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.


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, thermostaenaceans, hadziid amphipods, ciriolanid isopods, remipeds, thau- matocypridid ostracods, and a vast array of copepods such as epacteriscid, pseudocyclopid, and ridgewayiid calanoids, halicycloine cyclopoids, speleophriid misoph- rioids, 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...
Australia. The crustacean assemblage in these waters includes the following: remipede *Lasionectes exleyi* Yager & Humphreys, 1996; the thaumatocypridid ostracod *Danielpolina kornickeri* Danielpol, Baltanás & Humphreys, 2000; the epacteriscid calanoid copepod *Bunderia misophaga* Jaume & Humphreys (2001), the halicyclopid cyclopoids *Halicyclops spinifer* Kiefer, 1935; *H. longifurcatus* Pesce, De Laurentiis & Humphreys, 1996; the atyid shrimps *Stygicoarhis stilyfera* Holthuis, 1959 and *S. lancifera* Holthuis, 1959; the thermosbaenacean *Halosbaena tulki* Poore & Humphreys, 1992; the hadziid amphipod *Liagoceradocus branchialis* Bradbury & Williams, 1995, and the cir- olanid 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 pseudocyprid calanoid of the genus *Stygocyclopa* 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 STYGOCYCLOPA JAUME & BOXSHALL, 1995

*STYGOCYCLOPA 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 spines on anterior half of lateral margin.

Urosome 4-segmented, with surface of somites covered with both lamellar and ordinary spines, easily lost during manipulation of specimens. Genital double-somite (Fig. 1C) externally symmetrical, with lobate hyaline frill along rear margin and paired ovicducts, seminal receptacles, and shell ducts; seminal receptacles asymmetrically disposed. Transverse row of slender spines 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 spines along medial margin and patch of similar spines 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 spines; seta VII displaced to ventromedial side of ramus.
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 setae. 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 surface. 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:

<table>
<thead>
<tr>
<th>Leg</th>
<th>Coxa</th>
<th>Basis</th>
<th>Exopod</th>
<th>Endopod</th>
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<tr>
<td>Leg 1</td>
<td>0–0</td>
<td>0–0</td>
<td>I–0; I–1; I,1,3</td>
<td>0,2,3</td>
</tr>
<tr>
<td>Leg 2</td>
<td>0–1</td>
<td>0–0</td>
<td>I–1; I–1; III,1,4</td>
<td>0–1; 1,2,2</td>
</tr>
<tr>
<td>Leg 3</td>
<td>0–1</td>
<td>0–0</td>
<td>II–1; I–1; III,1,4</td>
<td>0–1; 0–1; 1,2,2</td>
</tr>
<tr>
<td>Leg 4</td>
<td>0–1</td>
<td>0–0</td>
<td>I–1; I–1; III,1,4</td>
<td>0–1; 0–1; 1,2,2</td>
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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...
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 setae 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 aesthetasc on segments 2, 4 and 6, and of 6 setae plus 5 aesthetasc 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 spines on anterior surface near outer margin, and transverse row of short spines 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 spines 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 spines 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 spines 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 spines 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 spines 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 spines and setules as figured.

Etymology

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

Remarks

The genus Stygocyclopia 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 al., 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 form 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. australis). 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 desalinized 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 Neocopoda. 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 pseudocyclopioids 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 pseudocyclopioids 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 SPELOPHRIIDAE BOXSHALL & JAUME, 2000**
**GENUS SPELOPHRIA BOXSHALL & ILIFFE, 1986**

**SPELOPHRIA 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 copepods 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. Proosomal 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 sensilla; 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 trapezoidal 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, heterogeneous 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.
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 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.
dites with 4 setae each. Basal exite unarmed. Endopod 1-segmented, with remnants of articulation between ancestral segments and distribution of setae sug
gesting 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 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.
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.
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; precoxal 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
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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:

<table>
<thead>
<tr>
<th>Coxa</th>
<th>Basis</th>
<th>Exopod</th>
<th>Endopod</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leg 1</td>
<td>0–1</td>
<td>1–1</td>
<td>I–0; I–1; III, I, 3 0–1; 1, 2, 3</td>
</tr>
<tr>
<td>Legs 2</td>
<td>0–1</td>
<td>1–0</td>
<td>I–1; I–1; III, I, 4 0–1; 0–2; 1, 2, 3 &amp; 3</td>
</tr>
<tr>
<td>Leg 4</td>
<td>0–1</td>
<td>1–0</td>
<td>I–1; I–1; III, I, I, III 0–1; 0–2; 1, 2, 2</td>
</tr>
</tbody>
</table>

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 XXXI 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 + aesthetasc; segment 21 (XXVI), 1+1 setae; segment 22 (XXVII–XXVIII), 5+ae. Seta on anterodistal margin of segment 21 resembling slender aesthetasc. Aesthetasc 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)

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


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’.

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