buffalo in Victoria that is similar, particularly with respect to the structure and armature of the caudal rami, antenna and legs 1 to 5 of the female and the segmentation of the outer ramus of legs 3 and 4 in the male, to the material upon which our description is based. Morton's record, however, must be confirmed as his description was was not supported by a complete set of illustrations.

Order Harpacticoida Sars, 1903

Family Ameiridae Boeck, 1865

Genus *Nitocra* Boeck, 1865

Nitocra lacustris pacifica Yeatman, 1983

Material examined. Fridge Grotto Cave (YN81), Yanchep National Park, Western Australia (31°31'21"S, 115°40'17"E): 1 ♀, 17 July, 1992.

Remarks. This subspecies was established originally as *Nitocra lacustris pacificus* by Yeatman (1983) to accommodate specimens collected from crab holes in Fiji, Western Samoa and Tonga. Subsequently, Fiers (1986) corrected the subspecific name (i.e., from *pacificus* to *pacifica* to agree with the gender of the genus name) and documented a slightly variable form of *N. l. pacifica* from temporary brackish water pools on Laing Island, Papua New Guinea, and Karanovic (2004a) redescribed in great detail this subspecies (given as *Nitokra lacustris pacifica* [see Wells (2007) on the valid usage of *Nitocra* vs. *Nitokra*]) obtained from two bores in the Murchison Region of Western Australia. This subspecies is indeed relatively widespread in Western Australia, as we have examined five adult specimens of both sexes collected from one bore locality in the Shark Bay Region (Tang & Knott, unpublished data). There is a distinct possibility that *N. l. pacifica* occurs in other Australian States given that the nominate species *N. lacustris* (Schmankevitsch, 1895) was recorded previously, without descriptions or illustrations, from springs in South Australia by Mitchell (1985) and Zeidler (1989). Whether these authors' specimens represent *N. lacustris* s. str. or *N. l. pacifica* requires further investigation. The collection of just one female *N. l. pacifica* during our 18 year-study period supports Karanovic's (2004a) supposition that this species "is only an occasional guest in the subterranean waters of Western Australia."

***Paranitocrella* n. gen.**

Diagnosis. Ameiridae. Body elongate and cylindrical. Prosomal somites with smooth hyaline frill. Urosome 5-segmented in female, 6-segmented in male. Pre-anal somites with minutely serrated hyaline frill forming rectangular lappets. Genital double-somite with dorsal suture line representing ancestral division between genital somite and first abdominal somite. Anal operculum well developed, furnished with large spinules. Caudal rami short, with 7 setae. Rostrum with truncate tip, defined at base. Female antennule 8-segmented, with tubular pore on segment 1 and aesthetasc on segment 4. Male antennule 10-segmented, haplocerate, with tubular pore on segment 1 and aesthetasc on segment 5. Antenna with separate basis and endopod; exopod 1-segmented, with 1 apical seta. Mandible with 2-segmented palp, representing unarmed basis and endopod with 4 apical setae. Maxillule with 3 setae on coxal endite; basis with 1 subapical and 4 apical setae; endopod minute, with 2 setae; exopod absent. Maxilla with basal pilose seta representing proximal endite and trisetose distal endite on syncoxa; allobasis drawn out into into a claw; endopod 1-segmented, with 2 setae. Maxilliped subchelate; syncoxa with 1 seta; basis unarmed; endopod represented by long claw with 1 accessory setae.

Leg 1 with 3-segmented rami; basis with subapical flagellum on outer spine and sexually dimorphic inner spine; proximal and middle exopodal segments without inner seta; terminal exopodal segment with 4 elements; distal endopodal segment with 3 elements. Legs

2–4 with 3-segmented exopods and 2-segmented endopods. Proximal and middle exopodal segments without inner seta. Terminal exopodal segment with reduced inner apical seta. Proximal endopodal segment unarmed. Leg 2 basis with subapical flagellum on outer spine. Legs 3 and 4 bases with outer seta. Leg 2 endopod sexually dimorphic; fewer spinules on distal segment in male. Leg 3 endopod sexually dimorphic; 1 apical spine on distal segment in female; 2 elements on same segment in male. Terminal exopodal segment of leg 4 with 6 elements.

Leg 5 with separate basoendopod and exopod in both sexes; basoendopods fused medially in male; female with 4 elements on basoendopod and 5 elements on exopod; male with 2 elements on basoendopod and 6 elements on exopod. Female leg 6 vestigial, forming common genital operculum armed with 1 seta on either side. Male leg 6 asymmetrical, forming opercular plate armed with 2 setae.

Type and only species. *Paranitocrella bastiani* **n. gen. et n. sp.**

Etymology. The generic name is a combination of Greek “*para*” (meaning beside or near) and the existing genus name *Nitocrella*. Gender feminine.

***Paranitocrella bastiani* n. sp.**
(Figs)

Type material. Holotype ♀, allotype ♂, and 22 paratypes (11 ♀♀, 6 ♂♂, and 1 copepodite in alcohol; 2 ♀♀ and 2 ♂♂ dissected and mounted on one slide each), Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E), 28 August, 1994.

Other material examined. Boomerang Cave (YN99), Yanchep National Park, Western Australia (31°32'33"S, 115°41'24"E): 1 ♂, 17 July, 1992; Cabaret Cave (YN30), Yanchep National Park, Western Australia (31°32'31"S, 115°41'24"E): 1 ♂, 29 August, 1993; Carpark Cave (YN18), Yanchep National Park, Western Australia (31°33'08"S, 115°41'08"E): 18 ♀♀ (1 dissected and mounted on slide), 14 ♂♂ (1 dissected and mounted on slide), and 1 copepodite, 31 October, 1996; Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E): 3 ♀♀, 7 ♂♂, and 2 copepodites, 17 March, 1993; 5 ♀♀, 5 ♂♂, and 1 copepodite, 27 November, 1996; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 2 ♂♂, 27 August, 1994; 3 ♀♀ and 1 ♂, 27 November, 1996.

Description of female. Total body length (measured from tip of rostrum to posterior margin of caudal rami), based on 4 specimens, 425–430 µm, mean 428 µm; largest width (80 µm) measured at posterior end of cephalothorax. Body (Fig. 26A) cylindrical, without discrete delineation between prosome and urosome. Prosome composed of cephalothorax and 3 free pedigerous somites; all prosomal tergites with sensillae and smooth hyaline frill. Urosome comprised of fifth pedigerous somite, genital double-somite and 3 free abdominal somites. Urosomites 1–4 with minutely serrated hyaline frill forming rectangular lappets. Genital double-somite (Fig. 26B) wider (60–65 µm) than long (45–55 µm), with paired anteroventral spinular rows and 2 medioventral spinular rows; original segmentation represented by dorsal line furnished with minutely spinulated frill. Genital field situated anteriorly on genital double-somite, with large median copulatory pore and chitinized copulatory duct leading to pair of lobate seminal receptacles; median genital pore covered by modified sixth legs. Postgenital somites 1–2 (Fig. 26B) with paired ventrolateral spinular rows, numerous medioventral spinular rows, and posteroventral spinular row. Anal somite (Figs 26B, 27A) with paired lateral, anteroventral and anterodorsal spinular rows, spinules along hind margin of anal cleft, and spinules at insertion point of each caudal ramus; anal operculum with 7–8 large spinules along slightly convex distal margin.

Caudal ramus (Figs 26B, 27A) short, about 1.6 times as long as wide, armed with 7 setae. Seta I and II closely set near outer subdistal margin; seta II over 2 times as long as seta I. Setae III and VII longer than caudal ramus, inserted at outer and inner distal angle, respectively. Seta VI about 1.6 times as long as seta I. Spinules present at insertion point of setae III, V and VII. Setae IV and V spinulate, with proximal breaking planes; other setae naked.

Rostrum (Fig. 27B) elongated, demarcated at base, with truncate tip and 2 dorsal sensillae; longer than first antennulary segment.

Antennule (Figs 27C–E) 8-segmented, with armature as follows: 1, 8, 6, 4+ae, 2, 2, 4, and 7. Segment 1 with spinular row, large tubular pore, and distal spiniform seta. Segments 2–8 without surface ornamentation and armed with naked elements. Segment 8 with 2 apical setae fused at base.

Antenna (Fig. 27D) 4-segmented, comprising coxa, basis and 2-segmented endopod. Coxa naked and unarmed; basis with 2 large medial spinules and inner oblique spinular row. Exopod 1-segmented, cylindrical, armed with distal pinnate seta. Proximal endopodal segment naked and unarmed. Distal endopodal segment as long as proximal segment; furnished with 2 lateral hyaline frills and large spinules along medial margin; armed medially with 2 spines and naked seta and apically with 1 pilose, 1 naked and 5 geniculate setae (lateralmost geniculate seta fused basally with pilose seta).

Labrum (Fig. 27E) subtriangular, with denticulate membrane on distal margin.

Mandible (Fig. 28A) composed of coxa and 2-segmented palp. Coxal gnathobase with numerous unicuspidate teeth along distal margin and unilaterally denticulate seta on inner distal angle. Proximal and distal segments of palp equal in length; proximal segment unarmed and naked; distal segment armed with 2 pairs of basally fused setae.

Maxillule (Fig. 28B) composed of praecoxa and 3-segmented palp. Praecoxal arthrite bears proximal spinules near inner margin, 2 medial setae, 2 anterior surface setae, and 6 apical elements (1 unipinnate; 3 naked; 2 highly chitinized, with minute spinules along distal half of inner margin). Coxal endite elongated, with anterior surface spinules and 3 apical setae. Basis ¾ length of coxa, bears subapical naked seta and 4 apical naked setae. Endopod 1-segmented, small, armed with 2 unequal naked setae. Exopod absent.

Maxilla (Fig. 28C) 3-segmented, composed of syncoxa, allobasis and 1-segmented endopod. Syncoxa unornamented, with proximal endite represented by pilose seta; distal endite bears 1 pectinate and 2 naked apical setae. Allobasis drawn out into long claw furnished with spinules along distal half of inner margin; with proximal pectinate seta on posterior surface. Endopod 1-segmented, inserted on anterior surface of allobasal claw and armed with 2 long distal setae.

Maxilliped (Fig. 28D) 3-segmented, comprising syncoxa, basis and 1-segmented endopod. Syncoxa stout, with proximal spinules on posterior surface and distal naked seta. Basis equal in length to endopod, with few apical spinules along outer margin. Endopod drawn out into long claw furnished with denticles along distal half of inner margin; bears proximal naked seta.

Legs 1–4 biramous (Figs 28E–F, 29A–B); leg 1 with trimerous rami; legs 2–4 with trimerous exopod and bimerous endopod. Armature on rami of legs 1 to 4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	I-I	I-0; I-0; II,2	0-1; 0-0; I,2
Leg 2	0-0	I-0	I-0; I-0; II,I+1	0-0; I
Leg 3	0-0	1-0	I-0; I-0; II,I+1	0-0; I
Leg 4	0-0	1-0	I-0; I-0; II,I+1,2	0-0; I

Leg 1 (Fig. 28E) intercoxal sclerite slightly wider than long, without surface ornamentation. Coxa with 3 spinular rows (2 with long spinules; 1 with minute spinules) on anterior surface. Basis with 3 groups of long spinules on anterior surface; outer spine with

subapical flagellate element; inner spine short, furnished with few denticles. Outer distal angle of proximal and middle exopodal segments produced forming rounded spinulose protuberance. Setae on terminal exopodal segment geniculate. Inner seta on proximal endopodal segment highly chitinized, furnished with spinules distally. Middle seta on terminal endopodal segment geniculate. All spines on rami denticulate. Proximal and distal exopodal segments and middle endopodal segment with naked inner margin.

Leg 2 (Fig. 28F) intercoxal sclerite about 1.6 times as long as wide, without surface ornamentation. Coxa with 3 spinular rows (2 contains minute spinules; 1 with long spinules) on anterior surface. Basis similar to that of leg 1, except without spinules and spine on inner margin. Exopod ornamented as in leg 1, except with additional spinular row on inner distal angle of proximal and middle segments; inner apical seta on terminal segment naked, reduced, about 0.35 times as long as adjacent spine. Distal endopodal segment with large spinules flanking insertion point of apical spine.

Leg 3 (Fig. 29A) identical to leg 2, except basis with outer setulate seta.

Leg 4 (Fig. 29B) similar to leg 3, except basis with outer naked seta and terminal exopodal segment bears 2 more elements.

Leg 5 (Fig. 29C) biramous. Basoendopod with setophore bearing outer basal seta; endopodal lobe with median pore, few lateral spinules, 3 distal setae (2 spinulate, 1 spiniform) and inner spiniform seta. Exopod about 1.9 times as long as wide, with 3 lateral naked setae, weakly spinulate apical seta and inner element (position of missing inner element indicated by arrow in Fig. 29C).

Legs 6 (Fig. 26B) reduced, completely fused, forming genital operculum armed with 1 pinnate seta on either side.

Male. Total body length (measured from tip of rostrum to posterior margin of caudal rami), based on 4 specimens, 395–420 µm, mean 407.5 µm; largest width (75 µm) measured at posterior end of cephalothorax. Prosome composed of cephalothorax and 3 free pedigerous somites; ornamented as in female. Urosome comprised of fifth pedigerous somite, genital somite and 4 free abdominal somites. Genital somite (Fig. 30A) wider than long, with minutely serrated hyaline frill. Postgenital somites (Fig. 30A) ornamented as those of female, except without paired lateral spinular rows on first and second somites. Caudal ramus (Fig. 30A) about 1.7 times as long as wide; armed and ornamented as in female.

Antennule (Figs 30B–D) 10-segmented, haplocerate, with geniculation between segments 7 and 8. Armature as follows: 1, 9, 7, 2, 9+ae, 2, 3, 4, 4, and 8. Segment 1 with spiniform seta, spinular row and tubular pore as in female. Short spiniform seta present on segment 4. Short spinulate seta(e) present on segments 5–7. Aesthetasc and adjacent seta on segment 5 fused basally. One small and 2 large spines present on inner margin of segment 8. Two apical setae on segment 10 fused basally.

Inner basal spine of leg 1 (Fig. 30E) modified into stout, apically barbed spine.

Terminal endopodal segment of leg 2 (Fig. 30F) without large spinules near insertion point of apical spine.

Terminal endopodal segment of leg 3 (Fig. 30G) with apical fringe of minute spinules and extra naked seta; apical spine slightly deflected outward and lacks large spinules at insertion point.

Leg 5 (Fig. 31A) biramous, with basoendopods fused medially. Basoendopod with setophore bearing outer basal seta; endopodal lobe with median pore and 2 apical elements. One dissected paratype with abnormal basoendopod (Fig. 31B). Exopod about 1.9 times as long as wide, with 3 lateral naked setae, weakly spinulate apical seta and 2 inner elements (position of missing inner distal element indicated by arrow in Fig. 31A).

Leg 6 (Figs 30A, 31C) asymmetrical (both sinistral and dextral formations present) and unornamented; each side represented by articulating operculum armed with 2 setae on genital somite.

Etymology. This species is named for Mr. Lex Bastian, in recognition of his long-term involvement with the Yanchep Caves invertebrate monitoring program.

Remarks. The new species described herein shows a close resemblance to members of the genus *Nitocrella* Chappuis, 1923 [*sensu* Petkovski (1976)], *Novanitocrella* Karanovic, 2004 and *Abnitocrella* Karanovic, 2006 in having a 3-segmented endopod on leg 1, armature of I-0 on the proximal exopodal segment of legs 2 to 4, two outer spines on the distal exopodal segment of legs 1 to 4, bimerous endopod on legs 2 to 4, and sexually dimorphic leg 3. The new species also shares an apomorphic 1-segmented antennal exopod armed with an apical seta with *Nitocrella japonica* Miura, 1962 and *Abnitocrella halsei* Karanovic, 2006, armature of I-0 on the middle exopodal segment of legs 2 to 4 with *Nitocrella kunzi* Galassi & Pesce, 1997 and both *Novanitocrella* species, armature of 0-0; I on the endopod of legs 2 to 4 with *Nitocrella paceae* Pesce, 1980 and *N. africana* Chappuis, 1955, a plesiomorphic leg 5 in both sexes with *Nitocrella* and *Novanitocrella*, and sexually dimorphic leg 2 with *Nitocrella*. Despite these shared features, the new species here attributed to *Paranitocrella* **n. gen.** contains a suite of characters not known to occur in *Nitocrella*, *Novanitocrella* and *Abnitocrella*.

The hyaline frill on the urosomal somites of *Nitocrella*, *Novanitocrella* and *Abnitocrella* is a complete cuticular membrane that is, depending on the species, either smooth, highly serrated or minutely denticulated along the posterior margin. In *Paranitocrella* **n. gen.**, on the other hand, the hyaline frill on the urosomites is not only minutely serrated along the posterior margin but also incised longitudinally at regular intervals along its length to form a series of rectangular lappets.

The proximal antennulary segment of *Nitocrella*, *Novanitocrella* and *Abnitocrella* (and other ameirid genera) consistently bears a proximal row of spinules and a distal spinulate seta. The proximal antennulary segment in *Paranitocrella* **n. gen.** is unique among the Ameiridae in having, along with the two aforementioned features, a large tubular pore on the dorsal surface. This integumental structure was hitherto known to occur only on the body somites, antenna and post-maxillipedal limbs of some ameirid species, in *Psammameira hyalina* Noodt, 1952, *P. parasimulans* (Lang, 1965) and *Inermipes humphreysi* Lee & Huys, 2002 for example (see Conroy-Dalton & Huys 1998; Lee & Huys 2002).

The outer margin of the bases of legs 1 and 2 is armed with a spine in *Nitocrella*, *Novanitocrella*, *A. halsei* (this element is absent in the first two leg pairs of *Abnitocrella eberhardi* Karanovic, 2006) and *Paranitocrella* **n. gen.** This outer element is commonly furnished with minute denticles along the margins in the first three taxa. In *Paranitocrella* **n. gen.**, this outer element also bears an accessory flagellate element subapically. This accessory structure is not unique to the new species, as it has evolved independently in other copepod groups, such as the stygobitic calanoids *Bunderia misophaga* Jaume & Humphreys, 2001 and *Hondurella verrucosa* Suárez-Morales & Iliffe, 2007 and the parasitic cyclopoid *Naricolax chrysophryenus* (Roubal, Armitage & Rohde, 1983) (see Jaume & Humphreys 2001; Suárez-Morales & Iliffe 2007; Hutson & Tang 2007).

The inner apical seta on the distal exopodal segment of legs 2 to 4 is invariably pinnate and more importantly as long as the outer apical element in *Nitocrella*, *Novanitocrella* and *Abnitocrella*. This inner element is naked and reduced, being about one-third as along as the outer apical element, in *Paranitocrella* **n. gen.** This apomorphy is, however, not unique to the new species, as it has been documented in members of *Pseudoleptomesochrella* Lang, 1965 (see Sak et al. 2008).

Sexual dimorphism in the distal endopodal segment of leg 3 is similar between *A. halsei* (the male has yet to be described for *A. eberhardi*) and representatives of *Nitocrella* in that the length of one of the two apical elements on the distal segment is altered in the male. For example, the inner element is considerably shorter in the male than in the female in some *Nitocrella* species, such as *N. ensifera* Cottarelli, Bruno & Berera, 2007 and *N. japonica*, but conversely, longer in the male than in the female in *A. halsei* (Miura 1962a; Karanovic 2006; Cottarelli et al. 2007). Dimorphism in the distal endopodal segment of leg 3 in *Novanitocrella aboriginesi* Karanovic, 2004 (the male has yet to be described for *N. aestuarina* Coull & Bell, 1979) and *Paranitocrella* **n. gen.** is profoundly different from that of *Nitocrella* and *A. halsei*. In male *N. aboriginesi*, the distal segment is more elongate, and of the three rather than two apical elements, the outer element is modified into a curved spine and the inner seta is considerably reduced as compared to in the female (Karanovic 2004a). The distal endopodal segment in male *Paranitocrella* **n. gen.**, in contrast, lacks large spinules at the insertion point of the apical spine and bears additional structures such as an apical fringe of minute spinules and, more significantly, an inner subapical naked seta.

The fundamental differences, as discussed above, between the new species and *Nitocrella*, *Novanitocrella* and *Abnitocrella* are sufficient to justify the establishment of a new ameirid genus. *Paranitocrella* **n. gen.** can be distinguished from these related genera by the following combination of characters: 1) urosome with well developed hyaline frill forming rectangular lappets; 2) antennule with tubular pore on first segment; 3) antenna with 1-segmented exopod armed with an apical seta; 4) outer spine on the bases of legs 1 and 2 with accessory flagellate element; 5) legs 1 to 4 without inner seta on proximal and middle exopodal segments; 6) legs 2 to 4 with reduced inner apical seta on the terminal exopodal segment; 7) legs 2 to 4 with 2-segmented endopods, of which the proximal segment is unarmed and the distal segment bears an apical spine; 8) well developed leg 5 in both sexes;

and 9) male leg 3 endopod bears an additional apical fringe of minute spinules and inner subapical naked seta on the distal segment.

Family Canthocamptidae Brady, 1880

Subfamily Canthocamptinae Brady, 1880

Genus *Attheyella* Brady, 1880

Attheyella (*Chappuisiella*) *hirsuta* Chappuis, 1951

Material examined. Boomerang Cave (YN99), Yanchep National Park, Western Australia (31°32'33"S, 115°41'24"E): 19 ♀♀ and 17 ♂♂, 14 November, 1996; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 39 ♀♀ (1 dissected and mounted on slide), 19 ♂♂ (1 dissected and mounted on slide), and 10 copepodites, 17 July, 1992; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 14 ♀♀, 7 ♂♂, and 5 copepodites, 1995; 12 ♀♀ (1 dissected and mounted on slide) and 6 ♂♂ (1 dissected and mounted on slide), 9 October, 2006; 6 ♀♀, 7 ♂♂, and 2 copepodites, 9 October, 2007; Sue's spring (South), Bullsbrook, Western Australia (31°38'42"S, 115°58'17"E): 1 ♀ and 2 ♂♂, 1 February, 2008.

Remarks. *Attheyella* (*Chappuisiella*) *hirsuta* was established by Chappuis (1951) based on two specimens of each sex collected from a moss sample obtained by a waterfall along Guide River in Tasmania. Hamond (1987) subsequently redescribed in detail this species (as *Canthocamptus hirsutus*) based on specimens associated with wet moss samples collected from the type locality and inland waters of Victoria. As *A.* (*Ch.*) *hirsuta* was hitherto known only from Tasmania and Victoria, its collection in Western Australia represents a large range extension for this freshwater taxon. Furthermore, this is the first record of this species from the hypogean environment.

Genus *Australocamptus* Karanovic, 2004

Australocamptus hamondi Karanovic, 2004

Material examined. Boomerang Cave (YN99), Yanchep National Park, Western Australia (31°32'33"S, 115°41'24"E): 1 ♀, 17 July, 1992; 2 ♀♀ (1 dissected and mounted on slide), 28 August, 1994; Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E): 2 ♂♂ (1 dissected and mounted on slide), 28 August, 1994; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 1 ♀ and 1 ♂, 17 July, 1992; Egerton spring, Ellenbrook, Western Australia (31°46'18"S, 115°58'51"E): 2 ♂♂, 20 December, 1994.

Remarks. *Australocamptus hamondi* was established, along with *A. similis* and *A. diversus*, by Karanovic (2004a) based on samples collected from boreholes in the Murchison Region of Western Australia. The occurrence of *A. hamondi* in several caves and a spring in the Gnangara Mound Region extends its known distribution to the south-west of Western Australia and supports Karanovic's (2004a) premise that this species is stygobitic.

Genus *Elaphoidella* Chappuis, 1928

Elaphoidella bidens (Schmeil, 1894)

Material examined. Boomerang Cave (YN99), Yanchep National Park, Western Australia (31°32'33"S, 115°41'24"E): 1 ♀, 17 July, 1992; 1 ♀, 28 August, 1994; Spillway Cave (YN565), Yanchep National Park, Western Australia (31°32'41"S, 115°40'37"E): 6 ♀♀, 8 November, 2005; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 14 ♀♀ (1 dissected and mounted on slide) and 3 copepodites, 17 July, 1992; Edgecombe spring, Ellenbrook, Western Australia (31°47'39"S, 115°59'43"E): 1 ♂, 4 November, 1995.

Remarks. *Elaphoidella bidens* (Schmeil, 1894) is a cosmopolitan species that typically inhabits the littoral zone of large waterbodies (Gurney 1932; Lewis 1972). In Australia, this species is known to occur commonly in slow-moving streams or lakes in South Australia, Victoria, New South Wales and Queensland (Hamond 1987). The presence of *E. bidens* from the Gnangara Mound Region, accordingly, represents the first record of this species in Western Australia. Although the occurrence of this species in the hypogean environment of Western Australia is unusual, it is certainly not unique as it has been reported previously from caves in the Ryukyu Islands of Japan (Miura 1962b) and North America (Reeves et al. 2000).

Family Parastenocarididae Chappuis, 1940

Genus *Parastenocaris* Kessler, 1913

Parastenocaris eberhardi Karanovic, 2005

Material examined. Carpark Cave (YN18), Yanchep National Park, Western Australia (31°33'08"S, 115°41'08"E): 7 ♀♀ (1 dissected and mounted on slide) and 8 ♂♂ (1 dissected and mounted on slide), 31 October, 1996; Gilgie Cave (YN27), Yanchep National Park, Western Australia (31°34'07"S, 115°41'18"E): 1 ♀, 17 March, 1993; 1 ♂, 28 August, 1994; 1 ♀ and 4 ♂♂, 27 November, 1996; Orpheus Cave (YN256), Yanchep National Park, Western Australia (31°31'00"S, 115°40'10"E): 1 ♂, 17 July, 1992; Twilight Cave (YN194), Yanchep National Park, Western Australia (31°34'05"S, 115°41'21"E): 1 ♀ and 1 ♂, 9 October, 1992; 1 ♀, 27 November, 1996; YN7 bore, Yanchep National Park, Western Australia (31°33'17"S, 115°41'13"E): 18 ♀♀, 12 ♂♂, and 3 copepodites, 28 August, 1994; Edgecombe spring, Ellenbrook, Western Australia (31°47'39"S, 115°59'43"E): 1 ♀, 4 November, 1995.

Remarks. *Parastenocaris eberhardi* was established by Karanovic (2005a) to accommodate specimens of both sexes collected from Strongs Cave and Kudjal Yolgah Cave located in the Margaret River Region of Western Australia. The discovery of this species in the caves and spring of the Gnangara Mound Region, therefore, extends its known distribution northwards. Besides *P. eberhardi*, three other members of *Parastenocaris* Kessler, 1913 are known to exist, all from bore samples, in Western Australia: *P. solitaria* Karanovic, 2004, *P. kimberleyensis* Karanovic, 2005 and *P. jane* Karanovic, 2006. *Parastenocaris kimberleyensis* and *P. jane* occur north of the Tropic of Capricorn, whilst *P. eberhardi* and *P. solitaria* are distributed south of the tropics (Karanovic 2004a, 2005a, 2006).

DISCUSSION

Taxonomy

Although *Metacyclops arnaudi* (Sars, 1908) has been recorded on numerous occasions from Victoria and Western Australia following Sars (1908) original description, the morphological details of this species remained incomplete which made accurate comparisons with other taxa difficult (Fiers 2001). In this study, the description of both sexes of *M. arnaudi* from Western Australia, in conjunction with Morton's (1977) account and our recent observations of conspecific material from Victoria, revealed that this taxon is: a) undoubtedly a member of *Metacyclops* Kiefer, 1927; b) belongs to the "*trispinosus*"-group *sensu* Karanovic (2004a); and c) commonly exhibits variability in legs 3 and 4. The armature of the first antennulary segment of female *M. arnaudi* was also found to be highly unique in that the presence of seven setae and an aesthetasc on this limb segment has not been documented previously within the Cyclopidae. In this family, the first antennulary segment in the adult female is typically armed with eight setae, of which six are arranged essentially along the anterior margin and two vertically alongside each other on the ventral surface (Karaytug & Boxshall 1998; Schutze et al. 2000; Karaytug et al. 2004). Relatively few cyclopid species bear only seven (e.g., *Metacyclops pilanus* Karanovic, 2004 and *M. laurentiisae* Karanovic, 2004) or even six (e.g., *Goniocyclops uniarticulatus* Karanovic, 2004) setae on the first antennulary segment. It appears that the aesthetasc on *M. arnaudi* is, based on its position, homologous with the anteriormost seta of the ventral pair in other cyclopid species. Nevertheless, an investigation of the developmental stages of *M. arnaudi* is warranted to determine precisely the homology of this element and at which stage it appears during ontogeny. It is unclear at this juncture whether this aesthetasc is present or absent in Sars' (1908) specimens, as it was not depicted in his illustration of the antennule. Collection of topotype material is, therefore, also highly desirable to resolve this issue, as well as other morphological discrepancies noted previously between our specimens and Sars' material.

Prior to this study, the taxonomic affinities between members of the genus *Mixocyclops* Kiefer, 1944 were not firmly established (Lindberg 1954). Dr. Frank Fiers' recent observations on the type material of *Mixocyclops crozetensis* Kiefer, 1944 indicated that this taxon, together with *Mixocyclops minutus* Chappuis, 1951 and *Mixocyclops mortoni* **n. sp.**, form a natural group. There are currently 12 cyclopine genera that have a distinctly 2-segmented leg 5 similar to *Mixocyclops*. These genera are: *Cyclops* O. F. Müller, 1776, *Mesocyclops* G. O. Sars, 1914, *Acanthocyclops* Kiefer, 1927, *Diacyclops* Kiefer, 1927, *Megacyclops* Kiefer, 1927, *Thermocyclops* Kiefer, 1927, *Kieferiella* Lescher-Moutoué, 1976, *Caspicyclops* Monchenko, 1986, *Reidcyclops* Karanovic, 2000, *Abdiacyclops* Karanovic, 2005, *Zealandcyclops* Karanovic, 2005 and *Orbuscyclops* Karanovic, 2006. In the 11-segmented antennule, absence of an exopodal seta on the antenna, 2-segmented rami on legs 1 to 4 and sexual dimorphism in the exopod of legs 3 and 4, *Mixocyclops* resembles *Reidcyclops*. *Mixocyclops* is distinguishable from *Reidcyclops* by having a long apical seta and minute inner spine, as opposed to two long apical setae, on the distal segment of leg 5. *Mixocyclops* further differs from *Reidcyclops* by having one distomedial seta on the antennal coxobasis, the mandibular palp represented by a surface seta, two elements on the distal endopodal segment of the maxilla, one inner spinulate seta on the syncoxa of the maxilliped, absence of an inner seta on leg 1 basis, setal formula 3.3.3 on the distal exopodal segment of legs 2 to 4 in both sexes, and an unarmed inner margin on the proximal and middle exopodal segments of male legs 3 and 4. Of these, only the last two are autapomorphies of *Mixocyclops*. One or more of the remaining features occurs in species of other cyclopine genera. For instance, one distomedial seta on the antennal coxobasis and a seta inserted on the surface of the mandible have also been described in *Bryocyclops muscicola* (Menzel, 1926), *Fimbricyclops jimhensoni* Reid, 1993, *Itocyclops yezoensis* (Itô, 1953) and *Zealandcyclops fenwicki* Karanovic, 2005 (Reid 1993, 1999; Reid & Ishida 2000; Karanovic 2005b). It is highly plausible that a detailed redescription of *M. crozetensis* and *M. minutus*, which is currently being undertaken by Dr. Fiers (*in litt.*), will lead to further improvements in the concept of the genus *Mixocyclops*.

Copepod diversity of the Gnangara Mound Region

Examination of numerous copepod samples obtained predominantly from caves and springs within the Gnangara Mound Region revealed a total of 15 species, classified into two orders, four families and 14 genera (Table 1). Of these, one genus and four species are new to science. This collection has also generated several new records, of which one cyclopoid species, *Tropocyclops confinis* (Kiefer, 1930), is recorded from Australia for the first time and the canthocamptid harpacticoids *Attheyella* (*Chappuisiella*) *hirsuta* Chappuis, 1951 and *Elaphoidella bidens* (Schmeil, 1894) are newly recorded for Western Australia. The occurrence of the cosmopolitan *Paracyclops chiltoni* (Thomson, 1882) on the Australian continent is also confirmed. Of particular biogeographic interest was the discovery of *Paracyclops intermedius* **n. sp.**, a taxon that is undoubtedly affiliated with the *P. affinis*-group as it possesses a mixture of morphological details characteristic of both *Paracyclops* *affinis* (G. O. Sars, 1863) and *P. canadensis* (Willey, 1934). Karaytug (1998) hypothesized previously that the common ancestor of *P. canadensis* and *P. affinis* most likely had a Holarctic distribution, and subsequently split into these two species following the separation of North America from Eurasia during the Palaeocene. With the discovery of a new member of the *P. affinis*-group within Australia, it is now evident that a Pangaean distribution pattern for the ancestor of this group is more plausible than a Holarctic origin.

The cave and spring sites contained considerably more copepod species than the bore and surface sites (Table 1), which may be attributed to the much greater sampling effort applied at the former set of sites. Of the 58 samples examined, eight (14%) were obtained collectively from all bore and surface sites. Among individual sites, Twilight Cave (YN194) was the most species rich with seven taxa, followed closely by Egerton spring with six species. *Paracyclops chiltoni* was the most common species within the study area as it was collected from multiple caves, bores and springs. *Australoeucyclops* sp. was, however, the most common species in the Yanchep Caves, occurring in all but two cave sites. *Metacyclops arnaudi* (Sars, 1908) was the only species absent from groundwaters. Two species, *T. confinis* and *Nitocra lacustris pacifica* Yeatman, 1983, were rarely encountered; these taxa were collected on a single occasion during the entire sampling campaign. The abundance of individuals was also generally low (< 15 individuals) for most species found in groundwaters. This may be due to the fact that a limited number of root mat and sediment sweeps were taken at the caves and springs, respectively, during each sampling period in order to minimise the ecological impacts on these threatened habitats. Nonetheless, some copepod species did occur in relatively high densities as evidenced by the collection of 411 individuals of *Australoeucyclops* sp. and 68 of *A.* (*Ch.*) *hirsuta* in a single sample from Yellagonga Cave (YN438) and Twilight Cave (YN194), respectively.

The copepod fauna recorded in the caves and springs of the Gnangara Mound Region are comparable, with respect to species richness, the varying degrees of dependency on the subterranean environment and endemicity, to those reported from similar habitats in South Australia (Zeidler 1989) and the Leeuwin-Naturaliste and Pilbara Regions of Western Australia (Eberhard 2004; Halse et al. 2002b) (Table 2). At least 10 copepod species were found in the Gnangara Mound and Leeuwin-Naturaliste caves, as well as at the Gnangara Mound, Pilbara and Dalhousie springs. Only four copepod taxa were, however, recorded from all three Leeuwin-Naturaliste springs combined, but these sites were, according to Eberhard (2004), not sampled as intensively as the cave sites. Not all copepod species occurring in the caves and/or springs of these four areas are stygobitic either, as 50–100% of the taxa are facultative groundwater animals. In the Gnangara Mound Region, only *Eucyclops edytae* **n. sp.**, *P. bastiani* **n. gen. et n. sp.**, *Australocamptus hamondi* Karanovic, 2004 and *Parastenocaris eberhardi* Karanovic, 2005 are considered stygobites (4/15 or 27% of total species) (Table 1). The copepods from the caves and/or springs of these four areas are also comprised mostly of widespread taxa as evidenced by the low proportion (0–40%) of endemics. The only species endemic to the Gnangara Mound Region are *E. edytae* **n. sp.** (occurs primarily in springs and rarely in the Yanchep Caves), *P. bastiani* **n. gen. et n. sp.** (confined to Yanchep Caves) and *P. intermedius* **n. sp.** (found in springs so far but may be more widespread than the present collection indicates – see Remarks section) (3/15 or 20% of total species). The variable nature of groundwater dependency and geographical distribution exhibited collectively by the Yanchep Cave copepods, most of which belong to different lineages, is undoubtedly attributed to independent invasions of the caves by each taxon.

Despite the similarities discussed above, the species composition between the Gnangara Mound and the Pilbara, Dalhousie and Leeuwin-Naturaliste Regions differs considerably. Of the 10 and 12 species collected from the Pilbara and Dalhousie springs, respectively, only one (the cosmopolitan *P. chiltoni*) is shared with the Gnangara Mound springs. The caves and springs of the Leewuin-Naturaliste Region, on the other hand, have more taxa (*Australoeucyclops* sp., *M. albidus*, *Mesocyclops brooksi* Pesce, De Laurentiis & Humphreys, 1996, *N. l. pacifica* and *P. eberhardi*) in common with those of the Gnangara Mound Region. This is not unexpected given that these two areas have similar environmental histories, are separated by only 300 km and contain caves that occur in similar geological formations (Bowler 1976; Jasinska & Knott 2000). It is worth noting, however, that among the five aforementioned taxa, only *P. eberhardi* is unique to the Gnangara Mound and Leeuwin-Naturaliste Regions, as *Australoeucyclops* sp. occurs 200 km north of Yanchep National Park (Tang & Knott, unpublished data), *M. albidus* is a cosmopolitan species (Dussart & Defaye 2006), *M. brooksi* occurs throughout Western Australia, including the Pilbara Region (Hołyńska & Brown 2003; Karanovic 2006), and *N. l. pacifica* is widespread in Australasia (Yeatman 1983; Fiers 1986; Karanovic 2004a). The occurrence of the epigean *M. arnaudi* and stygophilic *A.* (*Ch.*) *hirsuta* in the Gnangara Mound Region further indicates faunal connections with southeastern Australia. *Metacyclops arnaudi* has also been reported from Victoria, South Australia and Tasmania (Geddes 1976; Morton & Bayly 1977; Morton 1977), whilst *A.* (*Ch.*) *hirsuta* was hitherto known only from Tasmania and Victoria (Chappuis 1951; Hamond 1987). According to Pinder et al. (2004), many aquatic invertebrates (about two-thirds of 957 taxa) inhabiting wetlands and rivers in the neighbouring Wheatbelt Region of southwestern Western Australia are also known to occur in southeastern Australia.

The 13 copepod species found in the Yanchep Caves must have originated from the interstices of the Gnangara Mound considering that there is no direct surface drainage into any of the caves (Jasinska & Knott 2000) and nearly all of these taxa were found in the springs further east (Table 1). With the exception of *Paranitocrella bastiani* **n. gen. et n. sp.**, all copepod species collected from the Gnangara Mound Region belong to lineages that have originated and radiated in fresh water. *Paranitocrella bastiani* **n. gen. et n. sp.** represents a relictual marine form as this taxon is almost certainly derived from *Nitocrella* Chappuis, 1923, a group that is known to occur in coastal and brackishwater habitats (Galassi 2001; Karanovic 2004a). As the present Swan Coastal Plain was repeatedly inundated by the sea during the Cretaceous (Frakes et al. 1987), it is not difficult to imagine, via the Two-step model (Boutin & Coineau 1990; Notenboom 1991), that the marine benthic ancestor of *P. bastiani* **n. gen. et n. sp.** invaded the interstices of the western margin of the Australian continent during one or more of these marine transgression episodes and became isolated within inland groundwater following regression of the sea. Whether the thalassostybiont ancestor speciated into the present form prior to or after invasion of the Yanchep Caves requires further investigation, but we speculate that *P. bastiani* **n. gen. et n. sp.** has had a long period of isolation in groundwater as evidenced by the numerous apomorphic features contained by this species.

The inventory of 15 copepod taxa provided herein is far from complete, particularly considering that only a fraction of the Gnangara Mound Region, which covers an area of about 2,200 km^2 (Western Australian Planning Commission 1999b), was investigated, viz. 17 (74%) of the sampling sites were restricted within Yanchep National Park, and sampling was limited primarily to the hypogean environment. Nevertheless, our findings indicate that the Gnangara Mound area contains a relatively rich copepod fauna. For comparison, Karanovic (2004a, 2006) found 30 and 41 subterranean copepod species amongst extensive bore and well samples obtained, respectively, throughout the dramatically larger Murchison and Pilbara Regions of Western Australia (respective total area of 316,239 km^2 and 178,017 km^2; Beard 1990). We predict that further sampling of hypogean and especially epigean habitats in the Gnangara Mound Region will almost certainly uncover additional copepod taxa.

Conservation

In Australia, groundwater ecosystems are under threat by human activities such as groundwater abstraction, mining, agriculture and land clearance, which often alters the quantity and quality of water available to subsurface animals (Boulton et al. 2003; Humphreys 2006). Indeed, Jasinska & Knott (2000) noted that the extraction of groundwater from the Gnangara Mound for Perth's public and industry needs has led to the progressive lowering of the water table, causing some habitats fed by the Gnangara Mound groundwater, such as the springs on the eastern side of this unconfined aquifer or Crystal Cave (YN1) in Yanchep National Park, to become seasonally or permanently dry.

Currently, the habitat and associated aquatic fauna of both Edgecombe and Egerton springs are under immediate threat by the recent land clearance and development of residential properties to within *ca*. 20 m west of each spring (Knott et al. 2008). Local recharge will likely cease at Egerton spring as the residential homes were constructed uphill from the discharge point. The present condition of Bevan Peter's and Mrs. King's springs is unknown, as these habitats have not been visited in recent times. In contrast to Edgecombe and Egerton springs, the newly discovered Sue's spring appears relatively undisturbed and, according to the landholder, flows constantly throughout the year. As such, this spring, along with the surrounding vegetation, should be protected to conserve the local flora and fauna, especially the endemic cyclopoid copepod *E. edytae* **n. sp.**

Although pumps, sumps and black plastic liners are currently used in Cabaret (YN30), Boomerang (YN99) and Carpark (YN18) Caves to combat the dehydration of the root mats, these artificial measures have proven to be ineffective due to frequent mechanical failure of the pumps and, more importantly, the unabated decline of the water table in the Gnangara Mound. As a result, Boomerang and Carpark Caves, along with Fridge Grotto (YN81) and Gilgie (YN27) Caves, have completely dried up. The water level in Cabaret, Lot 51 (YN555) and Water (YN11) Caves are also at all-time historic lows, leading to the reduction in extent and quality of root mats as well as a decrease in abundance and diversity of aquatic fauna at these sites (Knott et al. 2008). The continual degradation of these groundwater-dependent habitats is cause for concern, particularly for the locally endemic harpacticoid copepod *Paranitocrella bastiani* **n. gen. et n. sp.** This species has not been found in the Yanchep Caves since the 1990s (Knott & Storey 2001, 2002, 2003, 2004; Knott et al. 2006, 2007, 2008), which suggests that it may have already gone extinct. Clearly, alternative and effective management strategies need to be developed and implemented promptly by the appropriate governmental agencies to reestablish the natural environment of the caves. We anticipate that *P. bastiani* **n. gen. et n. sp.** will recolonise the Yanchep Caves, should it still occur in some unknown groundwater refuge of the Gnangara Mound, once root mats are restored and sufficient water levels are maintained permanently. As recharge of the Gnangara Mound is directly linked to rainfall infiltration (Davidson 1999), conservation of the caves, including the surrounding native vegetation (e.g. tuart trees), will be undoubtedly challenging given that southwestern Australia is predicted to receive less rainfall than other parts of the continent during this century (Hughes 2003).

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Figure Captions

FIGURE 1. Map of the Gnangara Mound Region of Western Australia showing the 23 sampling locations.

FIGURE 2. *Eucyclops edytae* **n. sp.**, adult female. (A) habitus, dorsal; (B) urosome, ventral; (C) anal somite and caudal rami, dorsal; (D) caudal ramus, ventral. Scale bars: A, 100 µm; B, 25 µm; C–D, 20 µm.

FIGURE 3. *Eucyclops edytae* **n. sp.**, adult female. (A) antennule, ventral; (B) antenna, frontal; (C) antennal coxobasis and proximal endopodal segment, caudal; (D) labrum, anterior; (E) mandible, posterior. Scale bars: A, 25 µm; B–C, E, 20 µm; D, 10 µm.

FIGURE 4. *Eucyclops edytae* **n. sp.**, adult female. (A) maxillule, posterior; (B) maxilla, posterior; (C) maxilliped, posterior; (D) leg 1 with exopod disarticulated from basis, anterior. Scale bars: A, 10 µm; B–C, 20 µm; D, 25 µm.

FIGURE 5. *Eucyclops edytae* **n. sp.**, adult female. (A) leg 2, anterior; (B) leg 3, anterior; (C) leg 4, anterior; (D) leg 4 intercoxal sclerite and coxa, posterior. Scale bars: A–C, 25 µm; D, 15 µm.

FIGURE 6. *Eucyclops edytae* **n. sp.**, adult female (A–B) and adult male (C–F). (A) leg 5, ventral; (B) leg 6, lateral; (C) habitus, dorsal; (D) antennule, ventral; (E) leg 3 basis, anterior; (F) urosomites 1 and 2 showing legs 5 and 6, ventral. Scale bars: A, D, F, 20 µm; B, E, 10 µm; C, 100 µm.

FIGURE 7. *Paracyclops intermedius* **n. sp.**, adult female. (A) habitus, dorsal; (B) same, dorsal; (C) urosomites 2–5 and caudal rami, ventral. Scale bars: A–B, 100 µm; C, 50 µm.

FIGURE 8. *Paracyclops intermedius* **n. sp.**, adult female. (A) anal somite and caudal rami, dorsal; (B) antennule, ventral; (C) antenna, caudal; (D) antennal coxobasis and proximal endopodal segment, frontal; (E) labrum, anterior; (F) mandible, anterior. Scale bars: A, 25 µm; B–C, 20 µm; D–F, 10 µm.

FIGURE 9. *Paracyclops intermedius* **n. sp.**, adult female. (A) maxillule with palp disarticulated from coxa, posterior; (B) maxilla, posterior; (C) maxilliped, anterior; (D) leg 1 with inner coxal seta shown separately, anterior; (E) leg 1 intercoxal sclerite and coxa, posterior. Scale bars: A–B, D–E, 20 µm; C, 10 µm.

FIGURE 10. *Paracyclops intermedius* **n. sp.**, adult female. (A) leg 2 (sockets of spinules indicated by arrowhead), anterior; (B) leg 2 intercoxal sclerite and coxa, posterior; (C) leg 3 (sockets of spinules indicated by arrowhead), anterior; (D) leg 3 intercoxal sclerite and coxa posterior. Scale bars: A–D, 20 µm.

FIGURE 11. *Paracyclops intermedius* **n. sp.**, adult female (A–D) and adult male (E). (A) leg 4 (sockets of spinules indicated by arrowhead), anterior; (B) leg 4 intercoxal sclerite and basis, posterior; (C) leg 5, ventrolateral; (D) leg 6, lateral; (E) habitus, dorsal. Scale bars: A–B, 20 µm; C–D, 10 µm; E, 100 µm.

FIGURE 12. *Paracyclops intermedius* **n. sp.**, adult male. (A) antennule, ventral (with dorsal view of segments 6, 7, 9 and 10 shown separately); (B) leg 6, ventrolateral. Scale bars: A, 20 µm; B, 10 µm.

FIGURE 13. *Tropocyclops confinis* (Kiefer, 1930), adult female. (A) habitus, dorsal; (B) genital double-somite, ventral; (C) anal somite and caudal rami (position of missing seta VII and II on right and left ramus, respectively, indicated by arrowheads), ventral; (D) antennule, ventral; (E) antenna (position of missing seta indicated by arrowhead), frontal; (F) antennal coxobasis, caudal; (G) labrum, anterior. Scale bars: A, 100 µm; B–C, E, 20 µm; D, 50 µm; F, 15 µm; G, 10 µm.

FIGURE 14. *Tropocyclops confinis* (Kiefer, 1930), adult female. (A) mandible, anterior; (B) maxillule, posterior; (C) maxilla with anterodistal element on proximal endopodal segment shown separately, posterior; (D) maxilliped, posterior; (E) leg 1 (socket of missing seta indicated by arrowhead), anterior. Scale bars: A, 10 µm; B–D, 20 µm; E, 25 µm.

FIGURE 15. *Tropocyclops confinis* (Kiefer, 1930), adult female. (A) leg 1 intercoxal sclerite and coxa, posterior; (B) leg 2 (socket of missing seta indicated by arrowhead), anterior; (C) leg 2 intercoxal sclerite and coxa, posterior; (D) leg 3 exopod, anterior; (E) leg 3 intercoxal sclerite and coxa, posterior. Scale bars: A, C, E, 15 µm; B, D, 25 µm.

FIGURE 16. *Tropocyclops confinis* (Kiefer, 1930), adult female. (A) leg 4, anterior; (B) leg 4 intercoxal sclerite and coxa, posterior; (C) leg 5, ventrolateral. Scale bars: A, 25 µm; B, 15 µm; C, 10 µm.

FIGURE 17. *Metacyclops arnaudi* (Sars, 1908), adult female. (A) habitus, dorsal; (B) urosomites 2–5 and caudal rami, ventral. Scale bars: A, 100 µm; B, 50 µm.

FIGURE 18. *Metacyclops arnaudi* (Sars, 1908), adult female. (A) postgenital somites, dorsal; (B) antennule, ventral; (C) antenna, frontal; (D) antennal coxobasis, caudal; (E) labrum, anterior; (F) mandible, anterior; (G) maxillule, posterior. Scale bars: A, C, F, G, 20 µm; B, 25 µm; D–E, 10 µm.

FIGURE 19. *Metacyclops arnaudi* (Sars, 1908), adult female. (A) maxilla, posterior; (B) maxilliped, anterior; (C) leg 1, anterior; (D) leg 2, anterior. Scale bars: A–D, 20 µm.

FIGURE 20. *Metacyclops arnaudi* (Sars, 1908), adult female. (A) leg 3, anterior; (B) leg 3 terminal endopodal segment, anterior; (C) leg 4, anterior; (D) leg 4 coxa, posterior; (E) leg 4 terminal endopodal segment; (F) leg 5, ventral; (G) leg 6, lateral. Scale bars: A–F, 20 µm; G, 10 µm.

FIGURE 21. *Metacyclops arnaudi* (Sars, 1908), adult male. (A) habitus, dorsal; (B) antennule, dorsal (with ventral view of segments 1, 4 and 9 shown separately); (C) leg 5, ventral; (D) leg 6, ventral. Scale bars: A, 100 µm; B, 25 µm; C–D, 10 µm.

FIGURE 22. *Mixocyclops mortoni* **n. sp.**, adult female. (A) habitus, dorsal; (B) urosome, ventral; (C) anal somite and caudal rami, dorsal; (D) antennule, ventral (with dorsal view of segment 5 shown separately). Scale bars: A, 100 µm; B, D, 25 µm; C, 20 µm.

FIGURE 23. *Mixocyclops mortoni* **n. sp.**, adult female. (A) antenna, frontal; (B) labrum, anterior; (C) mandible, anterior; (D) maxillule with palp disarticulated from coxa, posterior; (E) maxilla, posterior; (F) maxilliped, posterior. Scale bars: A, 15 µm; B–F, 10 µm.

FIGURE 24. *Mixocyclops mortoni* **n. sp.**, adult female. (A) leg 1, anterior; (B) leg 2, anterior; (C) leg 3, anterior; (D) leg 4, anterior; (E) leg 5, ventrolateral; (F) leg 6, dorsolateral. Scale bars: A–D, 20 µm; E–F, 5 µm.

FIGURE 25. *Mixocyclops mortoni* **n. sp.**, adult female (A–C) and adult male (D–F). (A) leg 3 exopod (break along inner cuticle layer indicated by arrowhead), anterior; (B) leg 4 exopod (lateral transverse suture and break along inner cuticle layer indicated by arrowheads), anterior; (D) leg 3 exopod, anterior; (E) leg 4 exopod, anterior; (F) leg 6, ventral. Scale bars: A–F, 10 µm.

FIGURE 26. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult female. (A) habitus, lateral; (B) urosomites 2–5 and caudal rami, ventral. Scale bars: A, 50 µm; B, 25 µm.

FIGURE 27. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult female. (A) anal somite and caudal rami, dorsal; (B) rostrum, dorsal; (C) antennule (armature omitted on segments 3 and

4), ventral; (D) antennulary segment 3, ventral; (E) antennulary segment 4, ventral; (F) antenna, anterolateral; (G) labrum, anterior. Scale bars: A, C, 20 µm; B, G, 5 µm; D–F, 10 µm.

FIGURE 28. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult female. (A) mandible, anterior; (B) maxillule, posterior; (C) maxilla, anterior; (D) maxilliped, posterior; (E) leg 1, anterior; (F) leg 2, anterior. Scale bars: A–D, 10 µm; E–F, 20 µm.

FIGURE 29. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult female. (A) leg 3, anterior; (B) leg 4 (inner apical seta indicated by arrowhead), anterior; (C) leg 5 (position of missing element indicated by arrowhead), ventral. Scale bars: A–B, 20 µm; C, 10 µm.

FIGURE 30. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult male. (A) urosomites 2–6 and caudal rami, ventral; (B) antennule (armature omitted on segments 4 and 5), ventral; (C) antennulary segment 4, ventral; (D) antennulary segment 5, ventral; (E) leg 1 basis, anterior; (F) leg 2 endopod, anterior; (G) leg 3 endopod, anterior. Scale bars: A, 25 µm; B, D, F–G, 10 µm; C, E, 5 µm.

FIGURE 31. *Paranitocrella bastiani* **n. gen. et n. sp.**, adult male. (A) leg 5 (position of missing element indicated by arrowhead), ventral; (B) abnormal leg 5 basoendopod, ventral; (C) leg 6, ventral. Scale bars: A, C, 10 µm; B, 5 µm.

TABLE 1. Occurrence of freshwater copepods in the Gnangara Mound Region of Western Australia.

		Caves												Bores			Springs					Surface		
Taxon	Ecology	Boomerang (2)	Cabaret (8)	Carpark (2)	Lot 51 (6)	Fridge Grotto (1)	Gilgie (3)	Yellagonga (1)	Mire Bowl (4)	Orpheus (1)	Spillway (1)	Twilight (5)	Water (2)	YN3 (1)	YN5 (1)	YN7 (2)	Bevan Peters' (4)	Edgecombe (2)	Egerton (5)	Mrs. King's (2)	Sue's (South) (1)	Pool at Loch McNess (2)	Lake Yonderup (1)	Swamp near Carpark Cave (1)
Order Cyclopoida																								
Family Cyclopidae																								
Australoeucyclops sp.	Sp		*	*	*	*	*	*	*	*	*	*	*							*				
Eucyclops edytae n. sp.	Sb		*														*		*	*	*			
Macrocyclops albidus	Sp										*									*	*			
Paracyclops chiltoni	Sp	*	*								*	*	*	*	*		*	*	*		*			
Paracyclops intermedius n. sp.	S*																*		*	*				
Tropocyclops confinis	E				*																			
Mesocyclops brooksi	Sp				*						*											*		
Metacyclops arnaudi	E																					*	*	*
Mixocyclops mortoni n. sp.	Sp				*		*									*		*	*					
Order Harpacticoida																								
Family Ameiridae																								

Nitocra lacustris pacifica	Sp					*																		
Paranitocrella bastiani n. gen. et n.	Sb	*	*	*			*					*												
Family Canthocamptidae																								
Attheyella (*Chappuisiella*) *hirsuta*	Sp	*										*							*		*			
Australocamptus hamondi	Sb	*					*					*							*					
Elaphoidella bidens	Sp	*									*	*						*						
Family Parastenocarididae																								
Parastenocaris eberhardi	Sb			*			*			*		*				*		*						

Ecological codes: E = epigean; Sp = stygophile; Sb = stygobite; S* = possible stygophile.
The number of samples examined at each site is given in brackets following each site name.

TABLE 2. Freshwater copepods from caves and/or springs of Western Australia (Gnangara Mound Region – present study; Leeuwin-Naturaliste Region – Eberhard (2004); and Pilbara Region – Halse et al. (2002b)) and South Australia (Dalhousie – Zeidler (1989)).

	Western Australia					**South Australia**
	Gnangara Mound caves	Gnangara Mound springs	Leeuwin-Naturaliste caves	Leeuwin-Naturaliste springs	Pilbara springs	Dalhousie springs
Total no. of sites examined	12	5	11	3	5	37
No. of sites containing copepods	12	5	10	3	5	13
Total no. of taxa	12*	10[†]	10	4[‡]	10	12
No. of stygobitic taxa	4	3	5	1	1	0
No. of endemic taxa	1	2	4	1	0	1

* = *Tropocyslops confinis* (Kiefer, 1930) was not included as its occurrence in Lot 51 Cave (YN555) is regarded as accidental.

[†] = Nine taxa are also present in one or more Yanchep Caves.

[‡] = Two taxa are also present in one or more Leeuwin-Naturaliste caves.

Figure 1

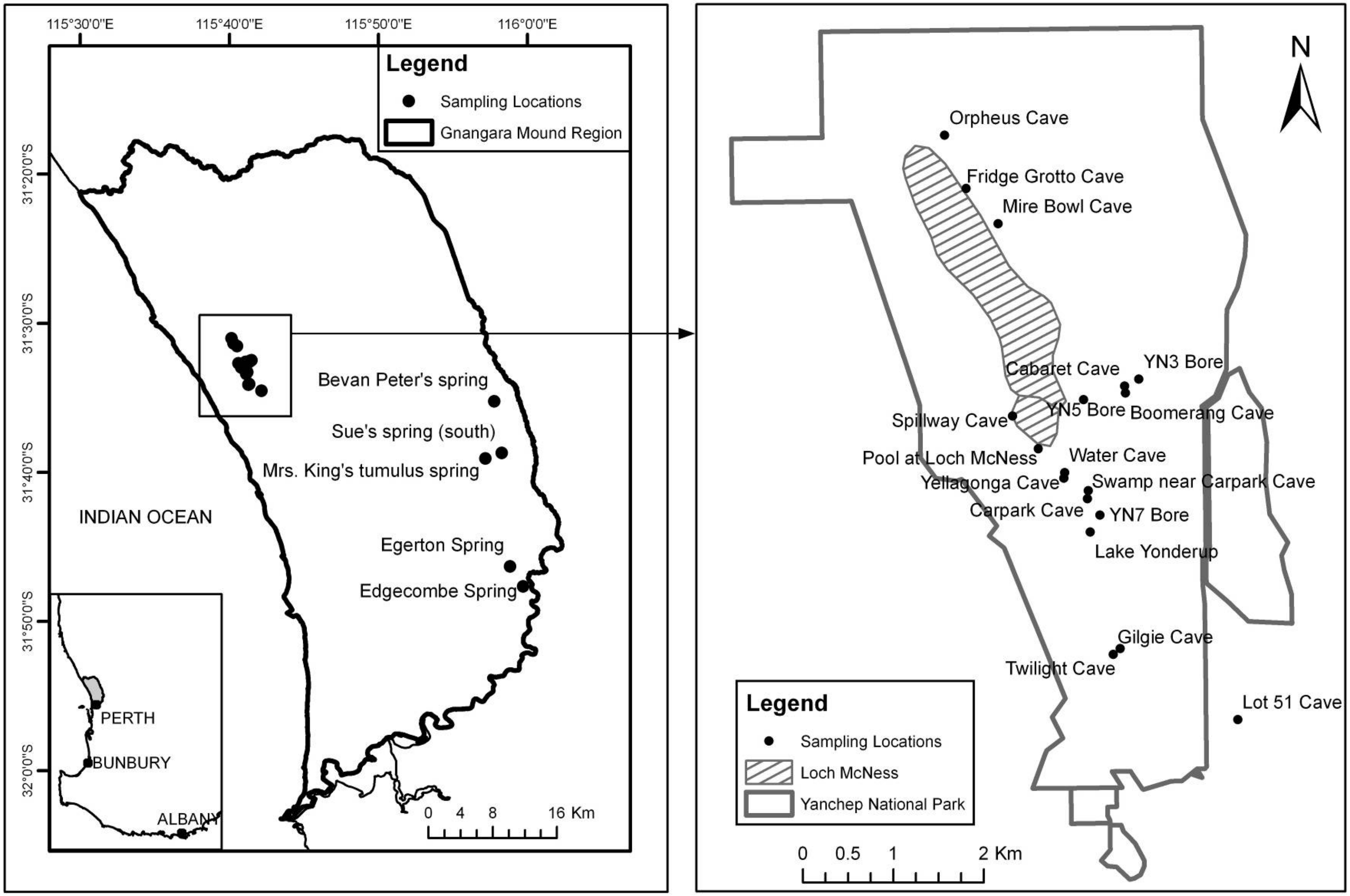
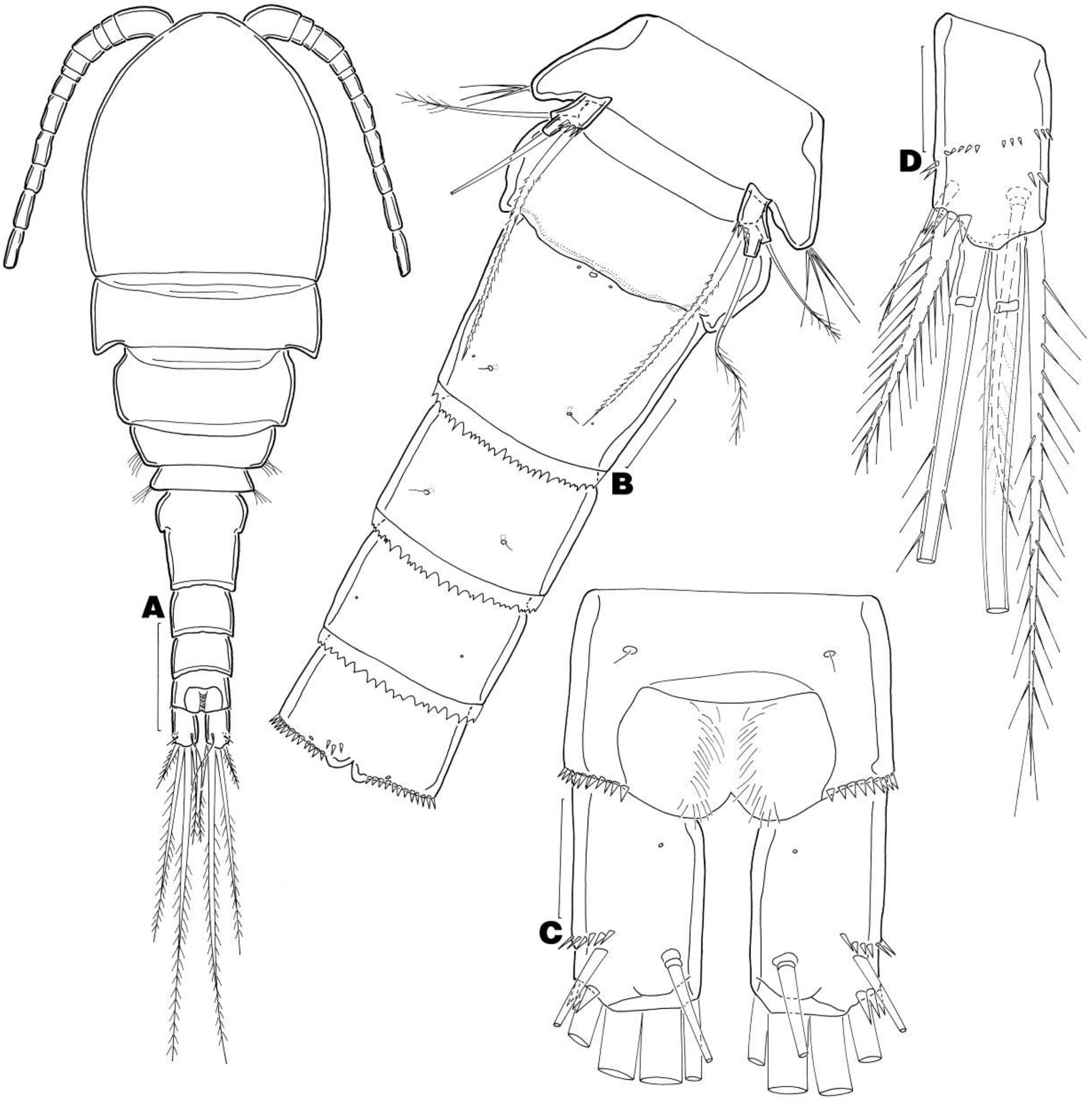

115°30'0"E
115°40'0"E
115°50'0"E
116°0'0"E
31°20'0"S
31°30'0"S
31°40'0"S
31°50'0"S
32°0'0"S
Legend
Sampling Locations
Gnangara Mound Region
Bevan Peter's spring
Sue's spring (south)
Mrs. King's tumulus spring
INDIAN OCEAN
Egerton Spring
Edgecombe Spring
PERTH
BUNBURY
ALBANY
0 4 8 16 Km
N
Orpheus Cave
Fridge Grotto Cave
Mire Bowl Cave
Cabaret Cave
YN3 Bore
YN5 Bore
Boomerang Cave
Spillway Cave
Pool at Loch McNess
Water Cave
Yellagonga Cave
Swamp near Carpark Cave
Carpark Cave
YN7 Bore
Lake Yonderup
Gilgie Cave
Twilight Cave
Lot 51 Cave
Legend
Sampling Locations
Loch McNess
Yanchep National Park
0 0.5 1 2 Km

Figure 2



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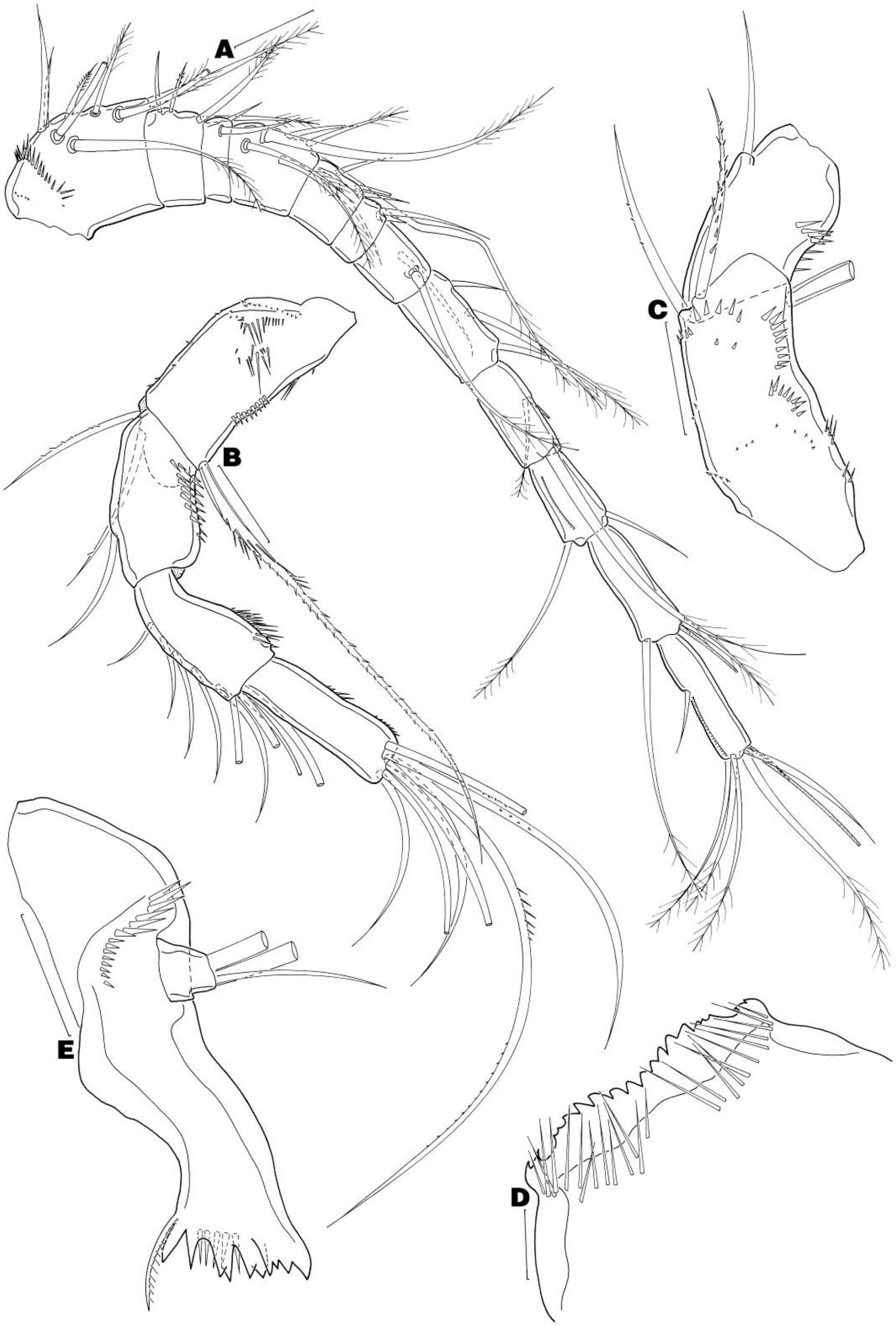

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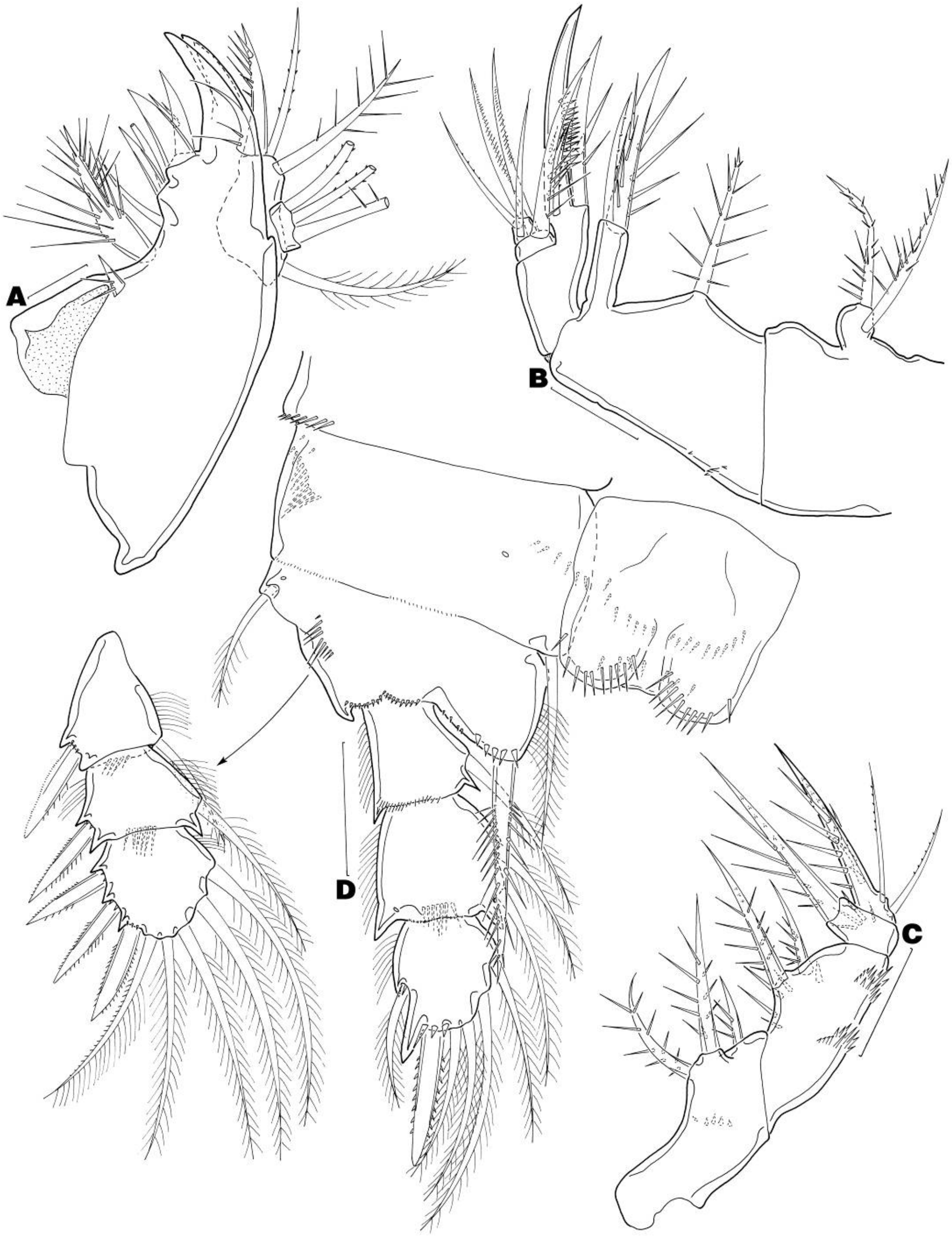

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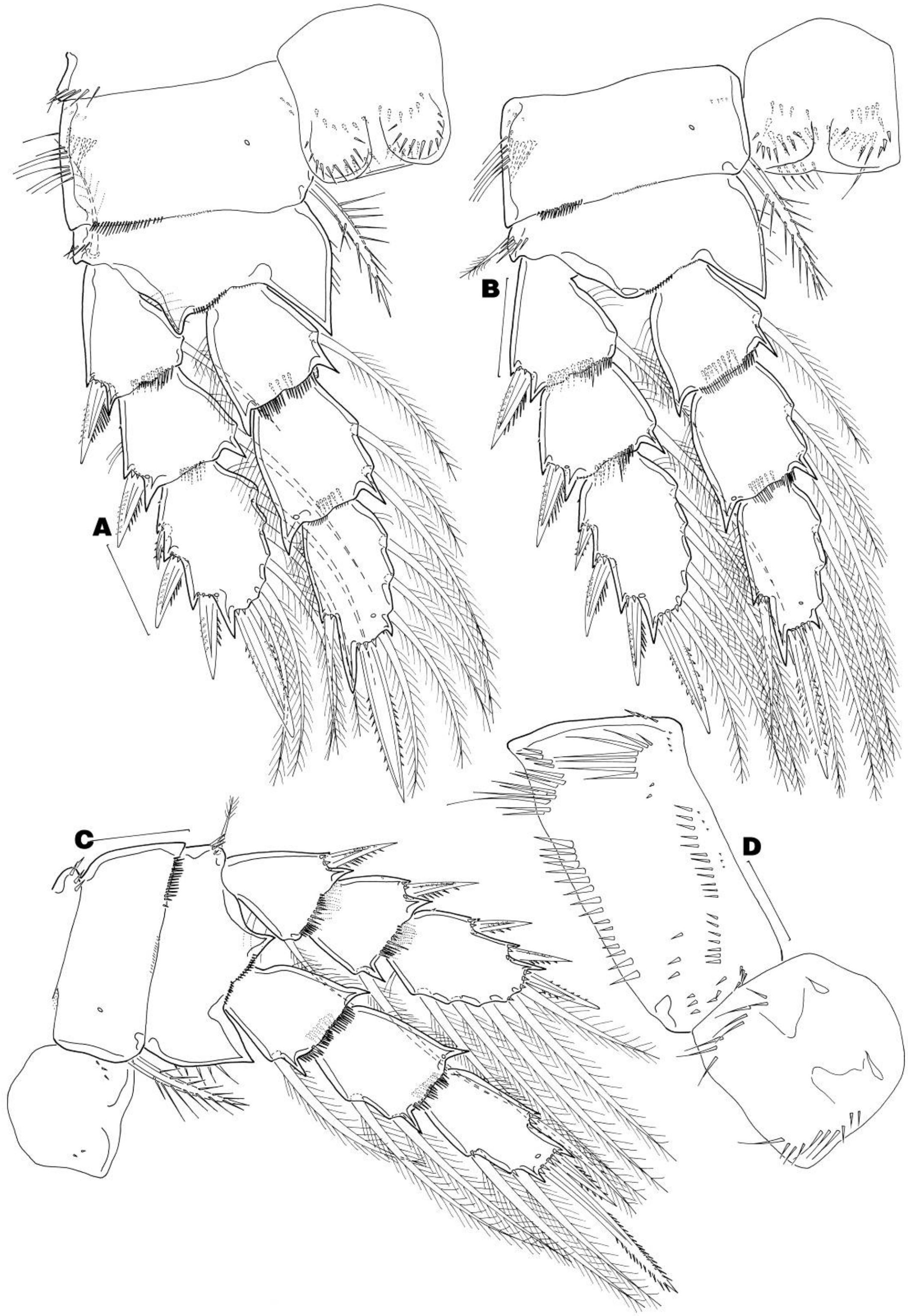

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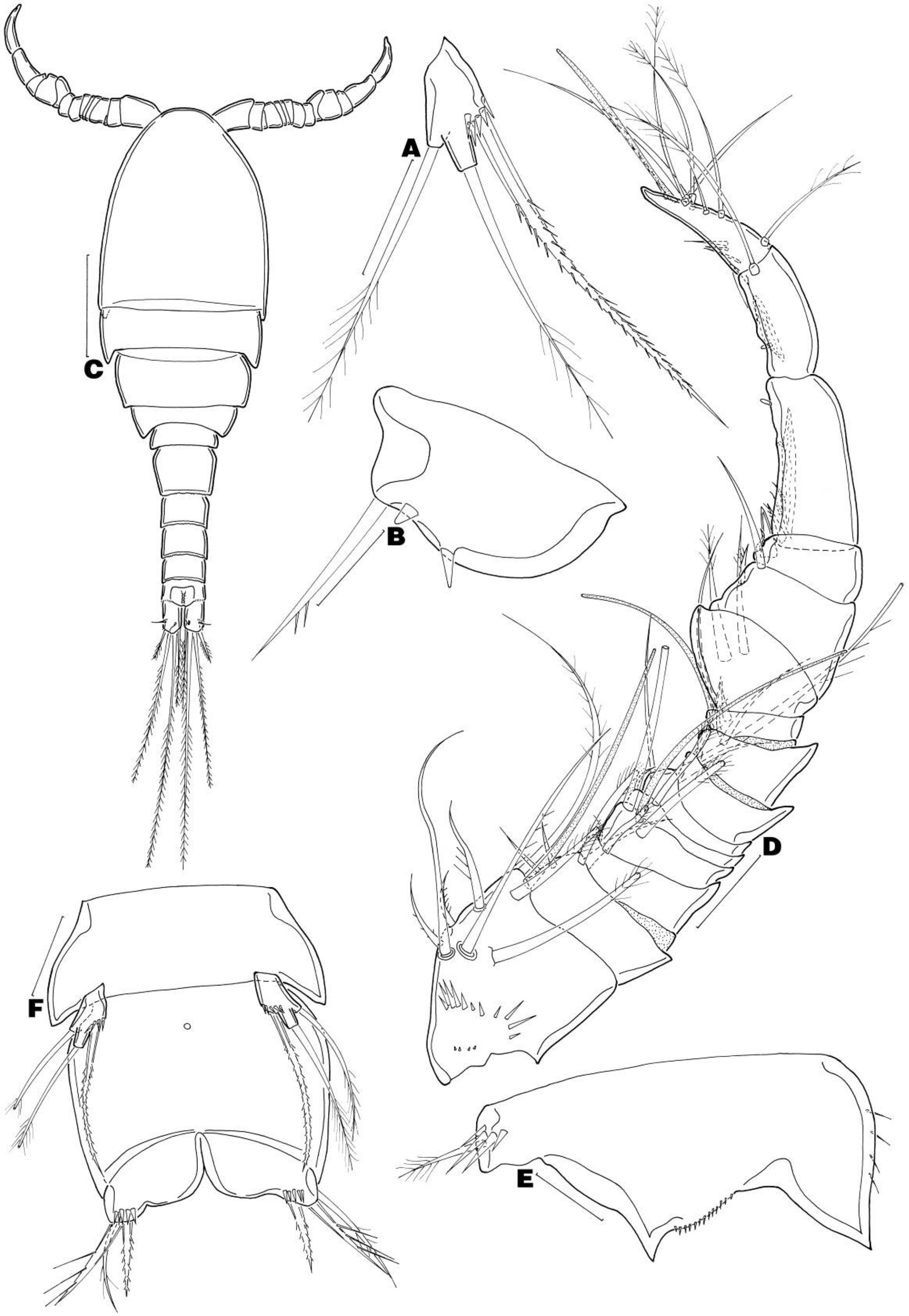

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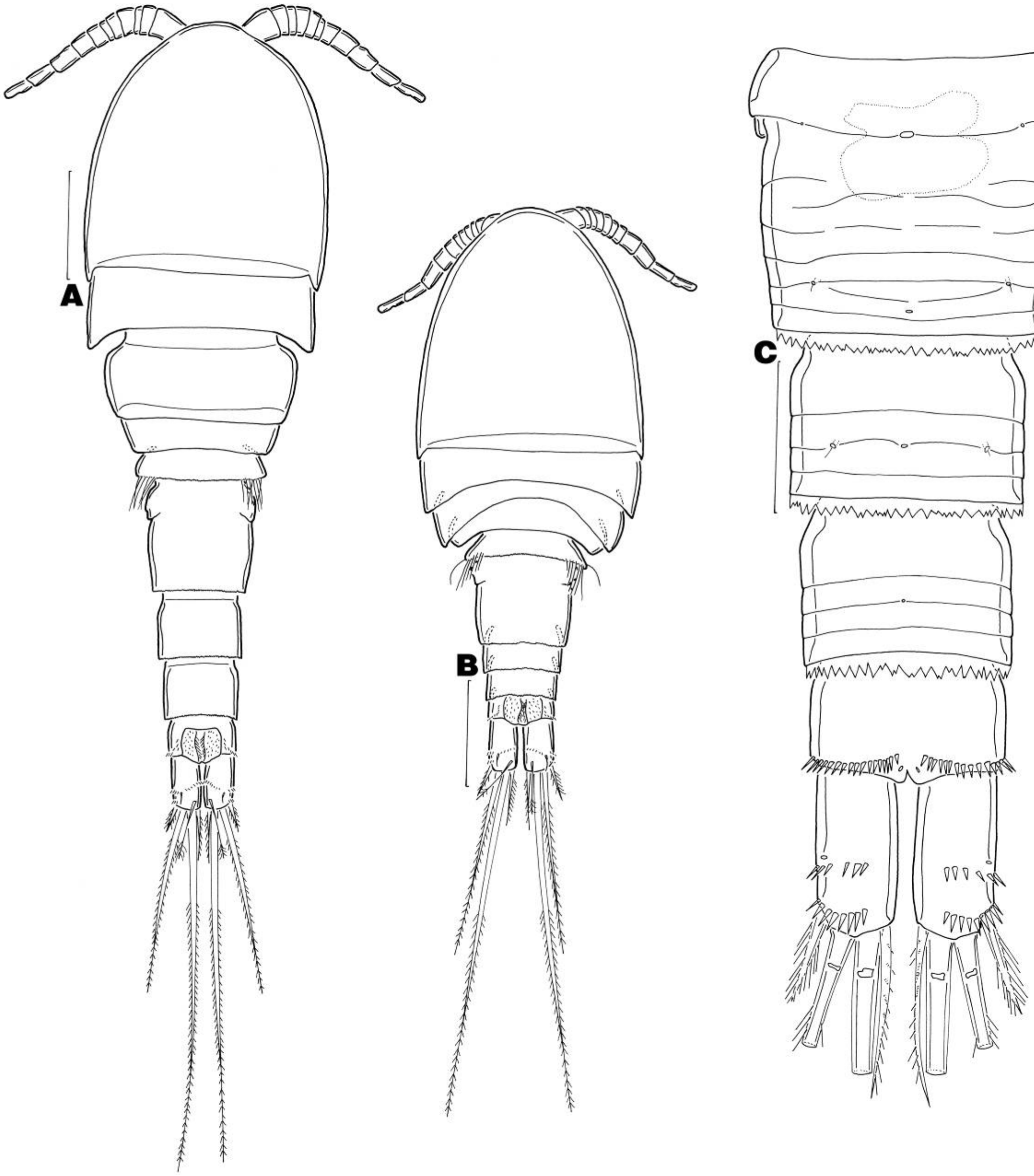

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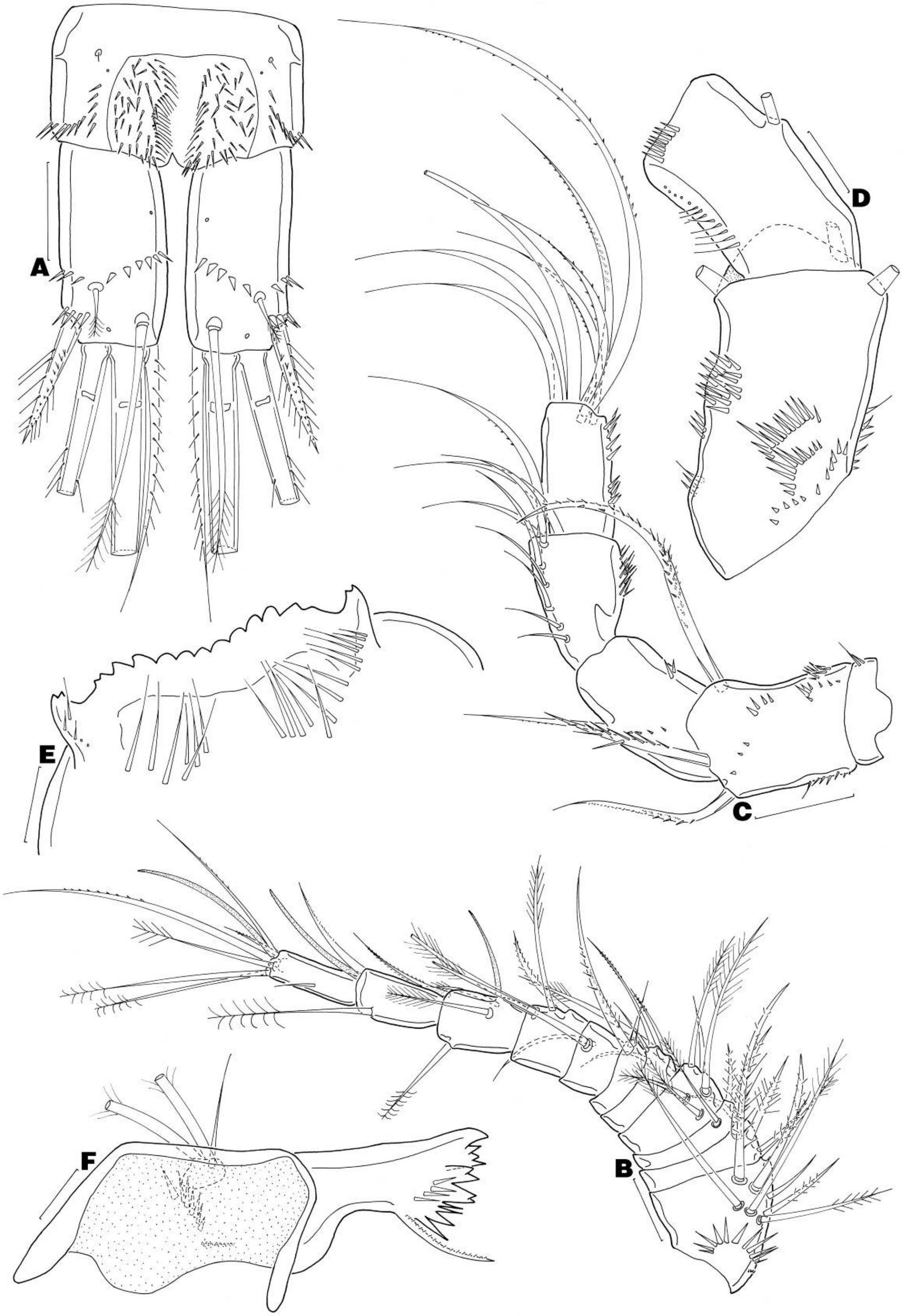

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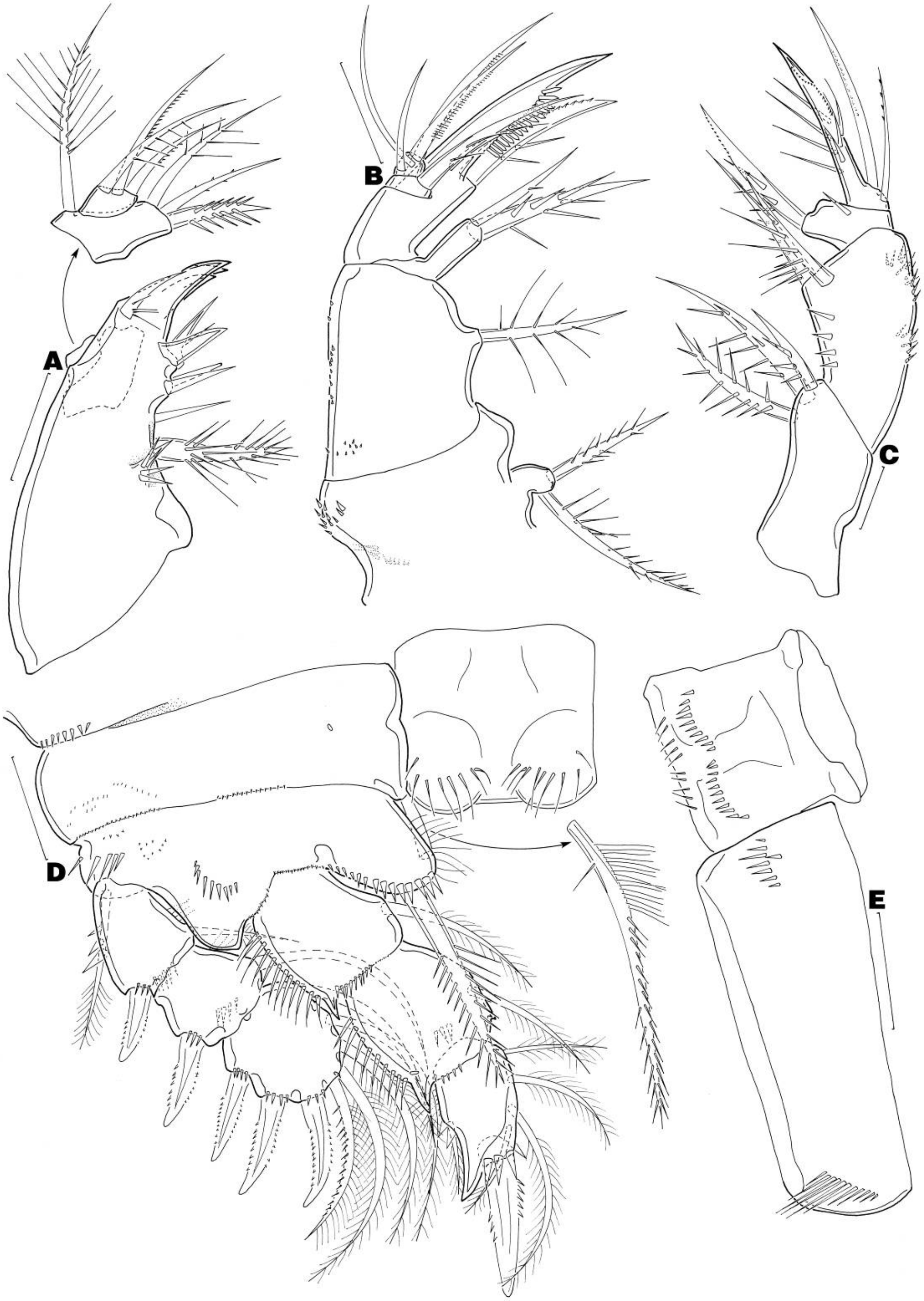

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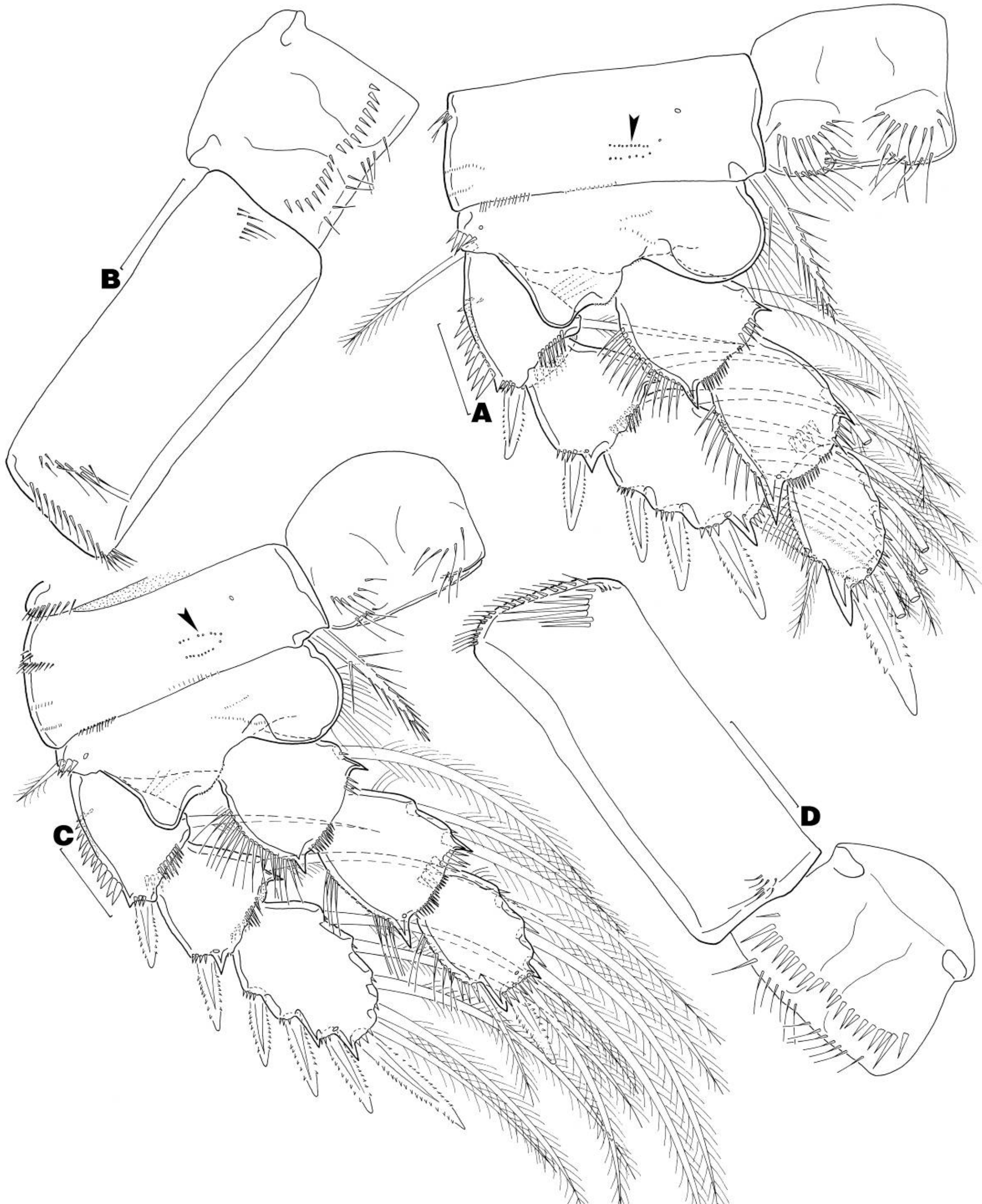

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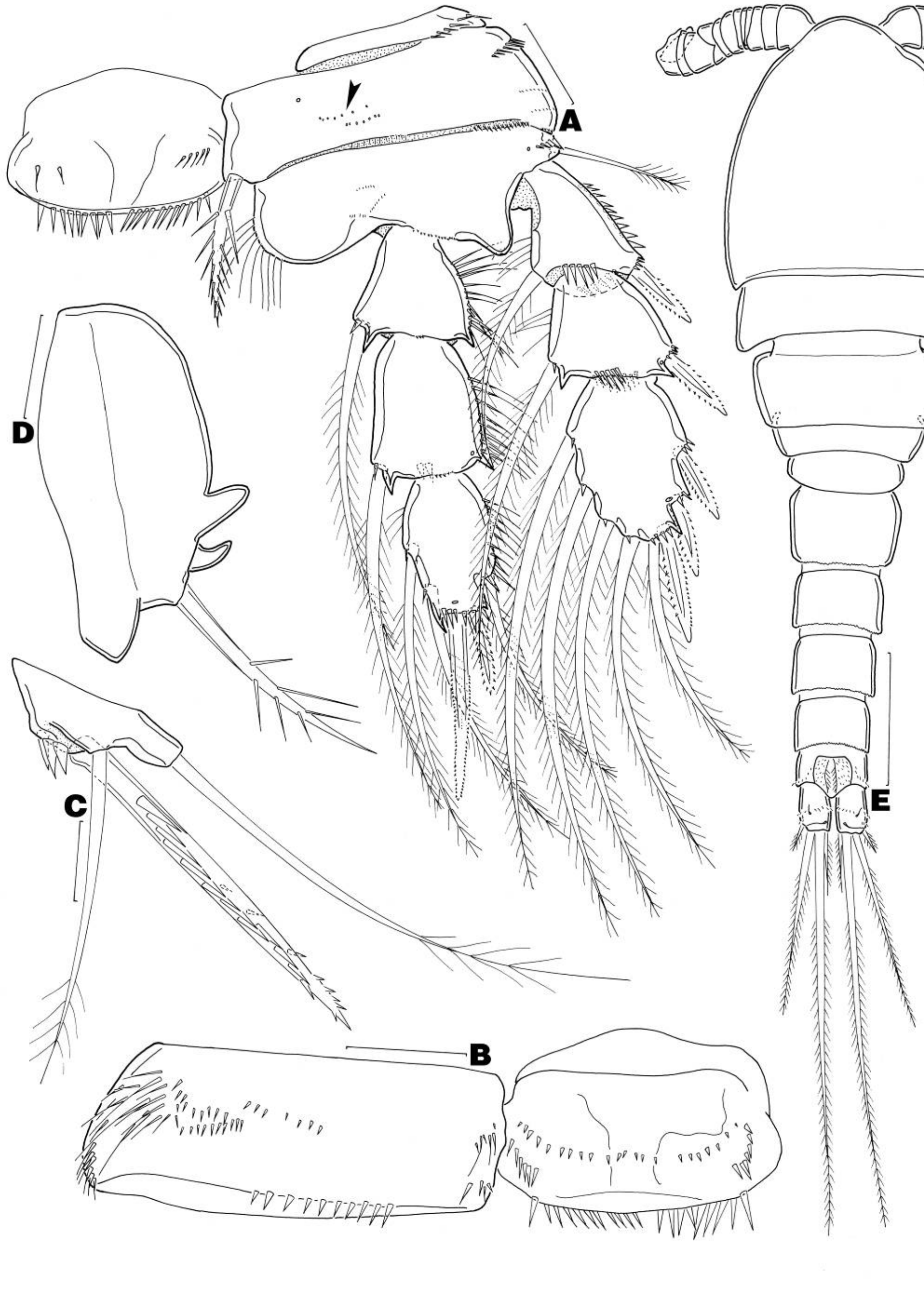

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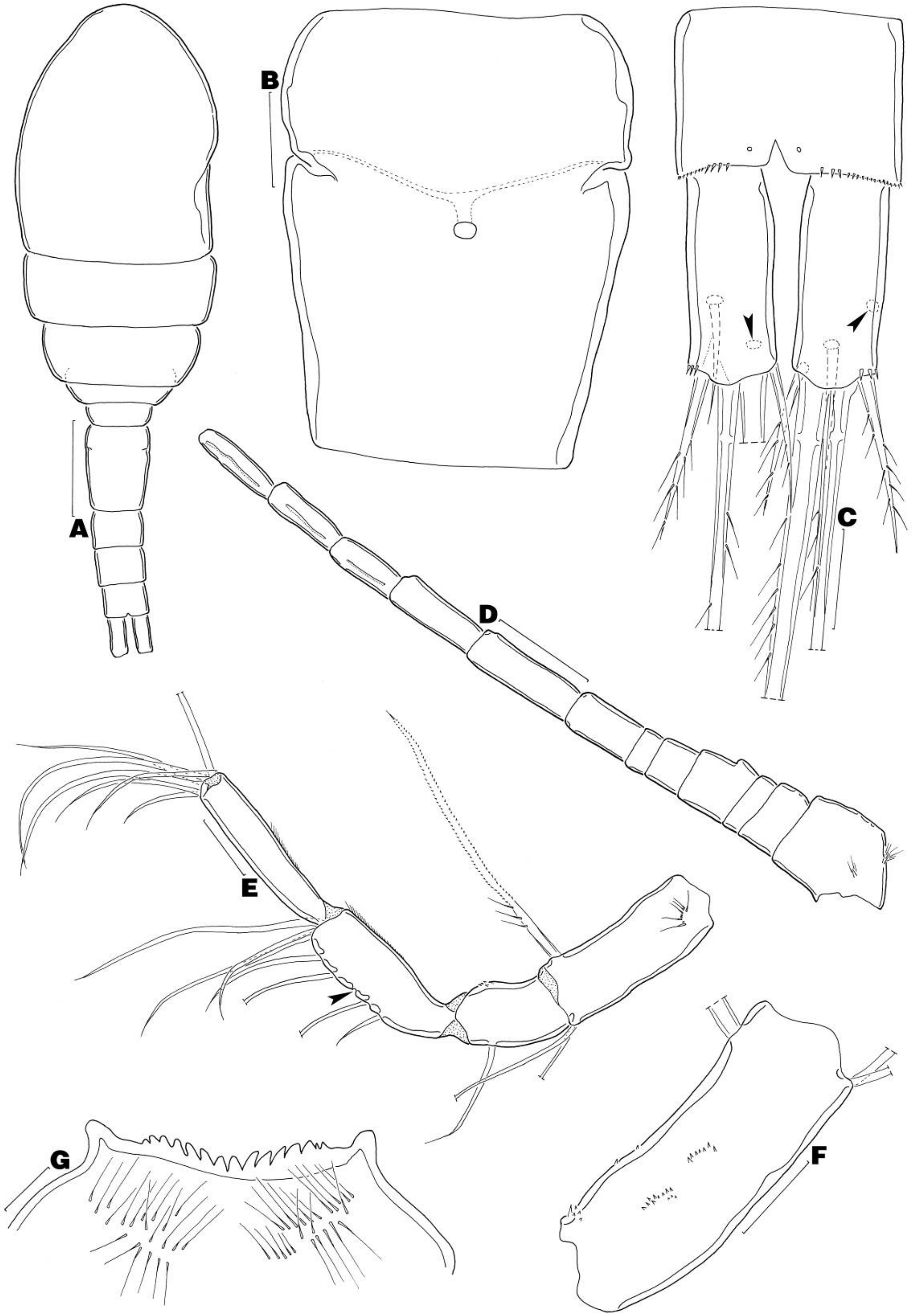
Figure 13



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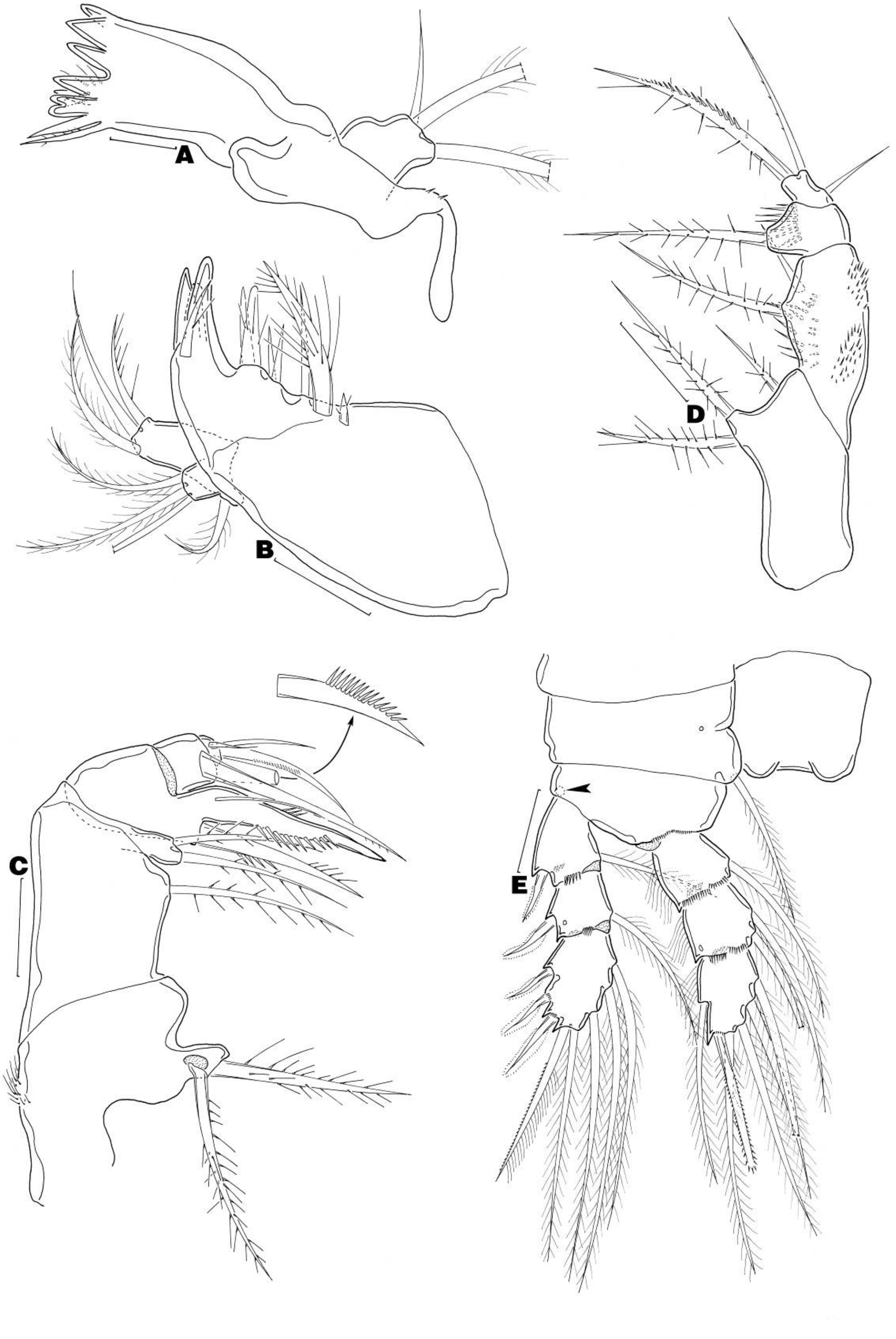

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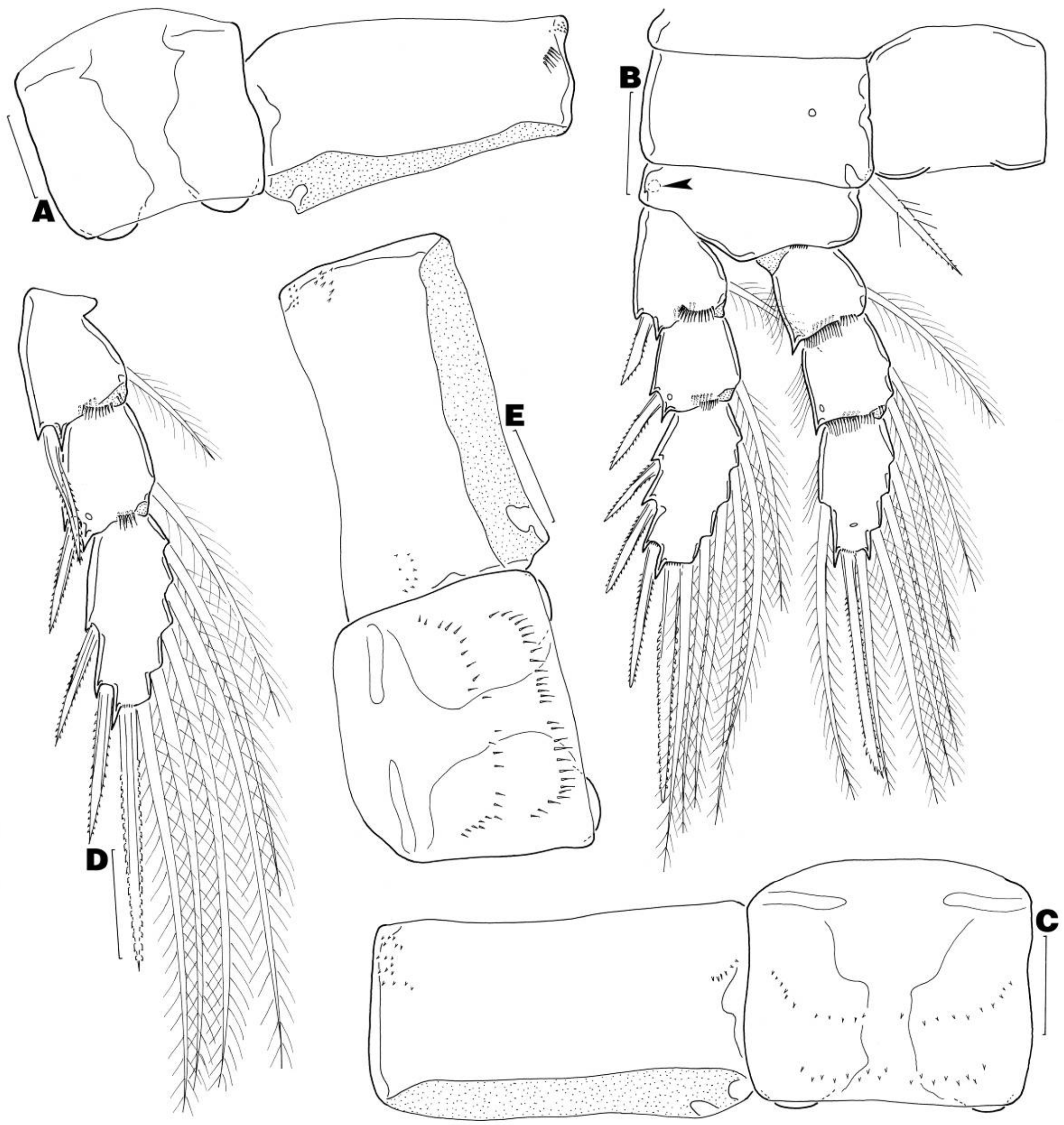

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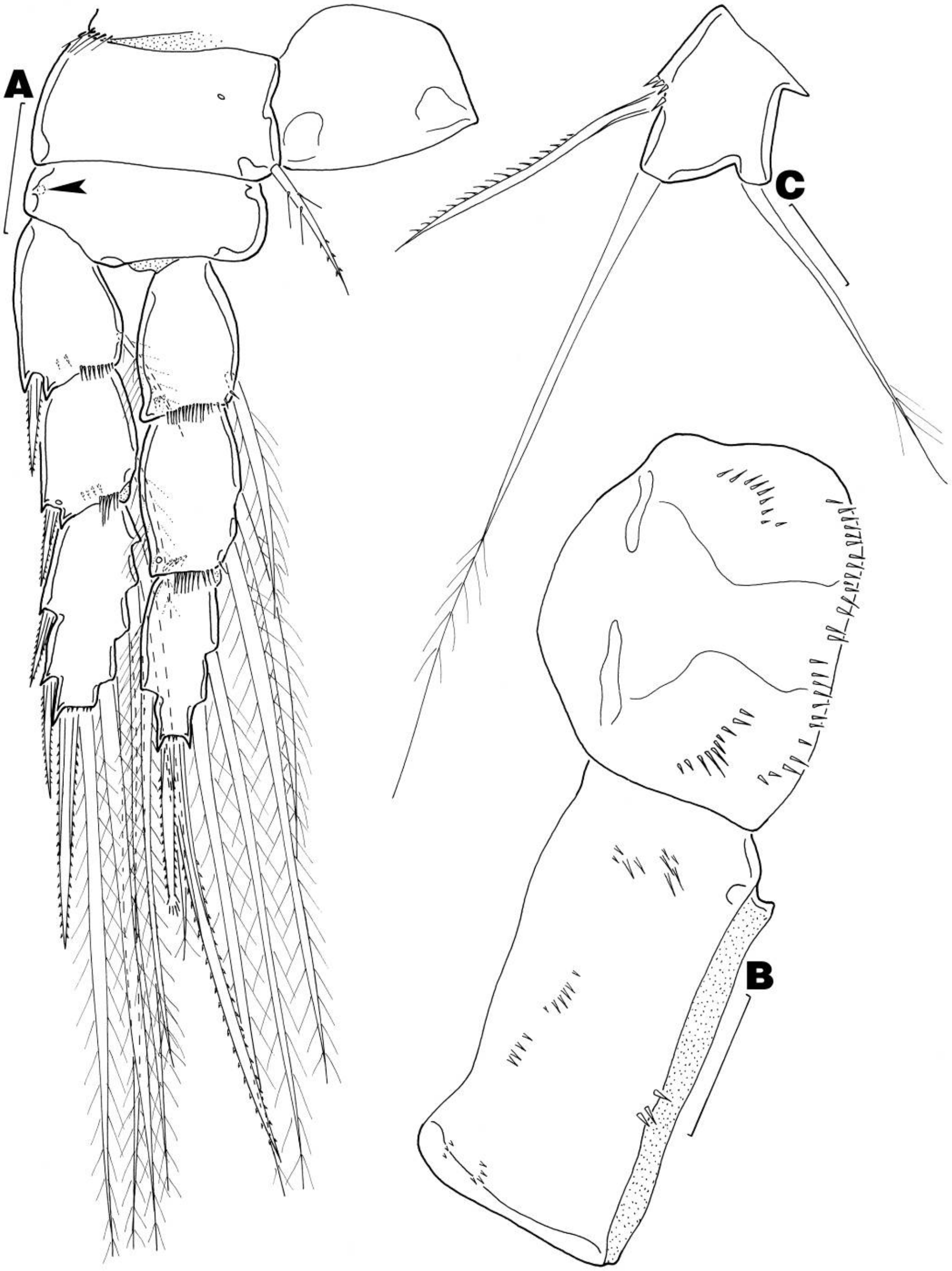

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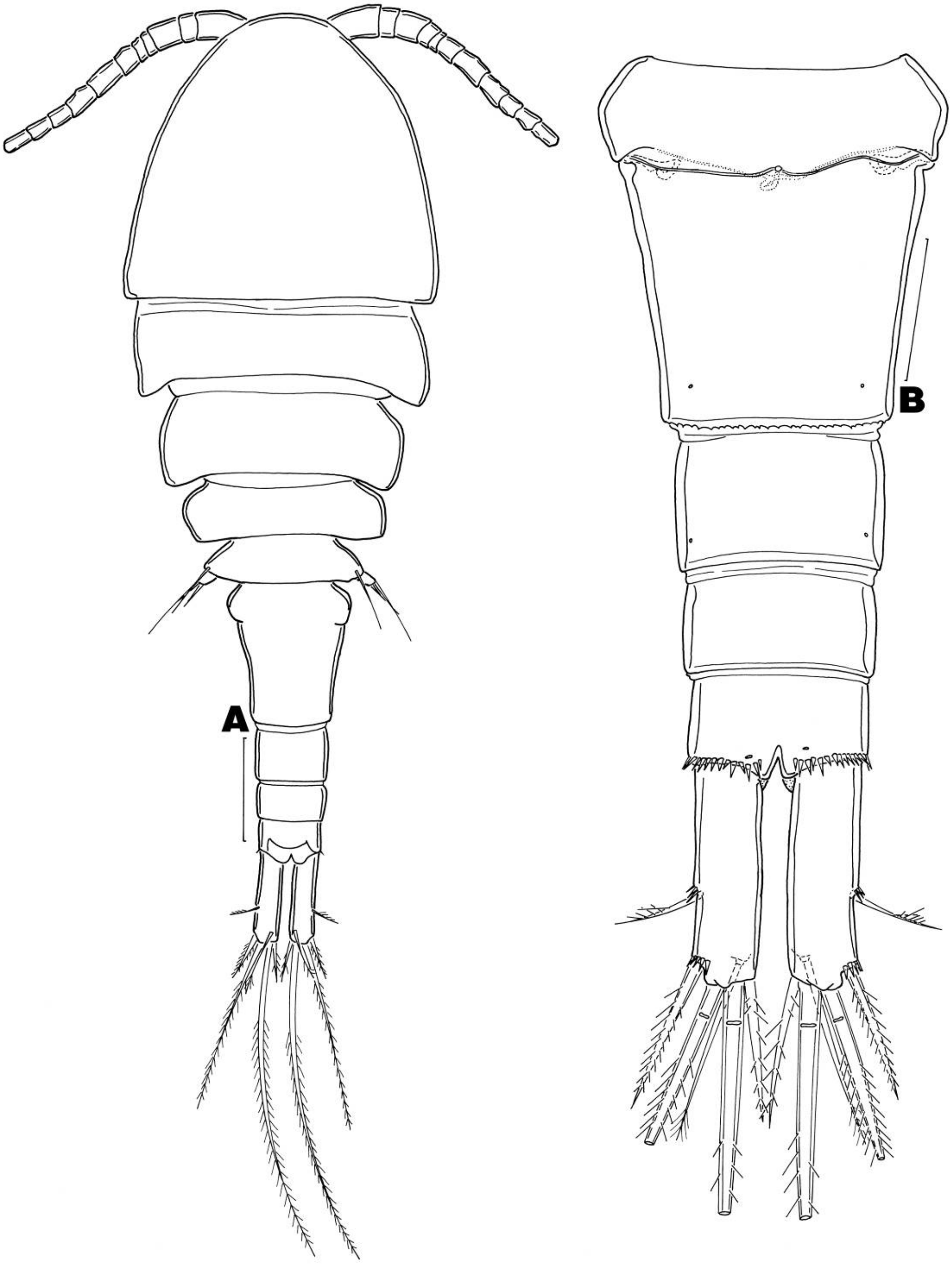

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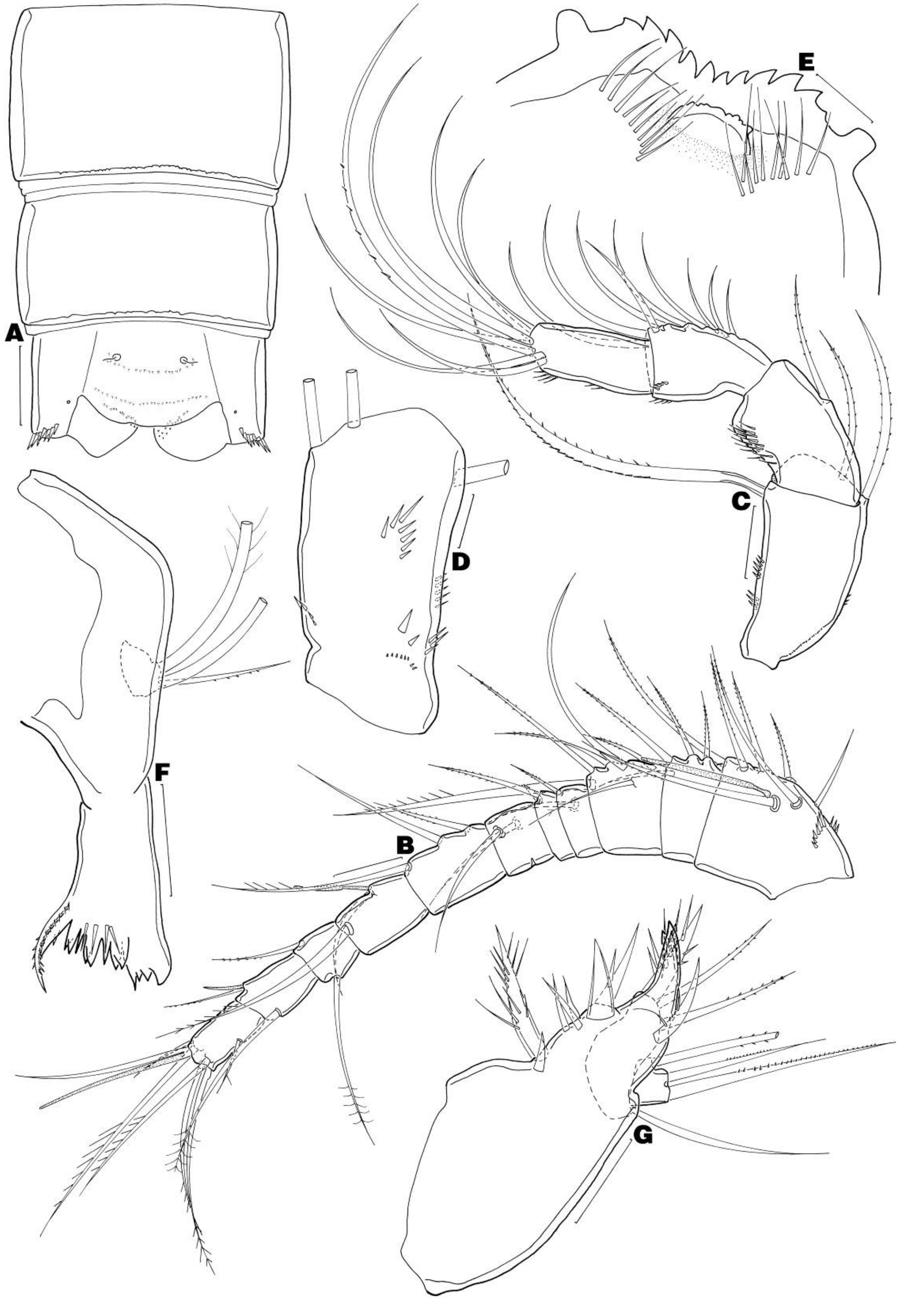

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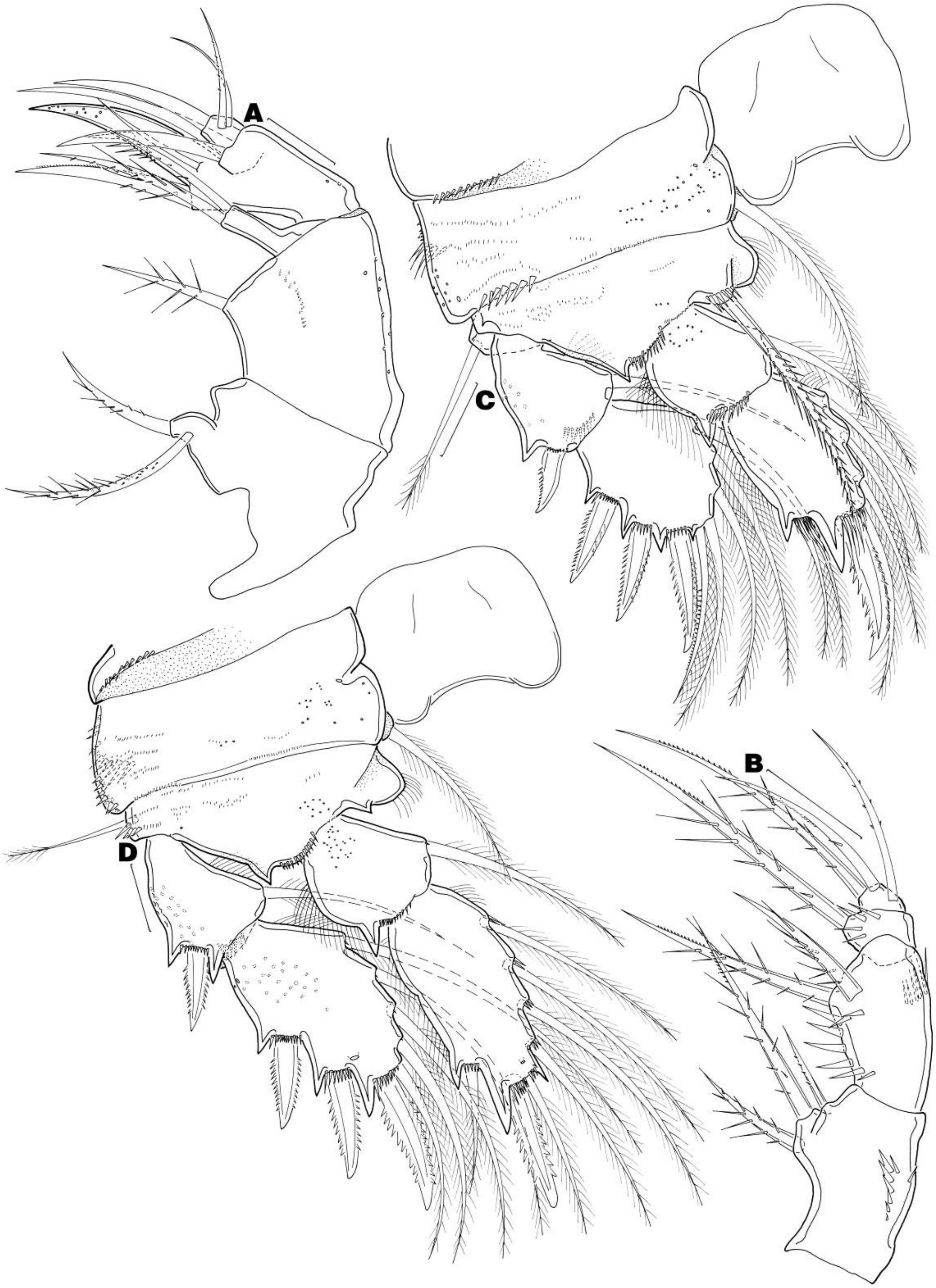

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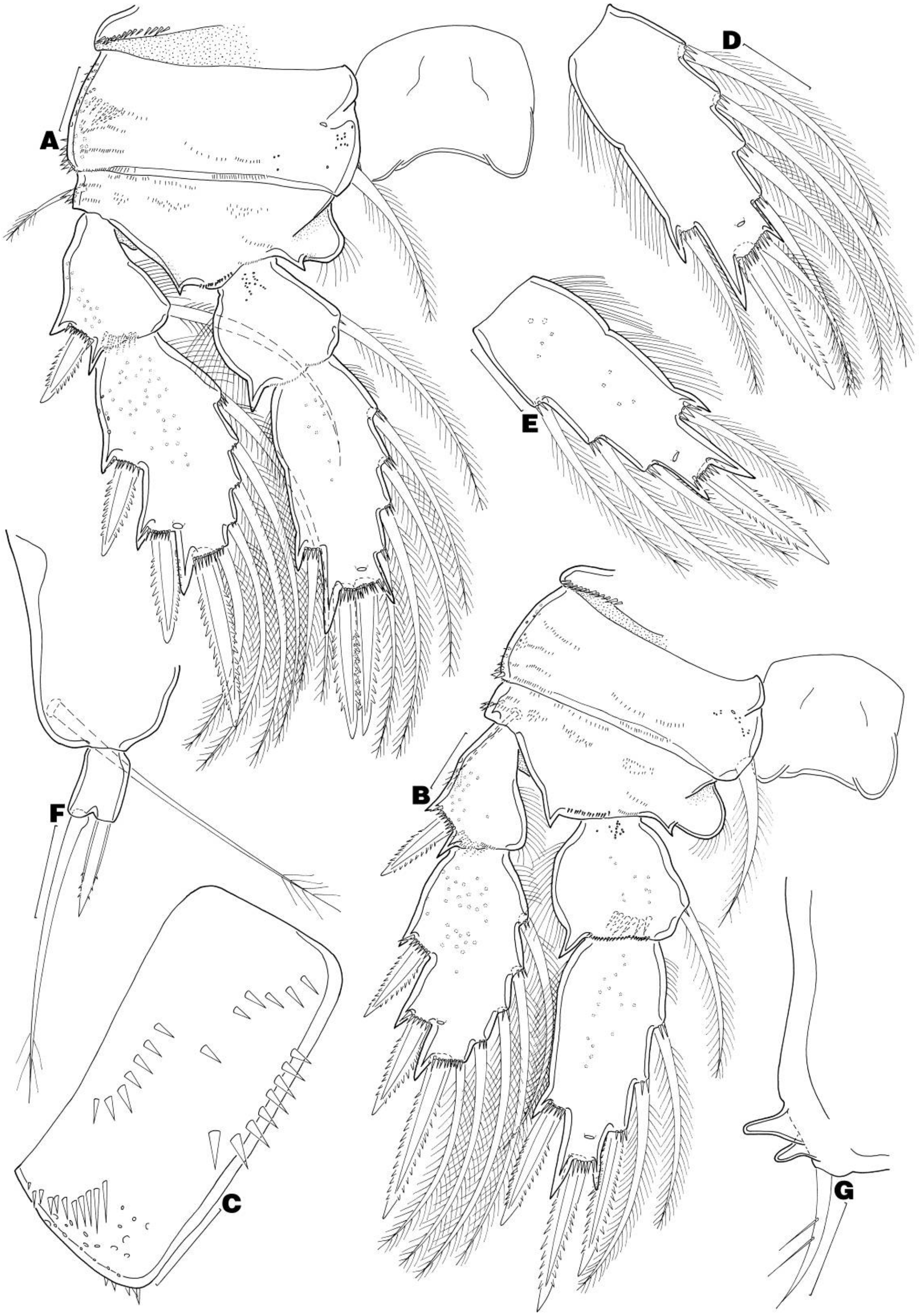

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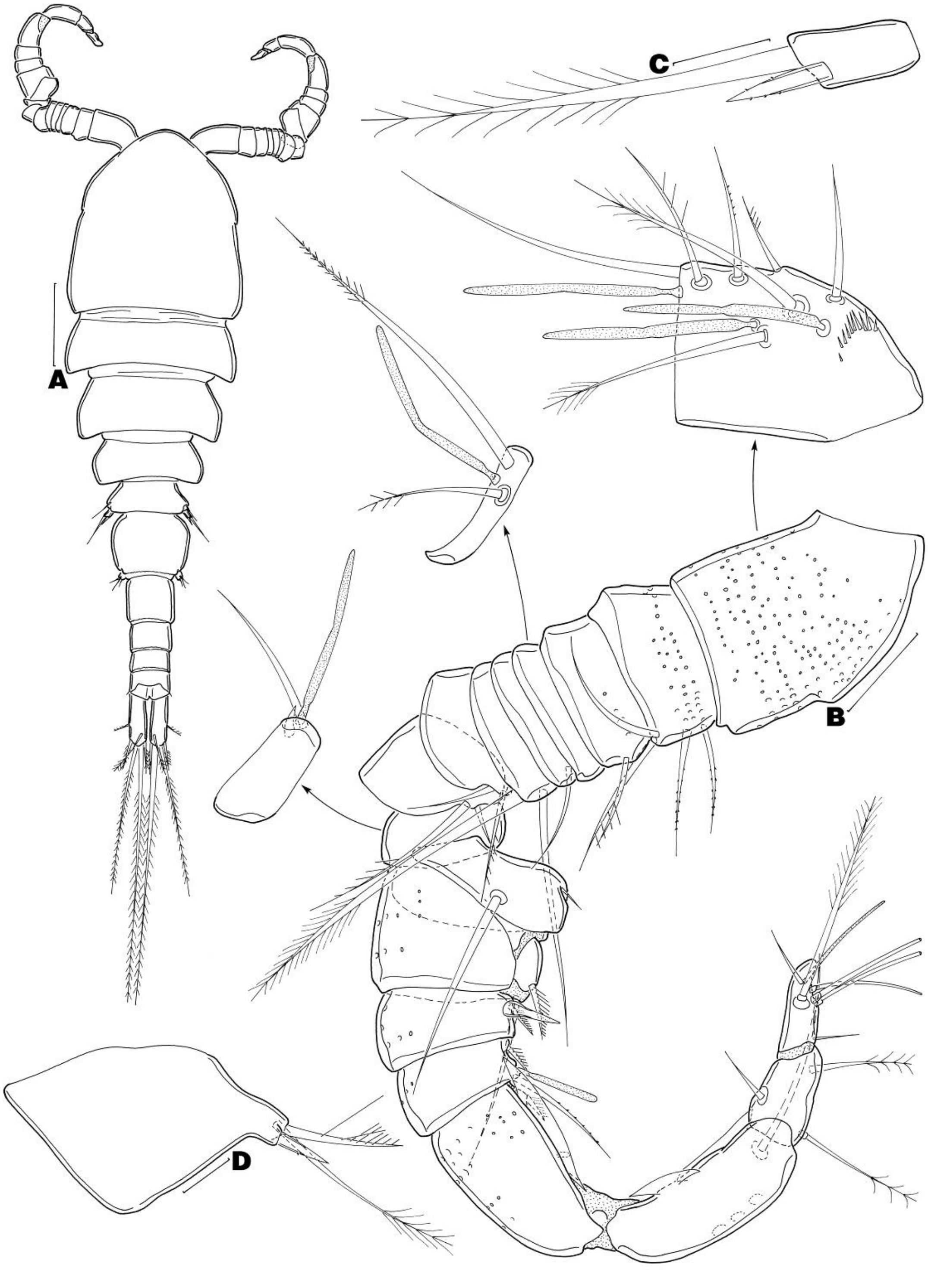

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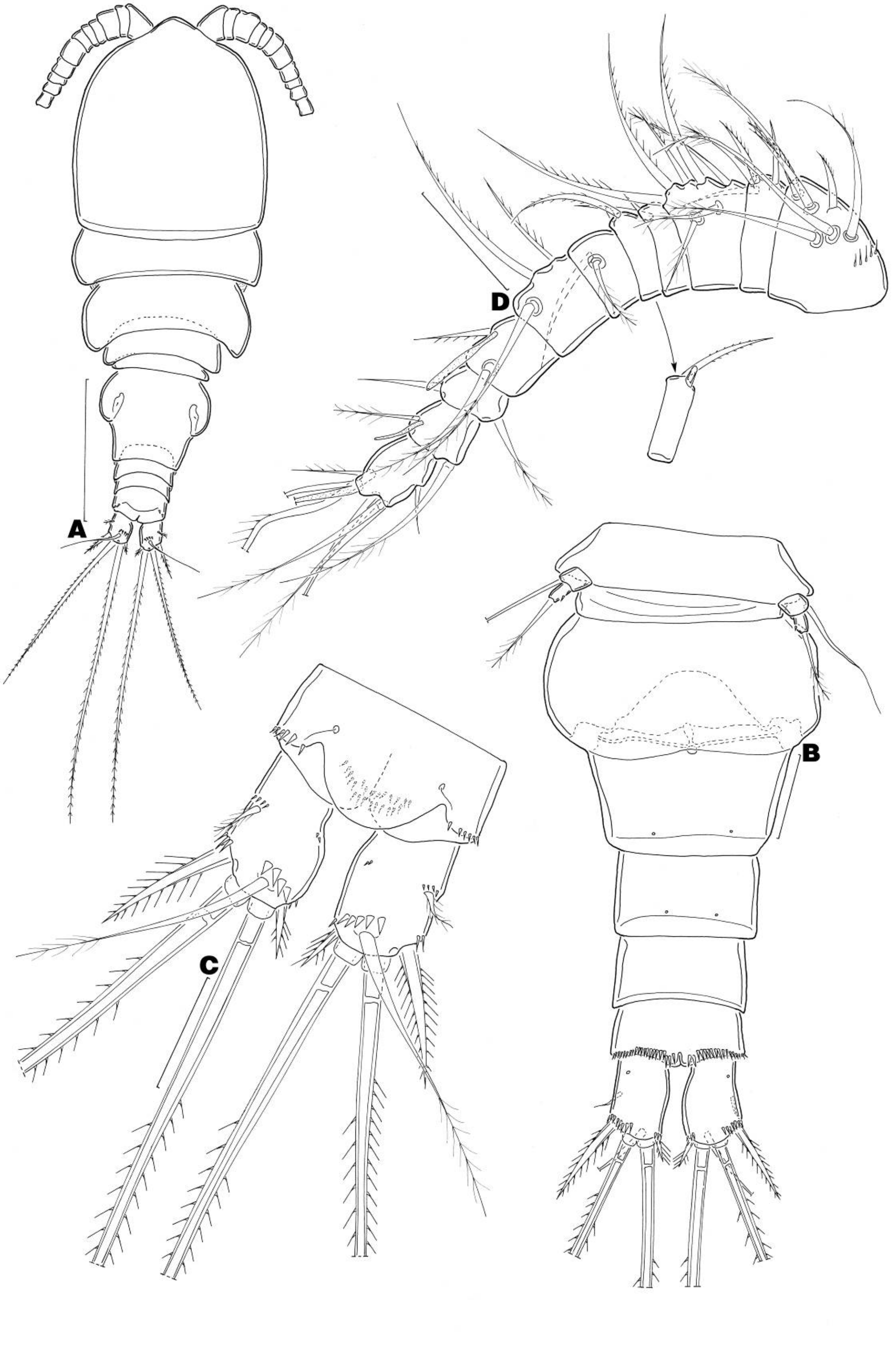

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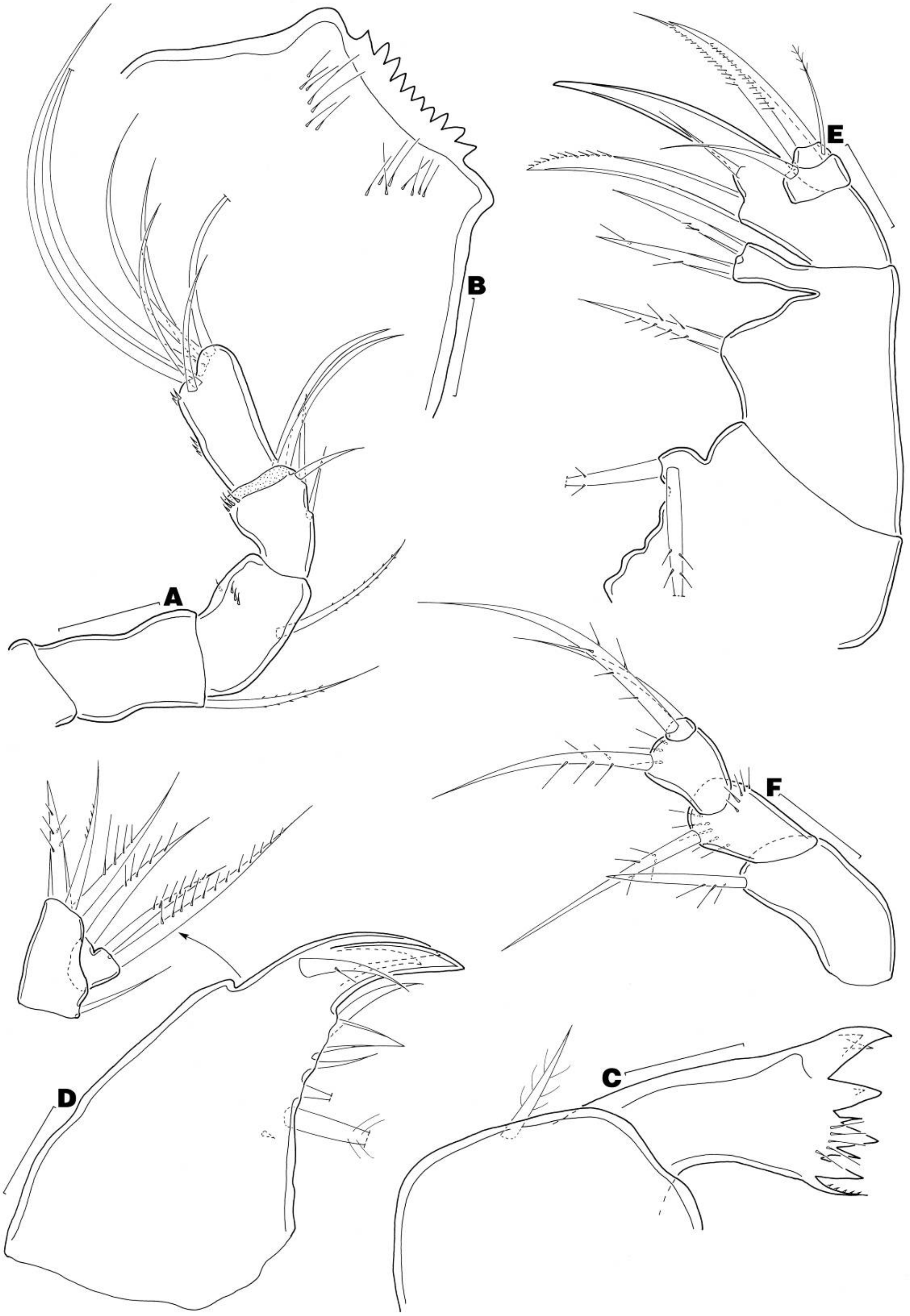

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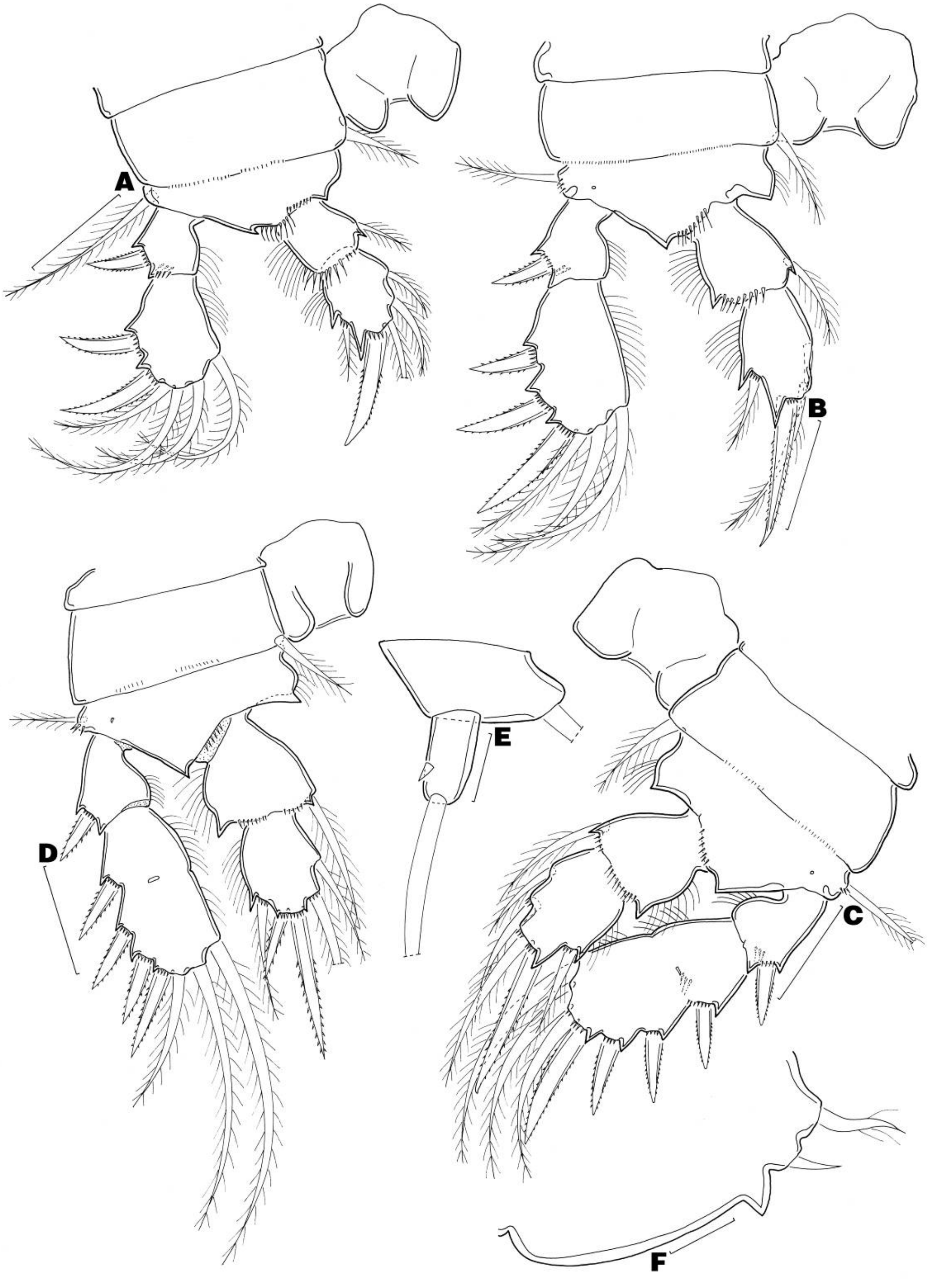

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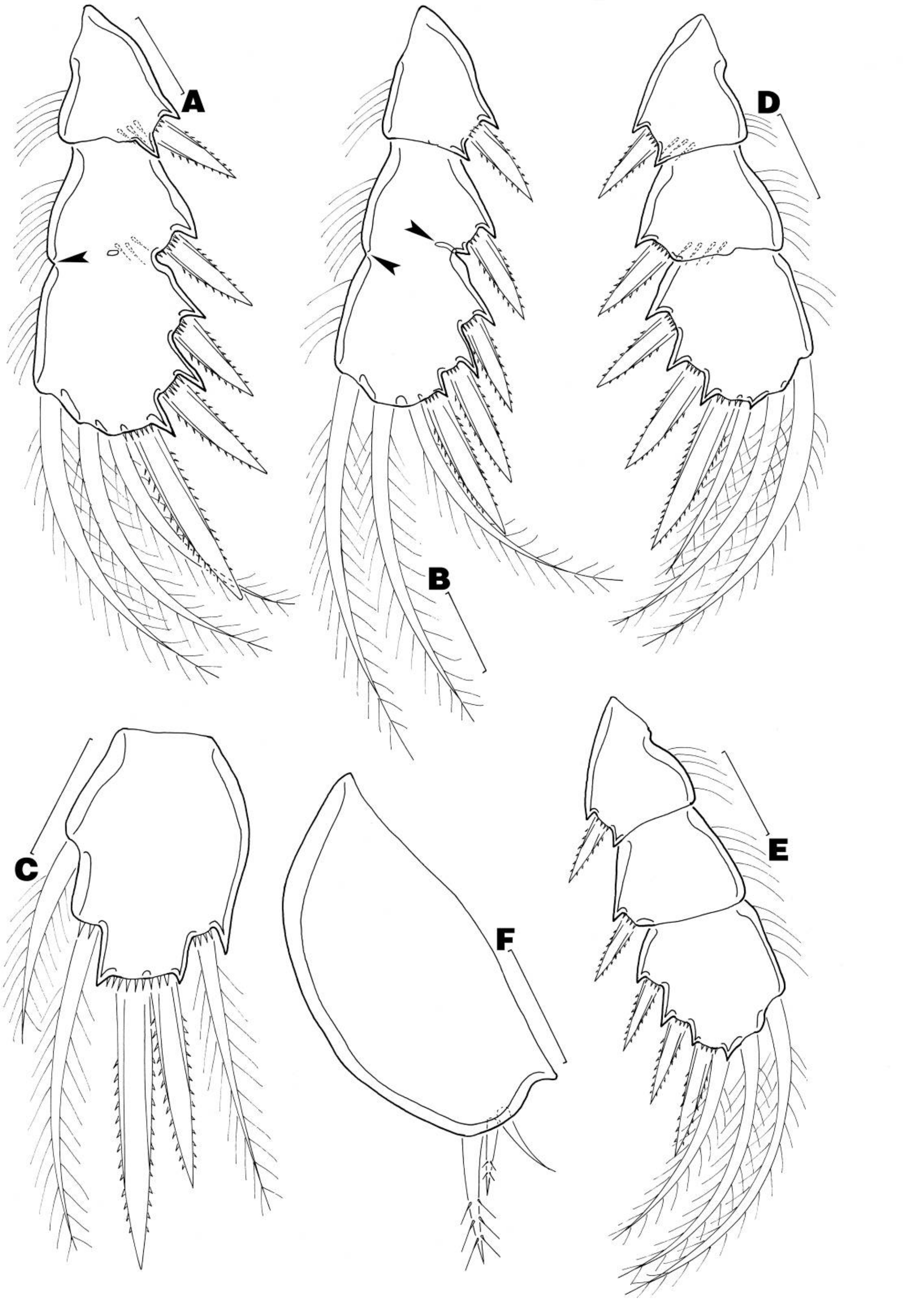

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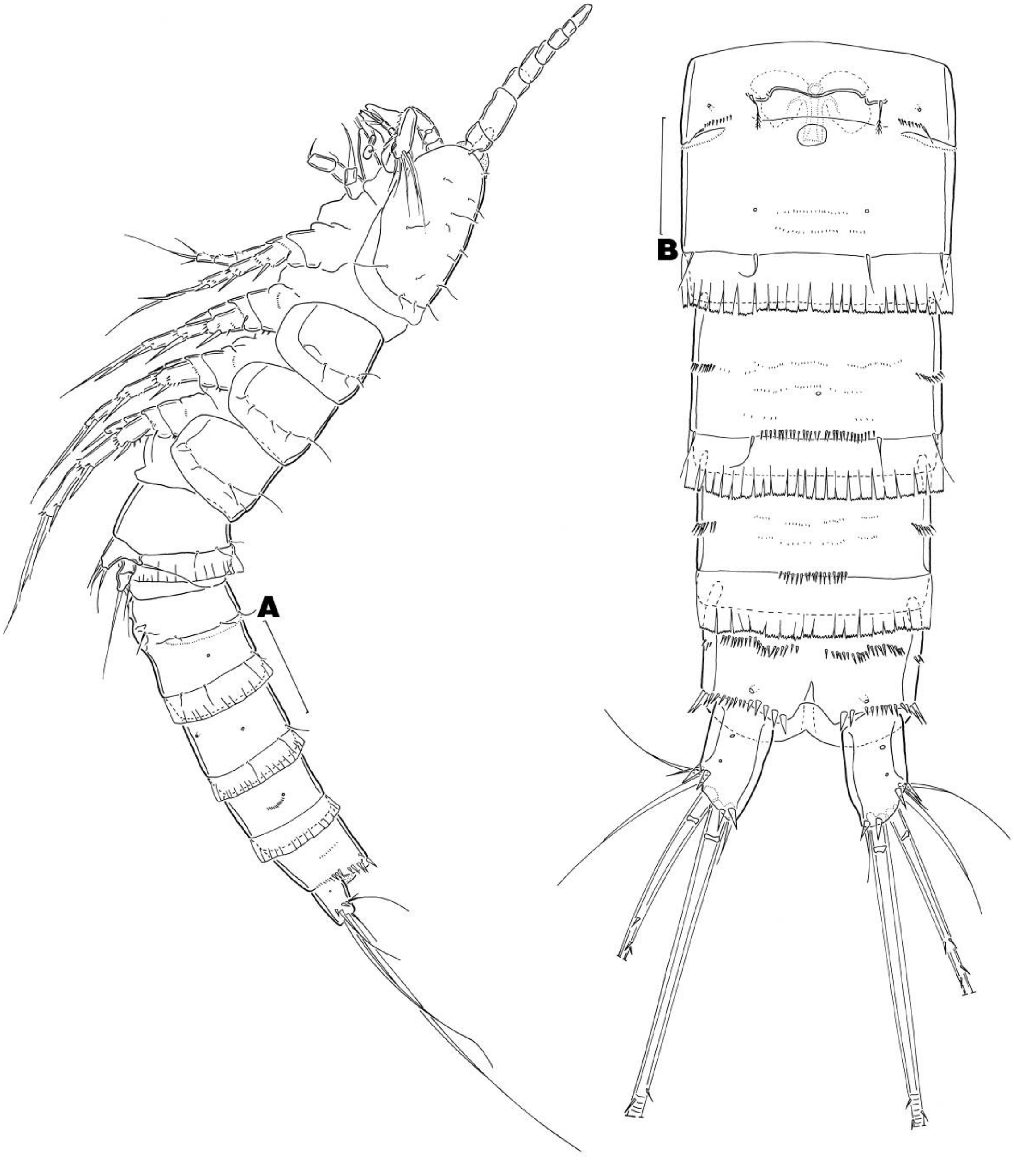

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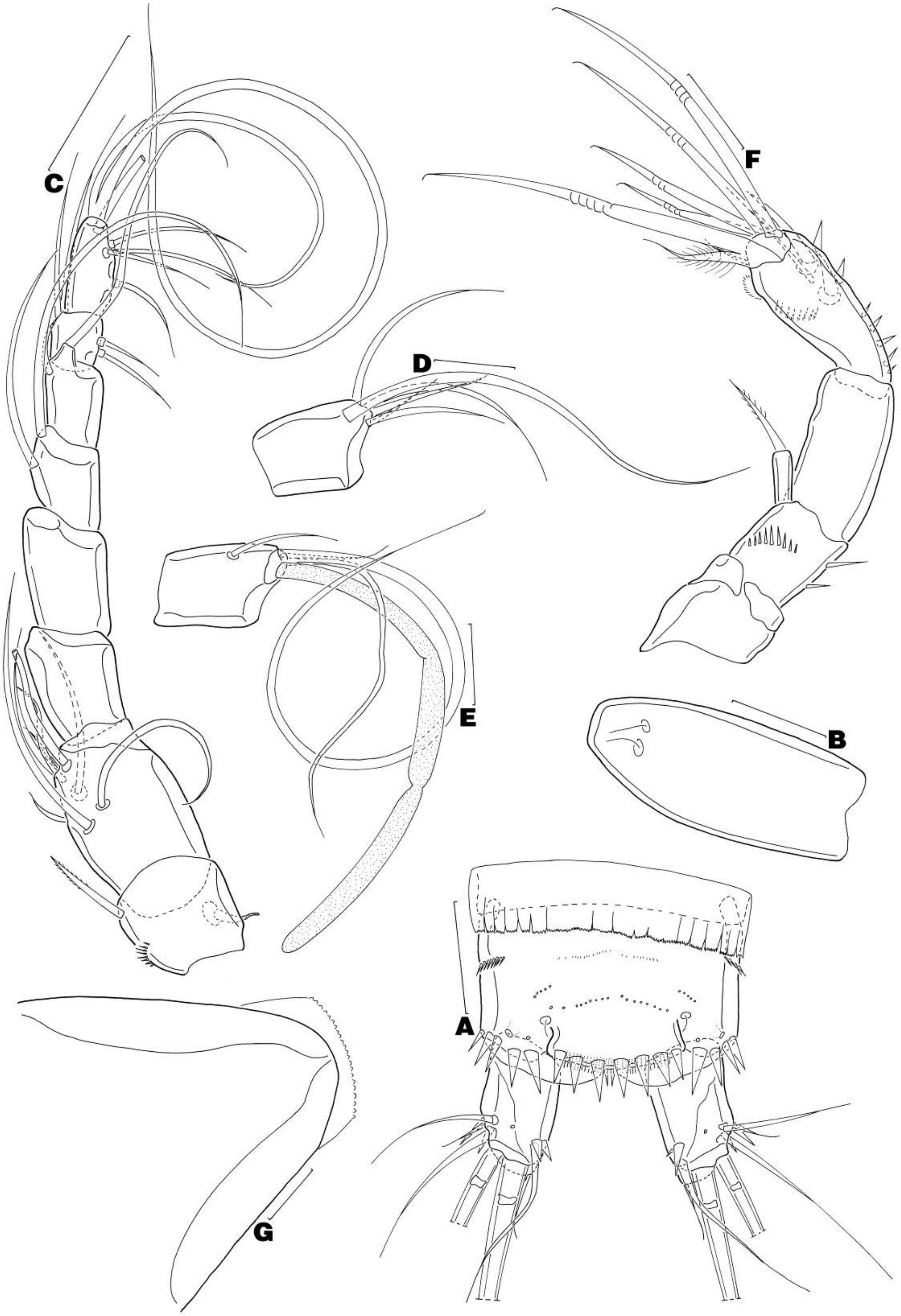

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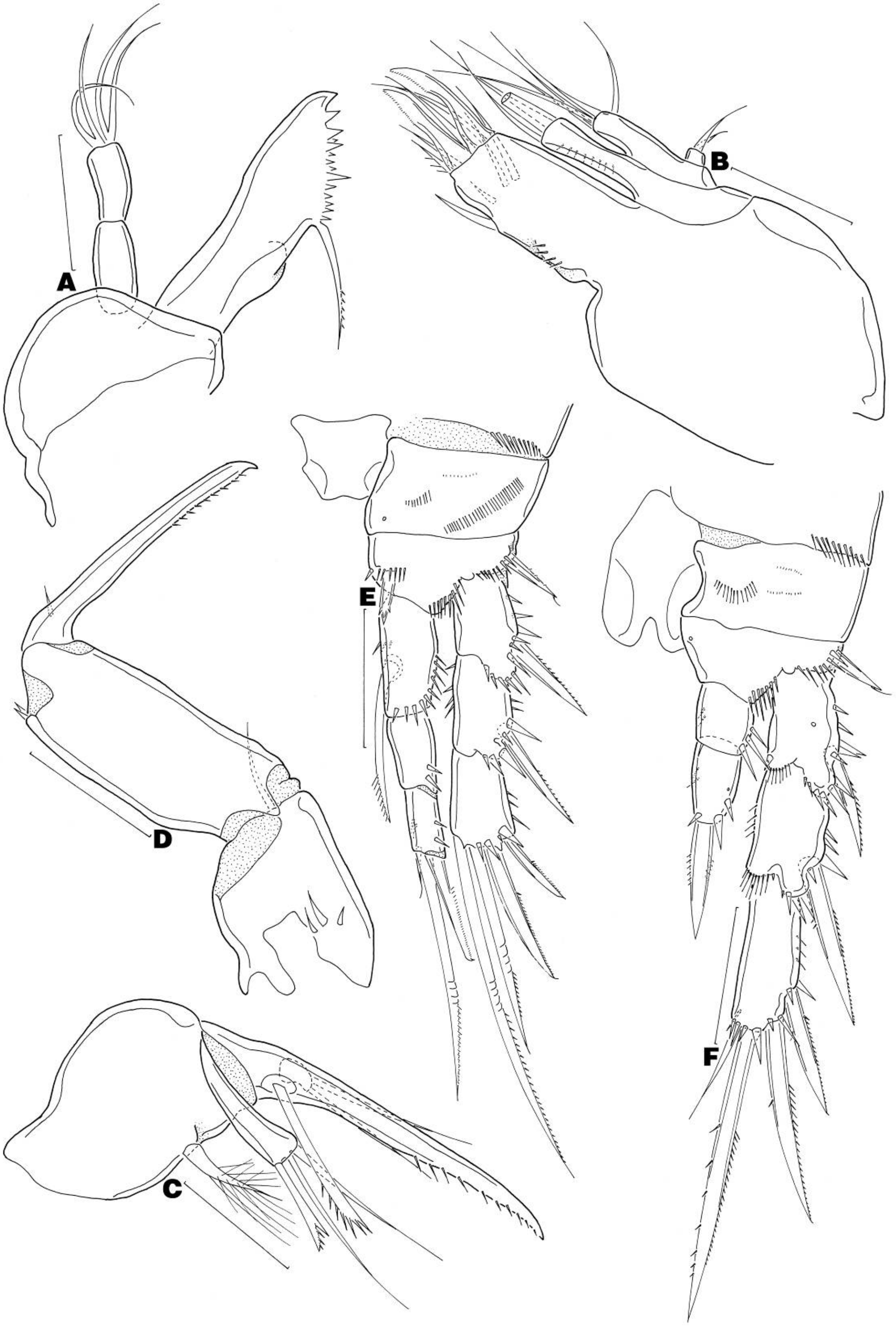

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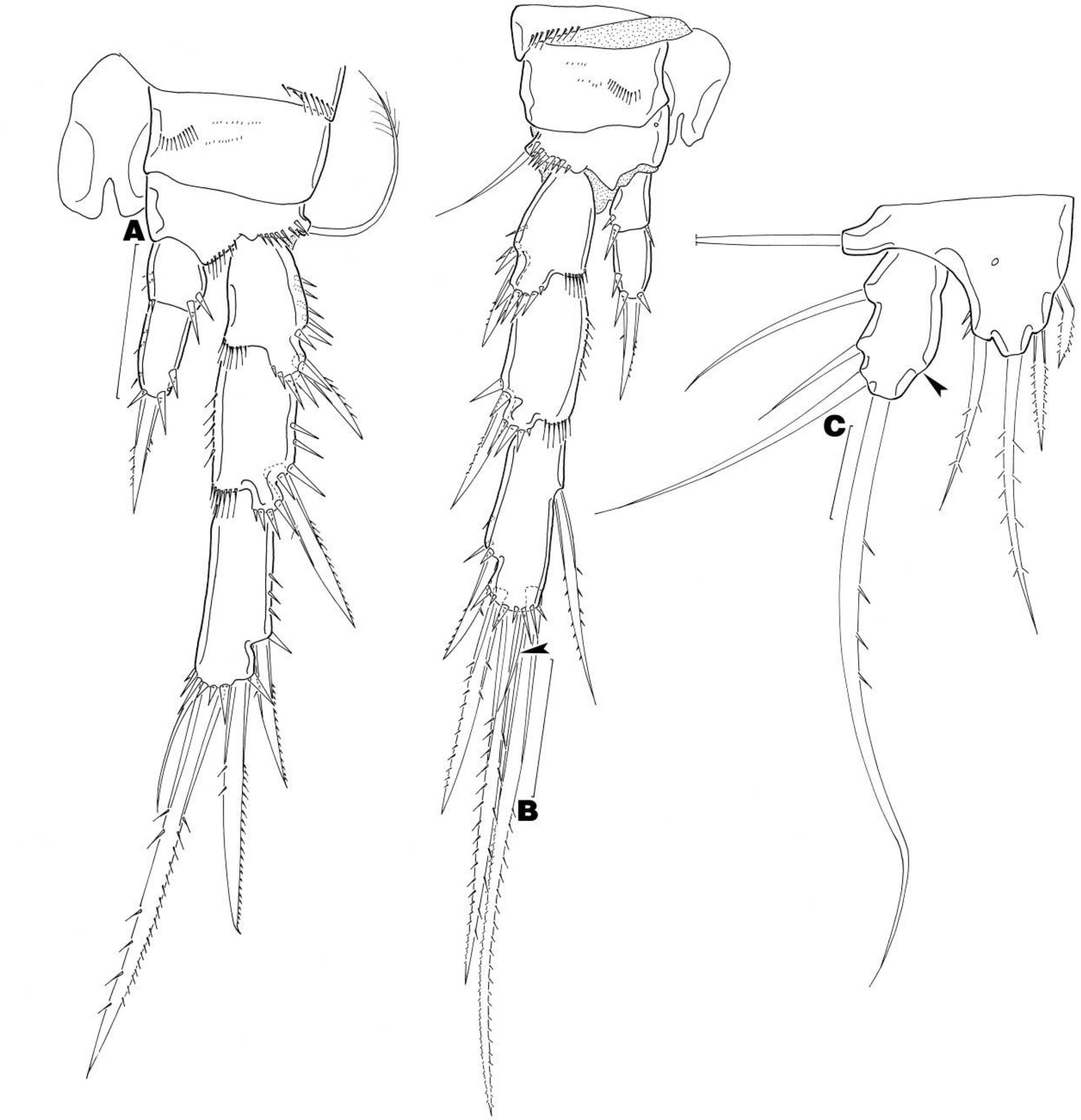

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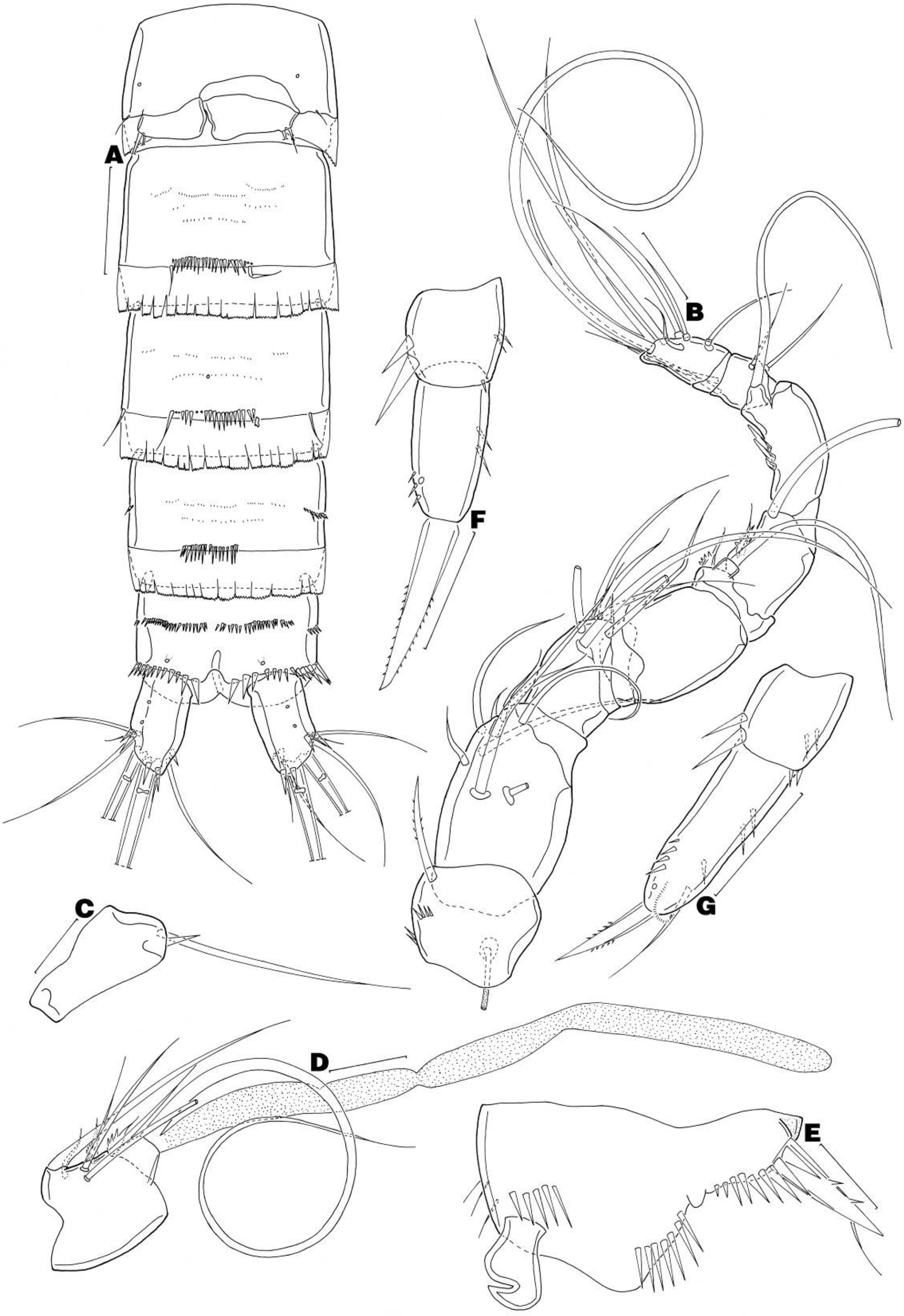

Figure 31