



Second representative of the order Misophrioida (Crustacea, Copepoda) from Australia challenges the hypothesis of the Tethyan origin of some anchialine faunas

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Abstract

A new species of the genus *Speleophria* is described from a cave in the Nullarbor region in southern Western Australia. Its congeners include species from the Balearics, Croatia, Bermuda, Yucatan peninsula and north-western Western Australia, all considered to be Tethyan relicts. However, the discovery of the new speleophriid in the Nullarbor region has important biogeographic and ecological implications.

From the biogeographic perspective, it either suggests dispersal as the process determining the current distribution pattern of the aquatic fauna found on the Roe Plains or significantly extends the Tethyan track across Australia, from the north-western coastal margin of the continent to the southern coastal margin. From an ecologic perspective, the new speleophriid suggests the possible existence of anchialine habitats in southern Australia.

Speleophria nullarborensis **sp. nov.** can be distinguished from its four congeners by its plesiomorphic 3-segmented endopod of the first swimming leg (2-segmented in other species) and unusually long innermost apical seta on the caudal ramus. Another character that easily distinguishes our new species, and seems to be an autapomorphic feature, is its constricted preanal somite.

Key words: *Speleophria*, new species, taxonomy, zoogeography, Western Australia, Nullarbor

Introduction

The Australian subterranean fauna was poorly known until recently, but during the last decade or so many stygal copepods have been described from freshwater habitats (Pesce *et al.* 1996a, 1996b; Pesce & De Laurentiis 1996; De Laurentiis *et al.* 1999, 2001; Karanovic 2003, 2004a, 2004b, 2005a, 2006). In Karanovic (2004a) alone, 24 new copepod species and five new genera were described from the Murchison region of Western Australia, while Karanovic (2006) included descriptions of five new genera, two new subgenera, 22 new species and one new subspecies of stygal copepods from the Pilbara region of Western Australia. Many more publications regarding freshwater copepods from Queensland, New South Wales, Northern Territory and Western Australia are in preparation by the senior author. Recently, intensive investigations of Australian sandy beaches also revealed an interesting marine interstitial copepod fauna (Karanovic 2008), which included many new poecilostomatoid and cyclopoid species and even one new cyclopoid family.

Although investigations of anchialine waters is still in the early phase of exploration in Australia (Humphreys 2006; Humphreys & Danielopol 2006; Bruce & Davie 2006; Seymour *et al.* 2007), an interesting anchialine copepod fauna has, nonetheless, been described from north-western Australia and Christmas Island (Jaume & Humphreys 2001; Jaume *et al.* 2001; Karanovic *et al.* 2001; Karanovic & Pesce 2002). In this paper

we describe a new species of the genus *Speleophria* Boxshall & Iliffe, 1986 from anchialine waters of the Nullarbor region, the occurrence of which challenges the hypothesis of the Tethyan origin of some anchialine faunas resulting from plate movements. High taxonomic predictability, combined with the strictly stygobiont condition of these taxa and the existence of enormous barriers to dispersal (entire continental landmasses or deep oceanic basins), suggested vicariance as the most plausible explanation for their current distribution (Jaume *et al.* 2001). A Tethyan origin was proposed as a result of vicariance by plate tectonics of an ancestral population widely distributed along the margins of the Tethyan Sea in the late Mesozoic era (Stock 1993) and the explanation has been widely adopted for various groups of organisms (Holthuis 1960; Humphreys & Adams 1991; Poore & Humphreys 1992; Bruce & Humphreys 1993; Jaume & Humphreys 2001; Karanovic 2004a, 2006). However, the Nullarbor region of Western Australia was not at any time part of the Tethyan seashore (Smith *et al.* 1994; Frakes 1999), which suggests dispersal as the process determining the current distribution pattern of the fauna found here. We explore the implications of these ideas further in the second part of this paper.

The Nullarbor region of Western Australia comprises Cainozoic carbonate sediments deposited in the Eucla Basin, and covering an area of approximately 200,000 km², it represents one of the largest continuous exposed karstlands in the world (Lowry & Jennings 1974). The remarkably flat surface of the plain mostly lies between 90 and 240 m above sea level, except in three locations where there are low lying coastal plains. One of these coastal plains, the Roe Plains, extends a distance of almost 300 km and is up to 40 km wide. Nurina Cave, where the material for the present study was collected, is located on the Roe Plains, about 30 km inland from the present coastline (Fig. 22). The entrance to Nurina Cave is situated at 25 m above mean sea level, and a passage descends steeply for about 20–25 m where it intersects the regional watertable and an extensive horizontal maze containing about 1000 m of air-filled and partially or completely submerged passages. The salinity and chemical composition of the cave waters is similar to seawater, except that it is enriched with calcium (James 1992).

Material and methods

The fauna collection in Nurina Cave was made from a watertable pool located directly below the entrance descent. Animals were baited overnight by placing tuna meat just below the water surface on the edge of the pool. Specimens were collected by sweeping a 250 µm mesh hand net in the vicinity of the bait. Samples were preserved in 70% ethanol and sorted for specimens under a dissecting microscope. At the collection site, physico-chemical characteristics (temperature, pH, salinity, dissolved oxygen) of the water column were profiled at 0.2 m intervals to a depth of 3m using calibrated portable instruments (WTW pH 320, WTW LF320 conductivity, WTW OXI 320). To check for possible tidal influences, water levels were closely observed during and between two visits to the cave (each visit spanning several hours), while possible fluctuations due to barometric pressure changes were accounted for using a Wallace and Tiernan field altimeter (model FA-112). The temperature ranged from 16.3 at surface to 17.2 °C at 3 m, the pH showed a cline from 7.38 to 6.83, while the salinity increased from 30.4 to 32.1‰ and dissolved oxygen declined from 6.9 to 2.3 mg/L. When diving in Nurina Cave, well defined haloclines and thermoclines were evident, including depths below 3 m (junior author, pers. obs.). The test for possible tidal influences in Nurina Cave did not detect any fluctuations in water level after accounting for barometric pressure changes.

Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock & von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal, two human hairs of the appropriate thickness were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination water slowly evaporated and appendages eventually remained in completely dry Faure's medium, ready for long term

storage. However, this dry medium can be rehydrated with a drop of distilled water after more than 50 years (Prof. Gordan S. Karaman, pers. comm.) and probably even much longer. All drawings were prepared using a drawing tube attached to a Leica-DMLS brightfield compound microscope, with C-PLAN achromatic objectives. Specimens that were not drawn were examined in a mixture of equal parts of distilled water and glycerol and, after examination, were again preserved in 70% ethanol.

Morphological terminology follows Huys & Boxshall (1991), except for small differences in the spelling of some appendages (antennula, mandibula and maxillula instead of antennule, mandible and maxillule), as an attempt to standardise the terminology for homologue appendages in different crustacean groups. Although we have followed the editor's and reviewers' recommendation to use the armature formula of the swimming legs as proposed in Huys & Boxshall (1991), we would prefer a much simplified version. The reason is a number of transitional forms between spine and seta exist in copepods and some examples are very obvious in the species presented in this paper (Figs 14, 17–18). To avoid any possible confusion we sometimes use the term "armature element" (or just "element") instead of spine or seta. Biospeleological terminology follows Humphreys (2000b). All examined material is deposited in the Western Australian Museum, Perth (WAM).

Systematics

Order Misophrioida Brady, 1878

Family Speleophriidae Boxshall & Jaume, 2000

Genus *Speleophria* Boxshall & Iliffe, 1986

Speleophria nullarborensis sp. nov.

(Figs 1–21)

Material examined. Holotype: adult female dissected on one slide (WAM C37311). Paratypes: two females dissected on one slide each (WAM C37312 & C37313); four females and six copepodids in 70% ethanol (WAM C37314). Australia, Western Australia, Nullarbor region, Roe Plains, Nurina Cave (32°00'28"S 127°00'58"E), 1–9 November, 2002, *leg.* S. Eberhard.

Description. HOLOTYPE FEMALE. Body length, excluding caudal setae, 0.493 mm. Habitus (Figs 1–2) cyclopiform, relatively slender, with prosome/urosome ratio 1.7 and greatest width between first and second free prosomites. Body length/width ratio about 3.4 (dorsal view); cephalothorax about 2.1 times as wide as genital double-somite. Posterior corners of cephalothorax and free prosomites without pronounced lateral expansions, except those of fourth free prosomite, latter somewhat expanded posterolaterally but not pointed. Urosome narrow, with fifth prosomite narrower than genital double-somite. Preserved specimen colourless, nauplius eye absent. Rostrum sickle-shaped from lateral aspect (Fig. 2), much longer than first antennular segment, triangular with rounded tip in frontal aspect.

Prosome (Fig. 1) comprising cephalothorax and 4 free prosomites (first pedigerous somite not incorporated into cephalothorax), ovoid, about twice as long as wide (dorsal view); length ratio of prosomal somites, beginning with cephalothorax, 100: 27: 18: 20: 4. Cephalothorax 1.2 times longer than its greatest width, representing 34% of total body length; surface of cephalic shield, as well as those of free prosomites, without any sensilla or pores visible. Hyaline fringe of prosomites narrow and smooth.

Urosome (Fig. 1) 5-segmented, with genital and first abdominal somites completely fused to form double-somite. First urosomite ornamented with 2 large dorsal sensilla and smooth fringe dorsally and ventrally. Sclerotized joint between first urosomite and genital double-somite well developed, almost as pseudosomite (Figs 7–9), but weakly sclerotized dorsally.

Genital double-somite (Figs 7–9) with anterior part slightly inflated laterally, about 1.5 times as long as wide (dorsal view), ornamented with 2 lateral and 2 dorsal sensilla at first third and four posterolateral sensilla



FIGURES 1–6. *Speleophria nullarborensis* sp. nov., holotype female: 1, habitus, dorsal view; 2, habitus, lateral view; 3, antennula; 4, antenna; 5, mandibula; 6, maxillula. Scales = 0.1 mm.

(two on each side). Single midventral copulatory pore relatively large, almost triangular when closed, situated at 3/5 of double-somite's length; copulatory duct wide, short and rigidly sclerotized, directed dorsally and then anteriorly and attached to posterior part of seminal receptacle. Seminal receptacle small, rounded, representing only 30% of double-somite's width and 22% of its length. Paired ovipores located ventrolaterally as narrow slits at each side of copulatory pore, covered by reduced sixth legs and connected to receptacle via weakly sclerotized, narrow receptacle ducts.

Third urosomite (Figs 7–9) ornamented with 2 posterolateral sensilla (one on each side), while fourth urosomite (preanal somite) unornamented. Preanal somite very short and narrow, only about 0.3 times as long as third urosomite and also much narrower than anal somite, acting like a clear urosomal constriction. Hyaline fringe of second to fourth urosomites narrow, not frilled and completely smooth. Anal somite with smooth, broad and convex anal operculum, representing 67% of somite's width and reaching its posterior margin; ornamented with 2 large dorsal sensilla and 2 posteroventral rows of minute spinules at base of each ramus.

Caudal rami (Figs 7–9) subcylindrical, about as long as wide and somewhat shorter than anal somite, almost parallel, with very small space between them; representing only about 3.5% of total body length. Distal margin dorsally smooth and convex, ventrally straight and ornamented with small spinules, without cuticular pores visible. Only additional ornamentation consisting of several minute spinules posteriorly at base of distolateral seta. Armature consisting of 7 setae: 1 dorsal, 2 lateral and 4 apical. Dorsal seta short and smooth, 1.3 times as long as ramus, inserted close to posteromedial margin, uniarticulate at base and arising from small setophore. Proximolateral seta minute, smooth, positioned ventrolaterally at 1/4 of ramus' length. Midlateral seta strong and bipinnate, twice as long as ramus and inserted laterally at 2/5 of ramus' length. Innermost apical seta strong and bipinnate, nearly twice as long as outermost apical one (also bipinnate) and 3.6 times as long as ramus. Principal apical setae broken at breaking planes.

Antennula (Fig. 3) short and slender, hardly reaching posterior 3/4 of cephalothorax, implanted on triangular pedestal, unornamented, incompletely 21-segmented. Intersegmental membrane less visible along thinner and highly armed anterior margin. First segment inflated, about as wide as long; twentieth segment 2.4 times as long as wide. Armature as follows: segment 1, 5 setae + aesthetasc; segments 2–4, 2 setae each; segment 5, 3 setae + aesthetasc; segment 6, 2 setae; segment 7, 9 setae; segments 8–9, 2 setae each; segment 10, 2 setae + aesthetasc; segments 11–14, 2 setae each; segment 15, 2 setae + aesthetasc; segments 16–17, 1 seta each; segment 18, 1 + 1 setae; segment 19, 1 + 1 setae + aesthetasc; segment 20, 1 + 1 setae; segments 21, 3 + 2 setae + aesthetasc. Aesthetasc hypertrophied on first and fifth segments, but slender on tenth, fifteenth, nineteenth and twenty-first segments. Only anterodistal seta on tenth segment hypertrophied. Setae without breaking planes or basal biarticulations; most setae smooth.

Antenna (Fig. 4) biramous, comprising coxa, basis, 2-segmented endopod and 6-segmented exopod (although first and second exopodal segments partly fused along anterior surface), with strong geniculation between first and second endopodal segments. Coxa and basis ovoid, unarmed and unornamented. Exopod nearly twice as long as coxa and basis combined, with second and last segments longest; setal formula 1.2.1.1.1.5. Endopod significantly longer than exopod, with both segments of about same length; first segment unornamented and armed with 2 medial setae; second segment ornamented with 4 transverse rows of slender setules, armed with 5 proximomedial and 7 apical setae. First endopodal segment 2.7 times as long as wide; second segment more than 3 times as long as wide.

Labrum (Fig. 2) not mounted satisfactorily to allow detailed examination, but appears large and complex, armed with several short rows of long setules.

Mandibula (Fig. 5) comprising coxa with well developed gnathobase and biramous palp; palp consisting of basis, 2-segmented endopod and indistinctly 4-segmented exopod. Coxal gnathobase cutting edge with isolated large tooth ventrally, plus row of 9 smaller, heterogeneous teeth and 2 dorsal setae. Basis large, 1.6 times as long as wide, unornamented and armed with 1 smooth seta medially. Endopod attached almost apically to basis (as its extension), with proximal segment somewhat shorter and wider than distal one, with setal formula 3.6. Exopod about as long as endopod, but somewhat wider, with setal formula 0.1.1.4.



FIGURES 7–12. *Speleophria nullarborensis* sp. nov., holotype female: 7, abdomen, ventral view; 8, abdomen, dorsal view; 9, abdomen, lateral view; 10, maxilla; 11, syncoxa and basis of maxilliped; 12, endopod of maxilliped. Scale = 0.1 mm.

Maxillula (Fig.6) composed of large praecoxa, smaller coxa, large basis and 1-segmented endopod and exopod. Praecoxa with massive arthrite, armed with 2 slender setae on posterior surface and 12 elements along inner margin (9 spines and 3 setae); dorsalmost marginal seta pinnate, almost 3 times as long as any of the spines and twice as long as other pinnate seta; third marginal seta small. Coxa with well developed endite, bearing 2 spiniform and 3 slender setae; epipodite small, armed with 8 plumose setae. Basis with single slender, smooth outer seta; proximal endite well developed, somewhat longer than coxal endite, armed with 4 setae (3 pinnate, one of which is strong; 1 slender and smooth); distal endite indistinct, armed with 4 smooth setae. Endopod half as long as basis, armed with 5 smooth setae along inner margin and cluster of 6 setae apically. Exopod slightly larger than basis (excluding endites), twice as large as endopod, armed with 2 outer, 4 apical and 3 inner plumose setae. Exopod ornamented with long spinules along both inner and outer margins; basis ornamented only along dorsal side; other segments unornamented.

Maxilla (Fig. 10) 6-segmented, comprising praecoxa, coxa, basis and 3-segmented endopod. Praecoxa quadriform, about as wide as long, unornamented, with 5 setae on proximal and 3 setae on distal endite. Coxa much smaller than praecoxa, also unornamented, armed with 3 setae on each endite. Basis slightly shorter than praecoxa, with strong proximal and small distal endite; distal endite armed with 3 slender setae, proximal one armed with 3 slender setae and 2 claw-like spiniform setae. All setae on praecoxa, coxa and basis pinnate. Endopodal segments very short, each armed with claw-like spiniform seta almost as long as entire maxilla; first and second segment additionally armed with slender smooth seta each, third segment additionally armed with 3 slender setae (2 smooth, 1 unipinnate).

Maxilliped (Figs 11–12) slender, 8-segmented, composed of syncoxa, basis and 6-segmented endopod. Syncoxa nearly 3 times as long as greatest width, unornamented, with proximal praecoxal endite weakly discernible, distal praecoxal and both coxal endites well developed; armature formula 1.2.3.3. Basis slightly shorter than wide, 0.3 times as long as syncoxa, ornamented with several long spinules on inner margin and armed with 3 pinnate setae. Endopod slender and twice as long as basis; proximalmost segment shortest, distalmost segment longest; armature formula 1.2.2.2.3.5.

All swimming legs (Figs 13–19) with 3-segmented exopod and endopod; their armature formula as follows:

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

All intercoxal sclerites without surface ornamentation, with slightly concave distal margin. Coxae unornamented, except posterior row of minute spinules on first leg, armed with plumose seta at inner distal corner. Basis of each leg also unornamented, armed with strong spine (first and second legs) or slender seta (other legs) on outer margin; basis of first leg with additional spine on distal inner corner, shorter than first endopodal segment; inner distal corners of second, third and fourth leg pronounced as blunt processes; similar but much sharper process also between exopod and endopod. All exopodal spines serrate on both sides. All exopodal and endopodal setae on first leg slender and plumose, except outer apical seta on third exopodal segment, plumose along inner margin and serrate along outer. Second, third and fourth legs with some setae plumose proximally and serrate distally; number of these setae smallest on second leg, largest on fourth (where 6 out of 8 endopodal setae ornamented like this). All endopodal segments with hair-like spinules along outer margin and all exopodal segments with minute spinules along outer margin. Third endopodal segment of fourth swimming leg about 1.7 times as long as wide; apical elements subequal, 2.2 times as long as segment.

Fifth leg (Fig. 20) with small intercoxal sclerite fused basally to somite, 4-segmented, comprising coxa, basis and 2-segmented exopod. Coxa about 1.5 times as wide as long, unarmed and unornamented. Basis

quadriform, somewhat longer than coxa, unornamented, but armed with unipinnate seta on outer distal corner. First exopodal segment narrower proximally and somewhat longer than basis, armed with bipinnate seta. Second exopodal segment longest, about 1.7 times as long as wide, 1.7 times as long as coxa, also unornamented, but armed with 3 setae; innermost subapical seta strongly serrate and spiniform, about as long as segment; inner apical seta plumose, 1.7 times as long as segment; outer apical seta bipinnate and somewhat shorter than segment.

Sixth leg (Figs 9 and 21) not clearly distinct, represented by trapezoidal cuticular plate, armed with inner smooth and minute spine, fused to plate, and 2 bipinnate setae; outermost seta 2.3 times as long as middle seta and 5 times as long as innermost spine.

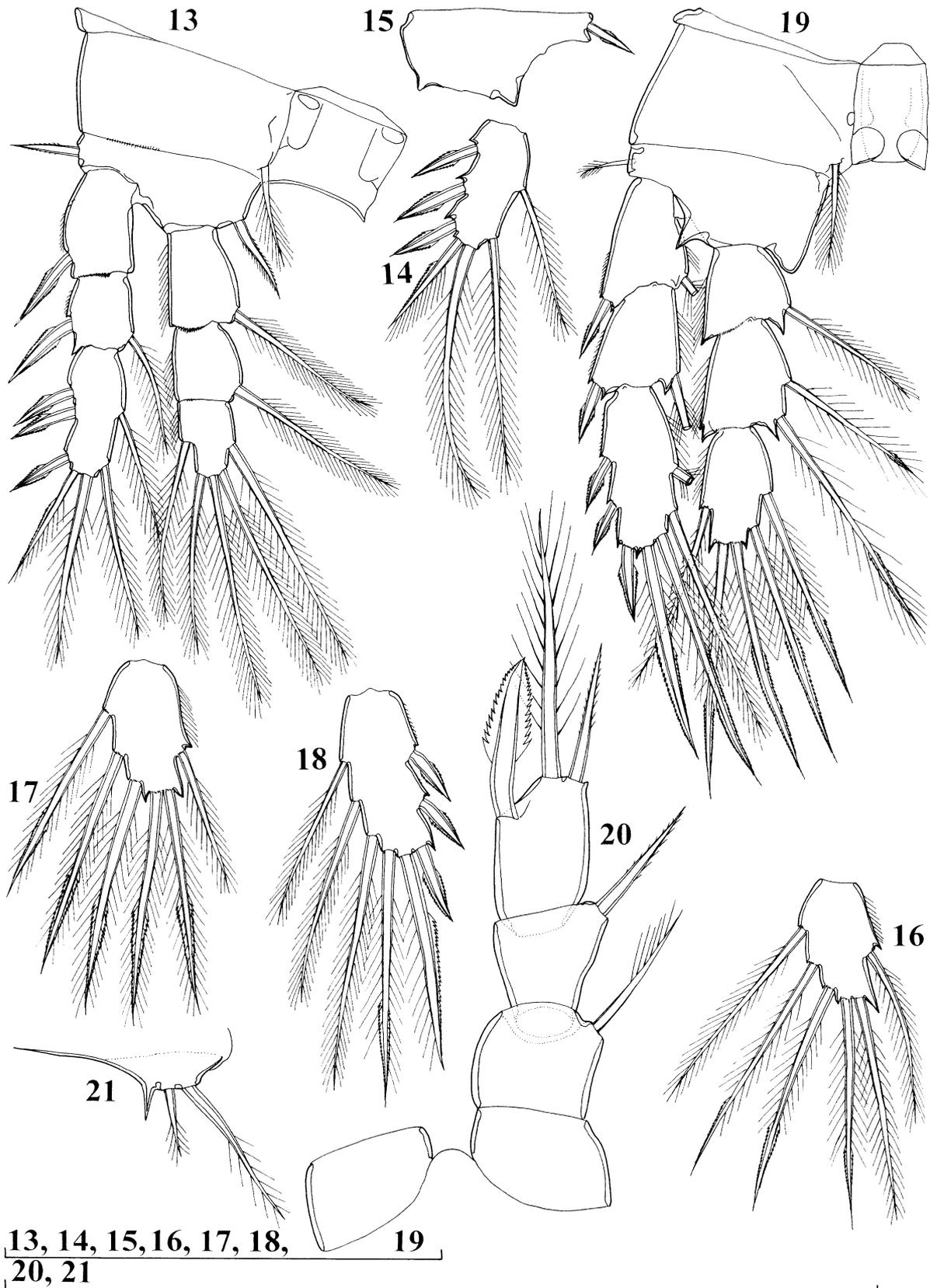
MALE. Unknown.

Variability. Body length of females ranges between 0.474 mm and 0.496 mm (average = 0.481 mm; n = 7). The third exopodal segment of the first swimming leg in the holotype has the proximal two outer spines spaced very close to each other on one side (Fig. 13), while the opposite leg has a normal appearance (Fig. 14). No other forms of variability or asymmetry were observed.

Etymology. The specific name comes from the Nullarbor region, where the type material was collected. The name is an adjective for place, made with the Latin suffix *-ensis*.

Affinities. Among the misophrioid genera, the new species fits well into the diagnosis of the genus *Speleophria* Boxshall & Iliffe 1986, as emended by Jaume & Boxshall (1996a), by its segmentation and armature of the mouth appendages, as well as by the shape, armature and ornamentation of the majority of body parts, except for the first leg endopod segmentation. A 3-segmented endopod of the first swimming leg is found in, beside our new species, the speleophriid clade (sensu Boxshall & Jaume 2000a) containing the genera *Archimisophria* Boxshall, 1983, *Boxshallia* Huys, 1988 and *Expansophria* Boxshall & Iliffe, 1987. Indeed, Boxshall & Halsey (2004) used this character alone in their speleophriid key to separate these three taxa from the other four genera having a 2-segmented leg 1 endopod (*Huysia* Jaume, Boxshall & Iliffe, 1998, *Protospeleophria* Jaume, Boxshall & Iliffe, 1998, *Speleophria* and *Speleophriopsis* Jaume & Boxshall, 1996). The plesiomorphic segmentation of the first leg endopod is, however, not enough to place our new species with the *Archimisophria-Boxshallia-Expansophria* clade, because our new species: a) differs from the latter three taxa in a number of very important characters that include armature and segmentation of the antenna, mandibula, maxilla, fifth leg, etc.; and b) shares many morphological characters with one of the *Speleophria* members, that we briefly considered a possibility of its subspecific status. It should be noted that the convenient division of speleophriid genera in Boxshall & Halsey's (2004) key is not supported by Boxshall & Jaume's (2000a) cladistic analysis of misophrioid genera, which showed that *Speleophriopsis* stands as a sister group to all other six speleophriid genera. Also the absence of the intersegmental membrane between the middle and distal endopodal segments of the first leg was not followed by the reduction of armature, as all *Speleophria* species have seven setae in total on the endopod.

So far only four *Speleophria* species are valid members of the genus, all of them described from anchialine caves: *S. bivexilla* Boxshall & Iliffe, 1986 from Bermuda, *S. gymnesica* Jaume & Boxshall, 1996 from the Balearic Islands, *S. bunderae* Jaume, Boxshall & Humphreys, 2001 from north-western Australia and *S. mestrovi* Kršinić, 2008 from Croatia (see Boxshall & Iliffe 1986; Huys & Boxshall 1991; Jaume & Boxshall 1996a; Jaume *et al.* 2001; Kršinić 2008). Two other anchialine species were originally described in this genus (*S. scottodicarloi* Boxshall & Iliffe, 1990 from Bermuda and *S. campaneri* Boxshall & Iliffe, 1990 from Palau Islands), but were later transferred to a newly established genus *Speleophriopsis* by Jaume & Boxshall (1996a). *Speleophria nullarborensis* **sp. nov.** can be easily distinguished from its four congeners by its plesiomorphic 3-segmented endopod of the first swimming leg (Fig. 13), which is 2-segmented in other species, and the unusually long innermost apical seta on its caudal rami (Fig. 7; nearly twice as long as the outermost apical seta). Another character that easily distinguishes our new species, and seems to be an autapomorphic feature, is its constricted preanal somite (Figs 7–9). This character was not variable in any of the seven adult females examined. *Speleophria bivexilla* differs additionally from *S. nullarborensis* **sp. nov.** by its lateral armature element on the second exopodal segment of the female fifth leg (absent in the new



FIGURES 13–21. *Speleophria nullarborensis* sp. nov., holotype female: 13, first swimming leg; 14, third exopodal segment of first leg; 15, basis of second swimming leg; 16, third endopodal segment of second swimming leg; 17, third endopodal segment of third swimming leg; 18, third exopodal segment of third swimming leg; 19, fourth swimming leg; 20, fifth leg; 21, sixth leg. Scales = 0.1 mm.

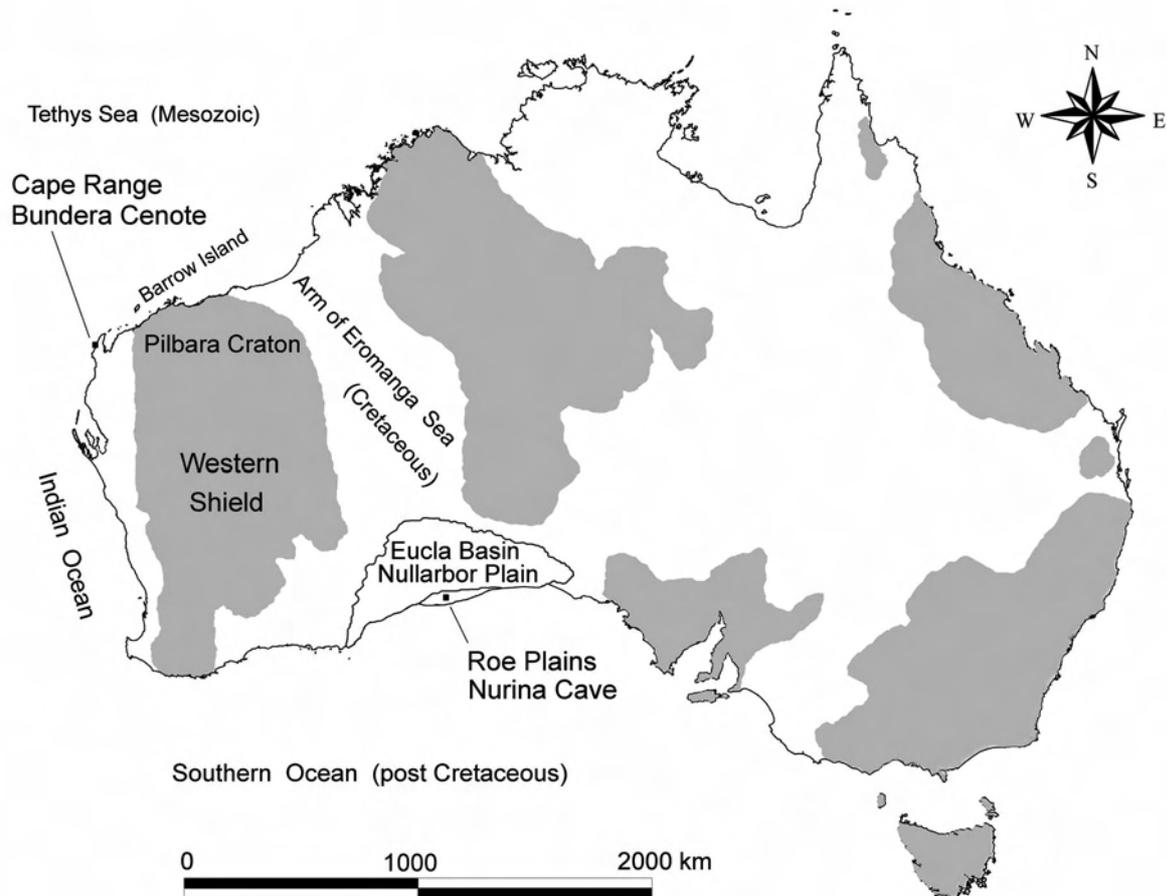


FIGURE 22. Map of Australia showing locations mentioned in text, including arm of the Eromanga Sea (Cretaceous) and areas (shaded) continually emergent since the Palaeozoic. Adapted and modified from Humphreys (2006).

species, as well as in the other three congeners), as well as by some other characters in the armature of cephalic appendages and the fourth swimming leg. The north-western Australian *S. bunderae* shares an unusually reduced proximolateral seta on each caudal ramus with the new species, but can be distinguished from it additionally by a number of minor characters, i.e.: antennula with hypertrophied seta also on the 14th segment and the penultimate segment much longer, antenna with only four proximomedial setae on the second endopodal segment (five in the new species), maxillula without outer seta on the basis, maxilla with a minute seta on the first two endopodal segments, more heavily ornamented swimming legs and more pointed posterolateral corners of the fourth free prosomite. The Croatian *S. mestrovi* can be easily distinguished from its congeners by a bulbous process on the first antennular segment, and differs additionally from *S. nullarborensis* **sp. nov.** by the size and ornamentation of anal operculum and genital double-somite. The Mediterranean *S. gymnesica* shares the greatest number of morphological characters with the new species and can be distinguished from it by the plesiomorphic armature of the third exopodal segment of the fourth leg, in addition to the three previously mentioned unique characters of *S. nullarborensis* **sp. nov.** It should be stressed here that morphological differences between *Speleophria* species, and especially between *S. nullarborensis* **sp. nov.** and *S. gymnesica*, are indeed very small. Unfortunately, males of only two *Speleophria* species (*S. bunderae* and *S. mestrovi*) are known, and a meaningful cladistic analysis would be very hard to perform here without male characters. Instead, we present below a key to species.

Key to species of the genus *Speleophria* (based on adult females)

- 1 Second exopodal segment of female fifth leg with three armature elements 2
- Same segment with four elements *S. bivexilla* Boxshall & Iliffe, 1986
- 2 Antenna with five lateral setae on the second endopodal segment..... 3
- Four setae on this segment.....*S. bunderae* Jaume *et al.*, 2001
- 3 First antennular segment without bulbous process 4
- This segment with bulbous process*S. mestrovi* Kršinić, 2008
- 4 Innermost apical seta on caudal rami shorter than outermost one*S. gymnesica* Jaume & Boxshall, 1996
- Innermost seta twice as long outermost *S. nullarborensis* **sp. nov.**

Discussion

Vicariance has been considered to be a more acceptable hypothesis for explaining zoogeographic connections of freshwater subterranean faunas with disjunct distribution patterns (Boxshall & Jaume 2000b; Karanovic 2004a, 2005a, 2006; Karanovic & Ranga Reddy 2005), while dispersal has been regarded traditionally as a better model for explaining recent distributions of marine and continental surface-water animals (Wilson 1999; Reid 2001; Waters & Roy 2004; Waters & Craw 2006; Karanovic 2008). Recent debate about New Zealand biogeography showed that we have unjustly underestimated recent long distance dispersal in favour of ancient vicariance (Sanmartin & Ronquist 2004; Waters & Craw 2006). Dispersal cannot be completely rejected even for some subterranean freshwater copepods with disjunct distributions (see Karanovic & Ranga Reddy 2004), although this can sometimes be a consequence of anthropogenic translocation associated with early shipping activities (Karanovic 2005b).

Our knowledge about distribution patterns of copepods is hindered by a lack of data. For example, Jaume & Boxshall (1996b) interpreted the lack of morphological variability between three "disjunct" island anchialine populations of the cyclopoid copepod *Muceddina multispinosa* Jaume & Boxshall, 1990 as a consequence of their highly conservative morphology over evolutionary time (thus employing the vicariance model), which was soon dismissed by Holmes & Gotto (2000) who found this species in the littoral habitats as well (see also Karanovic 2008). Thus, hypotheses about the Tethyan origin of copepod genera, that physically disrupt populations, should be taken cautiously.

Speleophria nullarborensis **sp. nov.** is the second representative of the order Misophrioida known from Australia. The first, *Speleophria bunderae* Jaume, Boxshall & Humphreys, 2001, was described from an anchialine cave (Bundera Cenote) at Cape Range in north-western Australia. Besides north-western Australia, species of *Speleophria* are known from anchialine caves in Mallorca (Mediterranean), Bermuda (NW Atlantic), the Yucatan in Mexico and Croatia (Boxshall & Iliffe 1986; Huys & Boxshall 1991; Jaume & Boxshall 1996a; Jaume *et al.* 2001; Kršinić 2008). *Speleophria* (and nearly all other speleophriid genera) are characterised by very localised and extremely disjunct distributions, with members confined almost exclusively to anchialine habitats (Boxshall & Halsey 2004) in regions flooded by late Mesozoic seas, which lent support to their interpretation as true Tethyan relicts (Jaume *et al.* 2001). The modern world distribution of described Speleophriidae has shown a 'Full Tethyan track', and was explained as a result of range fragmentation by plate tectonics and allopatric speciation from ancestral stocks widely distributed in suitable habitats along the late Mesozoic margins of the Tethys Sea (Boxshall & Jaume 2000a). These hypotheses naturally presume a reduced potential for dispersal of anchialine copepods, which has not been proved yet. It is interesting to note that *Speleophria bivexilla* Boxshall & Iliffe, 1986 is on the IUCN Red List (<http://www.iucnredlist.org/details/20461>) as critically endangered, i.e. category B1+2c (Iliffe 1996), probably because of this general assumption about reduced potential for dispersal in anchialine forms.

The discovery of this new speleophriid on the Roe Plains has important biogeographic and ecological implications. From the biogeographic perspective, it either suggests dispersal as the process determining the current distribution pattern of the aquatic fauna found on the Roe Plains or significantly extends the Tethyan

track across Australia, from the north-western coastal margin of the continent to the southern coastal margin (Fig. 22). From an ecological perspective, the new speleophriid suggests the possible existence of anchialine habitats within the Roe Plains.

No detailed study of Australian littoral copepods has been made, and what is known is fragmentary and mostly limited to Harpacticoida (Nicholls 1941, 1942, 1944, 1945; Hamond 1973; Harris 1994, 2002; Bartsch 1994, 1995; Walker-Smith 2001, 2005). As such, the possible presence of misophrioids in the Australian littoral cannot be dismissed. It should be noted as important for this discussion that *S. nullarborensis* **sp. nov.** is not morphologically most similar to its north-western Australian congener, but to the Mediterranean representative, *S. gymnesica*, and morphological differences between *Speleophria* species, and especially between *S. nullarborensis* and *S. gymnesica*, are indeed very small. This would certainly not suggest an evolutionary history of many millions of years, as normally postulated for the taxa that are considered to be Tethyan relicts. The Southern Hemisphere has been considered as having a fundamentally vicariant history, but recent biogeographic studies based on molecular estimates and more accurate paleogeographic reconstructions indicate that dispersal may have been more important than assumed traditionally (Sanmartin & Ronquist 2004). Boxshall & Jaume (1999) regarded the occurrence of misophriid copepods in anchialine caves as a landward extension of the habitat range from a shallow-water hyperbenthic ancestor, which was in contrast to Boxshall's (1989) previous hypothesis about the origin of anchialine misophrioids from the deep-sea (although it is fair to point out that many fewer misophrioid taxa were known at that time from anchialine caves) and was mostly influenced by the views of Stock (1986) and new data that became available. They also interpreted speleophriid distribution as resulting from a colonisation episode prior to the closure of the Tethys Sea.

Another possibility, which we would like to explore here, is that the Tethyan track somehow encompasses the Nullarbor region. Indeed, during the Early Cretaceous (ca. 120 Ma), when north-western Australia formed the eastern margin of the Tethys Sea (Howarth 1980), and after India separated from Australia's Western Australian margin and the sea entered the proto-Indian Ocean rift, a marine invasion began in the rifting zone formed where Australia began separating from Antarctica. Around the same time as this southern seaway (the proto-Southern Ocean) was developing, an arm of the Tethys Sea penetrated from north-western Australia and formed a vast shallow epicontinental sea (the Eromanga Sea) which connected with the southern seaway in the region of the Eucla Basin (White 1994). Thus two potential routes existed for colonisation of the Eucla Basin region by Tethyan fauna during the late Mesozoic (Fig. 22). The Tethyan hypothesis requires the persistence of suitable habitats over long geological time scales, as many Tethyan relicts are found in caves developed in rocks that are considerably younger than late Mesozoic, the Cainozoic limestones in the Eucla Basin and Cape Range being no exception. For the Tethyan fauna at Cape Range, Humphreys (1993) hypothesised their origin and persistence adjacent to much older (Proterozoic) rocks on the Pilbara Craton, part of the Western Shield, where some Tethyan elements have since been found, including thermosbaenaceans, cirrolanid isopods, halicyclopine cyclopoids and atyid shrimps (see Eberhard *et al.* 2005). There are several periods in the past when fauna may have colonised the Nullarbor region, including during the Oligocene, Miocene and late Pliocene-early Pleistocene. The limestone of the Nullarbor was deposited in the Eocene-Miocene Eucla Basin, a very extensive shallow shelf along the central part of Australia's southern margin (Webb & James 2006). The oldest limestone was deposited during the middle-late Eocene (ca. 43–36 Ma). In the early Oligocene, the sea withdrew and the surface of the limestone was exposed to subaerial weathering for over 10 Ma (Lowry 1970). From the late Oligocene to the early Miocene the sea returned and deposited more limestone, then retreated for less than 1 Ma, and advanced again in the middle Miocene (Lowry & Jennings 1974). The sea withdrew at the end of the late Miocene and the Nullarbor region was slightly uplifted. During the Pliocene-early Pleistocene (ca. 2 Ma), a marine transgression cut the Roe Plains and deposited the Roe Calcarene (Lowry & Jennings 1974). The localised distribution of stygofauna on the Roe Plain, and its apparent absence from parts of the Nullarbor karst not subjected to the late Pliocene-early Pleistocene marine transgression, would seem to suggest stranding of marine progenitors during this period, although earlier colonisations cannot be ruled out. Cave development could have occurred during the early to

late Oligocene (ca. 35 to 25 Ma), when the sea retreated for 10 Ma, and also during the late Miocene (ca 14 Ma), after the sea finally retreated and the area was uplifted (Webb & James 2006). Warm wet climates during the Oligocene would have supplied abundant run-off from rivers draining southwards into the karst which developed large conduits deep beneath the watertable that flowed southwards to major springs along the coast, and resulted in further cave development along the seawater-meteoric water interface, favouring the development of anchialine habitats. A Pliocene wet phase (5–3 Ma) likely coincided with a second phase of cave development (Webb & James 2006).

In anchialine caves, a diverse but highly predictable suite of marine taxa exhibits similarly extreme, disjunct distribution patterns with foci at locations including the Canaries, Bermuda, the Galapagos, the Bahamas, Belize, the Balearics, the Yucatan, the Turks and Caicos and Cape Range in north-western Australia (Boxshall & Jaume 2000a). The presence of some members of this faunal suite has been used to indicate that other members should be found, as in the case at Cape Range where the discovery of thermosbaenaceans (Poore & Humphreys 1992) led Wagner (1994) to predict the finding of a diverse community of phylogenetic and distributional relict Tethyan elements and other anchialine species, including remipedes, epacteriscid calanoids, speleophriids, hadziid amphipods, cirolanid isopods, thaumatocyprids, halicyclopine cyclopoids and atyid decapods (Humphreys 2000a). While other described species of *Speleophria*, and nearly all other described speleophriid genera are confined almost exclusively to anchialine habitats (Boxshall & Jaume 2000a), the existence of true anchialine conditions remains unclear in Nurina Cave. The term “anchialine” was coined by Holthuis (1973) and anchialine ecosystems are defined today as salinity-stratified coastal aquifers affected by marine tides but with no surface connection with the sea (Sket 1981, 1996; Stock *et al.* 1986). While Nurina Cave is salinity-stratified, evidence for strong hydrologic connections with the sea, for example tidal fluctuations, has not been established. Other caves on the Roe Plain, and caves up to 50 km inland on the Nullarbor Plain, are also salinity-stratified. In the Nullarbor Plain caves direct marine influences have not been invoked; instead the stratification is linked to processes of mixing corrosion at the vadose-phreatic interface and mixing precipitation at the shallow phreatic-deep phreatic interface (James 1992). Salinity-stratification is also characteristic in some other inland aquifers in arid parts of the Western Shield (e.g. Watts & Humphreys 2003).

One other stygobitic species is recorded from Nurina Cave, a melitid amphipod, *Nurina poulteri* Bradbury & Eberhard, 2000. Several other caves on the Roe Plain contain *Nurina* Bradbury & Eberhard, 2000, which bears many similarities to the marine genus *Melita* Leach 1814, and other taxa of marine provenance including bogidiellid amphipods (Bradbury & Eberhard 2000) and phallodriline oligochaetes (Adrian Pinder pers. comm.). While melitids and bogidiellids are associated with anchialine habitats at Cape Range (Bradbury & Williams 1997) and nearby Barrow Island (Bradbury & Williams 1996; Bradbury 2002), these taxa also occur in fresh groundwaters far inland on the Pilbara Craton (S. Halse, S. Eberhard, M. Scanlon, J. Cocking, H. Barron, unpublished data). In the Pilbara, melitids are found at elevations well above the late Eocene sea-level high (ca. 300 m) which appears to define the distribution limits for other marine faunal elements including thermosbaenaceans, cirolanid isopods, atyid decapods and halicyclopine copepods (see Poore & Humphreys 1992; Bruce and Humphreys 1993; Pesce *et al.* 1996b; Humphreys 2001; Karanovic 2006). Above this elevation the Pilbara Craton has remained continuously emergent since the Proterozoic, and the melitids most probably extended their range by active dispersal along river drainage systems which have existed since the late Cretaceous (Beard 1998; van de Graaff *et al.* 1977).

The Phallodrilinae (Tubificidae) are primarily marine interstitial worms, although some estuarine and freshwater species are known. Four species of phallodrilines from karst aquifers and caves along the west coast of Western Australia have recently been described, being the first records of this subfamily from non-marine waters in the Southern Hemisphere (Pinder *et al.* 2006). The described species were all collected in near coastal freshwater caves and springs in south-west Western Australia, and anchialine habitats at Cape Range. In contrast to the low lying Roe Plains, the more elevated plateau of the Nullarbor karst appears remarkably devoid of stygofauna despite its enormous size, Tertiary age and abundant potential habitat in the form of large water-filled caves with salinity conditions ranging from fresh to saline. The only life forms

recorded in the cave lakes of the Nullarbor plateau are microbial mantles (Contos *et al.* 2001) composed of biochemically novel, chemoautotrophic communities, which are dependent on nitrite oxidation (Holmes *et al.* 2001). These authors concluded that the low productivity in the Nullarbor cave lakes may explain the absence of macro-invertebrate grazers associated with the microbial communities; however, these lakes have not been sampled yet for meiofauna such as copepods. Discovery of the Roe Plain speleophriid raises the likelihood that other members of the anchialine “Tethyan” faunal suite will be found in the Eucla Basin, or in other groundwaters located near the palaeoshorelines of the Western Shield.

Can the Tethyan track be extended to the southern Australian coastline? If not, what mode of dispersal might have carried the animals there? Unfortunately, these questions would need much more investigation to be properly answered, including more sampling in the Nullarbor region, researching speleophriid biology and looking for these animals in littoral samples. Judging by the morphology of the five described *Speleophria* species alone, we clearly favour dispersal as an explanation for the presence of the newly described representative in the Nullarbor region. New evidence, which often includes molecular data, is mixed, but a swing towards dispersal is evident in explaining disjunct distributions of anchialine faunas. For example, Kornicker & Iliffe (1989) and others have argued for a Tethyan origin of the anchialine ostracod genus *Danielopolina* Kornicker & Sohn, 1976 in the Mesozoic with subsequent dispersal by plate tectonics, but the recent discovery of this genus on Christmas Island, a limestone-capped, volcanic seamount in the Indian Ocean, has fueled debate concerning the potential for oceanic dispersal of anchialine taxa to such otherwise isolated locations (Humphreys & Danielopol 2005). It should be mentioned here that one species of *Danielopolina* is also known from deep waters of South Atlantic. Anker *et al.* (2006) recently described a new species of alpheid shrimp from a callianassid shrimp burrow on a sand-mud intertidal area near mangroves in Vietnam. Other species of this genus are known from anchialine caves in Bermuda, the Balearic Islands and NW Western Australia. Kano and Kase (2004) have shown genetic exchange between anchialine cave populations of a neritiliid gastropod species from two isolated islands in the Philippines, most probably by means of larval dispersal. Kornicker *et al.* (2007) found some halocyprid ostracod species on opposite sides of the Great Bahama Bank, a distance of more than 150 km, and also reported similar disjunct distributions for several calanoid copepods within the Bahamas. They also discovered representatives of “typical anchialine fauna in the deep interior of open ocean submarine caves (blue holes), which are not considered an anchialine habitat at all. On the other hand, Santos (2006) studied population structure and demography of an endemic Hawaiian shrimp and found that little to no gene flow occurs between populations separated by more than 30 km. Finally, Page *et al.* (2008) used nuclear and mitochondrial analyses to study evolutionary relationships of Western Australian subterranean atyid shrimps and found evidence that some subterranean species have descended from localised surface relatives rather than morphologically similar subterranean species from further afield, while others have closest known relatives in anchialine waters of the Caribbean/North Atlantic/Mediterranean (thus supporting the hypothesis that they may descend from a common ancestor that lived in the coastal marine habitat of the ancient Tethys Sea). However, they admitted that the latter “on its own is only weak evidence for an imprint of the Tethys, especially as other atyids have proven to disperse over great distances”, but rather advocated “a more complex mixed-model approach”.

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