
Reprinted from: CRUSTACEANA
71,7 1998



Brill - P.O. Box 9000 - 2300 PA Leiden
The Netherlands

FIRST RECORD OF SPELAEGRIPHACEA FROM AUSTRALASIA:
A NEW GENUS AND SPECIES FROM AN AQUIFER IN THE ARID
PILBARA OF WESTERN AUSTRALIA

BY

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ABSTRACT

Spelaeogriphacea are reported for the first time from Australia. A new genus and species, *Mangkurtu mityula*, are described and the only other two genera diagnosed. The species, the third extant in the order, seems more similar to the Brazilian *Potiicoara brasiliensis* than to the South African *Spelaeogriphus lepidops* but all have unique apomorphies. The species is found in the aquifer in the Tertiary Millstream Dolomite of the Pilbara region of Western Australia. It is part of a fauna with clear Gondwanan affinities. This fauna is distinct from those found in aquifers in the lower and upper parts of the same drainage basin.

RÉSUMÉ

Des Spelaeogriphacea ont été découverts pour la première fois en Australie. Un nouveau genre et une nouvelle espèce, *Mangkurtu mityula* sont décrits et une diagnose est donnée pour les deux seuls autres genres. L'espèce, la troisième de l'ordre, apparaît plus proche de l'espèce brésilienne *Potiicoara brasiliensis* que de l'espèce d'Afrique du sud *Spelaeogriphus lepidops* mais toutes présentent des apomorphies uniques. L'espèce a été récoltée dans le système aquifère du dolomite tertiaire Millstream de la région de Pilbara en Australie Occidentale. Elle fait partie d'une faune présentant clairement des affinités gondwaniennes. Cette faune est distincte de celles trouvées dans les aquifères des parties inférieure et supérieure du même bassin de drainage.

INTRODUCTION

The peracarid crustacean order Spelaeogriphacea was erected on the basis of a single species, *Spelaeogriphus lepidops* Gordon, 1957 (Spelaeogriphidae), from a freshwater stream in a cave on Table Mountain, South Africa (Gordon, 1957). Later, the fossil *Acadiocaris novascotica* (Copeland, 1957) (Acadiocariidae) from marine sediments of Carboniferous age was recognized as a spelaeogriphacean by Schram (1974) who wrote that "no other [than *S. lepidops*] living

species have been found, though if others exist they should probably be sought in the Gondwana area". In 1987 *Potiicoara brasiliensis* Pires was described from a freshwater cave lake in the Mato Grosso, Brazil, and, with the current report of a new genus and species from Australia, comes close to fulfilling Schram's prediction of biogeographic affinities.

Here, the three extant genera are rediagnosed, the new Australian species is described, and its systematic and biogeographic relationships to other spelaeogriphaceans discussed. The environment that it inhabits is described and compared with those of other members of the order.

Material of the new species is lodged in the Western Australian Museum, Perth (WAM) and the Museum of Victoria, Melbourne (NMV).

SYSTEMATICS

SPELAEORIPHIDAE Gordon, 1957

Remarks. — Pires (1987) compared the two genera then known. We had difficulty in placing the new species in either and reluctantly erect a third. It is now necessary to rediagnose all genera on the basis of several characters, some not previously recognised. All genera are monotypic.

Spelaeogriphus Gordon, 1957

Spelaeogriphus Gordon, 1957: 32.

Diagnosis. — Antenna 1 peduncle sexually dimorphic; male peduncle article 2 medially lobed and papillose. Antenna 2 scale shorter and narrower than peduncle article 3. Mandibular palp 1-articulate. Maxilla 1 inner lobe with conical apices, each with clusters of short setae. Maxillipedal palp articles 2 and 3 with mesial row of plumose setae. Maxillipedal epipod cup-shaped, as long as endite. Pleopods 1-4 similar in both sexes; endopods without basal, laterally directed lobe. Pleopod 5 a single article. Oostegites on pereopods 2-5.

Type species. — *Spelaeogriphus lepidops* Gordon, 1957 by original designation and monotypy.

Potiicoara Pires, 1987

Potiicoara Pires, 1987: 226.

Diagnosis. — Antenna 1 peduncle not sexually dimorphic. Antenna 2 scale as long and broad as peduncular article 3. Mandibular palp 3-articulate. Maxilla 1

inner lobe with 2 apical pappose setae. Maxillipedal palp articles 2 and 3 with few mesial setae. Maxillipedal epipod thick, oval, as long as endite. Pleopods 1-5 all present and similar in juveniles and females; endopods without basal, laterally directed lobe. Pleopod 2 of male unknown. Oostegites on pereopods 1-5.

Type species. — *Potiicoara brasiliensis* Pires, 1987 by original designation and monotypy.

Mangkurtu n. g.

Diagnosis. — Antenna 1 peduncle not sexually dimorphic. Antenna 2 scale shorter and narrower than peduncle article 3. Mandibular palp 3-articulate. Maxilla 1 inner lobe with conical apices, each with clusters of short setae. Maxillipedal palp articles 2 and 3 with few mesial setae. Maxillipedal epipod short, digitiform. Pleopods 1-5 all present and similar in juveniles and females; endopods with basal, laterally directed lobe. Pleopod 2 of male with 2-articulate endopod and narrow exopod bearing few setae. Oostegites unknown.

Type species. — *Mangkurtu mityula* n. sp.

Etymology. — Mangkurtu is the name of the Fortescue River in the Yindjibarndi language of the region. Noun in nominative singular, feminine.

Remarks. — *Mangkurtu* n. g. is unique in the possession of a digitiform maxillipedal epipod and in having endopodal lobes on the pleopods. These are autapomorphies and the sexually dimorphic pleopod 2 would be as well unless it is found in *Potiicoara*.

Mangkurtu differs from *Spelaeogriphus* in most characters. In *Spelaeogriphus* the peduncle of antenna 1 of males bears tuberculate lobes mesially, the mandibular palp is 1-articulate and pleopod 5 is reduced to a small article. These three character states are autapomorphies. Other differences from *Mangkurtu* are the large and cup-shaped maxillipedal epipod, the pleopods which are not sexually dimorphic and absence of an endopodal lobe on the pleopods. These are characters shared with *Potiicoara*. *Mangkurtu* shares with *Spelaeogriphus*, and differs from *Potiicoara*, only the similar maxilla 1 inner lobe.

Mangkurtu differs from *Potiicoara* in fewer characters, the setation of maxilla 1 and the maxillipedal palp, and most significantly in the maxillipedal epipod and pleopodal endopods. The two genera share similar mandibular palps and non-dimorphic antenna 1. Sexual dimorphism of pleopod 2 has not been reported in *Potiicoara brasiliensis*. Careful examination by A. M. S. Pires (pers. comm.) of the original and new collections failed to find males or any characters which would differentiate individuals from the abundant oostegite-bearing females. Autapomorphies of *Potiicoara* are uncertain but having the antennal 2 scale as long and broad as peduncular article 3 is unique.

Mangkurtu mityula n. sp. (figs. 1-6)

Material examined. — Holotype: Western Australia, Pilbara region, Millstream aquifer, 21°36'S 117°04'E, CP3 11/81 Chinderwariner Pool A.B., W. F. Humphreys, 19.x.1996 (stn BES 4008), WAM C23278 (male, 3.1 mm).

Paratypes: Western Australia, Pilbara region, Millstream aquifer, 21°35'S 116°58'E, P4 haul net in piezometer, 19.x.1996 (stn BES 3998), WAM C23279 (male, 2.6 mm, with microslide), WAM C23280 (juvenile, with microslide), WAM C23281 (juvenile, with 2 microslides), WAM C23282 (7 juveniles, 1.5-2.8 mm), 21°38'S 117°01'E, 7C haul net in piezometer, 16.x.1996 (stn BES 3962), WAM C23283 (male, with 2 microslides), WAM C23284 (juvenile, with microslide), WAM C23285 (11 juveniles, 1.7-2.3 mm), 21°40'S 117°07'E, 5B haul net in piezometer, 18.x.1996 (stn BES 3981), WAM C23286 (male, 3.5 mm), 21°38'S 117°01'E, 7C north haul net in piezometer, 16.x.1996 (stn BES 3966), WAM C23287 (male, 2.8 mm), 21°36'S 117°01'E, 7B haul net in piezometer, 17.x.1996 (stn BES 3973), WAM C23288 (juvenile male, 2.7 mm; 2 posterior ends), 21°38'S 117°01'E, 7C haul net in piezometer, 17.x.1996 (stn BES 3972), WAM C23289 (4 abdomens), 21°35'S 117°01'E, 7A haul net in piezometer, 19.x.1996 (stn BES 4001), WAM C23290 (juvenile), 21°40'S 116°54'E, 4A haul net in piezometer, 17.x.1996 (stn BES 3980), NMV J44021 (juvenile), 21°45'S 117°15'E, 15B haul net in piezometer, 18.x.1996 (stn BES 3983), NMV J44023 (juvenile), 21°35'S 116°58'E, P4 haul net in piezometer, 19.x.1996 (stn BES 3999), NMV J44022 (4 males, 29 juveniles, with 3 specimens on SEM stubs), 21°35'S 116°58'E, haul net in piezometer, 19.x.1996 (stn BES 5230), NMV J44030 (2 juveniles). All collected by W. F. Humphreys.

Description of male. — Body about 5 times as long as greatest width; carapace : pereon : pleon ratio 0.18 : 0.30 : 52. Carapace with flat triangular rostrum, well defined cervical grooves visible dorsolaterally, and with deeply rounded lateral flaps covering bases of mouthparts. Pereonite 1 shortest, 2-5 longer, and 6-7 longest; all without lateral plates. Pleonites all longer than pereonites, more posterior ones longest; pleonite 6 narrower than others; 1-5 with lateral overlapping rounded epimera. Telson flat, slightly longer than wide at base, tapering to rounded apex with 4 pairs of marginal spiniform setae (sometimes extra 1 or 2 setae), most lateral the longest, and 1 pair submarginal-dorsal between 2 most lateral setae.

Eyelobe subcircular, little longer than wide, reaching beyond lateral margin of carapace.

Antenna 1 total length 0.75 of body; peduncle article 1 with few scattered short setae and longer plumose lateral seta; article 2 shorter, sparsely setose; article 3 about as long as 2, with short stout dorsal seta, longer stout lateral setae; outer flagellum subterminal, with broad proximal article and 27 other articles; inner flagellum 0.70 length of outer, of 22 articles.

Antenna 2 reaches at least to posterior of body; peduncle article 2 with medial row of short setae and lateral stout seta; article 3 longer, sparsely setose; article 4 longer than 3, with distal setae only; exopod width 0.35 length, with medial rows of alternating 6 plumose and 6 stout setae.

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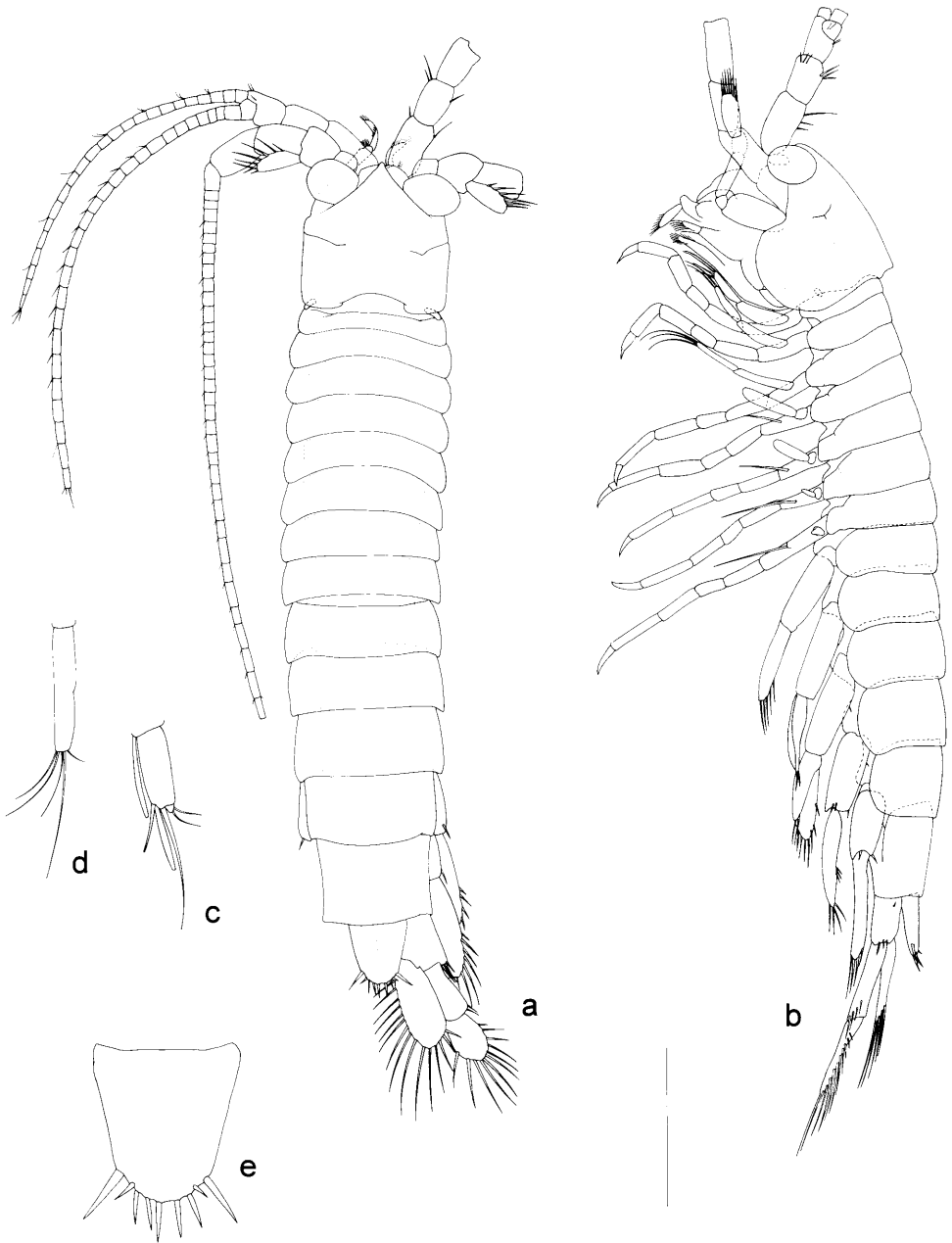


Fig. 1. *Mangkurtu mityula* n. sp., paratype male, 2.6 mm (BES 3998) WAM C23279. a, b, habitus (scale 0.5 mm); c, antenna 1, terminal article; d, antenna 2, terminal article; e, telson.

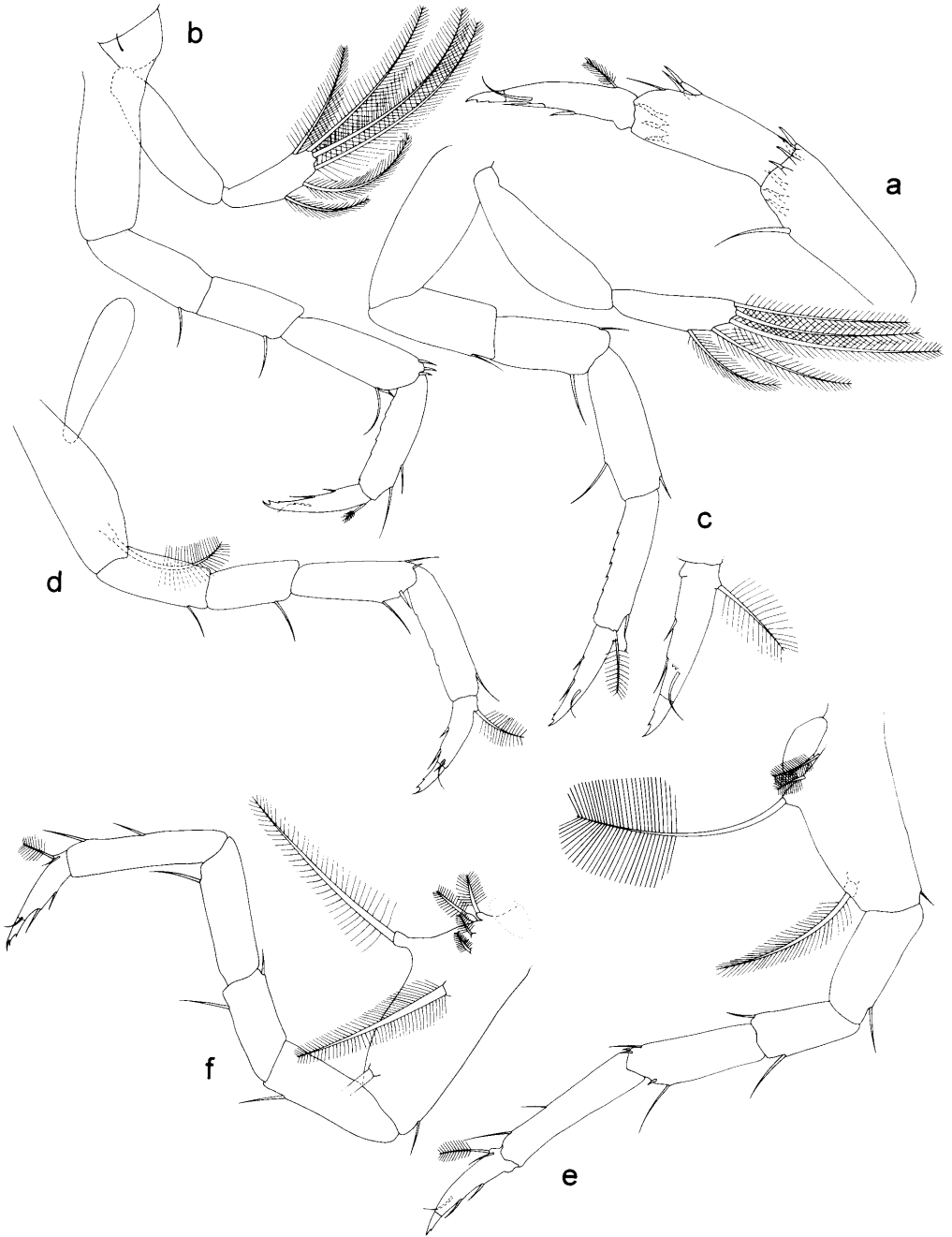


Fig. 2. *Mangkurtu mityula* n. sp., paratype male, 2.7 mm (BES 3973) WAM C23288. a, pereopod 1, carpus-dactylus; b, pereopod 2; c, pereopod 3 with detail of dactylus; d, pereopod 4; e, pereopod 6; f, pereopod 7.

Mandible substantial, forwardly directed; molar process prominent, cylindrical, with ridged and tessellate chitinised apex; curved spine row of 14 setae, each with basal setules; lacinia mobilis with 4-5 irregular distal denticles on left side, with major and minor tooth on right side; incisor process with 3-4 uneven teeth; field of long setules on anterior and posterior faces at base of spine row; palp with short article 1, article 2 reaching just beyond incisor process, with 5 short stalked setae along distal quarter of outer margin, article 3 with c. 16 stalked setae along outer curved margin.

Lower lip with 2 halves separated by deep angle, inner edge with straight-edged distal setose lobe; outer margin with angular lobe.

Maxilla 1 inner lobe with spinules scattered on both anterior and posterior faces, with 4 conical apices, each with clusters of short setae; outer lobe about 5 times as broad as inner, with 12 robust irregularly denticulate setae along oblique distomesial margin (simpler setae distally), with stout pappose seta covered with long setules on distolateral margin, and with long setules along lateral margin and on both faces near distal margin.

Maxilla 2 with mesial margin ending distally in an inner lobe, a middle lobe and an outer lobe; mesial margin with one row of c. 30 closely-spaced plumose setae near margin along posterior surface, second row of 6 widely spaced plumose setae marginally; apex of inner lobe with 4 long pectinate setae on anterior edge and with 6 pedunculate setae (each with numerous setules arising from a common point) alternating with simple setae and another pedunculate seta on posterior face, posterior face with strip of numerous setules; middle lobe with oblique mesial margin bearing a row of 1 denticulate seta proximally, 19 sinuous setae with complex denticulate heads, and 3 distal setae with pectinate heads; outer lobe with oblique mesial margin bearing a row of 1 denticulate seta proximally, 19 sinuous setae with complex denticulate heads, and c. 30 overlapping distal setae with pectinate heads.

Maxilliped basal endite 1.3 times as long (measured from base of palp) as greatest width, distally evenly rounded; row of 7-8 long plumose setae near inner margin of endite, leading to curved row of 7-8 shorter plumose setae on anterior face, 3 sigmoid coupling hooks, 2 oblique rows of pectinate setae on anterior face, 7-8 tooth-like setae on most of distal margin, and 7 complex setulate setae on distolateral margin. Maxilliped palp with very short article 1; article 2 widest distally, wider than long, with 2 long setae distolaterally; article 3 widest proximally, tapering to 40% of greatest width, 1.5 times as wide as long, with 4 long setae proximolaterally; article 4 40% width of article 3, articulated with it obliquely, with distal U-shaped row of 12 long setae around distal margin; article 5 articulated at right angles and on distal two-thirds of



Fig. 3. *Mangkurtu mityula* n. sp., paratype male, 2.6 mm (BES 3998) WAM C23279. a, left mandible; b, incisor and lacinia mobilis of right mandible; c, left maxilla 1, posterior view; d, left maxilla 2, posterior view; e, lower lip.

article 4, narrower than article 4 with partly paired rows of 16 long setae on distal margin. Maxilliped epipod a digitiform process high on side of maxillipedal somite.

Pereopod 1 linear; basis without setae; ischium with 1 posterodistal seta; merus with 2 posterodistal setae; carpus with 1 posterodistal seta, 5 lateral and 2 mesial pedunculate falcate setae; propodus with 1 anterodistal seta, 1 + 3 lateral and 1 anterior pedunculate falcate setae; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod article 1 without setae, article 2 with 5 plumose setae.

Pereopod 2 linear; basis without setae; ischium with 1 posterodistal seta; merus with 1 posterodistal seta; carpus with 1 posterodistal seta, 1 anterodistal seta, 1 + 2 lateral pedunculate falcate setae; propodus with 2 anterodistal setae, 1 lateral pedunculate falcate seta; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod article 1 without setae, article 2 with 5-6 plumose setae.

Pereopod 3 linear; basis with long mesial plumose seta; ischium with 1 posterodistal seta; merus with 1 posterodistal seta, 1 anterodistal seta; carpus with 1 posterodistal seta, 1 anterodistal seta, 1 lateral pedunculate falcate setae; propodus with 1 anterodistal seta; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod article 1 without setae, article 2 with 4-5 plumose setae.

Pereopod 4 linear, basis wider than more distal articles; basis with long mesial plumose seta; ischium with 1 posterodistal seta; merus with 1 posterodistal seta, 1 anterodistal seta; carpus with 1 posterodistal seta, 1 anterodistal seta, 1 + 1 lateral pedunculate falcate setae; propodus with 1 anterodistal seta; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod reaching beyond end of basis.

Pereopod 5 similar to pereopod 4; exopod 80% length of that on pereopod 4.

Pereopod 6 with basis much wider than more distal articles; basis with 1 mesial and 1 anterior long plumose setae, 3-4 shorter posteroproximal plumose setae; ischium with 1 posterodistal seta; merus with 1 posterodistal seta, 1 anterodistal seta; carpus with 1 posterodistal seta, 1 anterodistal seta, 1 + 1 lateral pedunculate falcate setae; propodus with 2 anterodistal setae; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod reaching about quarter length of basis.

Pereopod 7 with basis much wider than more distal articles; basis with 2 mesial and 1 anterior long plumose setae, 4-5 shorter posteroproximal plumose setae; ischium with 1 posterodistal seta; merus with 1 posterodistal seta, 1 anterodistal seta; carpus with 1 posterodistal seta, 1 anterodistal seta, 1 + 1 lateral

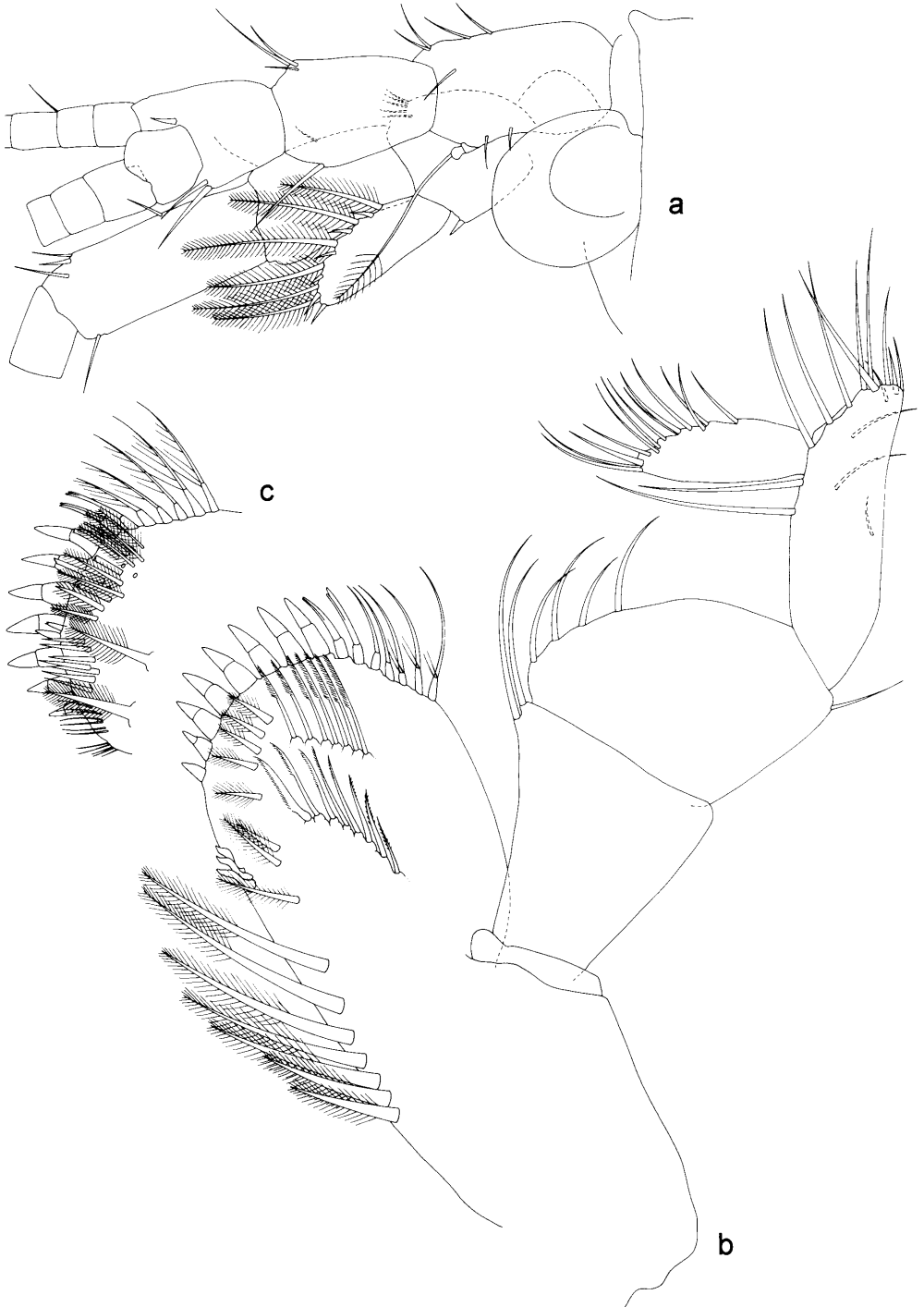


Fig. 4. *Mangkurtu mityula* n. sp., paratype male, 2.6 mm (BES 3998) WAM C23279. a, left antennae 1 and 2 and eye; b, right maxilliped, anterior view; c, left maxillipedal endite, posterior view.

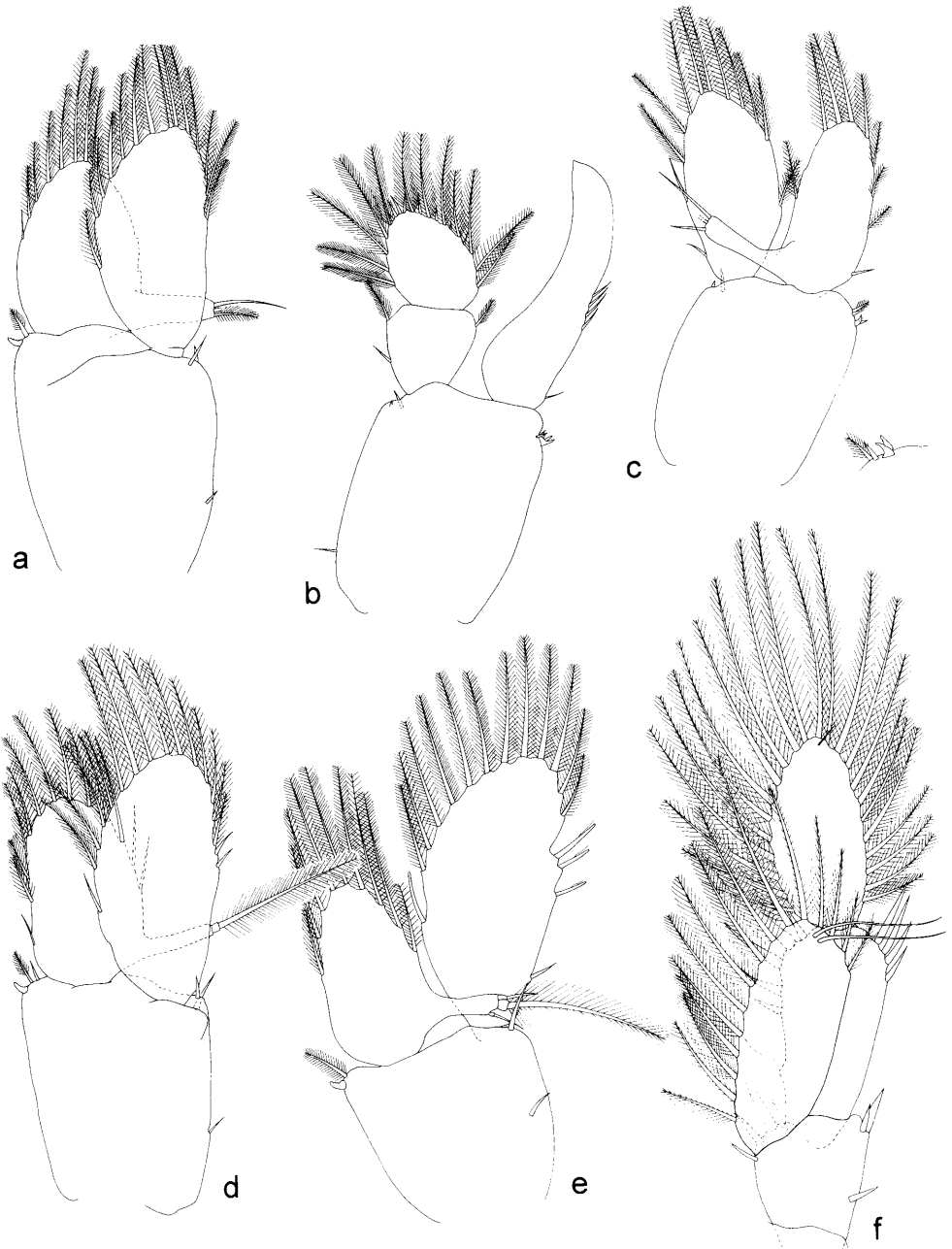


Fig. 5. *Mangkurtu mityula* n. sp. Paratype male, 2.6 mm (BES 3962) WAM C23283: a-d, pleopods 1-4. Paratype male, 2.7 mm (BES 3973) WAM C23288: e, pleopod 5. Paratype male, 2.6 mm (BES 3998) WAM C23279: f, left uropod.

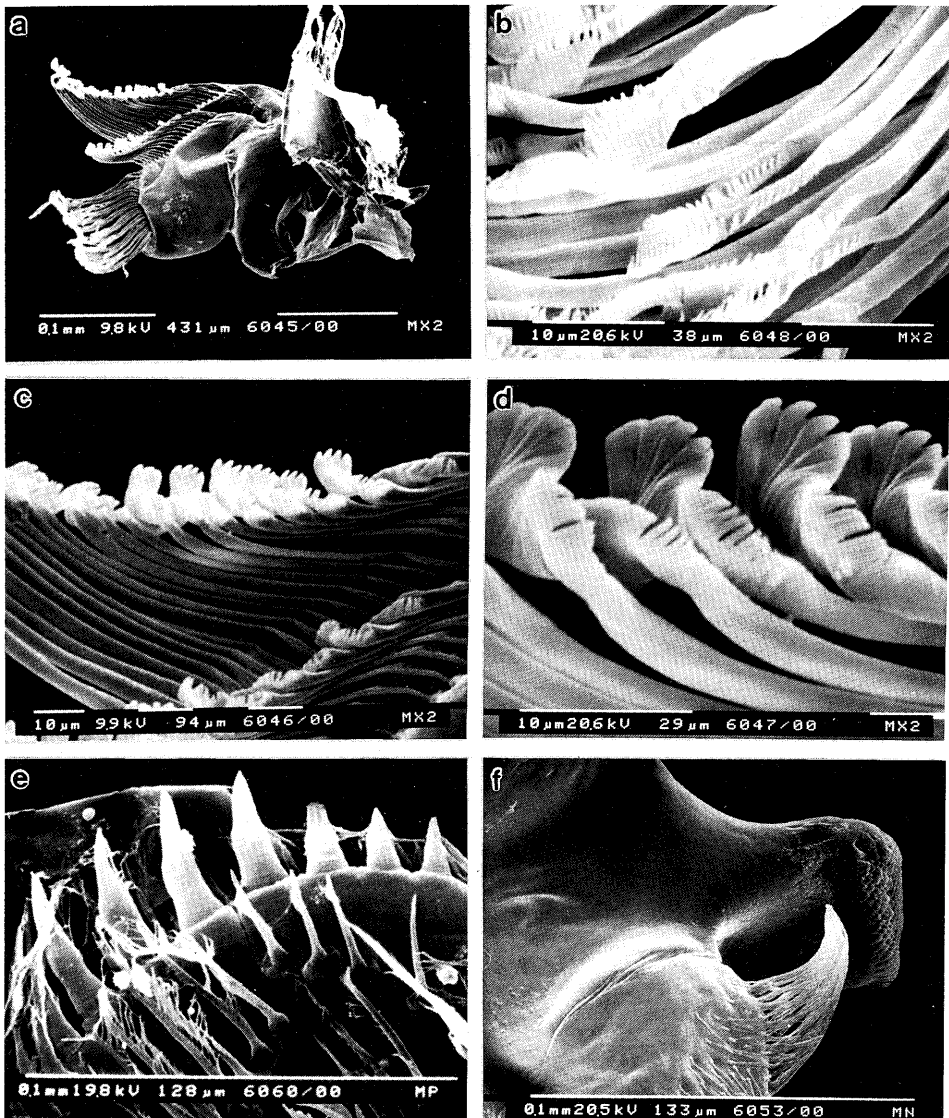


Fig. 6. *Mangkurty mityula* n. sp., paratype male (BES 3999) NMV J44022. SEMs: a, maxilla 2; b, maxilla 2, tips of setae on distal margin of outer lobe; c, maxilla 2, rows of setae on middle and outer lobes; d, maxilla 2, details of c; e, maxilliped, anterior face of apex of endite; f, mandible, distal view of spine row and molar.

pedunculate falcate setae; propodus with 2 anterodistal setae; dactylus with 1 plumose anteroproximal seta, 1 mesiodistal seta, 2 posterodistal setae; unguis with 2 secondary spines; exopod reaching about eighth length of basis.

Penes at bases of pereopods 7 cylindrical, meeting in midsternum.

Pleopod 1 peduncle thickened, longer than wide, with proximolateral short plumose seta, 2 distolateral short simple setae, 1 simple and 1 plumose distomesial short setae, 2 coupling hooks; exopod longer than endopod, with 1 lateral simple seta, 9-11 marginal plumose setae; endopod with 1 mesial simple and 8-10 marginal plumose setae, with proximal laterally-directed narrow lobe reaching lateral edge of exopod, with 1 long plumose and 2 shorter setae.

Pleopods 2-5 peduncles as in pleopod 1.

Pleopod 2 exopod 2-articulate, shorter than endopod; proximal article with 1 lateral simple seta, 1 distolateral plumose and 1 distomesial plumose setae; distal article with 12 marginal plumose setae and 9 shorter simple setae on distal margin; endopod broadly-falcate, curving laterally, with 1 proximomesial and 3-4 midmesial setae.

Pleopod 3 exopod longer than endopod, with (1 lateral simple seta), 9-14 marginal plumose setae; endopod with 1 proximal mesial simple, 9-12 marginal plumose setae, with proximal laterally-directed narrow lobe reaching beyond lateral edge of exopod, with 1 long plumose and 2 shorter setae.

Pleopod 4 exopod longer than endopod, with (1 proximolateral), 2-3 lateral simple setae, 11-13 marginal plumose setae, 1 mesial simple seta; endopod with 1 mesial simple and 10-13 marginal plumose setae, with proximal laterally-directed narrow lobe reaching beyond lateral edge of exopod, with 1 long plumose and 2 shorter setae.

Pleopod 5 exopod much longer than endopod, with 1 proximolateral, 2-3 lateral simple setae, 12 marginal plumose setae, 1 mesial simple seta; endopod with 8-9 marginal plumose setae, with proximal laterally-directed narrow lobe reaching beyond lateral edge of exopod, with 1 long plumose and 2 shorter setae.

Uropod peduncle with 4-5 distolateral, 2-3 distomesial, 1 proximomesial spiniform setae, 1 simple and 1 plumose setae ventrally on distal margin; exopod with 15-18 marginal plumose setae and 2-3 submarginal dorsal setae; endopod 2-articulate; proximal article as long as exopod, with 4 distolateral, 4-6 mesial spiniform setae; distal article with 18 marginal plumose setae, 1-2 simple apical setae.

Juvenile. — Pleopod 2 like pleopods 1 and 3.

Ovigerous female. — Unknown.

Etymology. — *Mityula* means 'hidden' in the Yindjibarndi language of the region and 'flood' in adjacent Ngarla language. An allusion to the recharging of the Millstream aquifer by major floods on the Fortescue River. Noun in apposition.

Distribution. — Found in 9 of 57 locations sampled in the Millstream aquifer and confined to the central part of the aquifer.

The environment. — Millstream is located in the arid tropics where the annual evaporation (3365 mm) exceeds rainfall (352 mm) by about an order of magnitude and is characterised by very high summer temperatures (the mean monthly maxima exceed 40°C for six months of the year). The vegetation covering the aquifer is predominantly tussock grassland (*Triodia* spp.) and *Acacia* scrub.

The ancestral Fortescue River formed by headward erosion along the strike of the Proterozoic Hamersley Group including the Wittenoom Dolomite. The original valley was in existence in the Late Jurassic. During the Early Cretaceous the Yarraloola Conglomerate — which comprises almost entirely of flood gravel and shingle similar to that found in the current lower Fortescue River (Williams, 1968) — was deposited by a river along the course of the original valley (Barnett, 1981). The Millstream Dolomite formed in a lake that developed within this valley, one of a series of valley-fill sediments of Cainozoic age, probably of Middle to Late Tertiary age (Barnett & Commander, 1985), that can be viewed as a single hydrological flow system (Barnett & Commander, 1985). The area has not been inundated by the sea since the Proterozoic (Hocking et al., 1987).

Mangkurty mityula is found in fresh groundwater contained in the Millstream Dolomite, a large aquifer in the western Fortescue plain and a major water resource for the towns of northwestern Australia. The aquifer is confined except where the Millstream Dolomite outcrops as it does over much of the central and northern part of the western Fortescue plain and in places there are small sink holes at the surface; all specimens were collected from areas of outcropping. The Fortescue plain catchment was captured from the northwest by the Fortescue River at the end of the Pleistocene or Holocene and in consequence the water table within the Millstream Dolomite fell from about 310 m to c. 294 m AHD. The aquifer, which mainly discharges through springs into the Fortescue River in the region of Millstream, covers c. 2000 km² and is estimated to contain about 1700 × 10⁶ m³ of water with the storage/discharge ratio c. 100 (Barnett & Commander, 1985). The rivers draining the region all flow through one or more water gaps due to incision of a superimposed drainage (Kriewaldt & Ryan, 1967) into the Precambrian base. The Proterozoic bedrock at the water gaps is effectively an hydrological boundary to the west, while to the east the groundwater flow is upstream so little groundwater flow occurs from the Upper Fortescue Valley (Barnett & Commander, 1985). Hence, the fauna is possibly confined to the western Fortescue plain — certainly the same river gravels and shingle, derived from the Yarraloola Conglomerate, of the Fortescue River to the west of the water gaps contain a distinct stygofauna of Tethyan origin.

The extensive cavities that lie above the water table (Barnett, 1981) may be expected to contain a terrestrial subterranean fauna as an integral part of the

TABLE I

Water chemistry parameters for the sample sites in Millstream aquifer from which spelaeogriphaceans were collected. The raw data are from pump tests (Barnett & Commander, 1985). Values are means and s.e. of 6 measurements in mg L^{-1} (save pH)

Parameter ²⁾	Mean	SE
pH ¹⁾	7.4	0.09
TDS	864	128.8
Na	99	24.5
K	10.5	2.42
Ca	66	6.60
Mg	50	8.00
Hardness	360	54.8
Cl	174	48.6
SO ₄	90	22.8
SiO ₂	53	2.3
HCO ₃	311	20.9
NO ₃	9.2	1.14

¹⁾ The pH was significantly lower (7.40 ± 0.086 s.e., $n = 6$ — $FS_{1,17} = 7.968$, $P = 0.012$) in sites where spelaeogriphaceans were collected than at sites where none was collected (7.71 ± 0.062 , 13).

²⁾ Other than pH, these values did not differ from the means of the 13 sites where spelaeogriphaceans were not collected.

hypogean ecosystem. Cavities up to 0.5 m high occur at the present water table where they are horizontally developed — similar development at higher elevation is indicative of a previously higher water level (Barnett, 1981) — and the extremely high hydraulic transmissivity shows that the voids and cavities form a conduit system typical of karst aquifers (Barnett & Commander, 1985).

The physicochemical characteristics of the waters inhabited by spelaeogriphaceans is poorly characterised. *Mangkurtu mityula* was found in sites at pH 7.40, significantly lower than sites where they were not collected (table I). However, the concentration of none of the remaining 11 parameters was associated with the presence of spelaeogriphaceans (table I).

Sampling and associated fauna. — In October 1996 a brief reconnaissance survey was conducted of the Millstream groundwater monitoring borefield (Water and Rivers Commission) and one augmentation bore (Water Corporation). The sites were sampled with haul nets (350 μm mesh) and the samples sorted while alive under a dissecting microscope. Forty-six locations were sampled in the Millstream aquifer of which 20 yielded fauna of some type (16 piezometers, three wells, one water bore). An additional 24 sites sampled in 1997 did not result in additional collections of spelaeogriphaceans but they extended the range of other species and revealed more species in other groups.

Between one and 18 individuals of *Mangkurtu mityula* were collected from eight locations encompassing about 200 km² of the unconfined aquifer. However, the additional sampling in 1997 did not infill the distribution and *M. mityula* cannot be assumed to occur throughout this range. A number of stygobitic taxa occurs in the aquifer of which some (denoted * below) are known from the same sampling points as the spelaeogriphaceans. Given that few samples were taken and no trapping was conducted the number of species found suggests that the aquifer will be shown eventually to be very species rich — it took nearly 50 years to achieve this species richness on the diverse Cape Range peninsula (Humphreys, in press) following the finding of the first stygofauna.

The associated fauna includes Oligochaeta: Phreodrilidae (generally with a cool climate Gondwanan distribution: A. Pinder, pers. comm., 1997); *Gastropoda: new hydrobioid (W. F. Ponder, pers. comm., 1997); *Syncarida: Bathynellacea; *Copepoda: Cyclopoidea (2 + species); Copepoda: Harpacticoidea; *Ostracoda (3 + species); *Isopoda: Phreatoicoidea (? closest to *Hyperoedesipus*, G. D. F. Wilson, pers. comm. 1996); *Amphipoda: Crangonyctoidea (does not align with known groups, J. Bradley, pers. comm. 1996; 2 + families, 4 + species); Acari: *Tiramideopsis* n. sp. (new genus for Australia, previously known only from India, M. S. Harvey, pers. comm. 1996).

The fauna so far determined has clear Gondwanan affinities as expected given its association with the spelaeogriphaceans. The presence in Tertiary strata of a fauna with clearly much older origins can be explained by the strata in places immediately overlying the Wittenoom Dolomite, which contains cavities up to 0.5 m deep, and is of Proterozoic age (table II). These voided strata could have supported the fauna throughout the Mesozoic. The situation is similar to that for the stygofauna of Cape Range peninsula to the southwest, where a clearly old fauna inhabits Tertiary strata (Humphreys, 1993, in press).

OTHER SPELAEOGRIPHACEANS

There are few published accounts of spelaeogriphacean biology (Botosaneanu, 1986; Grindley, 1976; Grindley & Hessler, 1971). They appear to feed on detritus and *Spelaeogriphus lepidops* has 10-12 eggs in a brood pouch but no juvenile forms have been described (Schram, 1986). Their geological context, habitat and associated faunas differ (tables II, III).

The fossil species, *Acadiocaris novascotica*, is from a shallow marine sediment of a laurentian plate of Carboniferous age in Canada. It is the only marine species. All Recent spelaeogriphaceans inhabit fresh water in a range of habitats, from shallow cave streams to at least 20 m depth in deep cave lakes, and in shallow

TABLE II
Global occurrence of extant and fossil spelaeogriphaceans

Species	Region	Country	Geological context	Coordinates
<i>Acadiocaris novascotica</i> (Copeland, 1957)	Atlantic Provinces	Canada	Shale:	46° 18' N 61° 21' W
<i>Spelaeogriphus lepidops</i> Gordon, 1957	Table Mountain	South Africa	Mississippian Carboniferous Table Mountain Sandstone (quartzite): Upper Silurian-Devonian	33° 56' S 18° 22' E
<i>Poticocara brasiliensis</i> Pires, 1987	Bodoquena Mountains	Brazil	White limestone: Corumba Group ¹⁾ , Upper Proterozoic ²⁾	21° 08' S 56° 35' W
<i>Mangkurta mityula</i> n. sp.	Fortescue River	Western Australia	³⁾ Millstream Dolomite: Tertiary/Wittenoorn Dolomite, Proterozoic	21° 35' S 116° 58' E
closest to <i>Spelaeogriphus</i>	Las Hoyas	Spain	Montes Universales, Barremian, Lower Cretaceous	40° 20' N 1° 40' W
closest to <i>Spelaeogriphus</i>	—	China	Shale: Jurassic	

¹⁾ E. Trajano, pers. comm., 1996; ²⁾ P. Gnaspini, pers. comm., 1996; ³⁾ The Millstream Dolomite overlies and is in contact with the Wittenoorn Dolomite in places (Barnett & Commander, 1985).

TABLE III
Habitat characteristics of extant and fossil spelaeogriphaceans

Species	Altitude m ASL	Water temperature	pH	Troglomorphic aquatic fauna	Occurrence
<i>Acadiocaris novascotica</i>	—	—	—	—	Core from borehole
<i>Spelaeogriphus lepidops</i>	700-800 m	c. 10 ¹⁾	4.5-6.0	<i>Paramelita barnardi</i> (Amphipoda); <i>Planaria</i> sp. <i>Dendricoelum</i> sp. (Platyhelminthes) ²⁾	Bats Cave, Giants Work- shop and Vivarium C.
<i>Potticoara brasiliensis</i>	450	22	—	Amphipoda: Hyalellidae; Dytiscidae (4 species); Oligochaeta	Gruta do Lago Azul, not in adjacent caves ³⁾
<i>Mangkurta mityula</i> n. sp.	300	c. 30	7.4	see text	Aquifer for c. 100 km ²
⁴⁾ closest to <i>Spelaeogriphus</i>	—	—	—	ostracods, isopods, decapods ⁵⁾	Aquifer for c. 100 km ²
⁶⁾ closest to <i>Spelaeogriphus</i>	—	—	—	—	—

1) Grindley (1976); ²⁾ Norma Sharratt, pers. comm., 1996; ³⁾ P. Gnaspini, pers. comm., 1996; ⁴⁾ E. Pinardo-Moyo, pers. comm. 1997; ⁵⁾ carideans and reptantians (plus insects, fishes, frogs, salamanders, lacertilians, crocodiles, dinosaurs and birds); ⁶⁾ F. Schram & R. Taylor, pers. comm., 1997.

aquifers. A more modern looking spelaeogriphacean has recently been found in China from a freshwater Jurassic environment (F. Schram, pers. comm. 1997) and a specimen is being described from lower Cretaceous freshwater deposits in Spain (E. Pinardo-Moyo, pers. comm. 1997) (tables II, III).

Spelaeogriphus lepidops occurs in caves on Table Mountain, South Africa, which emerged permanently from the sea long before the dissolution of Gondwana. The Early Triassic Cape Fold Belt is a pre-drift feature (Dingle et al., 1983) that is part of a much more extensive zone of deformation covering parts of Gondwana, possibly extending as far as the sub-Andean ranges to the west and the Hunter-Bowen orogeny in Australia to the east — Du Toit's (1937) Gondwanide orogeny. The orogenesis of the Table Mountain Group was of lower to middle Triassic age (234-200 Ma), and largely post-dates the folding and cleavage formation in the Permian (Dingle et al., 1983: 96). The caves occur in Table Mountain Sandstone, Ordovician sandstones that are mainly subaerial fluvial sandstones deposited near sea level. These are overlain by a glacial tillite (Pakhuis Formation) that was deposited variously in shallow marine, fluvial and terrestrial environments during the Upper Ordovician when the Cape Basin was tectonically extremely stable, a stability which persisted until the Silurian (Rust, 1981). The caves are at an altitude (c. 900 m ASL) where they would have been little influenced by the last major marine inundation of the southern tip of Africa during the Maastrichtian Epoch (c. 70 Ma) in the Late Cretaceous, when the palaeo-sealevel was c. +200 m (Smith et al., 1994), or by the marginal uplift during the Pliocene of c. 100-200 m (estimated from Partridge & Maud, 1987: fig. 24).

Spelaeogriphus lepidops occurs in a cave stream in two caves on Table Mountain. Bats Cave is connected to a cave known as Giants Workshop and the spelaeogriphaceans are also found in the Vivarium on the other side of a ridge, but not in Wynberg cave in the ridge between (P. Swart & N. Sharratt, pers. comm., 1996). While relative sealevels in this region are confused by local tectonism in the Tertiary (Burke, 1996), Table Mountain is unlikely to have been inundated since well before the Cretaceous (J. Rogers, pers. comm., 1997). It has been suggested that the low pH waters, typical of the Table Mountain Sandstone (pH 4.5-6.0; Du Toit, 1954) minimised fouling and accounted for the lack of grooming in *Spelaeogriphus lepidops* (cf. Schram, 1986).

Pottiocoara brasiliensis is found in Upper Proterozoic limestone, Brazil; the region has not been inundated by the sea since the limestone was laid down (I. Karmann, pers. comm. to E. Trajano, 1997) and hence only freshwater organisms colonised the karst region. They occur in Gruta do Lago Azul and Mimoso Cave between which non-soluble rock exists and they appear to be in

currently separate aquifers (E. Trajano, pers. comm., 1996). The species occurs in a >50 m deep lake in a large inclined cave in which daylight penetrates to the water table. Specimens are found to at least 20 m depth but seem to concentrate where light reaches the lake shore. They are not found in other caves believed to have underwater connections with Gruta do Lago Azul (P. Gnaspini, pers. comm., 1996) but spelaeogriphaceans do occur in Mimoso Cave not known to be in hydrological continuity with Gruta do Lago Azul. They have recently been found in a cave 250 km from the type locality (E. Trajano, pers. comm., 1997). No data on water chemistry are available for the Brazilian sites (E. Trajano, pers. comm., 1996).

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All known spelaeogriphaceans occur in geological contexts that are earliest Cretaceous or older, except for *Mangkurtu mityula* which occurs in Tertiary deposits. However, these overlie and are in direct contact with such strata. The three modern sites are located on parts of the continents that have not been inundated by the sea since the dissolution of Gondwana. All extant spelaeogriphaceans occur with very circumscribed distributions in subterranean freshwater habitats on Gondwanan fragments (Africa, South America and Australia). Schram (1974) considered that the spelaeogriphaceans represent a repetition of the classic situation for many crustacean groups which originate in a marine habitat (probably in Laurasian waters), and later disperse into Gondwana and freshwater refugia.

In the Late Carboniferous all of Australia (save for immediate area around North West Cape and the west Kimberley: Purcell & Purcell, 1994) and much of Gondwana was beneath an ice sheet. The colonisation of Gondwanan fresh water is likely to have occurred after the retreat of the Gondwanan ice sheet (after 320 Ma) and prior to the dissolution of Gondwana during which the separation of Africa from Antarctica (i.e., of west- from east-Gondwana — 142-133 Ma) predated the opening of the Atlantic Basin between Africa and South America (127 Ma; Partridge & Maud, 1987).

ACKNOWLEDGEMENTS

We thank, for information in the field: Phil Roberts, Ross Dougherty and Paul Crogan (Water and Rivers Commission, Karratha); Steve Dejusting (Water Corporation, Karratha) and Geoff Kregor (Department of Conservation and Land Management), and for identifications: Drs M. S. Harvey (Acarina), G. D. F. Wil-

son (Isopoda), W. F. Ponder (Mollusca), and A. Pinder (Oligochaeta). Julianne Waldoock provided invaluable support in Perth. Kate Thompson inked the figures. We thank Joan Clark, Department of Zoology, University of Melbourne, for preparing the SEMs and A. M. S. Pires, University of São Paulo, Brazil, for further comment on her species.

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