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New stygobiont copepods (Calanoida; Misophrioida) from Bundera Sinkhole, an anchialine cenote in north-western Australia

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Two new taxa in the copepod orders Calanoida and Misophrioida are described from the flooded coastal karst of north-western Australia. ***Stygocyclopia australis* sp. nov.** is the first pseudocyclopiid calanoid to be reported from the continent, with other congeners distributed in anchialine environments of the Philippine, Balearic, and Canary archipelagos. The presence of a supernumerary spine on the outer margin of the first exopod segment of leg 3 in this species is discussed in the context of the Neocopepodan groundpattern. ***Speleophria bunderae* sp. nov.** is the first representative of the order Misophrioida known from Australia, with other congeners in the Balearics, Bermuda, and the Yucatán peninsula of México. Both taxa co-exist in the deeper higher salinity layers of a single sinkhole in Cape Range peninsula. The placement of these taxa in strictly stygobiont genera represented by very localized and disjunct species distributed over regions flooded by the late Mesozoic seas, lends support to their interpretation as true Tethyan relicts, and hence to the inclusion in the past of the Northwest portion of Australia in the Tethyan realm. The remains of *S. bunderae* in the gut contents of a stygobiont epacteriscid calanoid is recorded.
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ADDITIONAL KEY WORDS: Copepoda – Pseudocyclopiidae – *Stygocyclopia* – Speleophriidae – *Speleophria* – stygobionts – caves – Tethyan relicts – biogeography – systematics.

INTRODUCTION

Anchialine habitats are noteworthy for their very diverse crustacean assemblages, especially those restricted to the oligoxic reaches of the water column, where most of their members represent biogeographic and/or phylogenetic relicts (Iliffe, 1992). The structure of these assemblages is highly predictable, being typically composed of atyid shrimps, thermosbaenaceans, hadziid amphipods, cirolanid isopods, remipeds, thaumatocypridid ostracods, and a vast array of copepods such as epacteriscid, pseudocyclopiid, and ridgewayiid calanoids, halicyclopine cyclopoids, speleophriid misophrioids, and superornatiremid harpacticoids. Most striking of all is that this predictability frequently extends to the generic composition (Wagner, 1994): no matter how far apart and isolated a new anchialine locality is from the rest, one can expect a high proportion of the eventual new taxa discovered to be congeneric of those already known from other anchialine localities. This high taxonomic predictability, combined with the strictly stygobiont condition of these taxa, and the existence of enormous barriers to dispersal between the locations of congeneric species (such as entire continental landmasses and/or deep and wide oceanic basins), point more to vicariance than to dispersal as the process determining their current distribution patterns. In fact, their perfect fit with the areas previously covered by the sea in the late Mesozoic suggests that their present distributions could have resulted from vicariance by plate tectonics (Stock, 1993).

A rich anchialine biota of this type has recently been discovered by the junior author in the Cape Range peninsula and nearby Barrow Island, in north-western

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Australia. The crustacean assemblage in these waters includes the following: remipede *Lasionectes exleyi* Yager & Humphreys, 1996; the thaumatocypridid ostracod *Danielopolina kornickeri* Danielopol, Baltanás & Humphreys, 2000; the epacteriscid calanoid copepod *Bunderia misophaga* Jaume & Humphreys (2001), the halicyclopine cyclopoids *Halicyclops spinifer* Kiefer, 1935; *H. longifurcatus* Pesce, De Laurentiis & Humphreys, 1996; the atyid shrimps *Stygiocaris stylifera* Holthuis, 1959 and *S. lancifera* Holthuis, 1959; the thermosbaenacean *Halosbaena tulki* Poore & Humphreys, 1992; the hadziid amphipod *Liagoceradocus branchialis* Bradbury & Williams, 1995, and the cirolanid isopod *Haptolana pholeta* Bruce & Humphreys, 1993 (see Humphreys, 2000; Jaume & Humphreys, 2001).

We report here on the discovery of two new copepods belonging to this highly predictable assemblage in Bundera Sinkhole, an anchialine cenote on Cape Range peninsula: a new species of pseudocyclopiid calanoid of the genus *Stygocyclopia* Jaume & Boxshall, 1995 and a new speleophriid misophrioid *Speleophria* Boxshall & Iliffe, 1986.

MATERIAL AND METHODS

The animals were collected in Bundera Sinkhole, an anchialine cenote 1.7 km inland from the Indian Ocean in Cape Range peninsula, north-western Australia. A detailed description of the cave is provided by Yager & Humphreys (1996), of the water column in Humphreys (1999a), and some effects of diving on the environment in Humphreys *et al.* (1999). The animals were found under a pycnocline placed at *c.* 8 m depth in oligoxic waters (oxygen <1 mg l^{-1} of near-marine salinity (33–34‰) below sulphidic layers, collected by scuba using hand-held nets and bottles, and fixed in 70% ethanol.

Figures were prepared with a camera lucida on an Olympus BH-2 microscope equipped with Nomarski differential interference contrast. Terms used in descriptions are adopted from Huys & Boxshall (1991). The material is deposited in the Western Australian Museum, Perth, Australia (WAM). Material preserved on permanent glass slides is mounted in lactophenol sealed with nail varnish. BES is a prefix for field numbers from WAM Biogeography, Ecology and (Bio)-speleology unit.

SYSTEMATICS

SUBCLASS COPEPODA H. MILNE EDWARD, 1830
ORDER CALANOIDA G.O. SARS, 1903
FAMILY PSEUDOCYCLOPIIDA T. SCOTT, 1892
GENUS *STYGOCYCLOPIA* JAUME & BOXSHALL, 1995

STYGOCYCLOPIA AUSTRALIS **SP. NOV.**

(*Figures 1–7*)

Material examined

Bundera Sinkhole (Australian Karst Index number C-28), Cape Range peninsula, north-western Australia. Coordinates: 22°25′S/113°46′E.

Holotype: adult female 0.79 mm in 70% ethanol vial [WAM C24512]. Paratypes: two adult males (0.71 and 0.78 mm), two adult females (0.83 and 0.78 mm), plus single copepodid III; one of female paratypes completely dissected and mounted on 10 slides [WAM C24513]; one of male paratypes with rostrum, both antennules, antenna, mandibular palp, maxillule, maxillae, and legs 2 to 5 dissected and mounted on 5 slides [WAM C24514]; rest of paratype specimens preserved in 70% ethanol in single vial [WAM C24515]. BES no. of female paratype of 0.83 mm: 4729.0; BES no. of rest of material: 4719.0. Collected by A. Poole, S. Eberhard and W. F. Humphreys, 23 September 1997.

Description of adult female

Body (Fig. 1A) colourless in preserved specimens, compact, with prosome slightly compressed in dorsal aspect. Eyes absent. Rostrum (Fig. 1B) fused to cephalosome, short, triangular in frontal aspect, with pair of short, blunt filaments on tip. Transverse slit near base of rostrum resembling structure present on head shield of chydorid anomopod branchiopods (see Alonso, 1996). First pedigerous somite incorporated with cephalosome forming cephalothorax. Dorsal fold of cuticular membrane resembling posterior extension of cephalothorax, covering anterior dorsal half of second pedigerous somite. Second and third pedigerous somites with rounded posterolateral margins; margin of third pedigerous somite with robust sensilla. Fourth and fifth pedigerous somites fused, symmetrical, with patch of long setules along posterolateral margin. Pedigerous somites each with submarginal cluster of tiny spinules on anterior half of lateral margin.

Urosome 4-segmented, with surface of somites covered with both lamellar and ordinary spinules, easily lost during manipulation of specimens. Genital double-somite (Fig. 1C) externally symmetrical, with lobate hyaline frill along rear margin and paired oviducts, seminal receptacles, and shell ducts; seminal receptacles asymmetrically disposed. Transverse row of slender spinules disposed posterior to quadrangular genital operculum. Anal somite (Fig. 2A,B) shorter than preceding somite, with faint, smooth anal operculum. Caudal rami (Figs 1D, 2A–C) symmetrical, about as long as wide, with transverse row of long spinules along medial margin and patch of similar spinules distally on lateral margin; ventral rear margin of each ramus with small pointed projection. Caudal rami setae symmetrical, seta I reduced and partly hidden by lateral patch of spinules; seta VII displaced to ventromedial side of ramus.

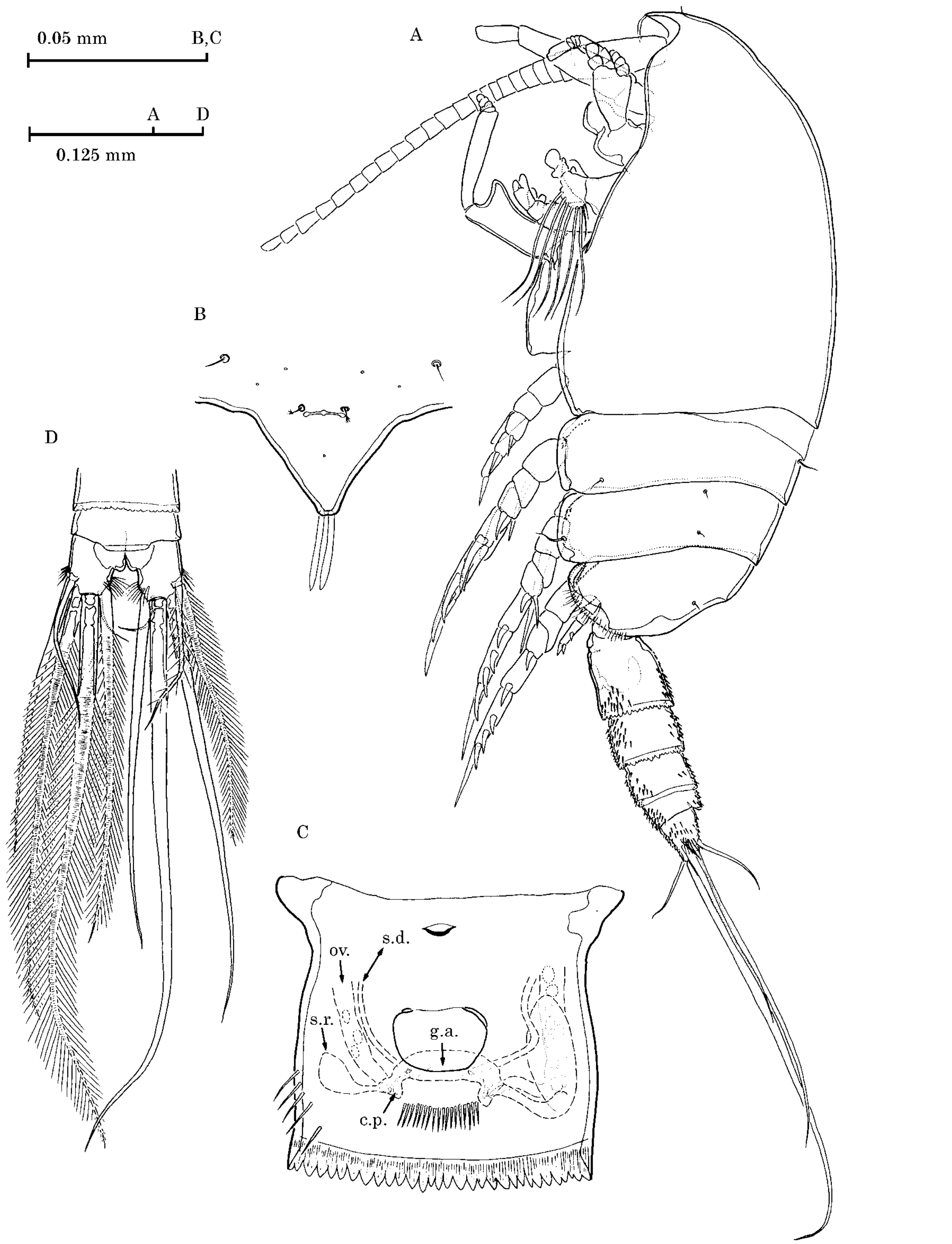

Figure 1. ***Stygocyclopia australis*** **sp. nov.,** adult female. A, body, lateral view; B, rostrum, frontal; C, genital double-somite, ventral (c.p.: copulatory pore; g.a.: slit-like single genital aperture; s.d.: shell duct; s.r.: seminal receptacle; ov.: oviduct); D, anal somite and caudal rami, dorsal.

Antennules (Fig. 3A) symmetrical, 23-segmented, each attached to sclerotized pedestal (arrowed in figure), reaching posterior end of cephalothorax (see Fig. 1A). First segment largest, representing ancestral segments I–IV; other compound segments X–XI and terminal XXVII–XXVIII. Armature elements on segments

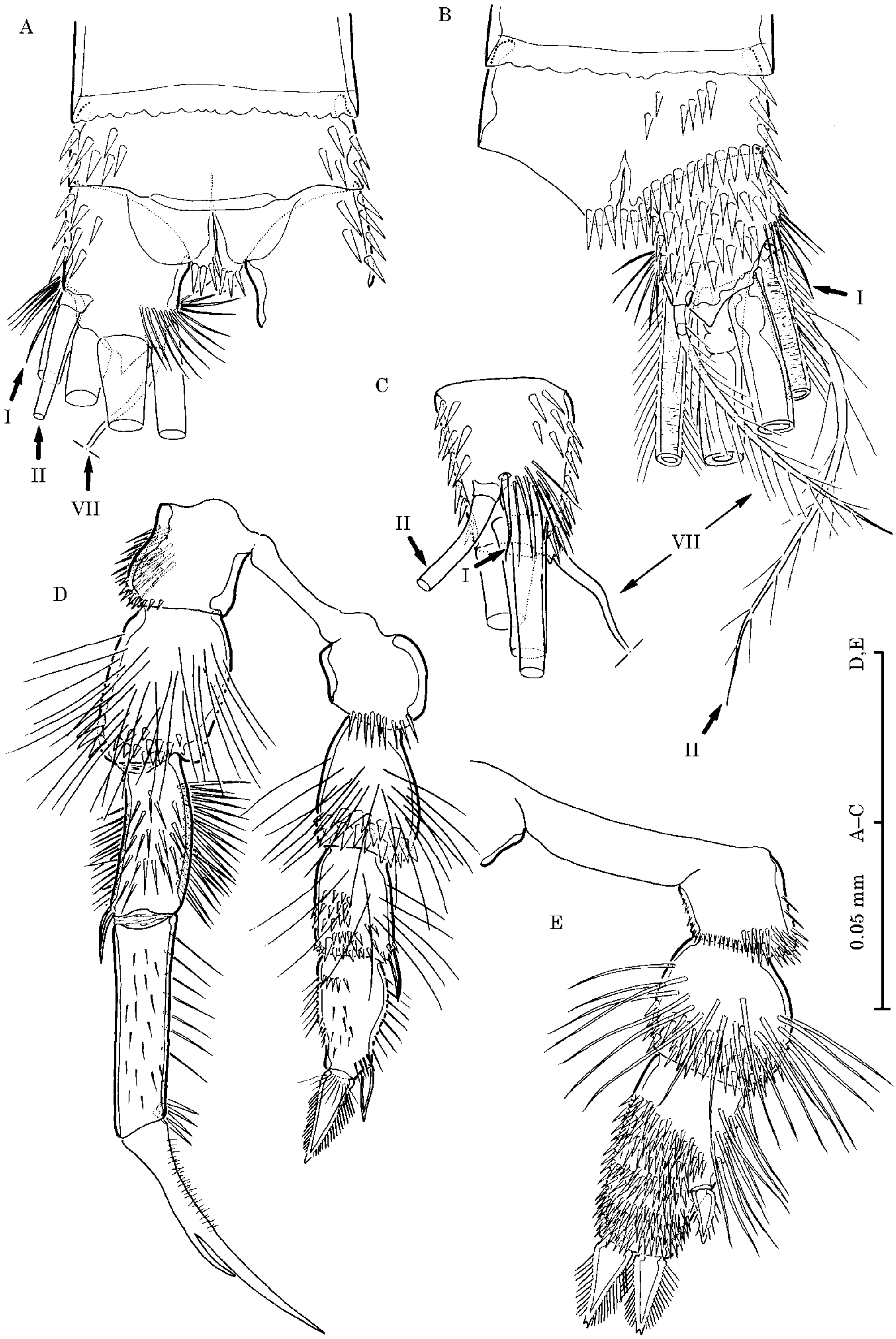

Figure 2. ***Stygocyclopia australis* sp. nov.,** adult female. A, anal somite and left caudal ramus, dorsal; B, same, ventral; C, lateral view of right caudal ramus (seta VI omitted); D, male fifth legs, posterior; E, right female fifth leg, posterior.

as follows: segment 1 (compound I–IV), 8 setae + aesthetasc; segments 2 and 3 (V and VI), 2 setae each; segment 4 (VII), 2 + ae; segment 5 (VIII), 1 seta; segment 6 (IX), 2 setae; segment 7 (compound X–XI), 3 + ae; segment 8 (XII), naked; segment 9 (XIII), 1 seta; segment 10 (XIV), 2 setae; segment 11 (XV), 1

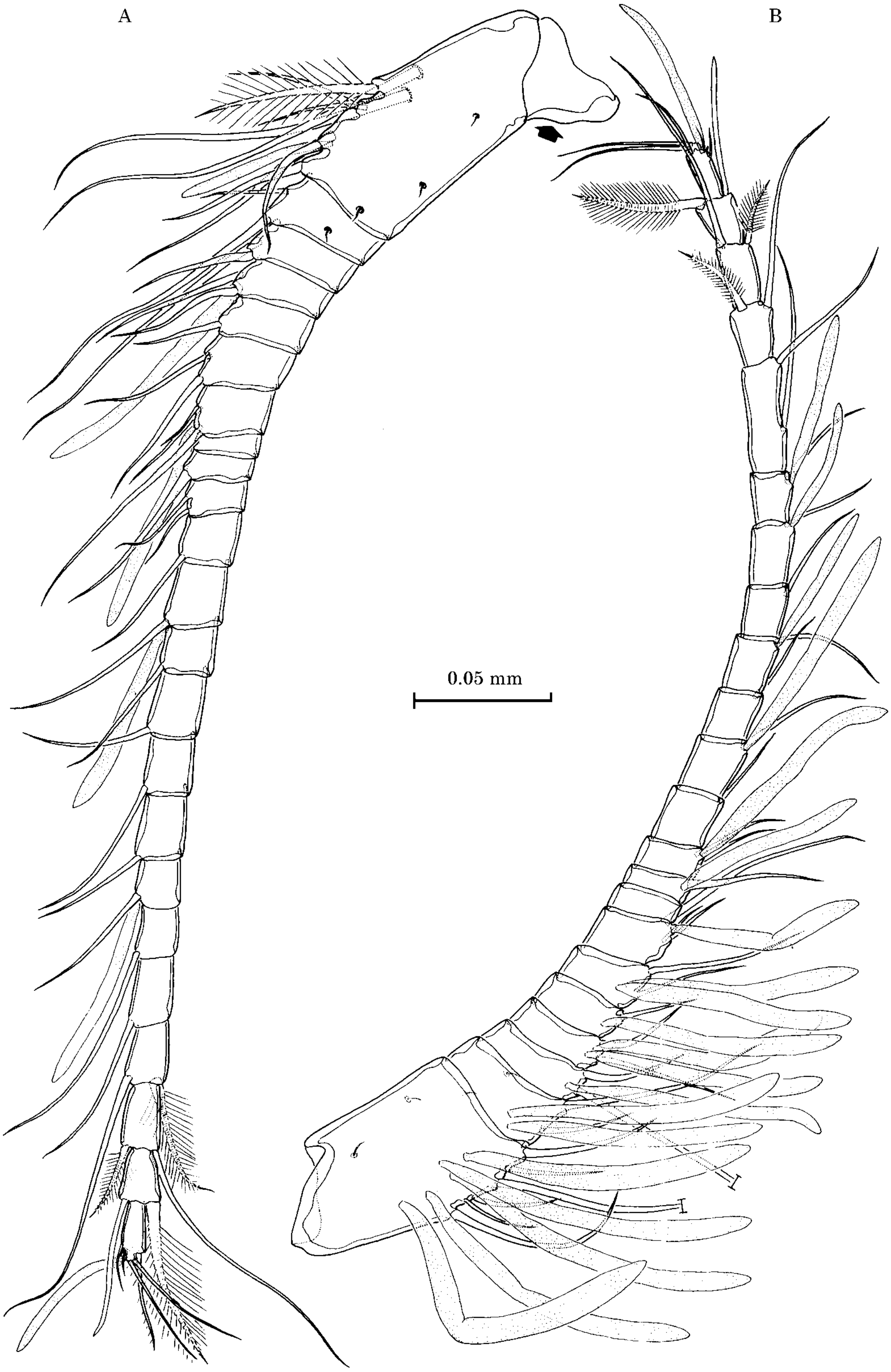

Figure 3. ***Stygocyclopia australis*** **sp. nov.** A, adult female left antennule attached to pedestal (arrowed), lateral; B, adult male right antennule, medial.

seta; segment 12 (XVI), 1 + ae; segments 13–16 (XVII–XX), 1 seta each; segment 17 (XXI), 1 + ae; segments 18 and 19 (XXII and XXIII), 1 seta each; segments 20–22 (XXIV–XXVI), 1 + 1 setae each; segment 23 (compound XXVII–XXVIII), 6 + ae. Three sensillae on dorsal surface of first segment, one sensilla on second segment. Posterodistal seta on segments 20 and 22, and anterodistal seta on segment 21, each densely pinnate, stout, with long and stiff pinnules. Anterodistal seta on segment 22 resembling slender aesthetasc. One of setae on distal segment extremely reduced.

Antenna (Fig. 4A) biramous, with endopod slightly longer than exopod. Coxa discrete, with patch of long spinules on medial margin and long distomedial plumose seta. Basis with 2 distomedial setae; articulation with proximal endopod segment interrupted medially. Exopod indistinctly 6-segmented, segmentation and armature formula as follows: segment 1 (I), 1 seta; segment 2 (compound II–IV), 3 setae; segment 3 (partially incorporated segments V–VIII), 4 setae; segment 4 (compound IX–X), 1 + 3 setae. Endopod 2-segmented, proximal segment longer than distal, with 2 setae implanted about two thirds of distance along medial margin. Compound distal segment bilobed, medial lobe (corresponding to ancestral segment II) with 9 setae (two of them reduced); distal segment corresponding to ancestral segments III and IV, with 7 setae (one of them reduced). Lateral margin of segment ornamented with short, stout spinules along proximal two thirds, and with row of short setules along distal third.

Mandible (Fig. 4B) with powerful coxal gnathobase, cutting edge with 6 unequal sharp teeth, plus 4 unequal, unipinnate dorsalmost spines; three transverse rows of spinules submarginally as figured. Palp with expanded basis, bearing three unequal setae plus proximal patch of short spinules. Exopod longer than endopod, located on pedestal and indistinctly 4-segmented, distal segment corresponding to ancestral IV–V; setal formula: 1, 1, 1, 1 + 2. Endopod 2-segmented, proximal segment with single distomedial seta and transverse row of spinules on lateral margin. Distal segment with 11 setae, two of them reduced.

Maxillule (Fig. 5A) well developed, with praecoxal arthrite bearing 10 stout, heterogeneously ornamented marginal spines plus submarginal row of 4 bipinnate setae on posterior surface. Coxal epipodite with 8 plumose setae on margin, two proximalmost reduced; coxal endite with two setae. Proximal basal endite discrete, with 4 setae; distal endite incorporated into segment, with 5 setae and two unequal rows of spinules. Endopod fully incorporated into basis forming lobe with 11 distal setae and two unequal rows of spinules. Exopod discrete, with 8 marginal setae; posterior surface of segment hirsute.

Maxilla (Fig. 5B,C) with articulation between praecoxa and coxa expressed laterally only; surface of syncoxal endites each with submarginal row of spinules and patch of setules as in Figure 5C; proximal syncoxal endite with 5 long setae and short triangular spine; remaining syncoxal endites each with three setae, one of them shorter (those represented *in toto* in Fig. 5C); soft process of uncertain homology between two proximal syncoxal endites. Basal endite with 4 setae, one of them stout and expanded proximally. Endopod short, 2-segmented, with distal segment reduced; setal formula: 4, 3.

Maxilliped (Fig. 4C) powerfully developed, reflexed distally (see Fig. 1A). Syncoxa stout, with 9 unequal setae on medial surface of segment distributed in 4 groups corresponding to armature of praecoxal and coxal endites: 1, 2, 3, 3; distomedial corner of syncoxa produced into rounded lobe with microtuberculate integument surface; patch of long spinules implanted proximally on lateral surface of segment. Basis slender, about as long as syncoxa, with three setae along medial margin, and row of submarginal short spinules along medial surface. Endopod 5-segmented, compound proximal segment corresponding to ancestral segments I–II, with intersegmental articulation defined on medial surface only; setal formula: (2 + 4), 4, 3, 3 + 1, 4; transverse row of stout denticles along distomedial margin of second and third segments, and of slender denticles along same margin of fourth segment.

Legs (Figs 6, 7) increasing progressively in size, each with 3-segmented exopod; praecoxa present on each leg. Endopod of first leg 1-segmented, that of second leg 2-segmented, those of third and fourth legs 3-segmented. Intercoxal sclerites smooth. Spine and seta formula as follows:

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

Distal seta on third exopod segment of first leg (Fig. 6A) with hyaline frill along outer margin. Distal spine on third exopod segment of second leg (Fig. 6B) with coarse denticles along outer margin; outer spine on second segment elongated. Inner coxal seta on leg 3 (Fig. 7A) stout, reaching midway of third endopod segment, with inner margin denticulate distally. Leg 4 (Fig. 7B) with posterior surface of segments densely setulose; inner coxal seta reduced. Surface of swimming legs richly ornamented with spinules and setules as figured.

Fifth legs (Fig. 2E) symmetrical, uniramous, reduced, with smooth intercoxal sclerite fused to coxae. Coxa and basis unarmed, each with posterior surface

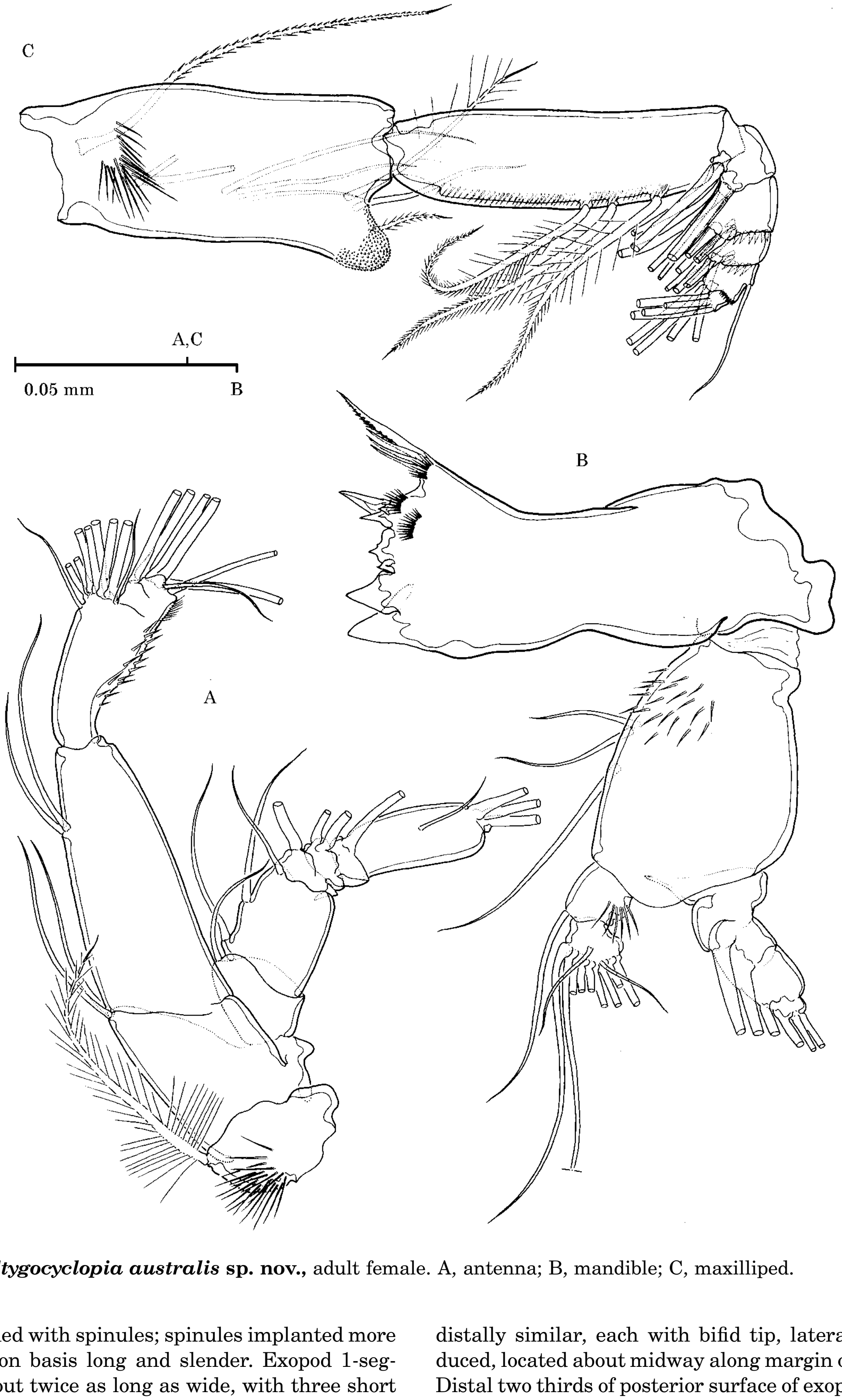

Figure 4. ***Stygocyclopia australis* sp. nov.,** adult female. A, antenna; B, mandible; C, maxilliped.

richly adorned with spinules; spinules implanted more proximally on basis long and slender. Exopod 1-segmented, about twice as long as wide, with three short and stout triangular pinnate spines; pair implanted distally similar, each with bifid tip, lateral more reduced, located about midway along margin of segment. Distal two thirds of posterior surface of exopod densely covered by short spinules.

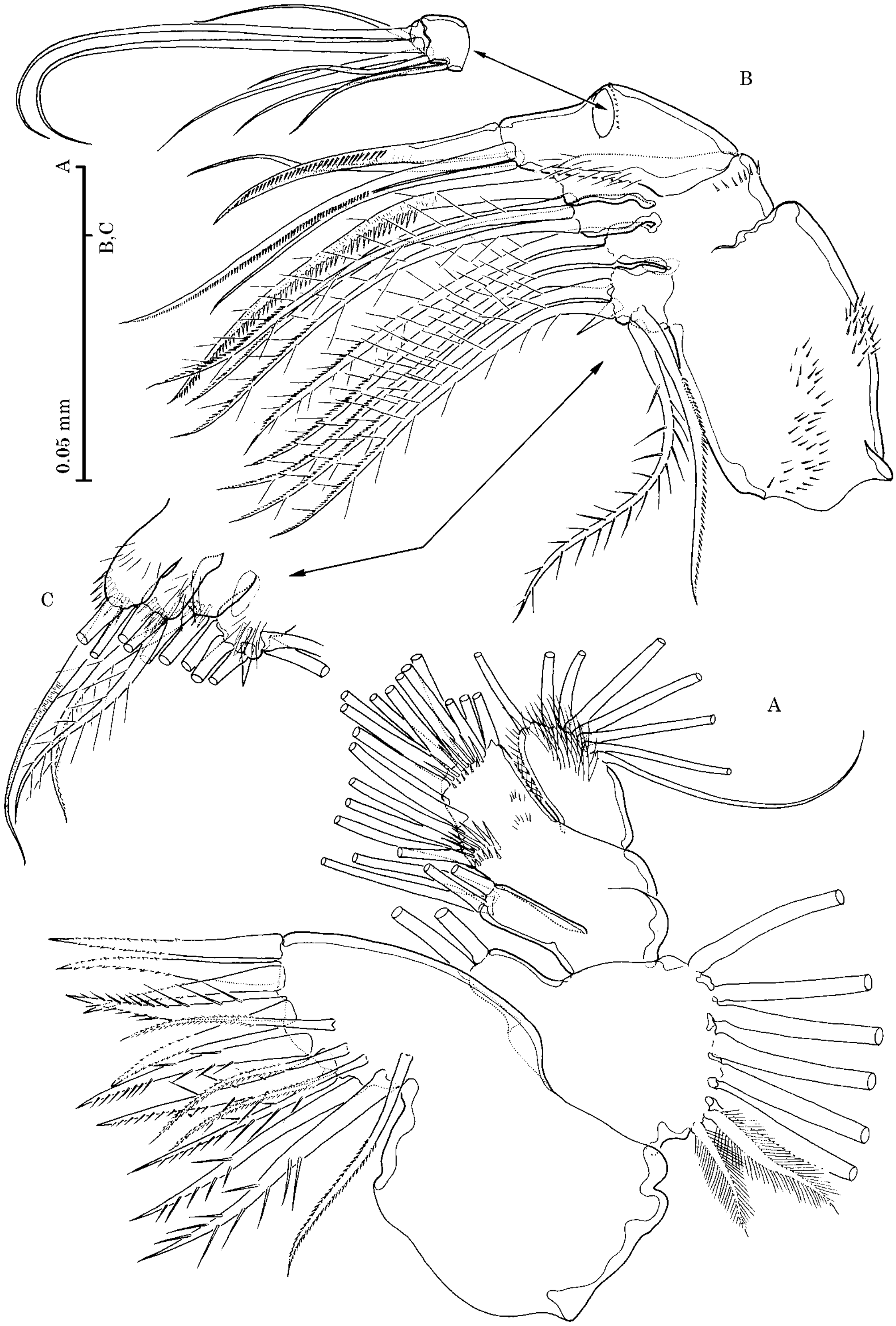

Figure 5. ***Stygocyclopia australis* sp. nov.,** adult female. A, left maxillule, posterior view; B, maxilla with disarticulated endopod and with shorter seta on each of three distal syncoxal endites omitted; C, detail of maxillary syncoxal endites, showing setae omitted in B.

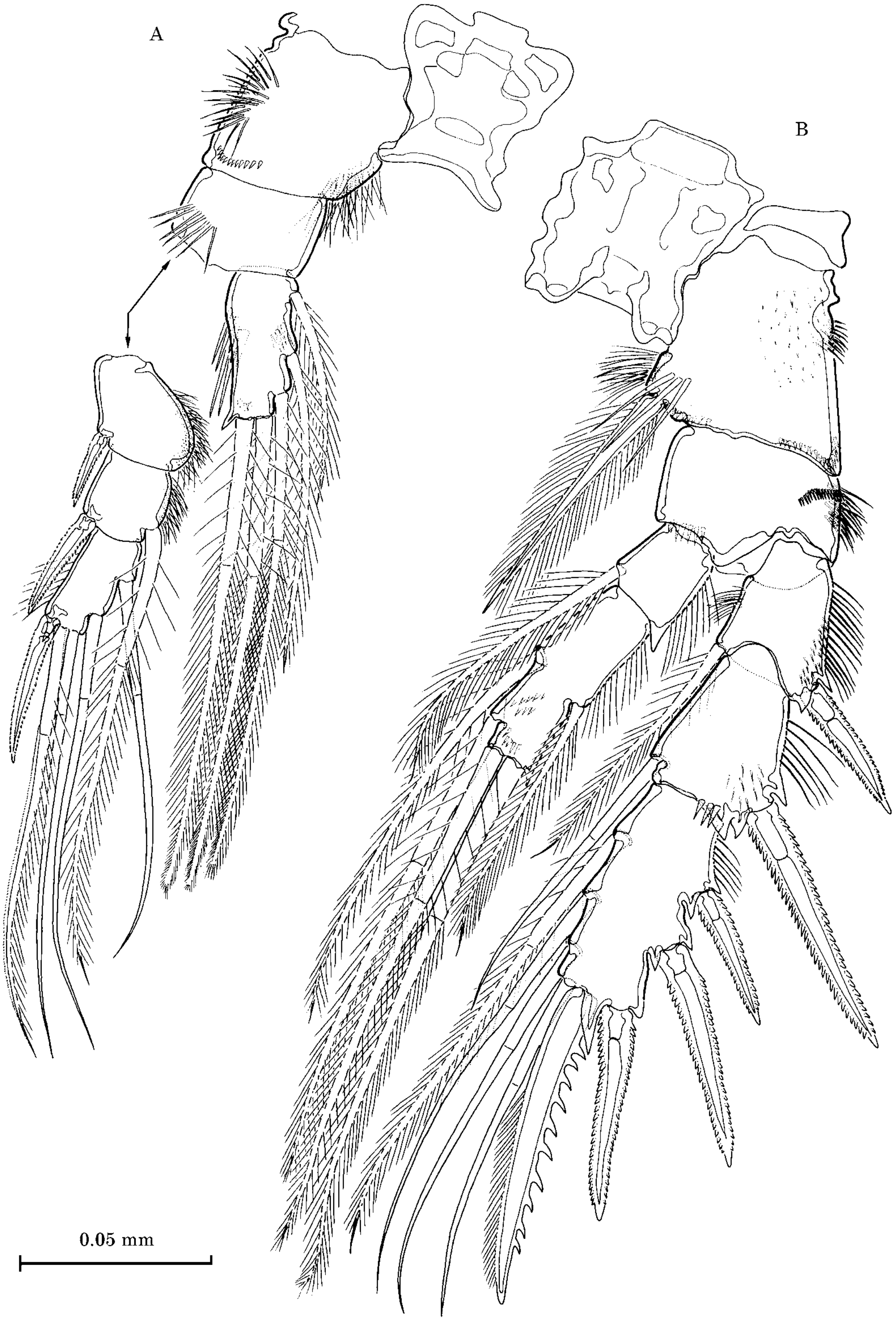

Figure 6. ***Stygocyclopia australis*** **sp. nov.,** adult female. A, first leg with disarticulated exopod, anterior view; B, second leg, anterior.

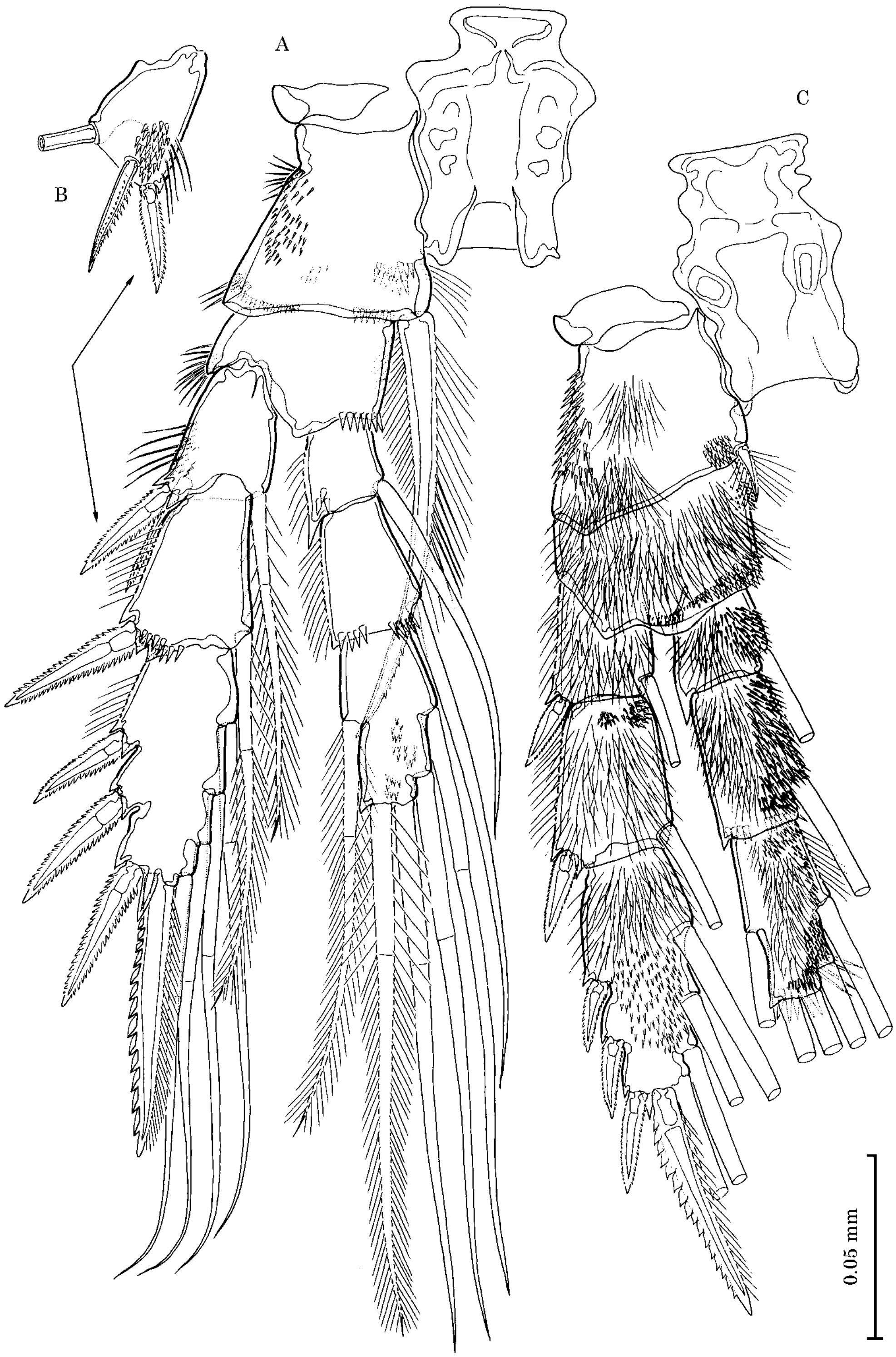

Figure 7. ***Stygocyclopia australis*** **sp. nov.,** adult female. A, third leg, anterior view; B, detail of proximal exopod segment of third leg, posterior; C, fourth leg, posterior.

Description of adult male

Body similar to female except for 5-segmented urosome, and by morphology of antennules and fifth legs.

Antennules (Fig. 3B) symmetrical, without any trace of geniculation, 22-segmented, resembling female except for compound segment 18 (XXII–XXXIII), presence of 1 aesthetasc on each of segments 5, 9, 10, 14 and 16, of 2 aesthetascs on segments 2, 4 and 6, and of 6 setae plus 5 aesthetascs on segment 1 instead of 8 + ae as in the female.

Fifth legs (Fig. 2D) asymmetrical, reduced, uniramous, with smooth intercoxal sclerite fused to coxae. Left leg longer than right, 5-segmented. Coxa subquadrate, unarmed, with patch of densely set, long spinules on anterior surface near outer margin, and transverse row of short spinules on outer distal corner of posterior surface. Basis unarmed, longer than preceding segment, 1.3 times as long as wide; posterior surface adorned with long setules proximally and patch of short and stout spinules distally. Exopod 3-segmented, segments elongated. Proximal segment as long as basis, 2.3 times as long as wide, with short, smooth curved spine distally on outer margin; long spinules along both margins and on posterior surface of segment, as figured. Second segment longer than preceding segment, 3.4 times longer than wide, unarmed; row of long setules along inner margin, 4 long and stout spinules on inner distal corner; posterior surface of segment covered with short setules. Third segment constricted about midway, with two terminal spines completely incorporated basally into segment, innermost more than twice as long as outer spine; inner margin of segment covered with sparsely set, short setules; total length of segment (inner seta included) clearly greater than preceding segment. Right leg 4-segmented, with three proximal segments homologous to left counterparts and differing from them in (shorter) proportions and in integumental ornamentation. Coxa differing from left counterpart in ornamentation, reduced to single row of long spinules at posterior margin. Basis somewhat shorter than left counterpart. First exopod segment shorter than preceding segment, with posterior surface ornamented with long setules proximally and with short, stout spinules on its distal half. Distal segment corresponding to incorporated second and third ancestral exopodal segments, slightly longer than preceding segment; armature consisting of stout triangular bipinnate spine 0.8 times as long as segment displaying transverse row of setules on posterior surface near insertion, and subdistal spine similar, but somewhat stouter, to spine on previous segment on outer margin; integument of segment ornamented with spinules and setules as figured.

Etymology

Species name referred to the Australian continent, where the species lives.

Remarks

The genus *Stygocylopia* comprises two strictly anchialine stygobiont species located at widely separate stations. *Stygocyclopia balearica* Jaume & Boxshall, 1995 is known from the flooded coastal karst of the Balearic Islands (Jaume & Boxshall, 1995; Carola & Razouls, 1996), and from a flooded lava tube and an anchialine well on Lanzarote (Canary Islands; Jaume, Fosshagen & Iliffe, 1999). A second species, *S. philippensis* Jaume, Fosshagen & Iliffe, 1999 has recently been described from a karstic anchialine cave on Panglao Island (Philippines). The new species from northwestern Australia falls, as the foregoing taxa, within an area displaying undeniable geological and biological connections with the Tethyan realm (Yeates *et at.*, 1987; Humphreys, 1999b), and could thus be considered as a relict of late Mesozoic seas (Fig. 14). In fact, the genus exactly conforms to the 'Full Tethyan track' (i.e. circum-tropical in the entire region of the former Tethys Sea) of Stock (1993), a covariant distribution pattern common to many stygobiont crustaceans interpreted elsewhere as Tethyan relicts.

The new species differs from *S. philippensis* by the structure of the fifth legs in both sexes, and by the presence in the former of the inner coxal spine on leg 4. In addition, the armature of the proximal segment of the female antennule is 8 + ae in the new species versus 6 + ae in *S. philippensis*. The female fifth legs differ mainly in the normal condition (versus reduced) of the outer spine on the distal segment, the bifid tips of the terminal spines (tips unicuspid in *S. philippensis*), the smooth intercoxal sclerite, and by the different ornamentation of the posterior surface of segments. The male fifth legs of the new species have the right limb 4-segmented (only 3-segmented in *S. philippensis*, due to failure to express articulation between third and fourth segments), whereas the left limb displays a slender, elongate distal segment with two non-articulated terminal spines (this segment is subquadrate and the two spines articulate at base in *S. philippensis*).

Stygocyclopia australis sp. nov. seems nevertheless to be much more closely related to *S. balearica* from the western Mediterranean and the Canary Islands than to its geographically closer relative from the Philippines. In fact, they display identical segmentation and armature on all limbs except for the failure to express the outer basal seta on leg 1 in the new species. Both can be easily differentiated from each other by the fifth legs of both sexes and, among other characters, by the densely setulose posterior surface of the fourth legs of the new species (coxa, basis and exopod of *S. balearica* lacking long setules). In addition, the ornamentation of the hypertrophied inner coxal spine of leg 3 differs in both taxa (inner distal margin coarsely serrate and outer distal margin smooth in the new species, versus spine homogeneously bipinnate in *S. balearica*). The female fifth legs of the new species differ in the smooth intercoxal sclerite (sclerite adorned with marginal row of setules in *S. balearica*), the shorter and stouter spines on the distal segment, the terminal pair having bicuspid tips whereas the lateral spine being somewhat smaller compared to the terminal ones (spines longer and more slender, of similar length, terminal pair with unicuspid tips in *S. balearica*), in addition to differences in ornamentation of the posterior surface of segments. The male fifth legs of the new species differ in the more slender, elongate, constricted-about-midway distal segment of the left limb, the articulate condition of the spines on the distal segment of the right leg, and in the bipinnate, expanded-at-base condition of the terminal spine on that segment (spine smooth and uniformly slender in *S. balearica*.

As the rest of representatives of the genus (see Jaume, Fosshagen & Iliffe, 1999), *Stygocyclopia australis* seems to be restricted to waters of raised salinity (>18‰), avoiding the more desalinated reaches of the anchialine system.

On the armature of the proximal exopod segment of the third leg of pseudocyclopiids

All the adult specimens available of *Stygocyclopia australis* sp. nov. displayed a supernumerary outer spine on the first exopod segment of leg 3 (Fig. 7A). There is no doubt that this supernumerary spine represents a genuine armature element since it is articulated at the base and inserts into a hole passing through the integument, and it has a hollow axial core. A similar spine on exactly the same segment and leg had been reported previously for other pseudocyclopiids (e.g. *Pseudocyclopia crassicornis* T. Scott, 1894; *Pseudocyclopia giesbrechti* Wolfenden, 1902 (see Sars, 1919–1921), *Paracyclopia naessi* Fosshagen & Iliffe, 1985, to which three sympatric, not yet described species of *Pseudocyclopia* T. Scott, 1892 from off Lyroddane (Norway) can be added (D. Jaume and A. Fosshagen, pers. obs.). The display of this supernumerary spine in these species has been interpreted elsewhere as an aberration displayed by isolated individuals, although it proved to be relatively extended within the populations analysed. But the present report confirms the putative fixation of this character state in the single known population of *S. australis* sp. nov. (and in one of the as yet undescribed, new *Pseudocyclopia* from Norway), and could lend credence to the interpretation of this feature as a relict character from the ancestral copepod groundplan (as retained in the exopod armature of legs 2–5 in the Platycopioida; see Huys & Boxshall, 1991) which had also persisted through into the Neocopepoda. This was already suggested by Huys (1996) when remarking on the coincidence of expression in exactly the same leg and segment as in pseudocyclopiids of a supernumerary spine on one out of the three individuals known of the arietellid calanoid *Crassarietellus huysi* Ohtsuka, Boxshall & Roe, 1994. A closer examination of this supernumerary spine in *S. australis* and in other pseudocyclopiids (Fig. 7B and pers. obs.) reveals nevertheless that its precise placement on the segment differs from the condition displayed in platycopioids. In the latter, it is located about midway along the outer margin of the segment, whereas in pseudocyclopiids it is invariably on the posterior surface of segment near to its distal rim, behind the normal outer margin (distal) spine. On the other hand, the condition exhibited in the aberrant *Crassarietellus huysi* specimen figured by Ohtsuka, Boxshall & Roe (1994) differs from both pseudocyclopiids and platycopioids in having the supernumerary spine inserted in close contact with the normal outer distal spine, and it is interpreted here as a teratology. Although the copepodid III of *S. australis* has only 2-segmented rami on the third legs, the first exopod segment is already differentiated and carries a single outer spine distally. The supernumerary spine is absent and must appear at a subsequent moult. Based on what is known about the ontogeny of platycopioid legs (see Ohtsuka & Boxshall, 1994), we infer from this later appearance that the supernumerary spine does not represent a secondary duplication of the normal outer distal spine, as is possibly the case in *C. huysi*.

The discovery of a supernumerary spine on the proximal exopod segment of leg 3 in the genus *Stygocyclopia* leaves representatives of the genus *Thompsonopia* Jaume, Fosshagen & Iliffe, 1999 and the monotypic *Frigocalanus rauscherti* Schulz, 1996 as the only pseudocyclopiids apparently not expressing this feature. Even though there are no solid grounds to determine whether it is a relict character of the copepod groundplan shared with the platycopioids, or only the result of a secondary, novel multiplication of armature elements, the extra spine on pseudocyclopiids is, as remarked above, not topologically homologous to its platycopioid counterpart. Ohtsuka & Boxshall (1994) in discussing *Platycopia orientalis* Ohtsuka & Boxshall, 1994 in which the second (proximal) outer spine appears on the first exopodal segment of leg 3 at the moult to copepodid IV, also concluded that the supernumerary spines are not homologous in these two taxa. It is notoriously difficult to find autapomorphies for calanoid families, so the expression of a supernumerary spine on the posterior surface of the proximal exopodal segment of leg 3 near its distal rim, behind the normal outer margin spine, is proposed here as a robust autapomorphy to be added to the diagnosis of the family (see Jaume, Fosshagen & Iliffe, 1999).

ORDER MISOPHRIOIDA GURNEY, 1933
FAMILY SPELEOPHRIIDAE BOXSHALL & JAUME, 2000
GENUS *SPELEOPHRIA* BOXSHALL & ILIFFE, 1986

SPELEOPHRIA BUNDERAE SP. NOV.
(*Figures 8-13*)

Material examined

Bundera Sinkhole (Australian Karst Index number C-28), Cape Range peninsula, north-western Australia. Coordinates: 22°25′S/113°46′E.
Holotype: adult female 0.63 mm [WAM C24516]; preserved in ethanol 70% vial.
Paratypes: 8 adult males, 3 adult females, and 2 copepodids preserved in ethanol 70% in single vial [WAM C24517]; two additional adult male paratypes [WAM C24518 and WAM C24519] plus 1 additional adult female paratype [WAM C24520] completely dissected and mounted on 3, 2, and 1 slide, respectively. Collected by A. Poole, S. Eberhard and W. F. Humphreys, 23 September 1997. BES nos. 4719.0 and 4717.0.

Description of adult female

Body length of 4 individuals 0.63, 0.58, 0.56, and 0.63 mm. Body (Fig. 8A,B) cyclopiform, colourless, nauplius eye absent. Prosome 5-segmented, with first pedigerous somite not incorporated into cephalosome; cephalosome bell-shaped in dorsal aspect, not extended posteriorly into carapace. Prosomal somites with evenly rounded posterolateral corners except fourth pedigerous somite, with pointed corners. Rostrum (Fig. 11A) powerfully developed, not incorporated into cephalic shield, triangular with rounded tip in frontal aspect (about 1.4 times longer than wide), sickle-shaped from lateral aspect (Fig. 8B).

Urosome 5-segmented, with genital and first abdominal somites completely fused to form double-somite. Genital field (Fig. 8C) located anteriorly, with single, small midventral copulatory pore communicating with fused seminal receptacles. Gonopores separate, positioned laterally as narrow slits at each side of copulatory pore; each covered by vestigial leg 6 armed with dorsalmost seta and two innermost reduced setae; patch of spinules positioned anterior to each gonopore (Fig. 8B). Anal somite (Fig. 9B,C) with weakly developed anal operculum with smooth rim, plus two dorsolateral sensillae; posteroventral margin of somite fringed with serrate hyaline frill. Caudal rami (Figs 8A, 9B,C) short, symmetrical, about as long as wide, with 7 caudal setae; anterolateral accessory seta (seta I of Huys & Boxshall, 1991) very reduced; terminal accessory seta (seta VI) moderately reduced, implanted submarginally on posterior surface of ramus.

Antennule (Fig. 10A) implanted on trapezoid pedestal, 21-segmented. Ancestral segments I to III with failure to express intersegmental articulations resulting in single, inflated compound segment (segment 1) with short, rounded lobe protruding dorsolaterally (see Fig. 8A). Other compound segments: 7 (due to failure to express intersegmental articulations between ancestral segments IX to XII), 10 (failure to express intersegmental articulation XV–XVI), and 21 (failure to express intersegmental articulation XXVII–XXVIII). Segments 2 to 6 short and densely packed; segment 20 slender, elongate, about 6 times longer than wide. Segmentation pattern and armature formula of antennule as follows: segment 1 (corresponding to ancestral I–III), 5 setae + aesthetasc; segments 2 to 4 (ancestral IV to VI, respectively), 2 setae each; segment 5 (VII), 2 + ae; segment 6 (VIII), 2 setae; segment 7 (IX–XII), 8 + ae; segments 8 and 9 (XIII and XIV), 2 setae each; segment 10 (XV–XVI), 3 + ae; segments 11 to 14 (XVII to XX), 2 setae each; segment 15 (XXI), 2 + ae; segments 16 and 17 (XXII and XXIII), 1 seta each; segment 18 (XXIV), 1 + 1 setae; segments 19 and 20 (XXV and XXVI), 1 + 1 setae plus aesthetasc each; segment 21 (XXVII–XXVIII), 5 + ae. Seta on anterodistal margin of segment 20 resembling slender aesthetasc. Aesthetascs on segments 1 and 5 hypertrophied, as characteristic for genus. Anterodistal setae on segments 10 and 14 hypertrophied.

Antenna (Fig. 11B) biramous, with endopod clearly longer than exopod. Coxa and basis separate, unarmed. Exopod indistinctly 6-segmented, setal formula: (1 + 2), 1, 1, 1, 5. Endopod indistinctly 2-segmented, with outer margin of proximal segment partially incorporated into basis; segment armed with two setae at about two thirds of distance along inner margin. Distal endopodal segment as long as proximal segment, about 4.1 times longer than wide, adorned with 4 transverse rows of slender setules along lateral margin, 4 unequal setae proximally on lateral margin, plus 7 setae on tip.

Mandibular coxal gnathobase cutting blade (Fig. 11C) with isolated, unicuspid tooth ventrally, plus row of 9 smaller, heterogeneus teeth and two dorsal setae. Palp (Fig. 11D) biramous, with basis longer than wide, armed with single seta on medial margin. Exopod indistinctly 6-segmented, setal formula: 0 + 1 + 1 + (1 + 1 + 2). Endopod 2-segmented, with distal segment elongate, about twice longer than wide; setal formula: 3, 7.

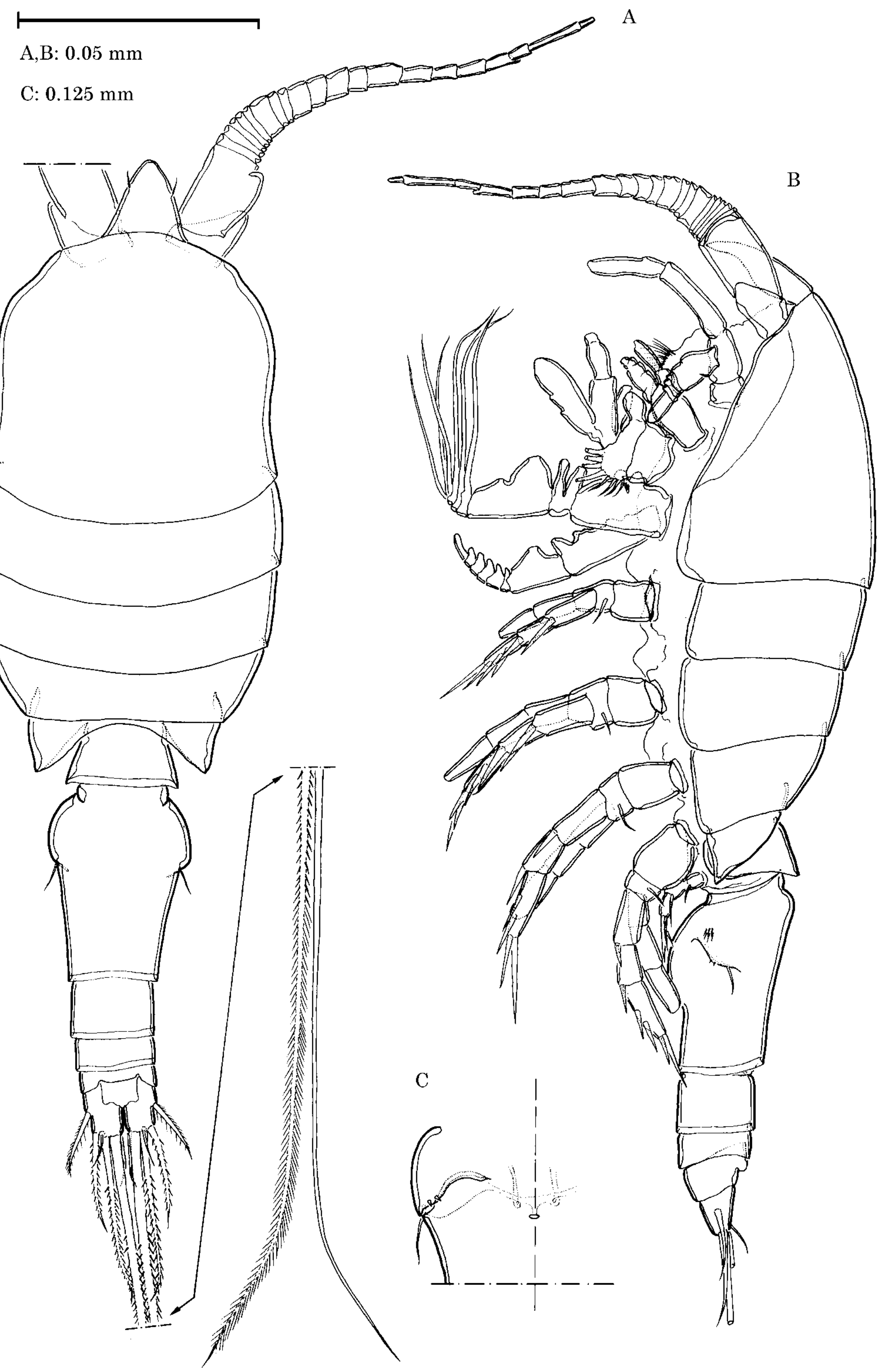

Figure 8. ***Speleophria bunderae*** **sp. nov.,** adult female. A, body, dorsal aspect; B, same, lateral; C, detail of copulatory pore, right gonopore, operculum, and associated internal genital apparatus, ventral.

Maxillule (Fig. 11E) well developed, with praecoxal arthrite bearing 8 stout spines and 4 setae on margin, plus two setae on posterior surface. Coxal epipodite with 8 plumose setae; coxal endite discrete, with two spines and three setae ornamented as figured. Proximal basal endite discrete, distal indistinct; both en-

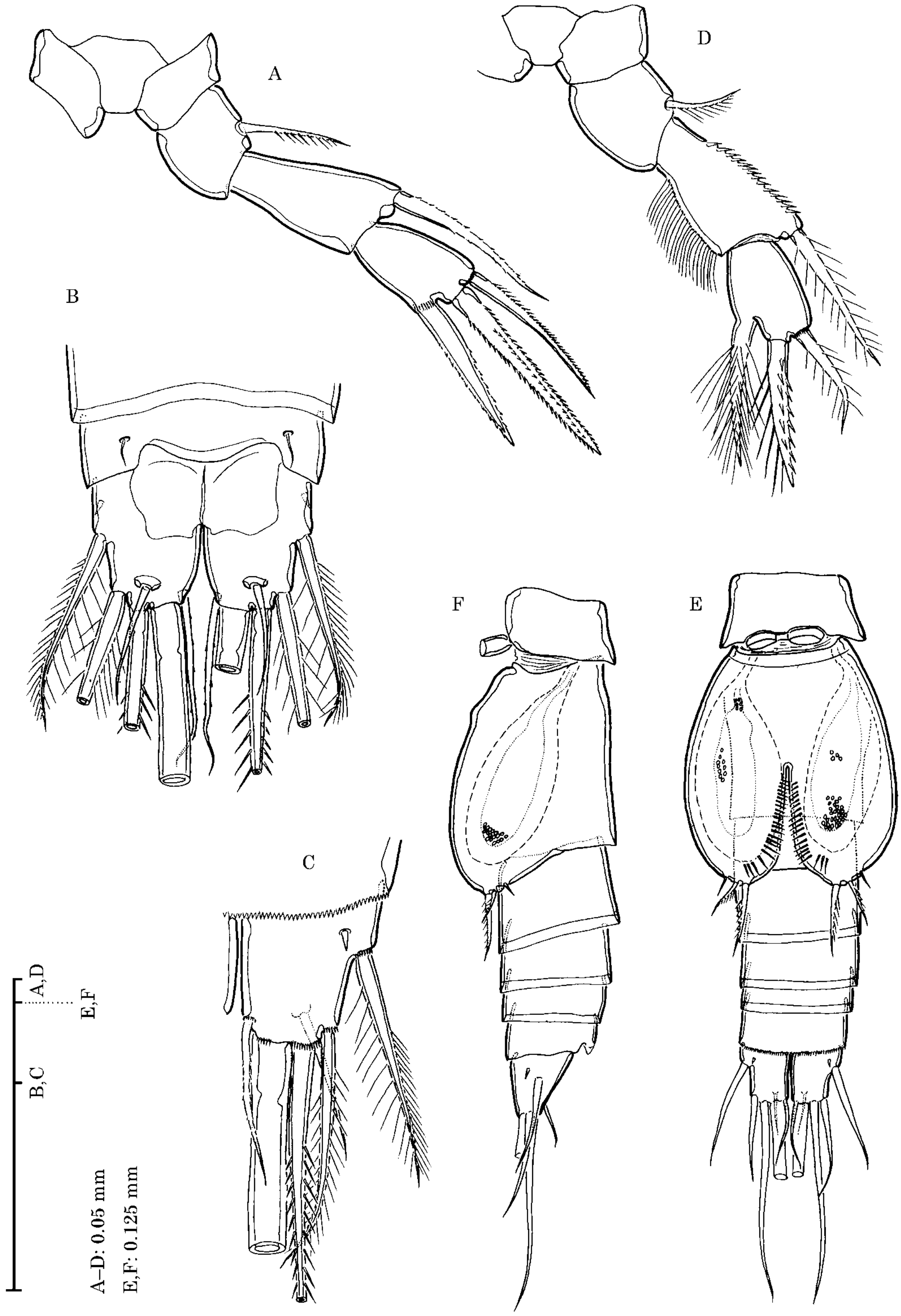

Figure 9. ***Speleophria bunderae*** **sp. nov.** A, adult female fifth leg, posterior; B, anal somite and caudal rami, dorsal; C, caudal ramus, ventral; D, adult male fifth leg, posterior; E, adult male urosome, ventral; F, same, lateral.

dites with 4 setae each. Basal exite unarmed. Endopod 1-segmented, with remnants of articulation between ancestral segments and distribution of setae suggesting derivation from 3-segmented ancestral condition with setal formula: 3, 2, 6. Exopod fused to basis, oar-shaped, with 4 distal, two lateral, and three

Figure 10. ***Speleophria bunderae*** **sp. nov.** A, adult female right antennule, lateral; B, adult male left antennule, medial.

medial setae; row of setules proximally along both margins of segment.

Maxilla (Fig. 12A) powerfully developed, 6-segmented. Praecoxa and coxa separate, endites with setal formula: 5, 3, 3, 3. Allobasis with proximal (=basal) endite powerfully developed, crowned by single stout seta flanked near insertion by two setae on each side; pair of setae on one side plumose, on other rake-like.

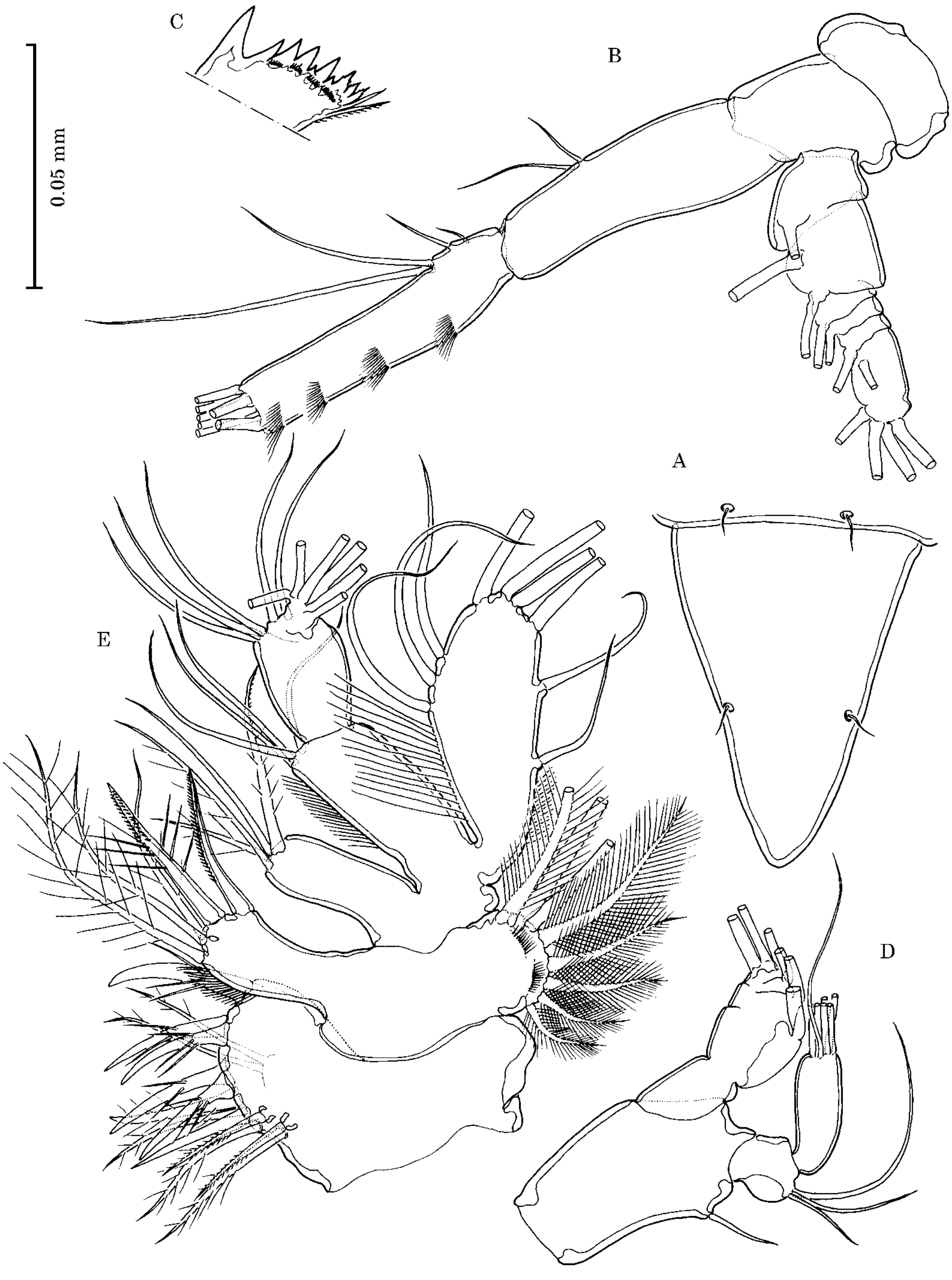

Figure 11. ***Speleophria bunderae* sp. nov.,** adult female. A, rostrum, frontal; B, left antenna; C, detail of mandibular gnathobase cutting edge; D, mandibular palp; E, right maxillule, anterior.

Distal (=endopodal) endite hardly developed, with one smooth, one plumose, and one rake-like seta. Free endopod 3-segmented, with setal formula: 2, 2, 4; one of setae on each of first and second segments reduced, other rake-like (Fig. 12B); third segment with two smooth and two rake-like setae.

Maxilliped (Fig. 12C) slender, 8-segmented. Surface of syncoxa ornamented with two rows of short spinules; praecoxal endite indistinct, represented by single seta; coxal endites almost completely incorporated into segment, setal formula: 2, 4, 3. Basis triangular, with two rows of slender spinules; three setae ornamented as

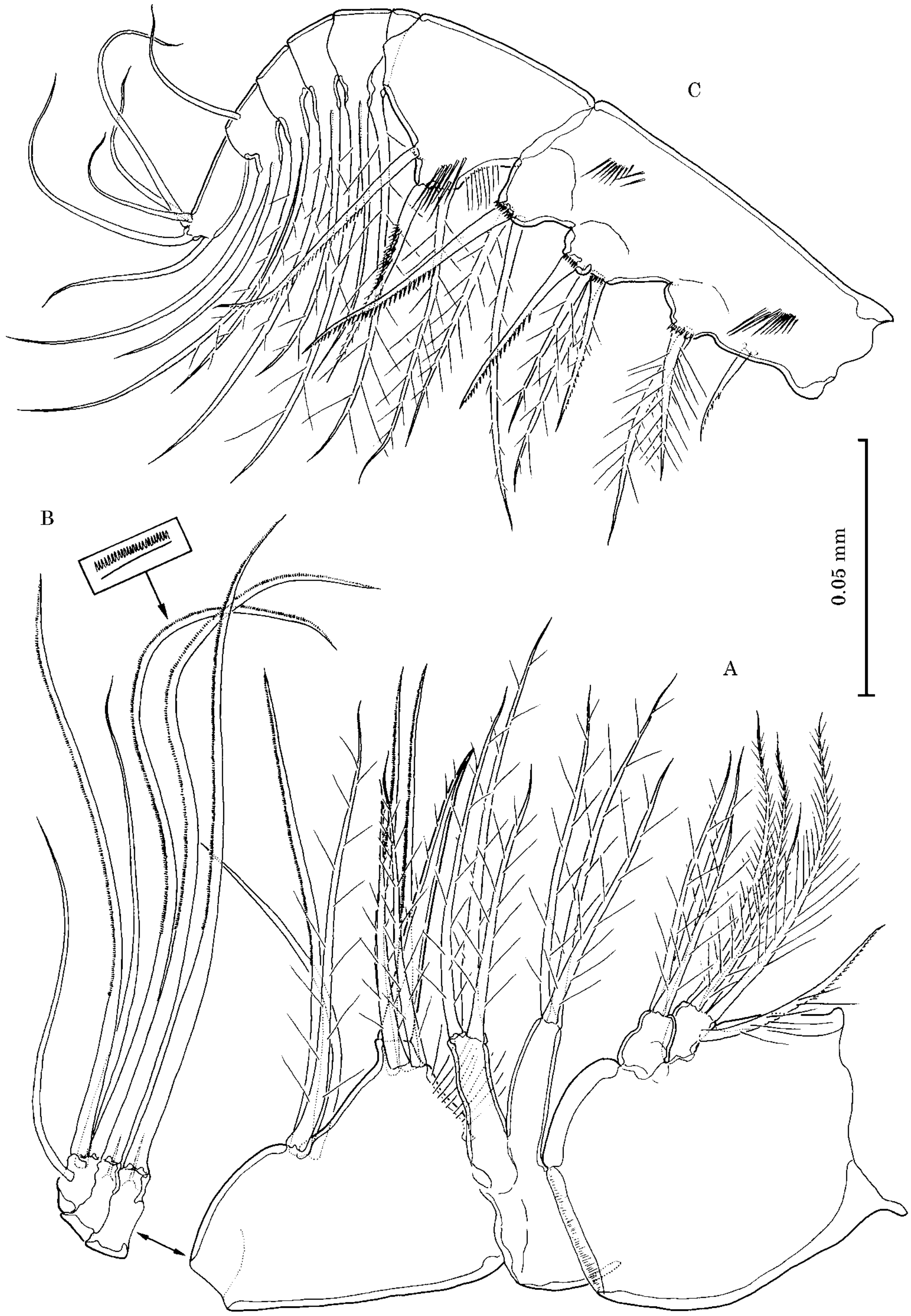

Figure 12. ***Speleophria bunderae* sp. nov.,** adult female. A, maxilla with disarticulated endopod; B, detail of one of rake-like setae on maxillary endopod; C, maxilliped.

figured on segment. Endopod 6-segmented, setal formula: 1, 2, 2, 2, 2+1, 5; distal segment elongate.

Legs (Fig. 13A–D) with 3-segmented rami except for 2-segmented endopod of leg 1. Legs increasing progressively in size from leg 1 to leg 3, with leg 4 about same size as leg 2. Intercoxal sclerites of first and second legs unadorned; those of legs 3 and 4 with two pairs of rows of short spinules on posterior surface.

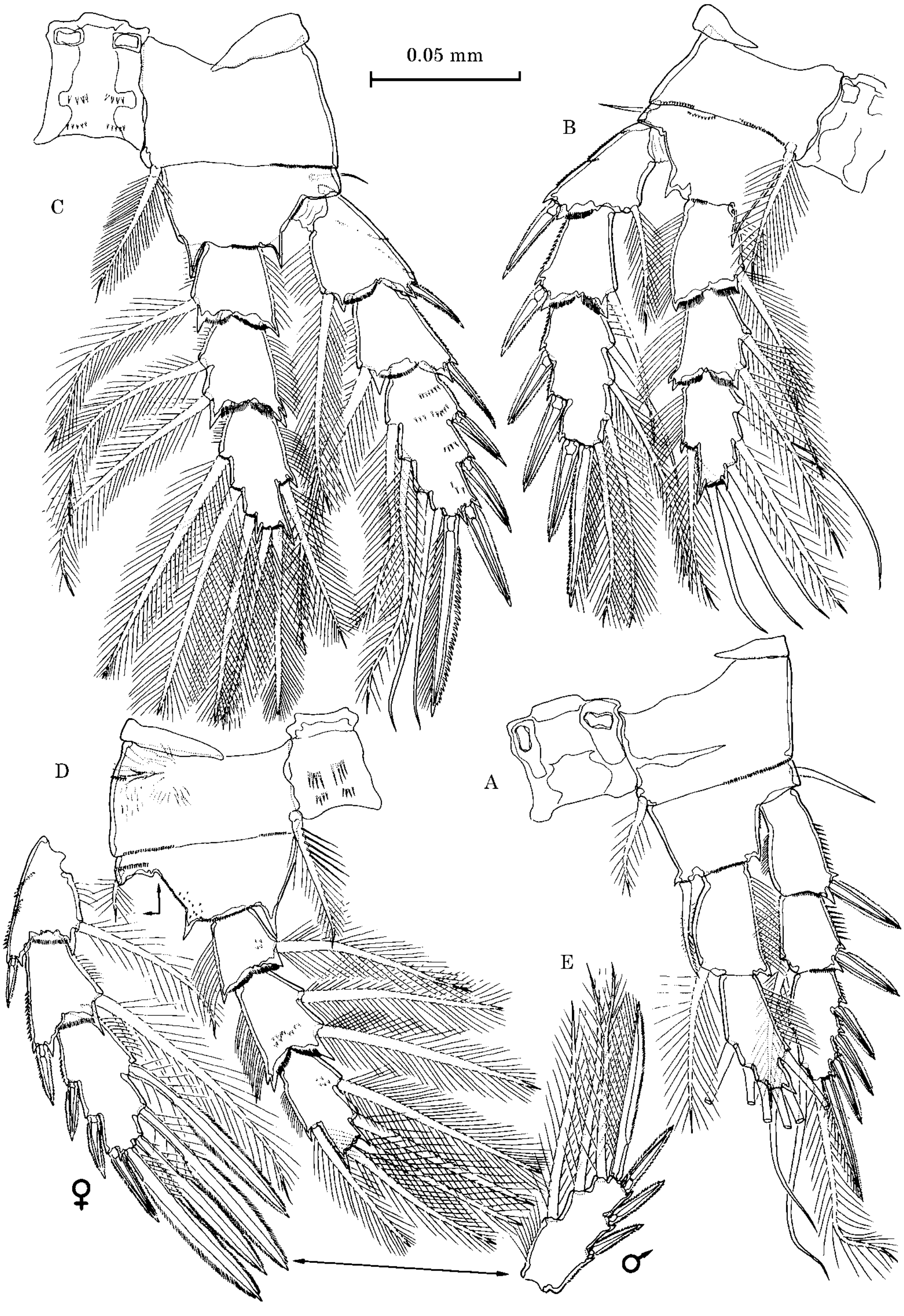

Figure 13. ***Speleophria bunderae*** **sp. nov.,** adult female swimming legs, anterior. A, leg 1; B, leg 2; C, leg 3; D, leg 4 with disarticulated exopod; E, detail of third exopodal segment of adult male leg 4, anterior.

Praecoxa retained on each leg. Posterior surface of both coxa and endopodal segments of leg 4 adorned with spinules and setules as figured; surface of other legs unadorned. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–1	I–0; I–1; III,I,3	0–1; 1,2,3
Legs 2 & 3	0–1	1–0	I–1; I–1; III,I,4	0–1; 0–2;1,2,3
Leg 4	0–1	1–0	I–1; I–1; III,I,III	0–1;0–2; 1,2,2

Fifth legs (Fig. 9A) positioned adjacent to ventral midline, uniramous, symmetrical, 4-segmented, with well developed intercoxal sclerite joining both legs. Coxa and basis separate, former unarmed, latter with short, slender distolateral seta implanted submarginally on posterior surface of segment. Exopod 2-segmented, proximal segment elongate, about 1.9 times as long as wide, with sparsely serrate, stout distolateral seta implanted on pedestal. Distal segment with long serrate seta distally; seta displaying row of denticles along midline of posterior surface in addition to ordinary serration along both margins. Other armature on distal segment consisting of inner stout, serrate spiniform process partially incorporated into segment (articulation line expressed only on anterior surface), plus finely unipinnate (along outer margin) slender outer seta.

Description of adult male

Body lengths of 5 specimens 0.54, 0.61, 0.56, 0.56, and 0.59 mm. Body similar to female except for 6-segmented urosome (Fig. 9E,F). Genital somite expanded ventrally, double length of succeeding abdominal somite. Sixth legs not articulating with somite, each bearing inner row of submarginal spinules; armature consisting of three unequal setae, innermost largest. Spermatophores paired, elongate.

Antennule (Fig. 10B) roughly similar to female, on trapezoid pedestal, 22-segmented, tri-geniculate, with geniculations positioned between ancestral segments XV and XVI, XX and XXI (Neocopepodan geniculation), plus additional one between XXIII and XXIV. Segment XV cup-shaped, forming sheath around proximal half of segment XVI. Segmentation pattern and armature formula of antennule as follows: segments 1 to 6 as in female; segments 7 and 8 (ancestral IX and X, respectively), 2 setae each; segment 9 (XI), 2 setae + aesthetasc; segments 10–13 (XII–XV), 2 setae each; segment 14 (XVI), 2 + ae; segments 15 and 16 (XVII and XVIII), 2 setae each; segment 17 (XIX–XX, with intersegmental articulation partially expressed), 2 short modified plate-like spines plus 2 setae (1 spine and seta per ancestral segment); segment 18 (XXI–XXIII, with intersegmental articulations partially expressed), 3 short modified plate-like spines plus 1 seta + ae (2 spines plus aesthetasc on ancestral segment XXI, 1 spine on segment XXII, and 1 seta on segment XXIII); segment 19 (XXIV), 1 + 1 setae; segment 20 (XXV), 1 + 1 setae plus aesthetasc; segment 21 (XXVI), 1 + 1 setae; segment 22 (XXVII–XXVIII), 5 + ae. Seta on anterodistal margin of segment 21 resembling slender aesthetasc. Aesthetascs on segments 1 and 5 hypertrophied, as characteristic for genus. Anterodistal setae on segments 14 and 17 hypertrophied.

Other cephalic appendages plus swimming legs as in female except for distal exopod segment of leg 4, armed with three medial setae instead of spines (see Fig. 13E).

Fifth legs (Fig. 9D) differing from that of female in proximal exopodal segment with row of stout denticles along outer margin, and row of long setules along inner margin (both margins naked in female); outer seta on segment bipinnate, versus sparsely serrate in female. Armature elements on distal exopod segment differing from those of female in both ornamentation and relative length, with both distal and outer setae comparatively shorter; distal seta with fewer and stouter denticles than in female, with ornamentation along inner margin here comprising row of long and slender stiff spinules instead of row of denticles; outer seta bipinnate (versus unipinnate in female); inner spiniform process brush-like, completely incorporated into segment proximally (process serrate and only partially incorporated into segment in female).

Etymology

Species name derived from the local name of the sinkhole where it was found.

Remarks

Speleophria is a very poorly diversified, strictly stygobiont genus, inhabiting karstic anchialine caves of raised salinity (>18‰) in widely separate territories. Only two described species were known to date, viz. *S. bivexilla* Boxshall & Iliffe, 1986, from Bermuda (NW Atlantic), and *S. gymnesica* Jaume & Boxshall, 1996, from Mallorca (Balearic Is., Mediterranean), although reports of the presence of unnamed species of the genus in the Yucatán peninsula of México have been made elsewhere (Boxshall & Iliffe, 1986; Jaume & Boxshall, 1996; Jaume, Boxshall & Iliffe, 1998). As previously commented for *Stygocyclopia australis* sp. nov., the discovery of a new species of *Speleophria* in northwestern Australia leads to a 'Full Tethyan track' (*sensu* Stock, 1993) distribution pattern for the genus, explained elsewhere as a result of vicariance by plate tectonics of an ancestral population widely distributed along the margins of late Mesozoic seas (Fig. 14).

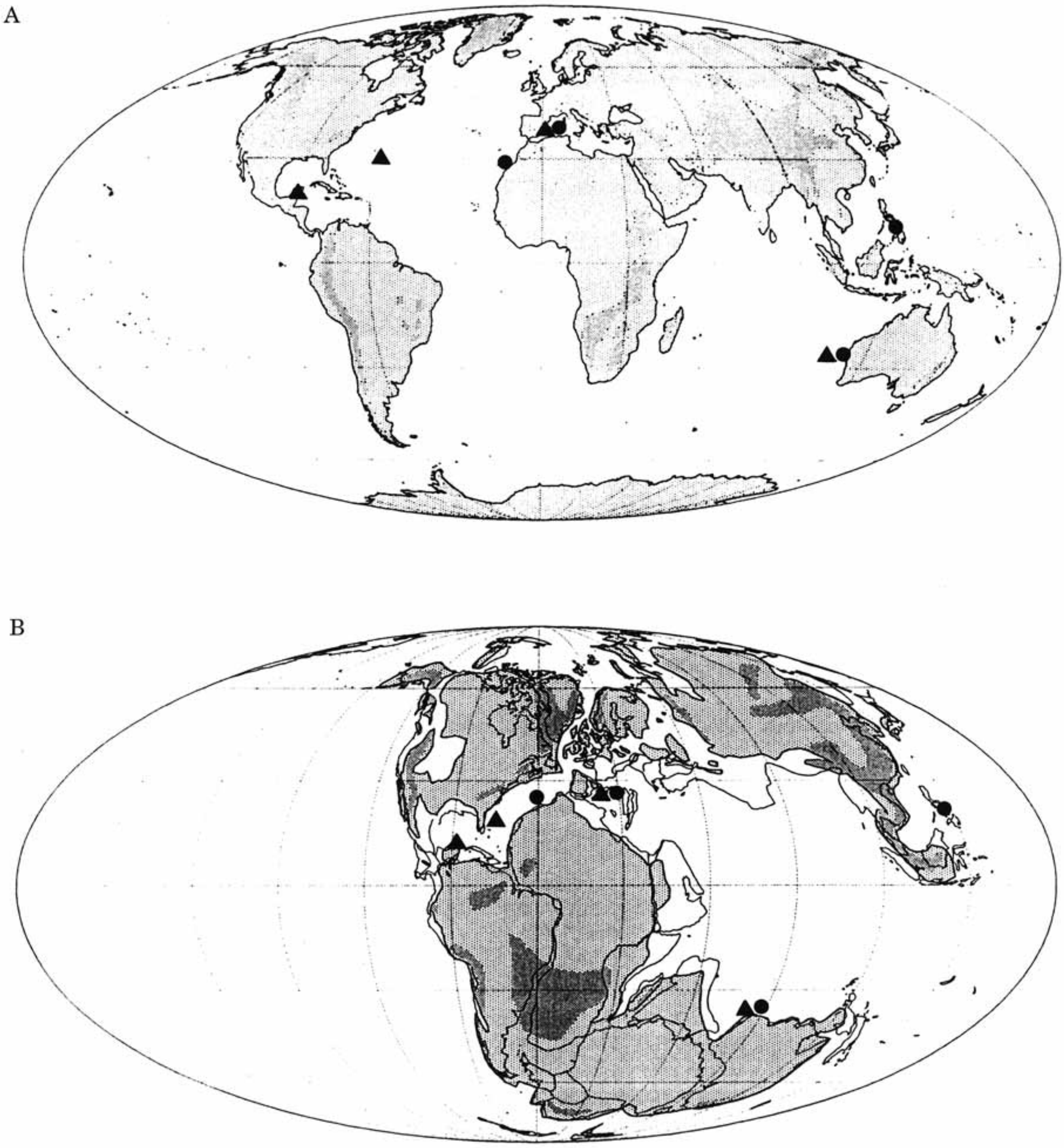

Figure 14. A, current known distribution of the calanoid genus *Stygocyclopia* (●) and the misophrioid genus *Speleophria* (▲). B, same stations translated on a 155 Myr BP palaeocoastline map. (Maps adapted from Smith, Smith & Funnel, 1994.)

The new Australian species can be easily distinguished from its congeners by the morphology of the fifth legs, the absence of the proximal armature element on the inner margin of the third segments of both rami of leg 4, and by the extreme reduction of caudal seta I. These and other diagnostic features of the new species are summarized in Table 1.

A single specimen of *Speleophria bunderae* was present in the gut contents of an adult female of the stygobiont epacteriscid calanoid *Bunderia misophaga* Jaume & Humphreys, another remarkable copepod endemic from Bundera Sinkhole (Jaume & Humphreys, 2001).

ACKNOWLEDGEMENTS

As volunteers to the Western Australian Museum of Natural Science, Jack Riley constructed sampling equipment and supported the diving operation in many ways and Andrew Poole developed the rebreathing

Table 1. Diagnostic characters of three known species of *Speleophria*. end- and exp-: endopodal and exopodal segments, respectively. (?): character states in need of verification. Character states of *Speleophria bivexilla* apparently in discordance with original description by Boxshall & Iliffe (1986) derived from subsequent emendations of species description by Huys & Boxshall (1991) and Jaume & Boxshall (1996)

	S. bivexilla	*S. gymnesica*	***S. bunderae* sp. nov.**
Antenna			
end-1	clearly shorter than end-2 (?)	about as long as end-2	about as long as end-2
end-2, no. of proximal setae	4	5	4
Mandible			
no. of setae on basis	1	0 (?)	1
no. of setae on palp end-1	1 (?)	3	3
end-2	subquadrate	long and slender	long and slender
Maxillule			
no. of setae on coxal epipodite	7	7 (?)	8
seta representing basal exite	present (?)	present (?)	absent
no. of setae on exopod	8	9	9
Maxilla			
no. of setae on proximal praecoxal endite	7	6 (?)	5
short seta on end-1 and -2	reduced	reduced	vestigial
Maxilliped			
praecoxal seta	absent (?)	absent (?)	present
no. of setae on end-1	2 (?)	1	1
Caudal seta I	well developed	well developed	vestigial
Leg 1			
outer basal armature	spine	seta	seta
exp-3 distal armature	spine	seta (?)	spine
Leg 2			
end-3 outer armature	spine	seta	seta
Leg 3			
exp-3 outer armature	spine	spine	seta
exp-3 distal armature	2 spines	2 spines	2 setae
exp-3 inner armature	spine + 2 setae	3 setae	3 setae
Leg 4			
exp-3 inner armature	4 setae	4 setae	3 spines
end-2 armature	spine + seta	2 setae	2 setae
end-3 outer armature	2 spines	2 spines	2 setae
end-3 distal armature	2 spines	2 spines	2 setae
end-3 inner armature	4 setae	4 setae	3 spines
Female leg 5			
exp-1 (length:width) ratio	1.5	1.3	1.9
exp-2 lateral seta	present	absent	absent
exopodal setae, each	shorter than corresponding segment	longer than corresponding segment except distal seta	longer than corresponding segment
exopodal spiniform process	short, plate-like	short, plate-like	long, slender
ornamentation of exopodal spiniform process	gently serrate	pinnate	gently serrate

equipment to minimize the effect of the research diving, which he conducted with Stefan Eberhard, on the fragile ecosystem. This paper is a contribution to DIVERSITAS-IBOY project, 'Exploration and Conservation of Anchialine Faunas'.

REFERENCES

Alonso M. 1996. Fauna Ibérica, 7. Crustacea. Branchiopoda. Madrid: Museo Nacional de Ciencias Naturales.

Boxshall GA, Iliffe TM. 1986. New cave-dwelling misophrioids (Crustacea: Copepoda) from Bermuda. *Sarsia* **71:** 55–64.

Boxshall GA, Jaume D. 2000. Discoveries of cave misophrioids (Crustacea: Copepoda) shed new light on the origin of anchialine cave faunas. *Zoologischer Anzeiger* **239:** 1–19.

Bradbury J-H, Williams WD. 1995. Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia. *Records of the Western Australian Museum* **17:** 395–409.

Bruce NL, Humphreys WF. 1993. *Haptolana pholeta*, sp. nov., the first subterranean flabelliferan isopod crustacean (Cirolanidae) from Australia. *Invertebrate Taxonomy* **7:** 875–884.

Carola M, Razouls C. 1996. Two new species of Calanoida from a marine cave on Minorca Island, Mediterranean sea: *Stephos balearensis* new species (Stephidae) and *Paracyclopia gitana* new species (Pseudocyclopiidae). *Bulletin of Marine Science* **58:** 344–352.

Danielopol DL, Baltanás A, Humphreys WF. 2000. *Danielopolina kornickeri* sp. n. (Ostracoda: Thaumatocypridoidea) from a western Australian anchialine cave: morphology and evolution. *Zoologica Scripta* **29:** 1–16.

Fosshagen A, Iliffe TM. 1985. Two new genera of Calanoida and a new order of Copepoda, Platycopioida, from marine caves on Bermuda. *Sarsia* **70:** 345–358.

Gurney R. 1933. Notes on some Copepoda from Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **19:** 229–304.

Holthuis LB. 1959. Two new species of atyid shrimps from subterranean waters of N.W. Australia (Decapoda Natantia). *Crustaceana* **1:** 47–57.

Humphreys WF. 1999a. Physico-chemical profile and energy fixation in an anchialine remiped habitat in north-western Australia. *Journal of the Royal Society of Western Australia* **82:** 89–98.

Humphreys WF. 1999b. Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In: Ponder W, Lunney D, eds. *The Other 99%. The Conservation and Biodiversity of Invertebrates.* Transactions of the Royal Zoological Society of New South Wales, 219–227.

Humphreys WF. 2000. The hypogean fauna of the Cape Range peninsula and Barrow Island, north-west Australia. In: Wilkens H, Culver DC, Humphreys WF, eds. *Ecosystems of the World. 30. Subterranean Ecosystems.* Amsterdam: Elsevier, 581–602.

Humphreys WF, Poole A, Eberhard SM, Warren D. 1999. Effects of research diving on the physico-chemical profile of Bundera Sinkhole, an anchialine remiped habitat at Cape Range, Western Australia. *Journal of the Royal Society of Western Australia* **82:** 99–108.

Huys R. 1996. Superornatiremidae fam. nov. (Copepoda: Harpacticoida): an enigmatic family from North Atlantic anchihaline caves. *Scientia Marina* **60:** 497–542.

Huys R, Boxshall GA. 1991. *Copepod Evolution.* London: The Ray Society.

Iliffe TM. 1992. Anchialine cave biology. In: Camacho AI, ed. *The Natural History of Biospeleology.* Madrid: Monografías del Museo Nacional de Ciencias Naturales, 614–636.

Jaume D, Boxshall GA. 1995. *Stygocyclopia balearica*, a new genus and species of calanoid copepod (Pseudocyclopiidae) from anchialine caves in the Balearic Islands (Mediterranean). *Sarsia* **80:** 213–222.

Jaume D, Boxshall GA. 1996. A new genus and two new species of cave-dwelling misophrioid copepods from the Balearic Islands (Mediterranean). *Journal of Natural History* **30:** 989–1006.

Jaume D, Boxshall GA, Iliffe TM. 1998. Two new genera of misophrioid copepods (Crustacea) from an anchialine cave in the Bahamas. *Journal of Natural History* **32:** 661–681.

Jaume D, Fosshagen A, Iliffe TM. 1999. New cave-dwelling Pseudocyclopiids (Copepoda, Calanoida, Pseudocyclopiidae) from the Balearic, Canary, and Philippine archipelagos. *Sarsia* **84:** 391–417.

Jaume D, Humphreys WF. 2001. A new genus of epacteriscid calanoid copepod from an anchialine sinkhole on northwestern Australia. *Journal of Crustacean Biology.* **21:** 157–169.

Kiefer F. 1935. Zur Kenntnis der Halicyclopiden (Crustacea Copepoda). *Zoologischer Anzeiger* **110:** 10–13.

Milne Edwards MH. 1830. Extrait de Recherches pour servir à l'Histoire naturelle des Crustacés amphipodes. *Annales des Sciences Naturelles* **20:** 353–399.

Ohtsuka S, Boxshall GA. 1994. *Platycopia orientalis*, new species (Copepoda: Platycopioida), from the North Pacific, with descriptions of copepodid stages. *Journal of Crustacean Biology* **14:** 151–167.

Ohtsuka S, Boxshall GA, Roe HSJ. 1994. Phylogenetic relationships between Arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. *Bulletin of The Natural History Museum (Zoology Series)* **60:** 105–172.

Pesce GL, De Laurentiis P, Humphreys WF. 1996. Copepods from ground waters of Western Australia, II. The genus *Halicyclops* (Crustacea: Copepoda: Cyclopidae). *Records of the Western Australian Museum* **18:** 77–85.

Poore GCB, Humphreys WF. 1992. First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. *Invertebrate Taxonomy* **6:** 719–725.

Sars GO. 1903–1911. *An account of the Crustacea of Norway. IV. Copepoda Calanoida.* Bergen Museum.

Sars GO. 1919–1921. *An account of the Crustacea of Norway. VII. Copepoda Supplement.* Bergen Museum.

Schulz K. 1996. *Frigocalanus rauscherti*, a new genus and species of hyperbenthic copepod (Calanoida: Clausocalanoidea) from the sublittoral of King George Island (Antarctica). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut* **93:** 73–82.

Scott T. 1892. Additions to the fauna of the Firth of Forth. Part IV. *Report of the Fishery Board for Scotland* **10:** 244–272, pls. 7–13.

Scott T. 1894. Additions to the fauna of the Firth of Forth. Part VI. *Report of the Fishery Board for Scotland* **13:** 231–271, pls. 5–10.

Smith AG, Smith DG, Funnel BM. 1994. *Atlas of Mesozoic and Cenozoic coastlines.*Cambridge: Cambridge University Press.

Stock JH. 1993. Some remarkable distribution patterns in stygobiont Amphipoda. *Journal of Natural History* **27:** 807–819.

Wagner HP. 1994. A monographic review of the Thermosbaenacea (Crustacea: Peracarida). A study on their morphology, taxonomy, phylogeny and biogeography. *Zoologische Verhandelingen* **291:** 1–338.

Wolfenden RN. 1902. The plankton of the Faroe Channel and Shetlands. Preliminary notes and some Radiolaria and Copepoda. *Journal of the Marine Biological Association of the United Kingdom* **6:** 344–372.

Yager J, Humphreys WF. 1996. *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. *Invertebrate Taxonomy* **10:** 171–187.

Yeates AN, Bradshaw MT, Dickins JM, Brakel AT, Exon NF, Langford RP, Mulholland SM, Totterdell JM, Yeung M. 1987. The Westralian Superbasin: An Australian link with Tethys. In: McKenzie SG, ed. *Shallow Tethys 2. Proceedings of the International Symposium on shallow Tethys 2. Wagga Wagga, 15-17 September 1986.* Rotterdam: Balkema, 199–213.