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A NEW GENUS AND SPECIES OF RIDGEWAYIIDAE (COPEPODA: CALANOIDA) FROM SUBTERRANEAN WATERS OF NORTHWESTERN AUSTRALIA

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ABSTRACT

A new ridgewayiid copepod, *Stygoridgewayia trispinosa* n. g. and n. sp., is described from continental ground waters of the Cape Range Peninsula and Pilbara regions of Western Australia, as the first occurrence of this family in fresh waters. The new genus can be distinguished from other ridgewayiid genera by a combination of characters that include three digitiform processes and striated membrane on each caudal ramus, fused ancestral segments II-IV and V-VI on the antennary exopod, leg 1 with a subterminal flagellum on the outer spiniform setae of the terminal exopodal segment, legs 3 and 4 with two outer spiniform setae on the terminal exopodal segment, and female leg 5 with reduced armature on the exopod, terminal exopodal segment inserted along the distal margin of the middle exopodal segment, and endopod absent. We postulate that this new ridgewayiid is a particle feeder living in close contact with the sediment surface, and originated in shallow coastal waters and secondarily colonized the freshwater hypogean environment.

KEY WORDS: Copepoda, ground water, Ridgewayiidae, *Stygoridgewayia trispinosa*

INTRODUCTION

The copepod family Ridgewayiidae, which currently consists of 27 species classified into ten genera, is considered to be one of the most primitive calanoid groups because its members usually possess plesiomorphic mouthparts and 3-segmented rami of legs 1-4 (Fosshagen and Iliffe, 2003). Of the ten nominal genera, only three are polytypic, viz., *Exumella*, *Ridgewayia*, and *Placocalanus*. Ridgewayiids have been reported from the hyperbenthos of tropical and subtropical seas (*Placocalanus*), anchialine caves (*Badijella*, *Brattstromia*, *Exumellina*, *Hondurella*, *Normancavia*, *Robpalmeria*, and *Stargatia*), and both the hyperbenthos and marine caves (*Exumella* and *Ridgewayia*). The ridgewayiid genera found solely in marine caves have a highly localized distribution pattern. *Badijella* was collected from Croatia, *Brattstromia* from the Caribbean region (Belize and Bahamas), *Hondurella* from the Hondurean island of Utila, and *Exumellina*, *Normancavia*, *Robpalmeria*, and *Stargatia* from the Bahamas (Fosshagen and Iliffe, 2003, 2004; Kršinić, 2005; Suárez-Morales and Iliffe, 2007). Those with members living in the hyperbenthic zone are more widely distributed. Species of *Placocalanus* and *Ridgewayia* are known to occur in both the Indo-Pacific and Atlantic Oceans, and members of *Exumella* are known from both sides of the North Atlantic, the Mediterranean, and the Indo-Pacific (Walter, 1986; Boxshall and Halsey, 2004).

To date only one ridgewayiid, *Ridgewayia flemingeri* Othman and Greenwood, 1988, has been described from Australia. This species, represented by two male specimens, was collected with a plankton net towed from near-bottom to the sea surface through 50 m of water in the Gulf of Carpentaria (Othman and Greenwood, 1988). In this paper a second member of Ridgewayiidae is described from Australia based on samples collected from ground waters of the Cape Range Pensinsula and Pilbara, two regions of Western Australia already known to contain a rich stygobiontic copepod fauna (Pesce and De Laurentiis, 1996; Pesce et al., 1996a, b; De Laurentiis et al., 1999; Jaume and Humphreys, 2001; Jaume et al., 2001; Karanovic and Pesce, 2002; Karanovic, 2004, 2006). This ridgewayiid copepod represents not only a new genus and species, but more importantly the first ridgewayiid ever to be reported from a freshwater habitat.

MATERIALS AND METHODS

Copepods were obtained from a total of 43 sites in Western Australia, of which five consisted of the Water Corporation's Monitoring (MB) and Dedicated Stygofauna (DSO) bores located near Exmouth in the Cape Range Peninsula and 38 from pastoral wells and bores (used for water supply and mining operation purposes) located in the Pilbara region (Fig. 1). Samples were collected between 2003 to 2006 using weighted fine-mesh nets (50 and 150 μm) lowered on a reel and 200 m rope device to the bottom of each bore. Specimens were sorted from debris under a dissecting microscope, preserved in 100% ethanol, and subsequently soaked in lactic acid for a minimum of 24 h prior to examination using an Olympus BX-51 compound microscope equipped with differential interference contrast. Selected specimens were measured using a calibrated eyepiece micrometer, and dissected and examined according to the wooden slide procedure of Humes and Gooding (1964). Drawings were made with the aid of a camera lucida. Anatomical terminology follows Boxshall and Halsey (2004).

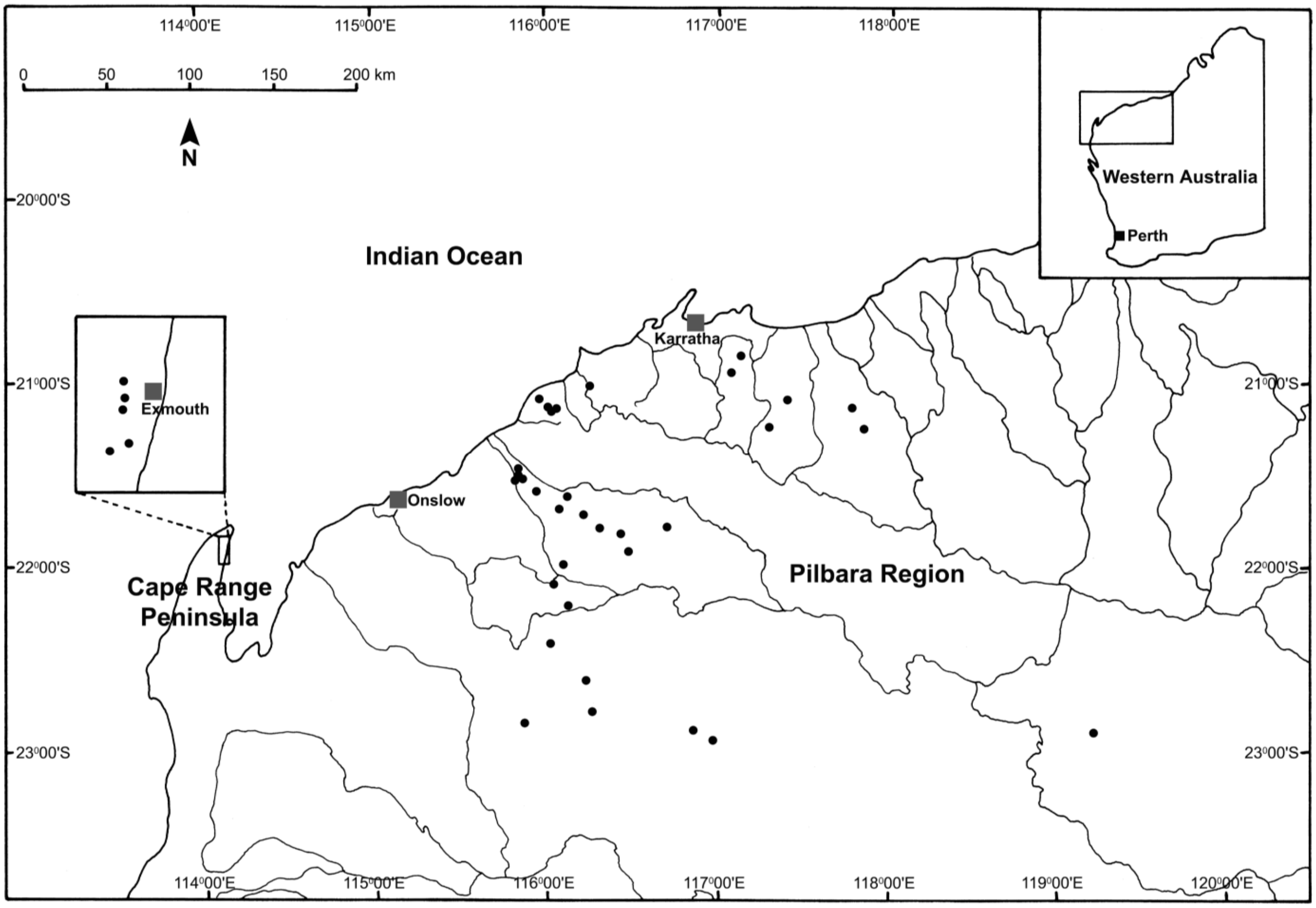

Fig. 1. Map of the Pilbara and Cape Range Peninsula regions of Western Australia showing the bore and well locations. [Note: five sites in the Pilbara share identical coordinates with at least one other site, thus 38 rather than 43 filled circles are shown].

Results

Order Calanoida G. O. Sars, 1901
Ridgewayiidae M. S. Wilson, 1958
Stygoridgewayia n. gen.

Diagnosis.—Body moderately slender. Naupliar eye absent. Prosome with cephalosome separated from first pedigerous somite, pedigerous somites four and five fused, and posterior corners symmetrical. Urosome 4-segmented in female, 5-segmented in male. Caudal rami symmetrical, each bearing 7 setae (seta I minute), striated membrane dorsodistally, and 3 processes ventrodistally. Rostrum lacking filaments. Female antennule 25-segmented, with articulations between ancestral segments II-IV and XXVII-XXVIII not expressed. Male right antennule 22-segmented, weakly geniculate, with articulations between ancestral segments II-IV, XXI-XXIII, XXIV-XXV, and XXVII-XXVIII not expressed. Antenna with 7-segmented exopod (articulations between ancestral segments II-IV and V-VI not expressed) and 2-segmented endopod. Mandibular palp unmodified, with 4-segmented exopod and 2-segmented endopod. Maxillulary endopod unmodified, 2-segmented. Maxilla 6-segmented. Maxilliped 8-segmented. Legs 1 to 4 biramous, and rami trimerous. Leg 1 with distolateral spinous process on middle exopodal segment and subterminal flagellum on each outer spiniform seta on terminal exopodal segment. Terminal exopodal segment of legs 3 and 4 with 2 outer spiniform setae. Female leg 5 uniramous, trimerous; middle exopodal segment lacking inner seta; terminal exopodal segment not constricted basally, articulates at joint located along distal margin of middle exopodal segment, and armed with 3 elements. Male fifth legs asymmetrical, biramous: right exopod 2-segmented, with distal segment elongate and tapered distally; right endopod 1-segmented, elongate, and armed with long element; left exopod 3-segmented, complex; left endopod a 1-segmented, unarmed lobe.

Type species.—*Stygoridgewayia trispinosa* n. gen., n. sp.

Etymology.—The generic name is a combination of Greek "*stygo*" (referring to its groundwater habitat) and *Ridgewayia* (the type genus of Ridgewayiidae). Gender feminine.

Stygoridgewayia trispinosa n. sp.
Figs. 2-7

Material Examined.—(a) Holotype ♀ (WAM C39301), allotype ♂ (WAM C39302), and 32 additional paratypes (WAM C39303-39307) (13 ♀♀, 9 ♂♂, and 6 copepodids in alcohol; 2 ♀♀ and 2 ♂♂ dissected and mounted on one slide each) from House Creek, bore NWSLK58 (22°27′S, 116°02′E), Pilbara, Australia, 22 November 2003, deposited

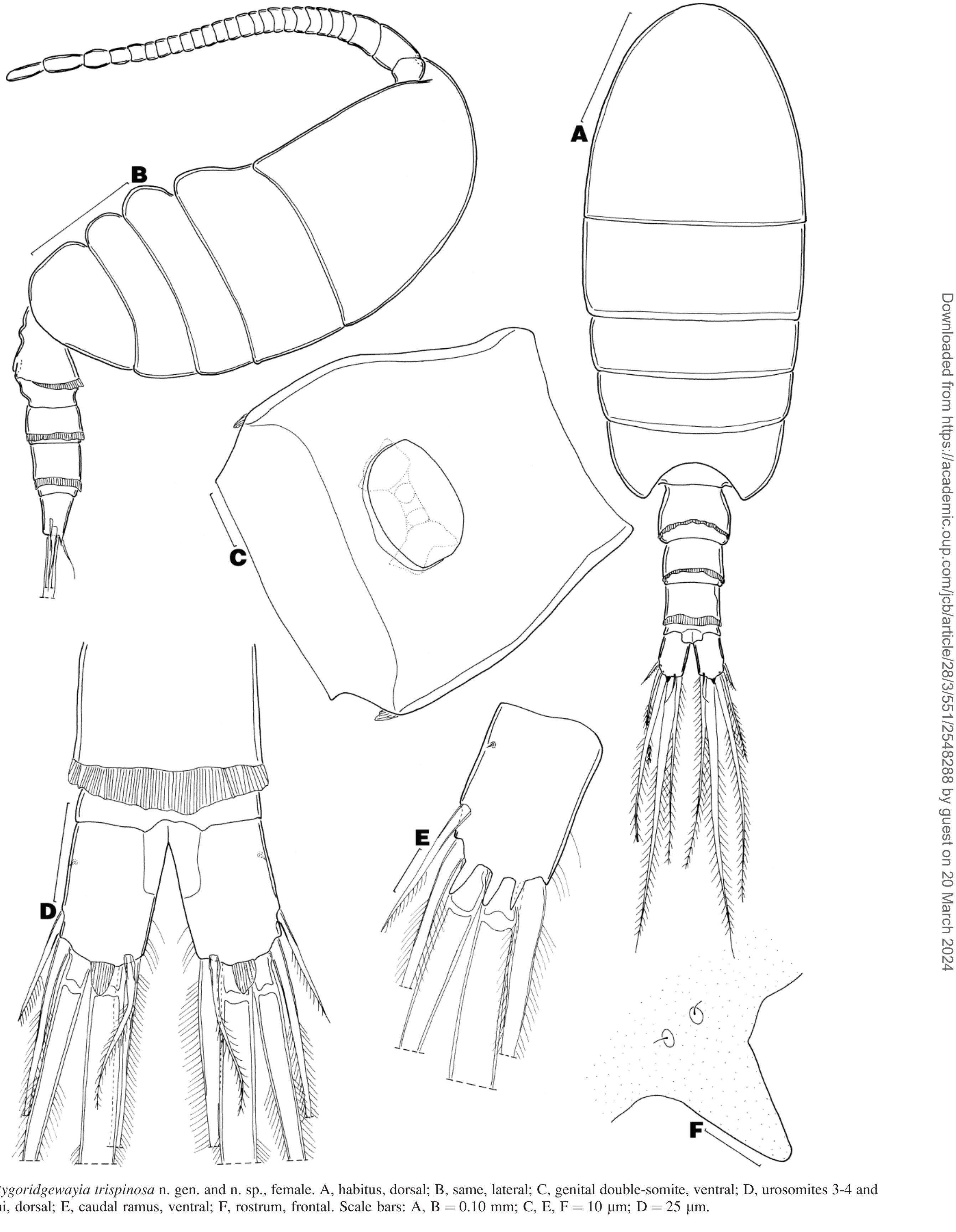

Fig. 2. *Stygoridgewayia trispinosa* n. gen. and n. sp., female. A, habitus, dorsal; B, same, lateral; C, genital double-somite, ventral; D, urosomites 3-4 and caudal rami, dorsal; E, caudal ramus, ventral; F, rostrum, frontal. Scale bars: A, B = 0.10 mm; C, E, F = 10 μm; D = 25 μm.

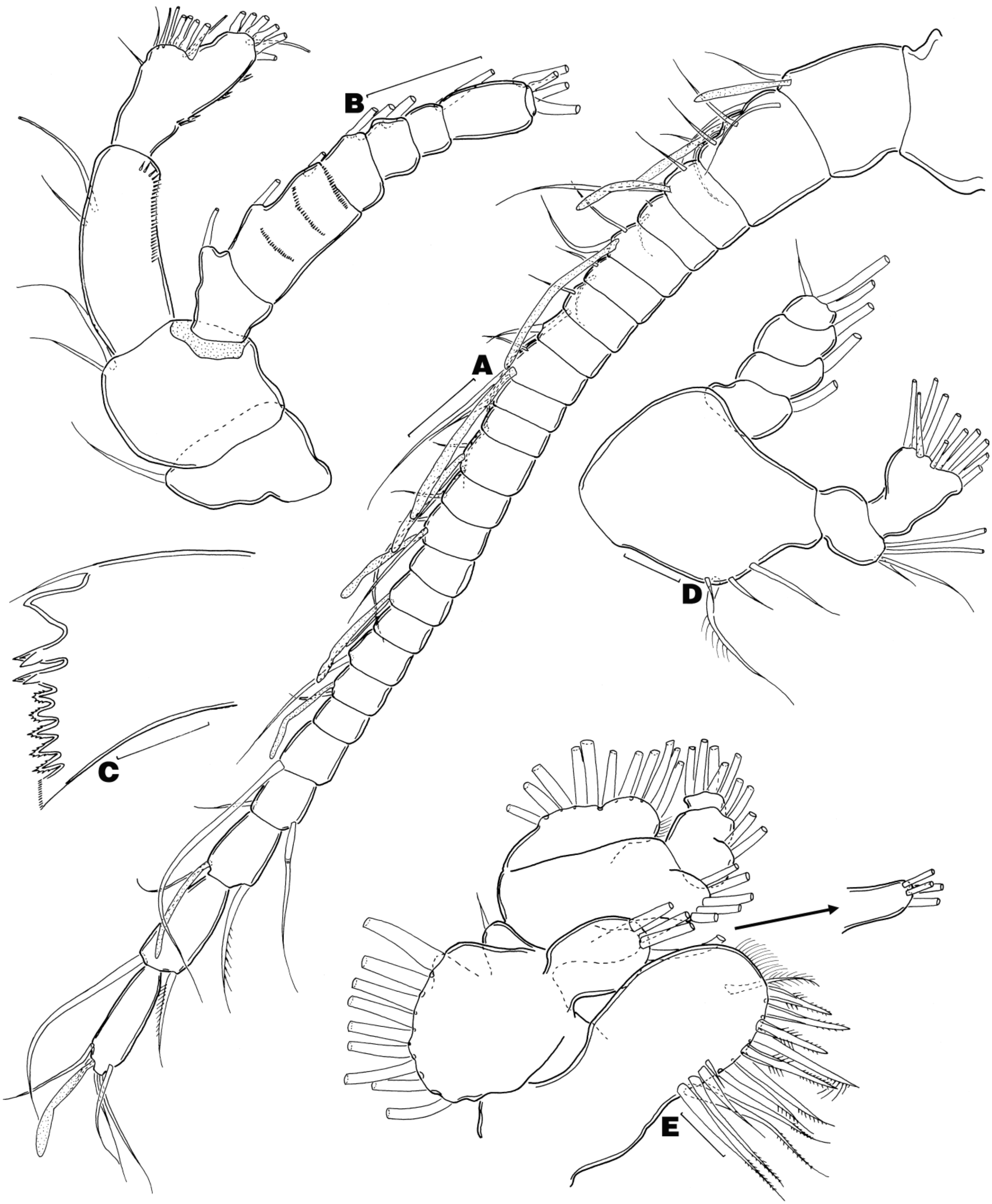

Fig. 3. *Stygoridgewayia trispinosa* n. gen. and n. sp., female. A, antennule, ventral; B, antenna, anterior; C, cutting edge of mandibular coxal gnathobase, posterior; D, mandibular palp, posterior; E, maxillule with proximal basal endite (arrowed) shown separately, anterior. Scale bars: A, B = 25 μm; C, D, E = 10 μm.

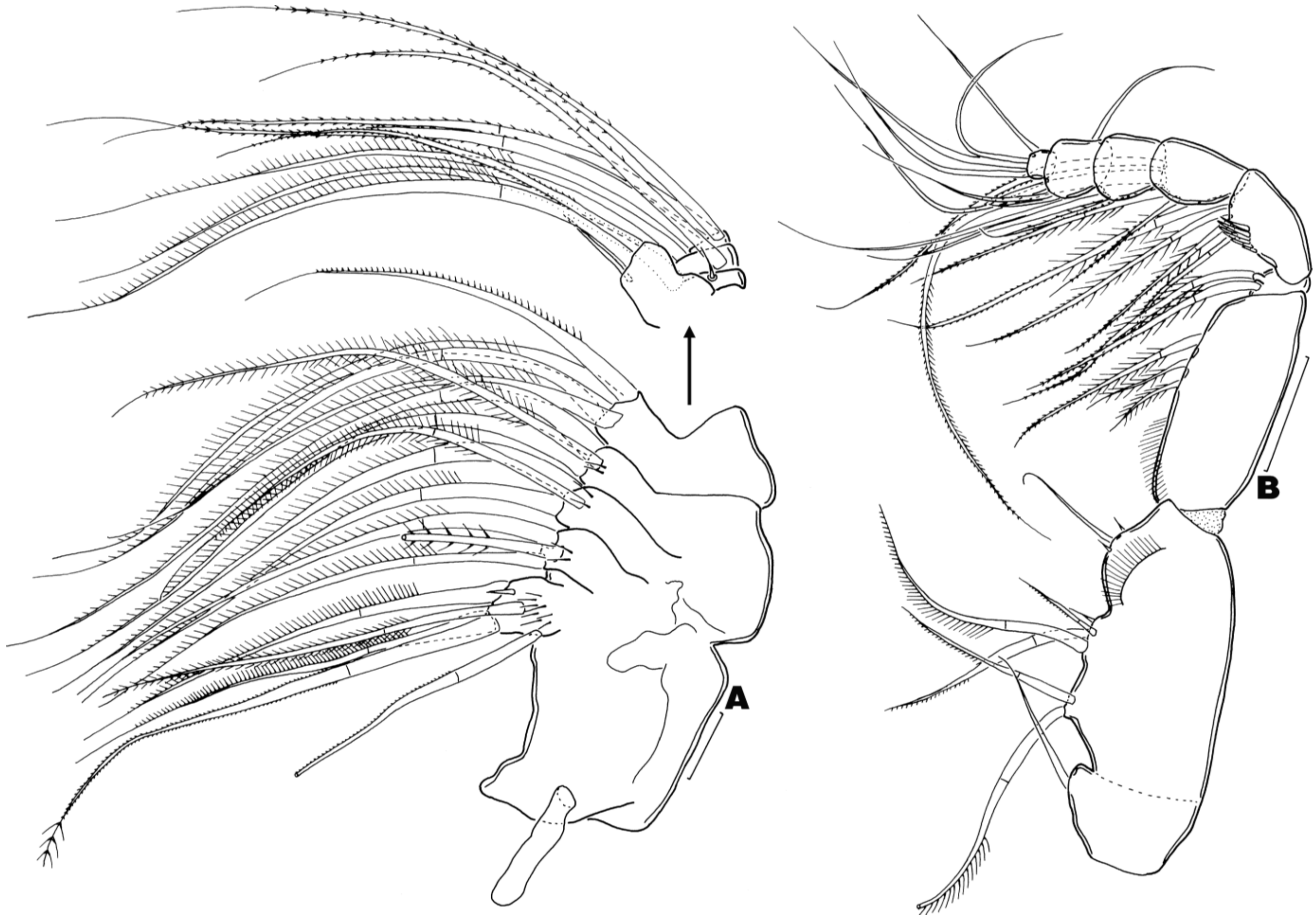

Fig. 4. *Stygoridgewayia trispinosa* n. gen. and n. sp., female. A, maxilla with endopod (arrowed) disarticulated from basis, posterior; B, maxilliped, anterior. Scale bars: A = 10 μm; B = 25 μm.

in the Western Australian Museum, Perth; (b) 42 ♀♀, 35 ♂♂, and 9 copepodids (AM P.75273) from Robe River, bore G70730104P (21°34′S, 115°50′E), Pilbara, Australia, 19 November 2003, deposited in the Australian Museum, Sydney; and (c) additional material from the Pilbara and Cape Range Peninsula regions of Western Australia (Appendix 1) are retained in the stygofauna collection of the Department of Environment, Woodvale, Western Australia and the Water Corporation, Leederville, Western Australia, respectively.

Female.—Body (Fig. 2A, B) 0.58 ± 0.03 mm long (range = 0.55-0.67 mm; n = 25), moderately slender. Naupliar eye absent. Prosome comprised of cephalosome, free 1st, 2nd, and 3rd pedigers, and fused 4th and 5th pedigers. Posterior corners of prosome symmetrical, rounded in lateral view. Urosome composed of genital double-somite and 3 free abdominal somites. Genital double-somite with striated hyaline frill along posterodorsal margin only; genital operculum (Fig. 2C) located ventromedially. Posterior margin of 1st and 2nd free abdominal somites with striated hyaline frill; anal somite considerably shorter than preceding somites. Caudal rami (Fig. 2D, E) symmetrical, each bearing 7 setae (seta I minute; seta II spiniform), a small striated membrane dorsodistally, and 3 digitiform processes ventrodistally; distomedial margin with short row of setules.

Rostrum (Fig. 2F) small, rounded at tip, lacking filaments. Antennule (Fig. 3A) 25-segmented, implanted on pedestal, and extending to 3rd pediger. Armature and fusion pattern as follows: I-1+ae, II-IV-6+ae, V-2+ae, VI-2, VII-2+ae, VIII-2, IX-2, X-1, XI-2+ae, XII-1, XIII-1, XIV-2+ae, XV-1, XVI-2+ae, XVII-0, XVIII-1+ae, XIX-0, XX-1, XXI-1+ae, XXII-0, XXIII-1, XXIV-2, XXV-2+ae, XXVI-2, and XXVII-XXVIII-5+ae. All setae simple, except posterodistal seta on segments XXV and XXVI with unilateral row of fine spinules.

Antenna (Fig. 3B) comprised of coxa, basis, 7-segmented exopod, and 2-segmented endopod. Coxa armed with distomedial seta, basis with 2 distomedial setae. Exopod setal formula 1, 1+1, 1+1, 1, 1, 1, 3; second segment with 3 transverse rows of spinules on anterior surface; ancestral segments II-IV and V-VI fused. Proximal endopodal segment bearing row of spinules laterally and 2 setae medially; compound distal endopodal segment bilobed, with 9 setae proximally and 7 setae distally. Cutting edge of mandibular coxal gnathobase (Fig. 3C) bearing naked seta, robust tooth, 2 bifurcate teeth, 5 serrate teeth, and spinulate process. Palp (Fig. 3D) unornamented, comprised of basis,

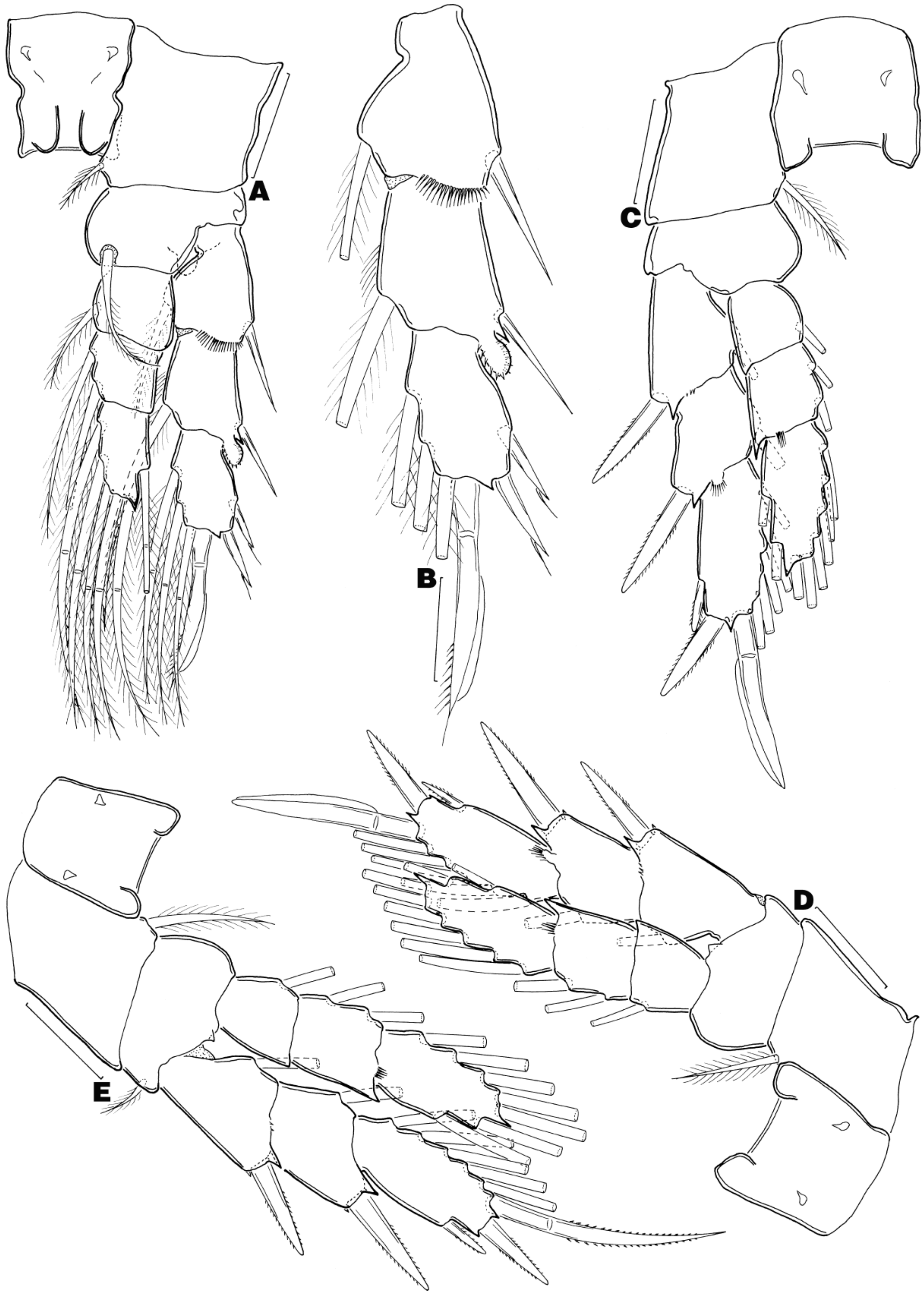

Fig. 5. *Stygoridgewayia trispinosa* n. gen. and n. sp., female. A, leg 1, anterior; B, leg 1 exopod, anterior; C, leg 2, anterior; D, leg 3, anterior; E, leg 4, anterior. Scale bars: A, C, D, E = 25 μm; B = 15 μm.

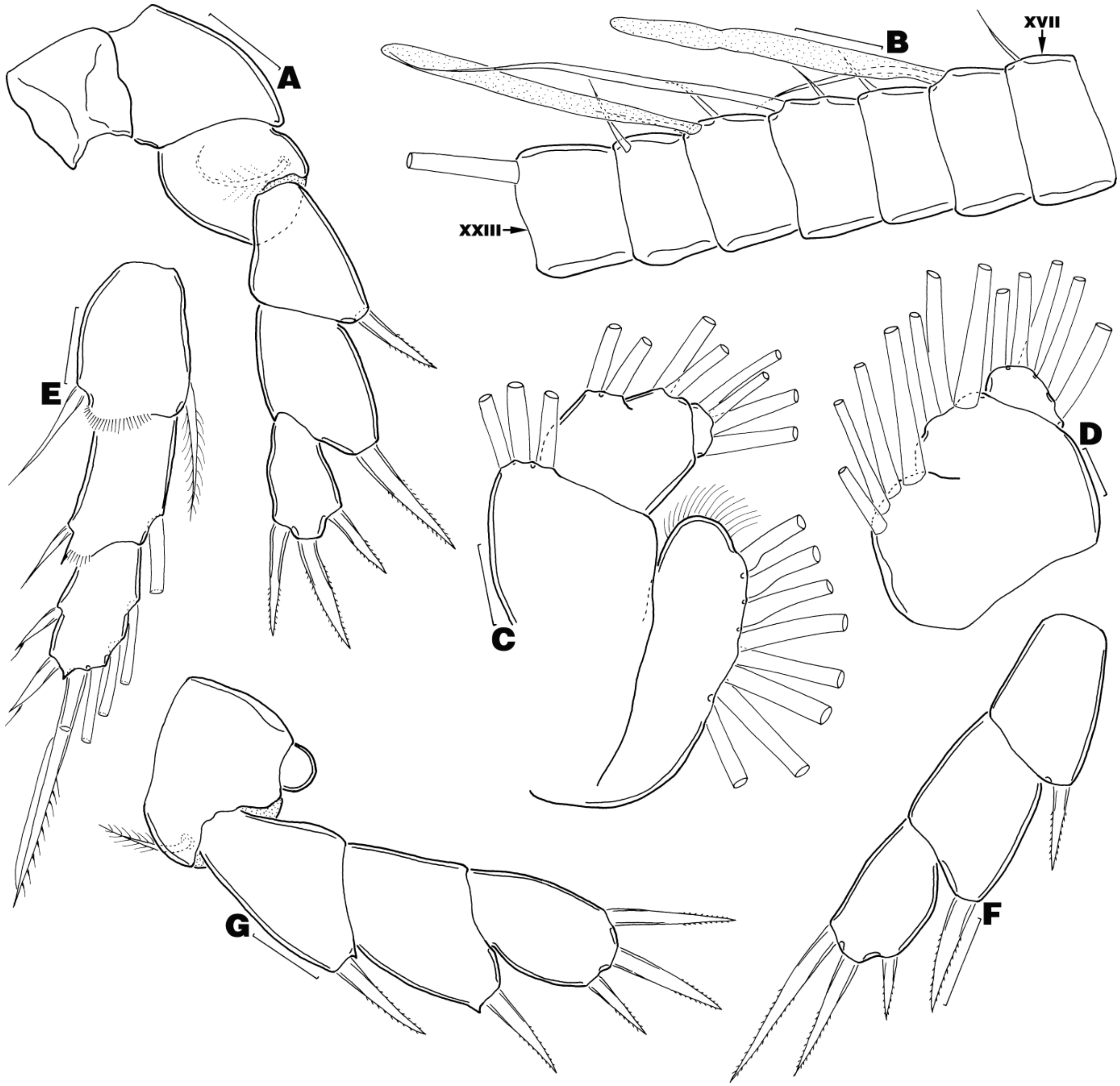

Fig. 6. *Stygoridgewayia trispinosa* n. gen. and n. sp., female. A, leg 5, anterior; B, antennulary segments XVII to XXIII, ventral; C, distal basal endite, exopod and endopod of maxillule, anterior; D, maxillulary endopod, anterior; E, leg 1 exopod, anterior; F, leg 5 exopod, anterior; G, leg 5, anterior. Scale bars: A, B, E, F, G = 15 μm; C = 10 μm; D = 5 μm.

4-segmented exopod, and 2-segmented endopod. Basis with 4 inner setae; exopod setal formula 1, 1, 1, 1+2; endopod setal formula 4, 11.

Maxillule (Fig. 3E) well developed, with praecoxal arthrite bearing 4 spines, 10 setae, and row of setules along distal margin. Coxal epipodite with 9 long setae; coxal endite with 4 setae. Basal exite with short seta; proximal and distal basal endites bearing 4 and 5 setae, respectively. Exopod unsegmented, bearing 11 lateral setae and short setules along distal margin. Endopod 2-segmented, with formula 2+2, 5.

Maxilla (Fig. 4A) composed of syncoxa, basis, and 4-segmented endopod. Armature formula of syncoxal endites 5+short spine, 3, 3, 3; all endites ornamented with fine spinules. Basis with 4 long setae; endopod setal formula 3, 2, 2, 3. Maxilliped (Fig. 4B) comprising syncoxa (although articulation between praecoxa and coxa visible on posterior surface), basis, and 6-segmented endopod. Syncoxa with semi-circular row of setules at base of distal (coxal) endite; setal formula of endites 1, 2, 4, 3. Basis nearly as long as syncoxa, furnished with row of setules basally, and armed with 3 medial setae. Endopod setal formula 2, 4, 4, 3, 3+1,

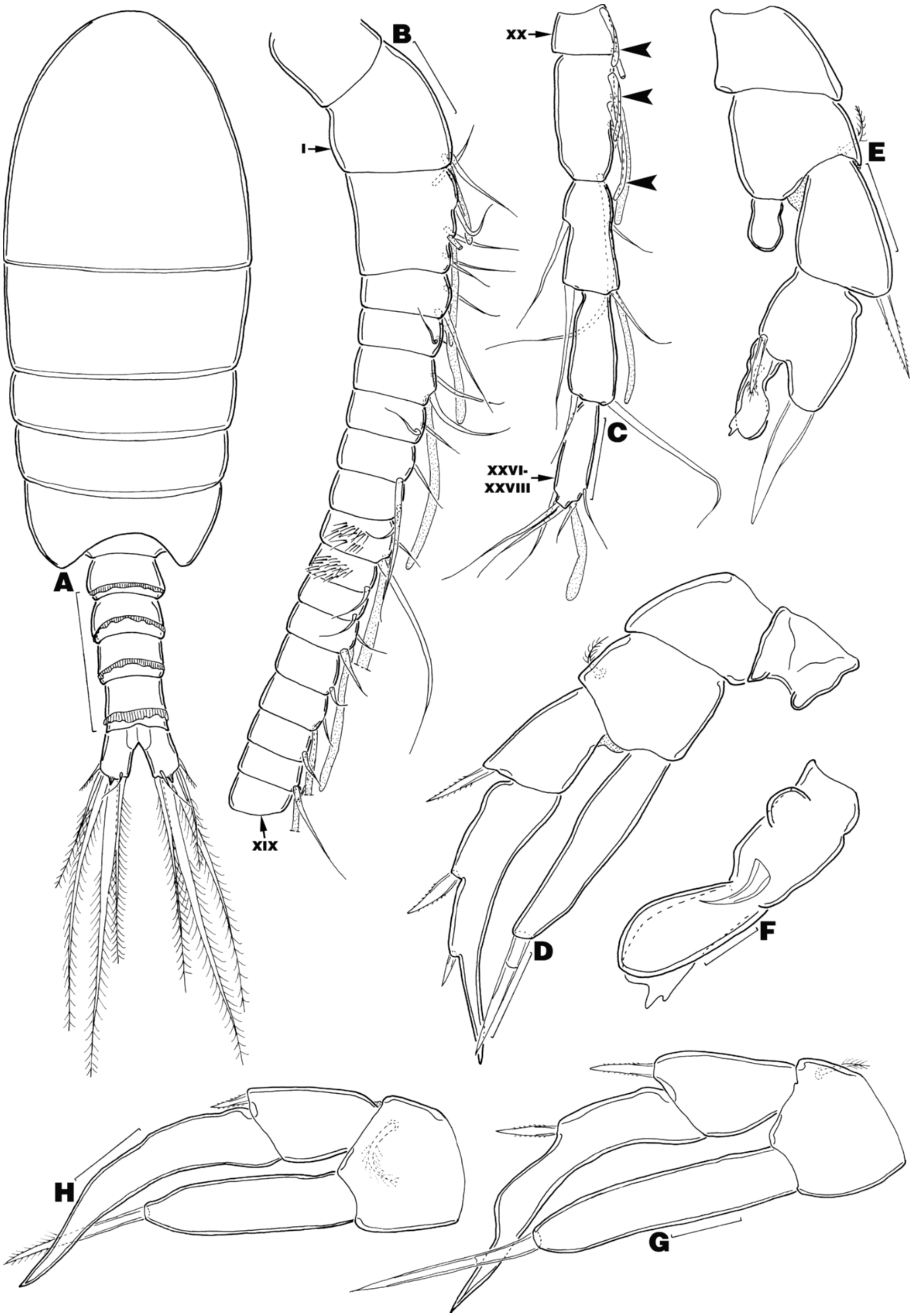

Fig. 7. *Stygoridgewayia trispinosa* n. gen. and n. sp., male. A, habitus, dorsal; B, antennulary segments I to XIX, dorsal; C, antennulary segments XX to XXVIII (arrowheads indicate sclerotized elements), dorsal; D, right leg 5, anterior; E, left leg 5, anterior; F, terminal exopodal segment of left leg 5, posterior; G, right leg 5, anterior; H, same, anterior. Scale bars: A = 0.10 mm; B, C = 25 μm; D, E, G, H = 20 μm; F = 5 μm.

4; first endopodal segment distinctly separate from basis; second endopodal segment with row of large spinules.

Legs 1-4 (Fig. 5A-E) biramous, with 3-segmented rami. Armature formula (spiniform setae represented by Roman numerals, setae represented by Arabic numerals) as follows:

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

Coxa and basis of legs 1-4 unornamented; intercoxal sclerites of legs 1-4 unornamented and bilobed posterolaterally. All natatory setae plumose (setules not drawn on setae of rami of legs 2-4).

Leg 1 (Fig. 5A, B) basis with rounded distomedial process on posterior surface. Proximal exopodal segment with row of spinules along distal margin; middle exopodal segment with acute process and spinous process distolaterally; terminal exopodal segment with small acute process between 2nd and 3rd spiniform setae. First two outer spiniform setae unornamented. Outer spiniform setae on terminal exopodal segment each bearing subapical flagelliform element; distal spiniform seta with lateral hyaline membrane and few long spinules distomedially. First endopodal segment with distolateral margin slightly protruded, extending to proximal 1/8 of second endopodal segment. Terminal endopodal segment with acute distal process.

Proximal exopodal segment of leg 2 (Fig. 5C) with acute process and few spinules distolaterally; middle exopodal segment with acute distolateral process and spinulated distomedial process; terminal exopodal segment with small acute process as in leg 1. All outer spiniform setae spinulate. Distal spiniform seta on terminal exopodal segment similar to that of leg 1, except lacking distomedial row of spinules. Distolateral corner of proximal endopodal segment slightly pointed; middle endopodal segment with acute distolateral process and distomedial row of long spinules; terminal endopodal segment with distal process as in leg 1.

Leg 3 (Fig. 5D) identical to leg 2, except basis with small triangular process between bases of rami, and outer spiniform seta on first 2 exopodal segments and distolateral spine on terminal exopodal segment each with 2 acute processes at base. Leg 4 (Fig. 5E) similar to leg 3, except basis with outer seta, second exopodal segment without distomedial spinulated process, distal spiniform seta curving inward and bilaterally furnished with spinules, and terminal endopodal segment armed with 7 setae. Leg 5 (Fig. 6A) uniramous, 3-segmented, and unornamented. Coxa unarmed; basis with outer seta. Proximal and middle exopodal segments each with outer spiniform seta; spiniform seta on middle segment extending beyond distal margin of terminal segment. Terminal exopodal segment inserted along distal margin of middle segment, armed with 3 unequal spiniform setae.

Male.—Body (Fig. 7A) 0.57 $\pm$ 0.01 mm long (range = 0.54-0.59 mm; $n = 15$), similar in shape to that of female. Urosome 5-segmented, ornamented as in female. All appendages similar to those of female, except for right antennule and leg 5. Right antennule (Fig. 7B, C) 22-segmented, weakly geniculate, and implanted on pedestal. Armature and fusion pattern as follows: I-1+ae, II-IV-6+ae, V-2+ae, VI-2, VII-2+ae, VIII-2, IX-2, X-1, XI-2+ae, XII-1, XIII-1, XIV-2+ae, XV-1, XVI-2+ae, XVII-1, XVIII-1+ae, XIX-0, XX-1+sclerotized element, XXI-XXIII-2+ae+2 sclerotized elements, XXIV-XXV-4+ae, XXVI-2, and XXVII-XXVIII-5+ae. Dorsal surface of segments XI and XII each furnished with patch of fine spinules.

Leg 5 (Fig. 7D, E) asymmetrical, biramous, and unornamented. Coxae unarmed; bases each with outer seta. Right exopod (Fig. 7D) 2-segmented; proximal segment bearing outer spiniform seta; distal segment about twice as long as proximal segment, curved inward, tapered distally, and armed with 2 unequal spiniform setae. Right endopod 1-segmented, as long as distal exopodal segment, and armed with long distal element. Left exopod (Fig. 7E) 3-segmented, complex in structure. Proximal segment robust, armed with outer spiniform seta; middle segment robust, with outer elongate process and weakly sclerotized inner element; terminal segment (Fig. 7E, F) rounded distally, bearing lamelliform process on anterior surface and proximal spine on posterior surface. Left endopod a 1-segmented, unarmed lobe.

Variability.—Morphological differences observed in Exmouth material as follows: 1) 4 females with an additional seta on antennulary segments XVII and XIX to XXII, i.e., 5 extra setae in all (Fig. 6B); 2) 1 female with maxillule bearing 3 setae on distal basal endite, 8 setae on exopod, and formula 2+2, 4 on endopod (Fig. 6C); 3) another female with formula 4+3, 5 on maxillulary endopod (Fig. 6D); 4) all specimens lacking distolateral spinous process on middle exopodal segment of leg 1 (Fig. 6E); 5) 17 females with leg 5 bearing relatively shorter outer spiniform seta on middle exopodal segment and relatively longer inner spiniform seta on terminal exopodal segment (Fig. 6F); 6) 4 females with leg 1 lacking inner seta on proximal exopodal segment (not figured), leg 2 bearing 7 setae on terminal endopodal segment (not figured), and leg 5 bearing relatively shorter outer spiniform seta on middle exopodal segment and rudimentary endopod (Fig. 6G); 7) 2 males with right leg 5 bearing only 1 outer spiniform seta on terminal exopodal segment and relatively longer apical element on endopod (Fig. 7G); and 8) 9 males with right leg 5 bearing relatively shorter spiniform seta on proximal exopodal segment, unarmed terminal exopodal segment, and setulate apical element on endopod (Fig. 7H).

Etymology.—The species name refers to the three armature elements on the terminal exopodal segment of the female fifth leg.

Habitat and Distribution.—The Cape Range Peninsula, located roughly midway along the Western Australian coastline, is bordered on the west by the Indian Ocean and to the east by the Exmouth Gulf. It encompasses an area of about 1600 km^2, reaches a maximum elevation of 314 m, and has an average rainfall of 250 mm per annum. This area is composed of a sequence of predominantly marine carbonate sediments (Mandu, Tulki, and Trealla Limestones) of Oligocene-Miocene age, and is underlain by a lens of fresh groundwater overlying seawater (Allen, 1993). The new calanoid was found approximately 2-5 km inland from the northeastern shoreline of the peninsula (Fig. 1), in salinities of 0.01-1.31‰ and 0.41-38.04‰ at the MB and DSO bores, respectively. Other fauna in the Cape Range Peninsula bore sites includes the atyid shrimp *Stygiocaris stylifera* Holthuis, 1960, the thermosbaenacean *Halosbaena tulki* Poore and Humphreys, 1992, the amphipod *Nedsia* sp., and the cyclopoid copepod *Diacyclops humphreysi* Pesce and De Laurentiis, 1996.

The Pilbara region encompasses the Ashburton, Fortescue, De Grey, Onslow Coast, and Port Hedland Coast Basins, covering approximately 178,000 km^2 in total area east of the Cape Range Peninsula. This vast region receives an average annual rainfall of 200-250 mm, with groundwater occurring in Precambrian rocks, Phanerozoic sedimentary basins, and Cenozoic deposits (Eberhard et al., 2005). Although the new species was collected primarily throughout the western, and some from the northern, section of the Pilbara, it was found at one bore site (Weeli Wolli) situated approximately 450 km southeast of the small coastal town of Onslow (Fig. 1). Salinity in the Pilbara sites ranged from 0.10 to 4.30‰. Tubificid oligochaetes, planorbid gastropods, thermosbaenaceans, syncarids, mites, candonid, cypridid and limnocytherid ostracods, cirolanid, phreatoicid and tainisopid isopods, bogidiellid, melitid, neoniphargid and paramelitid amphipods, ameirid, canthocamptid, diosaccid, ectinosomatid and parastenocaridid harpacticoid copepods, and cyclopoid copepods were also collected from the Pilbara sites.

Remarks.—With the exception of the apomorphic fifth legs in both sexes, *Stygoridgewayia*, new genus, exhibits many plesiomorphic features characteristic of the superfamily Epacteriscoidea. We consider the new taxon to be attributable to Ridgewayiidae rather than Epacteriscidae because it has symmetrical caudal setae, a well developed mandibular endopod, and higher number of setation elements on the mandibular endopod and maxillule as well as greater number of free endopodal segments on the maxilla and maxilliped than hitherto considered within the morphological range of the latter family (Fosshagen et al., 2001; Jaume and Humphreys, 2001; Boxshall and Jaume, 2003; Fosshagen and Iliffe, 2004; Suárez-Morales et al., 2006).

Stygoridgewayia shares a mixture of apomorphic character states with several ridgewayiid genera. For example, the loss of the endopod on the female fifth leg is shared with *Normancavia* and the presence of two outer spiniform setae on the terminal exopodal segment of legs 3 and 4 with *Stargatia* and *Exumellina*. The new genus can be distinguished from *Normancavia* by the absence of rostral filaments and modified setae on the maxilliped, reduced number of outer spiniform setae on the terminal exopodal segment of legs 3 and 4, and insertion of the terminal exopodal segment along the distal margin (rather than the medial margin) of the preceding segment of the female fifth leg. The new genus can be distinguished from *Stargatia* and *Exumellina* by structural differences in the mandibular endopod (unmodified vs. enlarged), maxillulary endopod (unmodified vs. elongate), female leg 5 (uniramous vs. biramous), and male leg 5 endopods (1-segmented vs. 2- or 3-segmented).

Hondurella and *Ridgewayia* share several features, such as an uncompressed prosome, pointed rostrum lacking filaments, unmodified antennule, maxillule with outer basal seta, unmodified leg 1 endopod, and male leg 5 with highly reduced endopods, in common with *Stygoridgewayia*. Indeed *Hondurella* appears to be a transitional form between the other two genera. *Hondurella* shares a well-developed distolateral lobelike extension on the first endopodal segment of leg 1 and three outer spiniform setae on legs 3 and 4 with *Ridgewayia* and a subterminal flagellum on the outer spiniform setae of the terminal exopodal segment of leg 1 with *Stygoridgewayia*. More importantly, for female leg 5: a) the terminal exopodal segment is constricted basally and inserted into a socket on the medial margin of the second segment in *Ridgewayia*, has a relatively wider base that articulates at a joint located distomedially on the second segment in *Hondurella*, and is basally broad and inserted along the distal margin of the second segment in *Stygoridgewayia*; and b) the endopod is two- or three-segmented, armed with six or seven setae on the terminal segment, in *Ridgewayia*, one-segmented and unarmed in *Hondurella*, and entirely absent in *Stygoridgewayia*.

The most outstanding feature of *Stygoridgewayia* is the highly reduced armature on the female leg 5 exopod; the inner seta on the middle segment is absent and the terminal segment bears only three spiniform setae. Members of the other ridgewayiid genera retain the inner seta on the middle exopodal segment and have an armature formula on the terminal exopodal segment of II, II, 4 (*Ridgewayia*, *Placocalanus insularis* Fosshagen, 1970, and *P. nannus* Fosshagen, 1970), II, II, 3 (*Badijella*, *Brattstromia*, *Exumella*, *Exumellina*, *Robpalmeria*, *Stargatia*), II, II, 2 (*Normancavia* and *Placocalanus longicauda* Ohtsuka, Fosshagen and Soh, 1996), II, I, 4 (*Hondurella*), or II, II (*Placocalanus inermis* Ohtsuka, Fosshagen and Soh, 1996). *Stygoridgewayia* can be readily separated from the other ten ridgewayiid genera by the following combination of apomorphic features: striated membrane and three digitiform processes on each caudal ramus; ancestral segments II-IV and V-VI fused on the antennary exopod; subterminal flagellum on the outer spiniform setae of the terminal exopodal segment of leg 1; two outer spiniform setae on the terminal exopodal segments of legs 3 and 4; loss of the inner seta on the middle exopodal segment of female leg 5; three spiniform setae on the terminal exopodal segment of female leg 5; and absence of female leg 5 endopod.

Discussion

Ridgewayiid genera, such as *Brattstromia*, *Exumella*, *Exumellina*, *Normancavia*, *Robpalmeria*, and *Stargatia*, with enlarged ventral teeth on the mandibular gnathobase and modified setae on the maxilliped are regarded as raptorial feeders, while those (*Hondurella* and *Ridgewayia*) with low teeth on the mandibular gnathobase and slender setae on the mandibular palp and maxillule are considered as particle feeders (Fosshagen and Iliffe, 1991, 1998, 2003; Suárez-Morales and Iliffe, 2007). We believe *Stygoridgewayia trispinosa* n. sp. is a particle feeder because its mandible, maxillule, and maxilliped are structurally similar to those of *Ridgewayia*.

Although the sampling methods used in this study precluded us from determining whether *S. trispinosa* was collected in situ from the bottom or water column of each bore/well, we believe this species is a hyperbenthic form based on its relatively shorter antennules (25-segmented, not extending beyond prosome) compared with those of *Exumellina* (27-segmented, extending well beyond prosome) and *Stargatia* (26-segmented, extending well beyond prosome), which were collected in the water column of anchialine caves (Fosshagen and Iliffe, 1998, 2003). This inference is further supported by the presence in the bore and well sites, from which specimens of the new species were found, of other crustacean taxa, e.g., thermosbaenacaens, syncarids, harpacticoid copepods, typically associated with the sediment surface.

The discovery of the new species in a freshwater hypogean environment is highly unusual within Ridgewayiidae, inasmuch as the other genera have been reported hitherto from anchialine or coastal environments. We propose that the new ridgewayiid is derived from a marine ancestor because its related genera, *Hondurella* and *Ridgewayia*, live in anchialine caves and both the marine hyperbenthos and anchialine caves, respectively, and the new species may indeed be euryhaline, having been collected from sites (DSO bores) in the Cape Range Peninsula that intersect fresh, brackish, and marine waters. The occurrence of the new species in subterranean waters is, therefore, interpreted as a secondary colonization of fresh water following the regression of the epicontinental sea that inundated a large part of Australia, including the Cape Range Peninsula and western and eastern margins of the Pilbara region, from the Aptian to Albian stages of the Lower Cretaceous (ca. 125-100 Ma) (Frakes et al., 1987). Similar thalassoid origins have been postulated for amphipod species collected from the Cape Range Peninsula (Knott, 1993), as well as for spelaeogriphaceans and some cyclopoid and harpacticoid copepods found in the Pilbara (Poore and Humphreys, 1998, 2003; Karanovic, 2006).

Given that *Stygoridgewayia* is more apomorphic than *Ridgewayia* and most likely originated during the lower Cretaceous as discussed above, the origin of the latter genus must also date back to at least the Cretaceous, as originally proposed by Ohtsuka et al. (2000), or more likely as far back as the Jurassic when the Tethys Sea existed as a large seaway that extended from the present Indo-Pacific through Mediterranean Europe and across the North Atlantic. This assumption is supported by the fact that members of *Ridgewayia*, in particular the *Ridgewayia marki* species-group, exhibit a full Tethyan track distribution (Ohtsuka et al., 2000). Although just one species, viz., *Ridgewayia stygia* Ohtsuka, Kase, and Boxshall, 2000, of the *Ridgewayia marki* species-group has been reported from the Indo-West Pacific thus far, we predict that extensive sampling of the shallow water hyperbenthos of continents bordering the tropical Indian Ocean will uncover additional species of this group within this area. This prediction also applies to *Stygoridgewayia*.

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Appendix 1. Additional material of *Stygoridgewayia trispinosa* n. sp. collected from bore and well sites within the Pilbara and Cape Range Peninsula regions of Western Australia.

Region	Locality	Bore Code	Coordinates	Date	Copepod Stages
Pilbara	House Creek	NWSLK58	22°27′S, 116°02′E	8 August 2005	23 ♀♀, 21 ♂♂, 6 copepodids
	Wyloo Station	NWSLK88	22°39′S, 116°14′E	3 August 2003	3 ♀♀, 3 ♂♂, 1 copepodid
	Calgara Bore	NWSLK176	22°58′S, 116°58′E	27 August 2003	6 ♀♀, 4 ♂♂, 2 copepodids
	Firestick Well	PYRAMID1	21°16′S, 117°18′E	24 June 2004	3 ♂♂, 1 copepodid
	Firestick Well	PYRAMID1	21°16′S, 117°18′E	15 August 2005	1 ♀, 2 ♂♂, 2 copepodids
	Demander Well	PYRAMID2	21°07′S, 117°24′E	15 August 2005	1 ♂
	Minson Well	PYRAMID6	21°10′S, 117°47′E	17 June 2004	1 ♂
	Minson Well	PYRAMID6	21°10′S, 117°47′E	14 June 2005	3 ♀♀, 6 ♂♂, 4 copepodids
	Johnie Walker	PYRAMID8	21°17′S, 117°51′E	14 June 2005	3 ♂♂
	Weewaddie Bore	GFS003	22°53′S, 115°52′E	4 June 2005	1 ♂, 1 copepodid
	Fortescue 2B	G70830103	21°11′S, 116°04′E	10 November 2004	8 ♀♀, 11 ♂♂, 1 copepodid,
	Fortescue 4A	G70830105	21°11′S, 116°03′E	10 November 2004	7 ♀♀, 10 ♂♂, 7 copepodids
	Fortescue 4P	G70830105P	21°11′S, 116°03′E	4 April 2003	1 ♀, 4 ♂♂, 2 copepodids
	Fortescue 4P	G70830105P	21°11′S, 116°03′E	19 November 2003	1 ♀, 12 copepodids
	Fortescue 6A	G70830107	21°10′S, 116°02′E	10 November 2004	1 copepodid
	Fortescue 6A	G70830107	21°10′S, 116°02′E	2 June 2005	8 ♀♀, 5 ♂♂, 1 copepodid
	Murry Camp Well	LHR1	20°53′S, 117°08′E	5 August 2005	1 ♀, 1 copepodid
	Six Mile Well	RED001	22°01′S, 116°06′E	11 August 2004	37 ♀♀, 24 ♂♂
	Red Hill Well	RED002	22°07′S, 116°03′E	11 August 2004	22 ♀♀, 14 ♂♂, 6 copepodids
	Red Hill Well	RED002	22°07′S, 116°03′E	15 May 2005	31 ♀♀, 40 ♂♂, 18 copepodids
	Cardo Outstation	RED003	22°14′S, 116°08′E	11 August 2004	2 ♀♀, 5 ♂♂
	Cardo Outstation	RED003	22°14′S, 116°08′E	15 May 2005	1 ♀, 1 ♂
	Little George River	NWCHSLK1180	20°58′S, 117°05′E	31 July 2003	19 ♀♀, 7 ♂♂
	Hardey Bore	WYL003	22°49′S, 116°16′E	16 May 2005	48 ♀♀, 56 ♂♂, 25 copepodids
	Weeli Wolli	BH32D	22°55′S, 119°12′E	11 April 2003	1 copepodid
	Harding Dam	HD1/81	20°58′S, 117°05′E	3 April 2003	1 copepodid
	Harding Dam	HD3/00	20°58′S, 117°05′E	11 October 2004	1 ♀, 1 ♂
	Yarraloola Station	PANNASLK4	21°37′S, 115°57′E	17 June 2003	15 ♀♀, 11 ♂♂, 7 copepodids
	Yarraloola Well	PANNASLK24	21°39′S, 116°08′E	5 April 2003	1 ♂
	Yarraloola Well	PANNASLK24	21°39′S, 116°08′E	21 October 2004	1 ♀, 1 ♂
	Yarraloola Well	PANNASLK24	21°39′S, 116°08′E	6 August 2005	2 ♀♀, 2 ♂♂
	Robe River	G70730101	21°34′S, 115°52′E	11 November 2004	26 ♀♀, 25 ♂♂
	Robe River	G70730102	21°34′S, 115°52′E	21 October 2004	13 ♀♀, 10 ♂♂
	Robe River	G70730102	21°34′S, 115°52′E	14 May 2005	16 ♀♀, 12 ♂♂
	Robe River	G70730103	21°32′S, 115°51′E	11 November 2004	3 ♀♀, 4 ♂♂
	Robe River	G70730104	21°34′S, 115°50′E	4 April 2003	85 ♀♀, 40 ♂♂, 4 copepodids
	Robe River	G70730104	21°34′S, 115°50′E	11 November 2004	46 ♀♀, 29 ♂♂, 2 copepodids
	Robe River	G70730104O	21°34′S, 115°50′E	19 November 2003	59 ♀♀, 39 ♂♂
	Robe River	G70730107P	21°31′S, 115°51′E	4 April 2003	1 ♀, 1 ♂
	Hilda Well	Mardi1	21°07′S, 115°58′E	25 June 2004	2 ♂♂
	Millstream-Yarraloola Road	MILLYARRA64A	21°44′S, 116°46′E	12 April 2003	8 ♀♀, 6 ♂♂, 2 copepodids
	Seven Mile Well	MILLYARRA1	21°49′S, 116°19′E	19 November 2003	30 ♀♀, 9 ♂♂, 10 copepodids
	Mesa G	ER81	21°43′S, 116°05′E	18 June 2003	1 ♂
	Jimmawarranda	JW011A	21°45′S, 116°13′E	18 June 2003	5 ♀♀, 25 ♂♂, 3 copepodids
	Bungaroo Creek	BUNW0774	21°51′S, 116°26′E	18 June 2003	5 ♀♀, 1 ♂
	Bungaroo Creek	BC62	21°57′S, 116°29′E	18 June 2003	3 ♀♀, 1 ♂
	Cheela Plains camp	CP1	22°55′S, 116°51′E	27 August 2003	1 ♀
	Eramurra Creek	NWCHSLK1033	21°03′S, 116°15′E	13 November 2002	13 ♀♀, 12 ♂♂
Cape Range	Exmouth	MB18	21°56′S, 114°06′E	April 2005	1 ♂
	Exmouth	MB18	21°56′S, 114°06′E	July 2005	1 ♀
	Exmouth	MB18	21°56′S, 114°06′E	December 2005	1 copepodid
	Exmouth	MB26	21°57′S, 114°06′E	April 2005	1 ♀
	Exmouth	MB26	21°57′S, 114°06′E	July 2005	1 ♀, 1 copepodid
	Exmouth	MB26	21°57′S, 114°06′E	December 2005	2 ♀♀
	Exmouth	MB26	21°57′S, 114°06′E	April 2006	1 ♂
	Exmouth	MB31	21°58′S, 114°06′E	April 2005	7 ♀♀, 1 ♂
	Exmouth	MB31	21°58′S, 114°06′E	July 2005	2 ♀♀, 1 ♂, 7 copepodids
	Exmouth	MB31	21°58′S, 114°06′E	December 2005	4 ♀♀, 7 ♂♂, 22 copepodids
	Exmouth	MB31	21°58′S, 114°06′E	April 2006	1 ♀
	Exmouth	DSO1/96	21°59′S, 114°06′E	July 2005	1 ♀
	Exmouth	DSO4/96	22°00′S, 114°05′E	April 2005	1 ♀