Lasionectes exleyi, sp. nov., the First Remipede Crustacean Recorded from Australia and the Indian Ocean, with a Key to the World Species

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Abstract

The first remipede crustacean from the Southern Hemisphere and the Indian Ocean is reported. *Lasionectes exleyi*, sp. nov., is described from an anchialine cave on the Cape Range peninsula of Western Australia. This is the eleventh species of modern remipede to be described and the second species to be described in the genus *Lasionectes*. A key to all known species is presented. The discovery of remipedes in Australia represents the first occurrence of a genus other than *Speleonectes* off the Bahamas Banks and only the second continental occurrence of extant remipedes. The species is known from below a density interface in a single nutrient-enriched cave.

Introduction

Recent investigations of coastal karst in Western Australia have led to the discovery of anchialine habitat with a rich troglobitic fauna composed primarily of crustaceans, but including two blind fishes (Humphreys and Adams 1991; Poore and Humphreys 1992; Bruce and Humphreys 1993; Humphreys 1993*a*; Knott 1993). The fauna consists of the same groups of crustaceans recorded from anchialine caves of the Bahamas, the Yucatan Peninsula of Mexico, and Cuba (Yager 1987*a*, 1987*b*, 1994), including cirolanid isopods, atyid shrimp, ostracodes, gammarid amphipods and thermosbaenaceans. This aquatic community composition has become predictable in anchialine habitats (Holsinger 1989, 1992; Yager 1994). The occurrence of additional relict taxa in north-western Australia was predicted owing to the presence of thermosbaenaceans (Poore and Humphreys 1992) and cirolanids (Humphreys 1993*a*); this prediction led specifically to the search for remipedes.

Remipedes are free-swimming, troglobitic crustaceans characterised by a short head and an elongate trunk lacking tagmosis and composed of numerous segments each bearing a pair of paddle-like swimming appendages. Their position in crustacean phylogeny is controversial; the many ancestral characters suggest that they belong to the base of the crustacean phylogenetic tree (Schram *et al.* 1986).

The discovery of a new class of crustacean, Remipedia, represented by a single species, *Speleonectes lucayensis* (Yager 1981), led to the subsequent recognition that the Enantiopoda, known from Carboniferous fossils (Mississippian–Pennsylvanian boundary, about 320 million years ago), also belong to the class Remipedia (Schram 1986). The collection of additional species of living remipedes in the Caribbean region and the Canary Islands firmly linked the remipedes with the ancient Tethys Sea and the subsequent formation of the Atlantic Ocean (Schram *et al.* 1986).

In this paper we describe the first occurrence of a remipede in the Indo-Pacific region and the Southern Hemisphere and only the second genus to be found off the Bahama Banks.

Materials and Methods

All diving was conducted under the standards of the Cave Divers Association of Australia. Collections were made by divers using hand-held nets and bottles. In 1993 water samples were taken from the open surface of the sinkhole, and immediately above and below the thermocline (Table 1). The water was analysed according to standard methods by the Scientific Services Branch of the Water Authority of Western Australia. In March 1994 and May 1995 a sonde (Yeo-Kal submersible data logger Model 606, Sydney) recorded conditions in the upper 14 m and 22 m of the cave respectively. In 1995 tethered conductivity, temperature (LC84 meter; TPS Pty Ltd, Springwood, Brisbane) and oxygen (Yellowstone Instruments) probes attached to separate instruments were used to independently monitor the more accessible parts of the cave.

All appendages were dissected from the right-hand side of specimens, with the exception of the mandibles, both of which were dissected.

Specimens are deposited in the Western Australian Museum, Perth (WAM), and the National Museum of Natural History, Smithsonian Institution, Washington (USNM).

Key to the Species of Remipedia

1. Trunk pleura rounded posterolaterally; head shield subrectangular . . . . Speleonectidae . . . 2
   Trunk pleura pointed posterolaterally; head shield subtrapezoidal or convex laterally. Maxilla 2 and maxilliped with long, narrow segments distal to point of flexure . . . . Godzilliidae . . . 9
2. Segment distal to point of flexure in maxilla 2 and maxilliped enlarged distally and bearing discoid sensilla . . . . Cryptocorynetes haptodiscus
   Segments distal to elbow of maxilla 2 and maxilliped consecutively shorter and smaller, not enlarged distally, lacking discoid sensilla 3
3. Segment distal to point of flexure in maxilla 2 and maxilliped rounded medially, bearing moderate to large setae along the medial margin; distal claw complex with 1–2 anterior spines and posterior horseshoe-shaped arrangement of smaller spines . . . . Speleonectes . . . 4
   Maxilla 2 and maxilliped with rows of setae of nearly equal length along entire margin of segment distal to point of flexure; distal claw complex with long central spine flanked by 2 shorter subterminal spines . . . . Lasionectes . . . 8
4. Caudal rami elongate, over 3× length of anal segment . . . . Speleonectes tulumensis
   Caudal rami less than 3× length of anal segment 5
5. Antenna 1 long, 1/2–2/3 body length. Maxilla 1 terminal fang long, slender, about 3× length of segment 6. Sternal plates with pointed posterolateral processes . . . . Speleonectes benjamini
   Antenna 1 short, less than 1/3 body length. Maxilla 1 terminal fang less than 3× length of segment 6. Sternal plates absent or without pointed posterolateral processes 6
6. Maxilla 1 segment 4 endite with 1–2 robust, broad-based setae 7
   Maxilla 1 segment 4 endite with 5 moderately stout to robust setae. Caudal rami about 1·4–2× length of anal segment . . . . Speleonectes ondinae
7. Caudal rami about equal to length of anal segment. Maxilla 1 terminal fang stout . . . .
   . . . . Speleonectes lucayensis
   Caudal rami about 2× length of anal segment. Maxilla 1 terminal fang slender . . . Speleonectes gironensis
8. Antenna 2 exopod with about 54 plumose setae along margin. Maxilla 1 segment 3 with 1 broad-based, stout apical seta and 5 robust anterior setae; segment 7 a single fang over 2× length of segment 6. Swimming appendages with spinoselike appearance on lateral margin of endopod segments 1 and 2
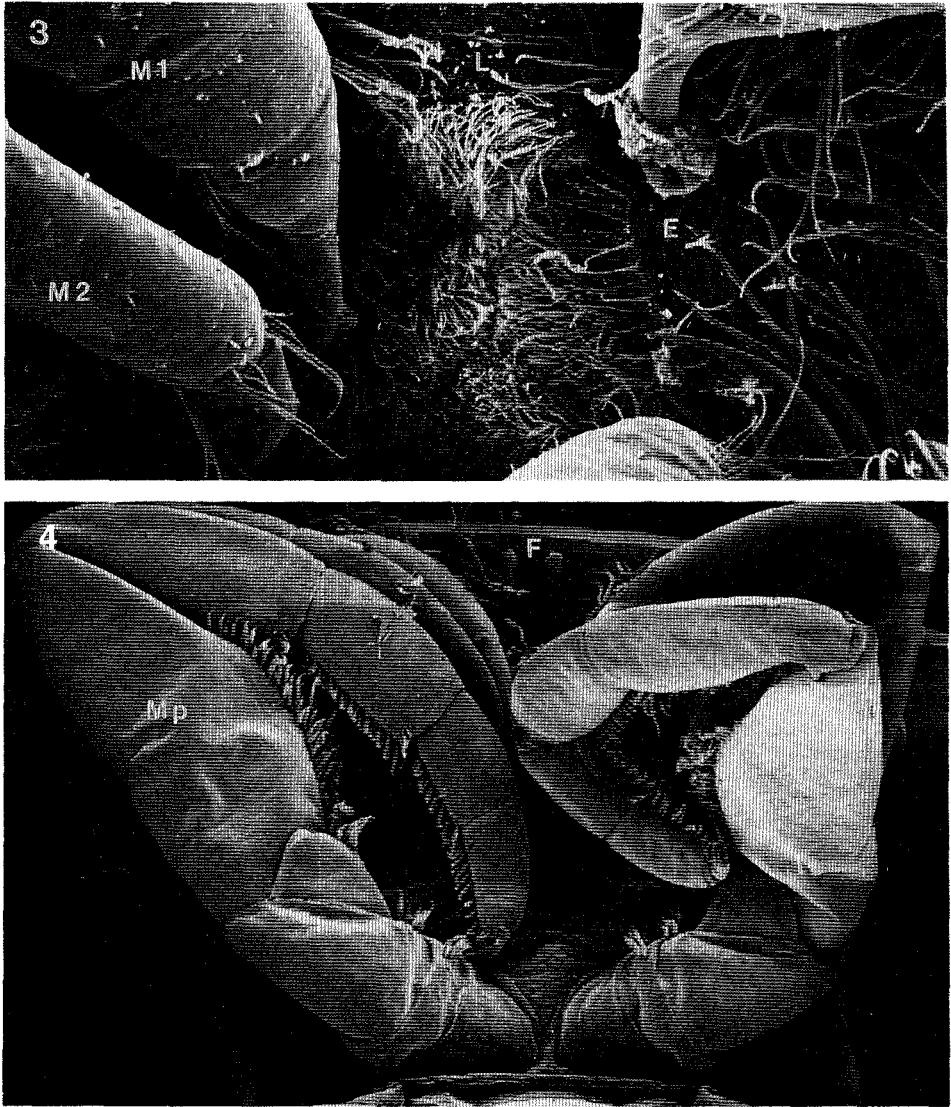   . . . . Lasionectes exleyi
   Antenna 2 exopod with about 35–40 plumose setae. Maxilla 1 segment 3 with 2 stout apical setae, segment 4 with 1 stout medial seta; segment 7 fang less than 2× length of segment 6 . . . .
   . . . . Lasionectes entrichoma
9. Head shield subtrapezoidal. Maxilla 1 large in comparison with maxilla 2 and maxilliped; segment 4 with endite 10
   Head shield convex midlaterally. Maxilla 1 segment 4 lacking endite. Maxilla 2 and maxilliped with leaflike setae on medial margin of segment distal to point of flexure. Body size small, less than 10 mm. Maximum number of trunk segments 16 . . . . Godzilliognomus frondosus
10. Maxilla 1 large, cheliform. Maxilla 2 and maxilliped with medial rows of candeliform setae; claw complex with 1 long medial spine and several shorter subterminal spines. Body length less than 20 mm . . . . Pleomothra apletocheles
    Maxilla 1 segment 4 endite clublike and perpendicular to margin of segment. Maxilla 2 and maxilliped with grappling-hook-shaped claw complex of subequal spines. Body length up to 40 mm or more . . .
    . . . . Godzillius robustus

Systematics

Phylum **CRUSTACEA** Pennant, 1777

Class **REMIPEDIA** Yager, 1981

Order **NECTIOPODA** Schram, 1986

Family **Speleonectidae** Yager, 1981

Genus *Lasionectes* Yager & Schram, 1986

Type species: *Lasionectes entrichoma* Yager & Schram, 1986.

Diagnosis

Maxilla 2 and maxilliped subchelate, segment proximal to point of flexure long, robust, expanded medially, bearing anterior and posterior rows of dense setae along medial margin; anterior setae longer than posterior setae; distal segments with uniform-length setae along medial margin; terminal segment of both appendages bears trifid claw with large central spine, flanked by 2 smaller robust spines.

Lasionectes exleyi, sp. nov.

(Figs 1–17)

Material Examined

Holotype.   Cave C-28, Cape Range peninsula, Western Australia (22°25′S 113°46′E), 26.v.1995, in saline water. A. A. Poole, D. Warren (WAM 147-95); body length 12·8 mm, 24 trunk segments.

Paratypes.   Same location, 12.viii.1993, in saline water, A. A. Poole, D. Warren, W. F. Humphreys, R. D. Brooks (WAM 169-94); body length 10·1 mm, 21 trunk segments. Same collection data (WAM 168-93), dissected; body length 14·2 mm, 24 trunk segments. Same collection data, except 7.viii.1993 (WAM 160-93) body length 14·5 mm, 24 trunk segments.

Other material examined.   Same collection data as holotype except 25.v.1995 (USNM 274190); body length 10·3 mm, 24 trunk segments.

Diagnosis

Antenna 2 exopod with about 54 long plumose setae along margin. Maxilla 1 segment 2 platelike endite with 8 spines on distal margin; segment 3 medial conical endite with 1 broad-based, stout apical seta and 5 robust anterior setae; distal half of setae serrate; segment 7 a single fang over 2× length of segment 6. Swimming appendages with spinose-like setae on lateral margin of segments 1 and 2 of endopod.

Description

Body elongate, slender (Figs 1–2). Maximum length of material examined 14·5 mm. Maximum number of postcephalic segments 24. Cephalon small, about 1/8 total body length, covered by dorsal subrectangular shield, tapered anteriorly. Trunk segments bear laterally directed swimming appendages. Trunk segments with rectangular tergites with prominent lateral pleura; segment 1 tergite reduced, half width of segment 2. Posterior margin of sternite has narrow rectangular bar on trunk segments 1–13, 14th (genital segment) with triangular, medial cuticular flap.

Frontal filaments (Fig. 4) long, slender, extending to anterior margin of cephalon, bearing slender medial process. Antenna 1 (Fig. 5) biramous, about 3 times length of cephalic shield. Protopod 2-segmented, proximal segment bulbous, with rows of densely packed fine, long esthetascs; distal segment bifurcate, bearing rami. Dorsal ramus 13-segmented; segments 1 and 2 short; joint between segments 2 and 3 oblique, other segments long, slender. Ventral ramus with 10–12 segments, proximal segments lacking distinct articulation. Both rami bear fine setules on surface and clusters of multi-tipped esthetascs on medial and distal margins of segments.

Figs 1–2. *Lasionectes exleyi*, sp. nov. (BES 4268), photographed in life; body length 11·8 mm. *1*, Ventral surface showing limb arrangement resulting from metachronal movement of the paddles; *2*, ventrolateral view showing the dorsal-side-down position adopted during swimming. Photos: Douglas Elford, Western Australian Museum.

Figs 3–4. *Lasionectes exleyi*, sp. nov. *3*, Mouth area (188×); E, endite 2 of maxilla 1; L, labrum; M1, maxilla 1; M2, maxilla 2; *4*, head, posteroventral view (56×). F, frontal filaments; Mp, maxilliped.

Antenna 2 (Fig. 6) paddle-like, biramous, with 2-segmented protopod; proximal segment with 3 medial setae; distal segment bears lateral exopod and 14 medial setae. Endopod 3-segmented; segment 1 with 10 setae, segment 2 with 14 setae, segment 3 with about 25 setae along margin, distalmost setae in double row. Exopod large, oval, with about 54 long setae on margin. All setae plumose.

Labrum (Fig. 12) prominent, lobular, with dense, short setae on posterior margin (Fig. 3). Mandibles well developed; left mandible (Fig. 7) with 4-cusped incisor process and crescent-shaped lacinia mobilis; right (Fig. 8) with 3-cusped incisor process and 3-cusped lacinia mobilis. Molar processes broad, with densely packed setae. Body of mandibles lateral; working processes insert ventromedially under paragnath. Paragnath paired, flattened lobe with dense setae along medial margin. Mouth area highly setose (Fig. 3).
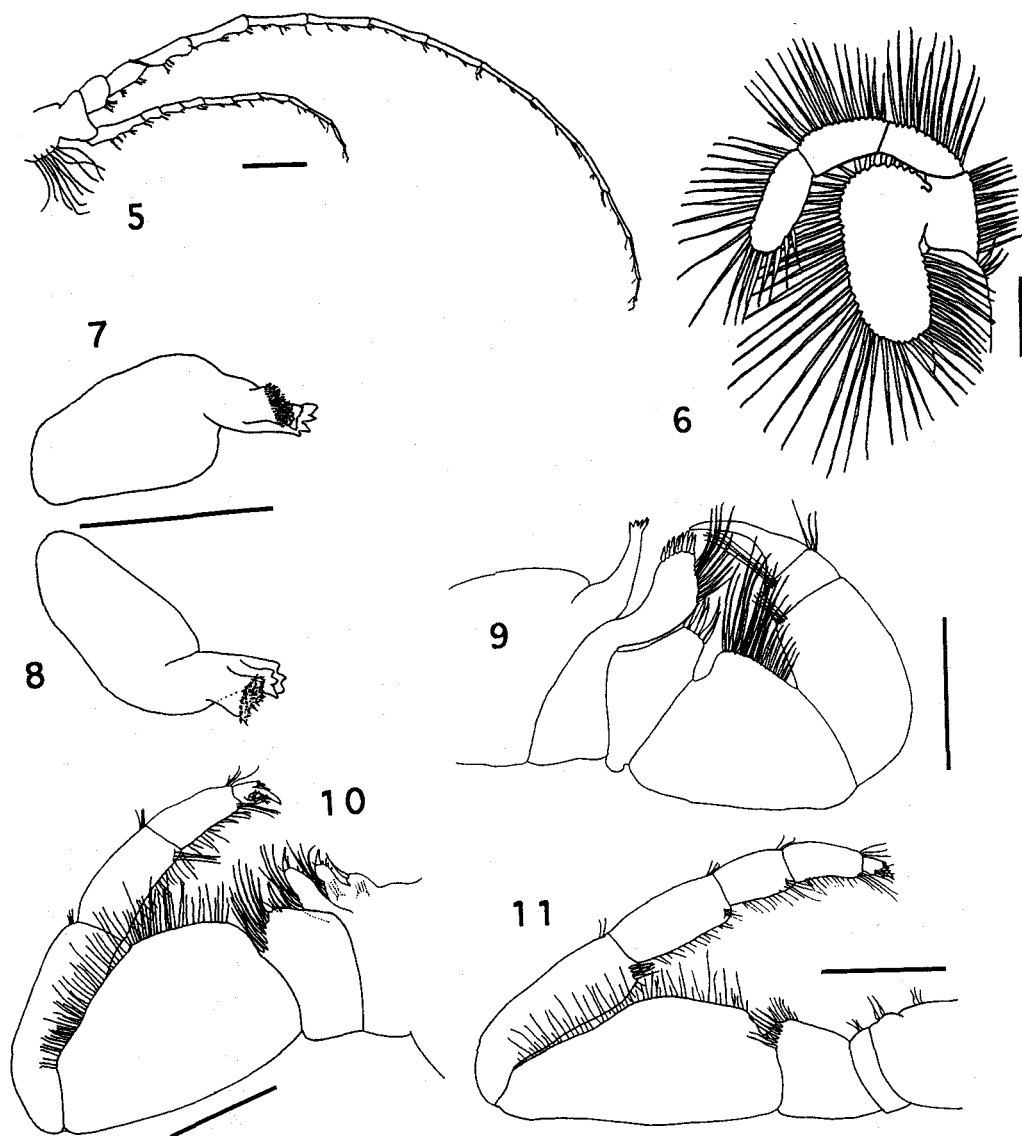
Figs 5–11. *Lasionectes exleyi*, sp. nov. *5*, Antenna 1; *6*, antenna 2; *7*, left mandible; *8*, right mandible; *9*, maxilla 1; *10*, maxilla 2; *11*, maxilliped. Scale bar for *5*, *7*, *8* = 0·5 mm; *6* = 0·2 mm; *9–11* = 0·4 mm.

First maxilla (Fig. 9) 7-segmented, uniramous, prehensile. Segment 1 with long, slender medial endite; distal margin terminates in spine complex with 1 robust anterior spine, 6 slightly smaller spines, 1 robust, serrate, posterior spine. Segment 2 with platelike medial endite (Fig. 4); posterior margin bearing 8 moderately long spines, medialmost spine serrate, and row of subterminal setules; about 12 setae on anterior margin; endite lies over paragnaths. Segment 3 short, with conical medial endite bearing 1 broad-based, serrated, apical seta, 5 moderately long, robust anterior setae serrated on distal half, and about 5 long, slender posterior setae. Segment 4 robust, expanded medially as flattened endite, with anterior and posterior rows of setae, about 10 long, robust anterior setae, posterior row shorter than anterior, with about 8 slender setae. Segment 5 robust, with clusters of anterior and posterior setae on distomedial margin. Segment 6 very short, with clusters of anterior and posterior setae on distomedial and distolateral margins; medial setae long. Segment 7 with long, slender fanglike terminal claw, slightly over 2 times length of segment 6; cluster of long setae medial to fang.
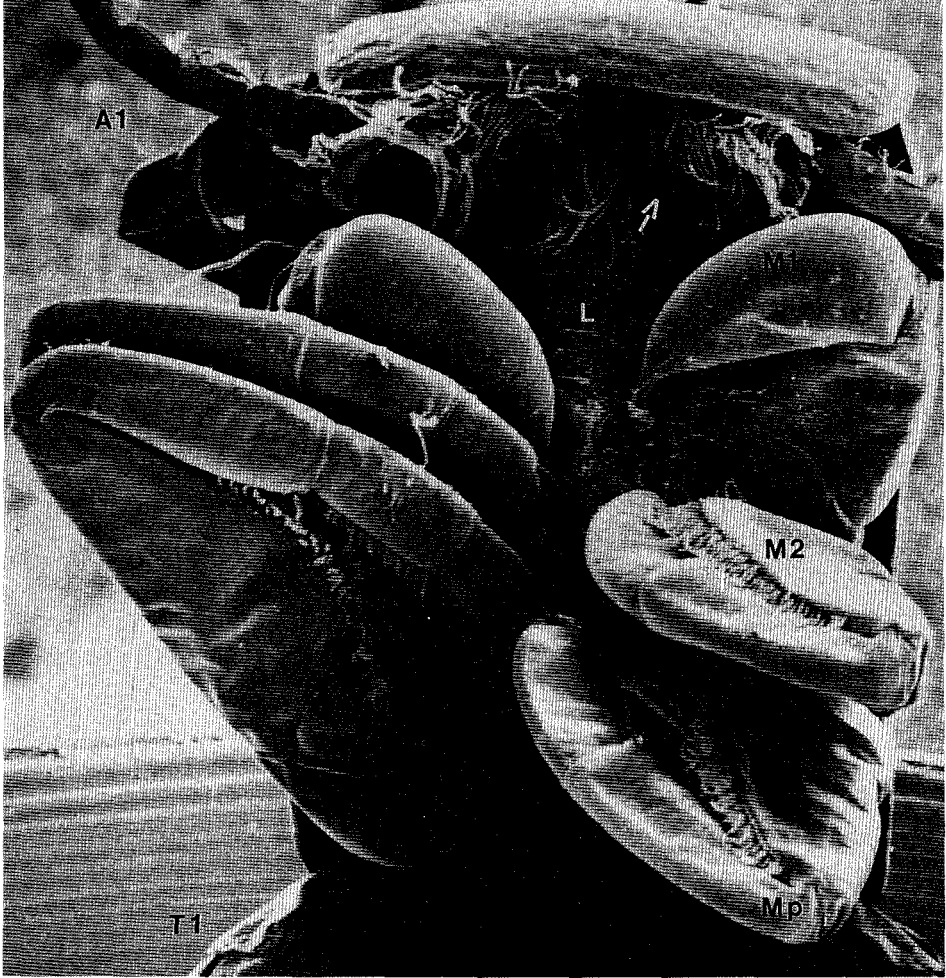
Fig. 12. *Lasionectes exleyi*, sp. nov. Head, ventral view (36×). A1, antenna 1; L, labrum; M1, maxilla 1; M2, maxilla 2; Mp, maxilliped; T1, swimming appendage 1. The white arrow indicates the position of antenna 2, beneath esthetascs of antenna 1.

Second maxilla (Fig. 10) 7-segmented, robust, uniramous with 4 segments beyond point of flexure. Segment 1 bearing 2 small posterior endites with clusters of 3–5 setae and 3 digitiform anteromedial endites that increase in size, each bearing apical curved spine, several subterminal setae, several long setae on anterior margin and several setae at base; oblique distal posterior articulation. Segment 2 short, conical, bearing 1 stout, apical spine and rows of at least 10 long anterior setae and cluster of about 15 smaller posterior setae. Segment 3 robust, long, rounded medially, with anterior and posterior ridges bearing dense rows of fairly uniform-sized setae along margin; anterior setae more dense, slightly longer than posterior; all setae finely plumose (Fig. 14). Point of flexure between segments 3 and 4. Segments 4, 5 and 6 consecutively shorter than segment 3, bearing rows of anterior and posterior medial uniform dense setae and clusters of several long setae on distomedial and distolateral anterior and posterior margins. Segment 7 short, terminating in sclerotised claw complex consisting of 1 long spine flanked by 2 shorter stout spines and posterior arc of 5–6 less robust spines; thumblike pad bearing many long, simple setae opposing claw complex.

Maxilliped (Figs 4, 11) 9-segmented, similar to maxilla 2, with 5 segments beyond point of flexure. Proximal 2 segments short, with weakly developed anterior and posterior endites
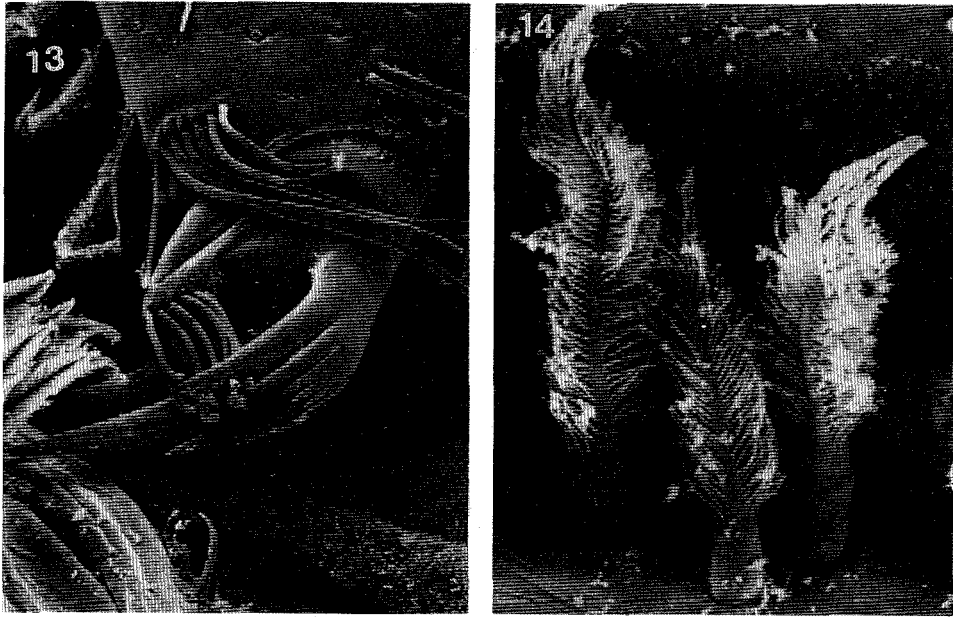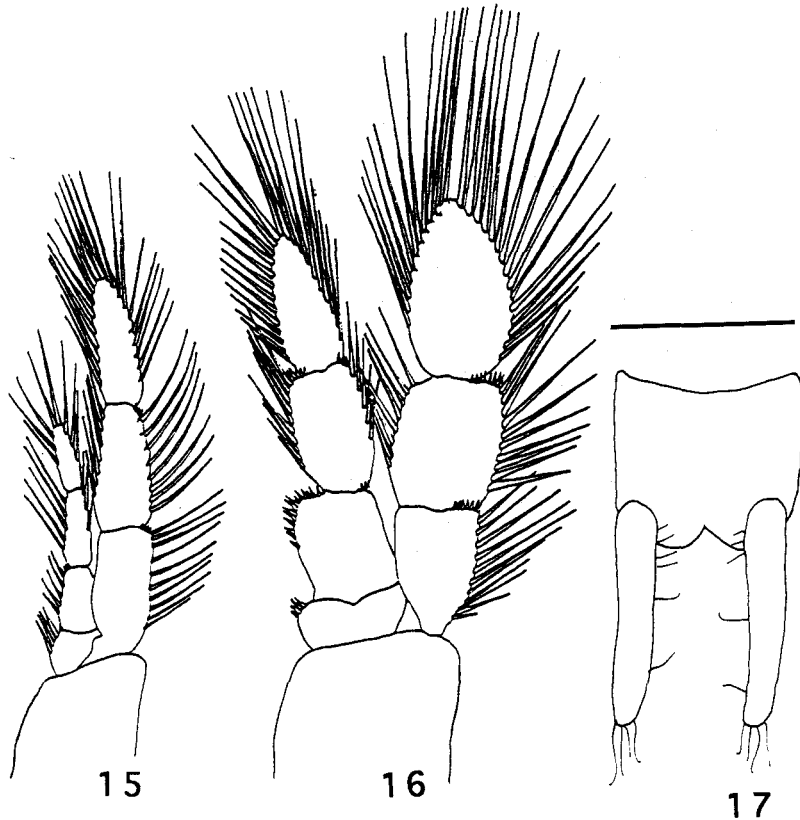
Figs 13–14. *Lasionectes exleyi*, sp. nov. *13*, Maxilliped, terminal claw complex, posterior view (528×); *14*, plumose setae along medial margins of maxilla 2 and maxilliped (1430×).

bearing 3–8 short setae. Articulation between segments 2 and 3 oblique posteriorly. Segment 3 short, with slightly expanded medial endite bearing rows of many anterior and posterior setae. Segment 4 long, robust, bearing ridges of anterior and posterior setae along medial margin, anterior slightly longer. Segments 5–8 progressively shorter, narrower, with anterior and posterior rows of dense setae along medial margin and clusters of anterior and posterior distomedial and distolateral setae. Segment 9 terminating in claw complex (Fig. 13) as in maxilla 2.

Trunk appendages (Figs 15–16) natatory, biramous, setose, paddle-like; protopod large. Endopod 4-segmented; segment 1 reduced, rectangular, segments 2 and 3 subrectangular, segment 4 oval. Exopod 3-segmented; segments 1 and 2 subrectangular to nearly square, segment 3 oval. Setation varies, with 3 types of setae: small comb setae, short plumose spinelike setae, and moderate to long plumose setae. In trunk appendage 10 (Fig. 15) endopod segment 1 bears 4 lateral spinelike setae; segment 2 with 5 distolateral comb setae, 3 distomedial comb setae, 1 medial seta, 11 lateral spinelike setae; segment 3 bears 10 lateral setae, 5 distolateral comb setae, and 3 distomedial comb setae, 6 medial setae; segment 4 with 24 long setae along entire margin. Exopod segment 1 with 11 lateral setae and 7 distolateral comb setae; segment 2 with 10 lateral setae, 8 distolateral comb setae; segment 3 with 30 long setae along margin. All setae plumose. Trunk appendage 1 (Fig. 16) with narrow segments, less setose. Protopod of 7th trunk appendage bears circular female gonopore; protopod of 14th appendage bears male gonopore on medial pedestal lying dorsal to triangular cuticular flap. Trunk appendages become smaller and less setose posteriorly. Anal segment (Fig. 17) about as long as wide; caudal rami about 1.5 times length of anal segment.

Etymology

The species is named to honour the memory of Sheck Exley, a pioneer cave diver who educated and inspired many.

Figs 15–17. *Lasionectes exleyi*, sp. nov. *15*, trunk appendage 10; *16*, trunk appendage 1; *17*, anal segment. Scale bar = 0·5 mm.

Comparisons

Lasionectes exleyi appears to be a much smaller species than *L. entrichoma*, the only other member of the genus. The maximum length of the specimens collected is 14·5 mm and the maximum number of post-cephalic trunk segments is 24. The largest individual of *L. entrichoma* measures 31·5 mm and has 32 trunk segments. Other differences include a more setose exopod of antenna 2 in *L. exleyi*, with 54 setae as compared with 35–40 in *L. entrichoma*. Maxilla 1, segment 2 bears 6 spines on the margins in *L. entrichoma*, 8 in *L. exleyi*. Segment 3 of maxilla 1 in *L. exleyi* bears 1 stout medial seta, segment 4 lacks a stout medial seta; *L. entrichoma* bears 2 robust setae on segment 3 and 1 short, spinelike medial seta on segment 4. The maxilla 1 terminal fang of *L. exleyi* is at least 2 times the length of segment 6 while in *L. entrichoma* the fang is less than 2 times the length. The maxilla 2 and maxilliped of both species are nearly identical. Segments 1 and 2 of the endopod on swimming appendages of *L. exleyi* bear many short, plumose setae on the lateral margins, giving the appearance of spines; the same segments in *L. entrichoma* bear only 1–2 tiny spinelike setae. The sternal bar of trunk segment 14 in *L. exleyi* is a cuticular medial triangular flap, while in *L. entrichoma* the lateral sides of the sternal bar are developed as triangular extensions. The caudal rami of *L. exleyi* are longer than *L. entrichoma*, which are equal to or slightly shorter than the length of the anal segment.

Habitat

Lasionectes exleyi was collected from a single site, 6C-28, on the Cape Range peninsula, Western Australia (Figs 18–19). The cave is registered in the Australian Karst Index as Bundera Sinkhole. C-28 is a water-filled cave located 1.7 km inland from the Indian Ocean. The cave has a single entrance from a flooded sinkhole and is inclined at about 30° to the horizontal. The cave was penetrated by cave divers to a depth of 31 m. Remipedes were collected at depths of 20–30·5 m, beneath a density interface.

The physico-chemical conditions in the cave are shown in Figs 20–23 and Table 1. The marked thermo-haloclines shown have been present in all three sampling years but the depth at which they occur varies between years as does the physical appearance of the water. In 1993 distinct thermoclines were noted at depths of 8 m and 13 m. Whispy suspensions, probably bacterial colonies, were seen in the water column at a depth of about 14 m, just below the cave entrance restriction. In 1994 the suspensions were barely visible and they were not present in 1995 when a distinct tannic layer occurred at a depth of 22 m. Strong H_2S is encountered in the vicinity of the density interface.

Lasionectes exleyi occurs in a habitat typical of remipedes (see Yager 1987a, 1994; Yager *et al.* 1994), known only from anchialine caves. These submerged caves are mainly found in coastal karst. They have a surface opening inland and subsurface connections with sea water. This marine influence typically consists of an hypoxic layer of sea water (*c.* 33–36 mg L^{-1}) beneath one or more layers of limnetic to polyhaline water (Yager *et al.* 1994). Remipedes have always been collected beneath a density interface (pycnocline) in hypoxic water. For example, remipedes from the Bahamas were reported in water with oxygen measured at 0·10 mg L^{-1} at a depth of 21 m (Yager 1994). The oxygen in Cuban cave water measured 0·22 mg L^{-1} at a depth of 22 m (Yager *et al.* 1994) and 0·14 mg L^{-1} at 16 m (Yager 1994). Remipedes have also been reported living beneath a layer of hydrogen sulphide (Yager 1994). Filamentous sulphur bacteria of the *Beggiatoa–Thiothrix* group have been reported as common in anchialine caves and may play a role in primary production (Yager 1991b).

From the comprehensive water analysis conducted in 1993 in the type location for *L. exleyi*, the deep cave water shows a number of major departures from the concentration found in sea water (Table 1). The cave water is not full sea water (the highest recorded value for any sample is about 28 g L^{-1} total filterable solids from a depth of 24 m. The concentrations of some components of the cave water clearly do not result from simple mixing of sea water and rain water (Table 1). Concentration of potassium is only 57% that of sea water while that of magnesium is 571% greater. The nutrient concentrations differ widely from those found in sea water: free reactive phosphorus (178%), nitrite (133%), nitrate (184%) and ammonia (467%) are all greatly elevated in the cave waters. This elevation is clearly reflected in the samples from the photic zone (samples from 0·2 and 6 m), which appears to be eutrophic.

These nutrient values fall within the range reported for anchialine caves on Bermuda considered to be grossly polluted (Iliffe *et al.* 1984a). Whereas on Bermuda nutrient enrichment is believed to result from seepage from cesspits and fertiliser application, C-28 is a remote site, far from habitation and not farmed, so the origin of this nutrient enrichment is unclear. It may result from feral goats utilising the pool for water. The conservation implications to the only known remipede habitat in the Southern Hemisphere are serious owing to the unique sensitivity of cave environments that results from slow water turnover and lack of photosynthesis. The site lies outside conservation reserves.

Associated Fauna

C-28 has been sparsely sampled and more species are expected. Several taxa in addition to the remipedes occur below the pycnocline in the cave: *Danielopolina*, sp. nov. (Ostracoda: Halocyprida:Thaumatocyprididae), *Liagoceradocus*, sp. nov. (Crustacea:Hadziidae, J. H. Bradbury, personal communication 1995), *Stygiocaris stylifera* Holthuis (Malacostraca: Decapoda:Natantia:Atyidae) and *Milyeringa veritas* Whitely (Perciformes:Eleotridae).

As most taxa were taken in a diver-hauled plankton net the exact location of the remaining biota is largely unknown, but the following probably occur only above the pycnocline: the algae *Rhizoclonium* ?*tortuosum* (Dillw.) Kuetz. (Chlorophyta:Cladophoraceae) and *Lamprothamnium*
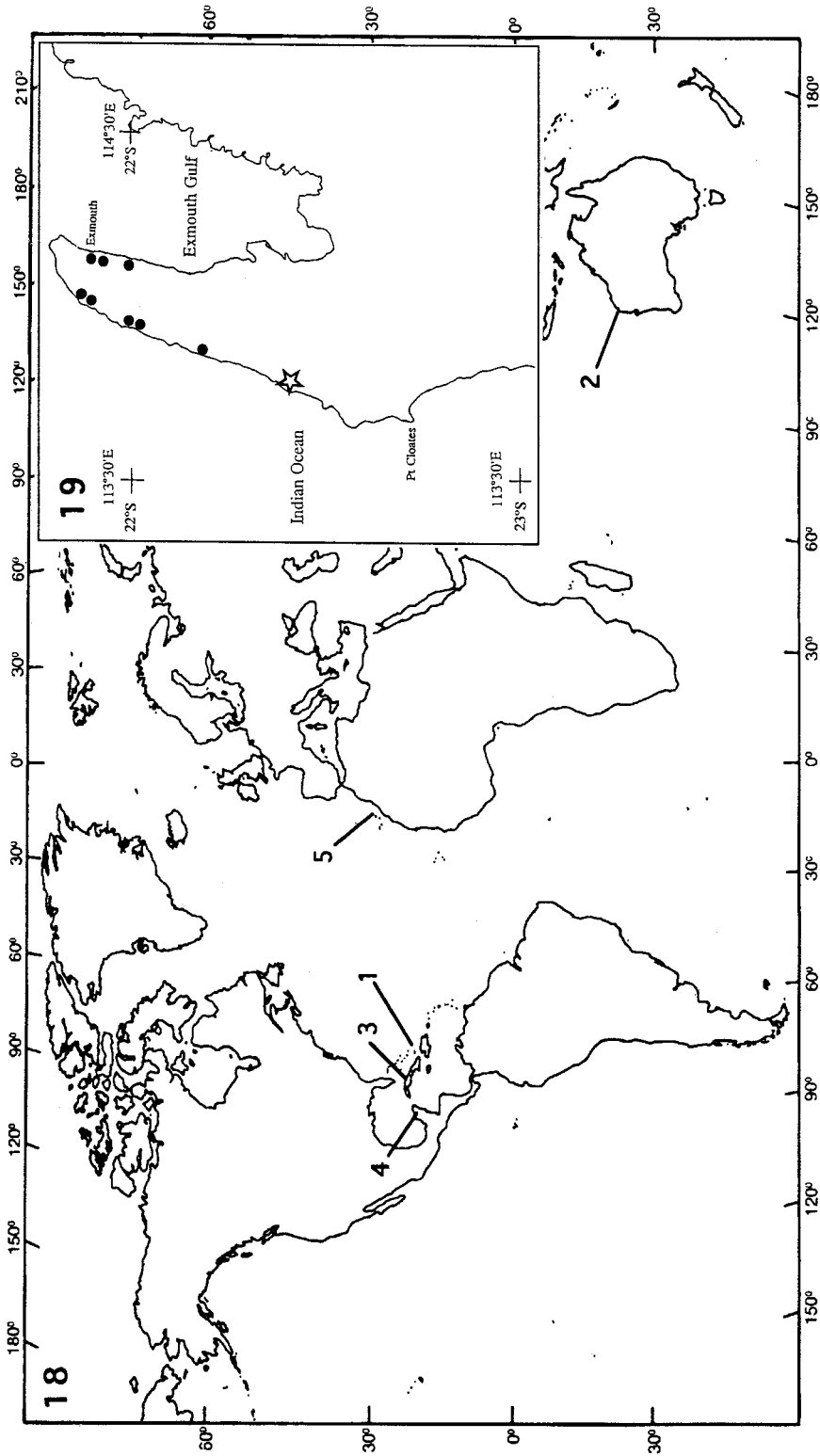
Figs 18–19. *18,* Distribution of extant remipedes: *1, Lasionectes entrichoma; 2, L. exleyi*, sp. nov.; *3, Speleonectes gironensis; 4, S. tulumensis; 5, S. ondinae.* The remaining species occur on the Bahamas Bank. *19,* Location of the collection site (star) of *L. exleyi,* sp. nov., on the Cape Range peninsula, north-western Australia. The distribution of thermosbaenaceans (as *Halosbaena tulki*) is also shown as they are indicative of remipede habitat (Yager 1994); *H. tulki* is also found on Barrow I. on the North West Shelf, 160 km to the north-east.
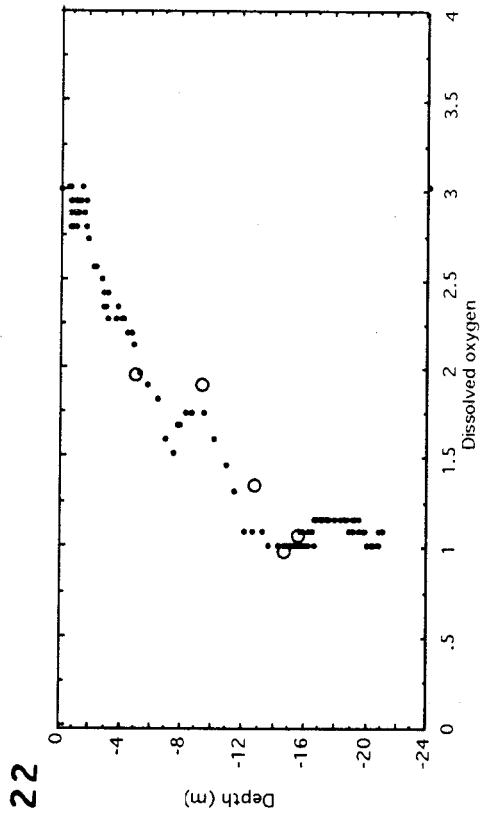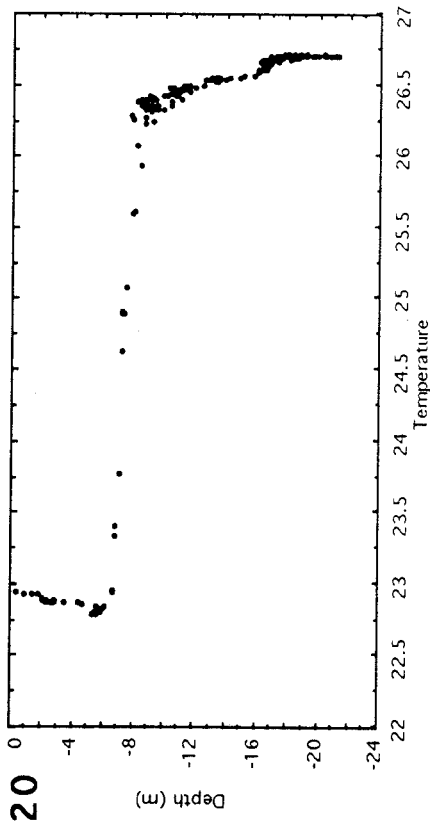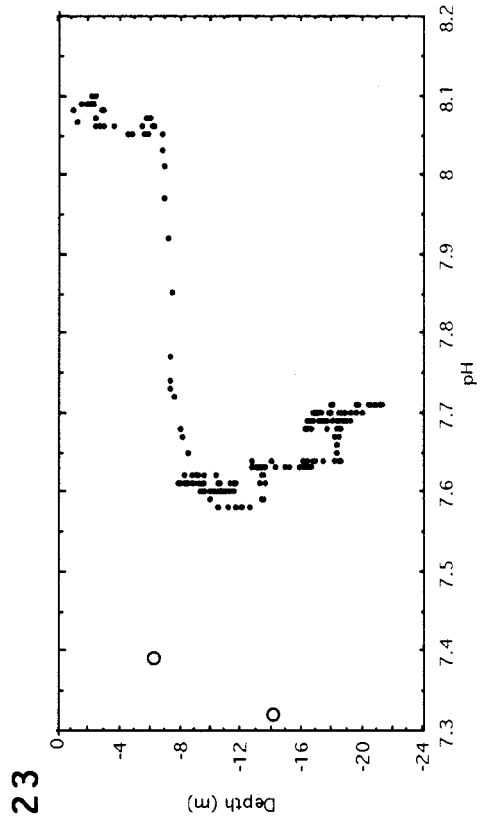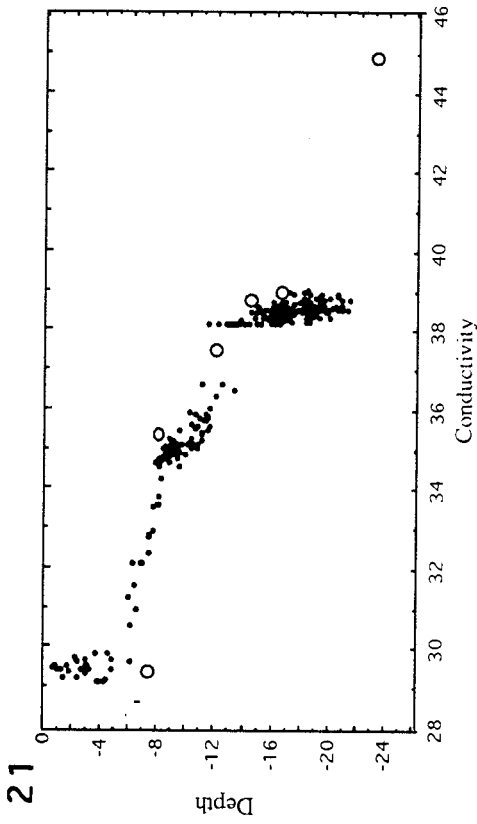
Figs 20–23. Physico-chemical profiles through the upper 22 m of water in C-28 in May 1995. *20*, Temperature (°C); *21*, conductivity (mS cm^{-1}); *22*, dissolved oxygen (mg L^{-1}); *23*, hydrogen ion concentration (pH). Solid points denote depth profiler data. Open circles denote independent samples collected the same day except for pH where they denote laboratory determinations from 1993.

Table 1. **Comparison of values from a comprehensive analysis of sea water from above and below the pycnocline in cave C-28**

Rain water (Exmouth) and inshore sea water (Learmonth) values are given for comparison. * denotes major departures from seawater concentrations. DL is the detection limit. All unit at in mg L^{-1} unless specified otherwise. Data from W. F. Humphreys, unpublished report 1994

Parameter	Sea	C-28 0.2 m	C-28 6 m	C-28 14 m	Rain
pH	8·1	8·08	7·44	7·27	6·47
Turbidity	1·6	1·7	0·7	1·2	1·2
Colour	1	2	2	0	21
Conductivity at 25°C	4950	3000	3050	4700	1
Total filterable solids-CO_2	36500	20000	20000	26500	15
Fe-unfiltered (DL 0·05)	0	0·14	0	0	0
Mn-unfiltered (DL 0·04)	0	0	0	0	0
Al	0·092	0·079	0·038	0·059	0·015
Na	12000	6090	6010	7780	0·5
K	540	210	200	*310	0·4
Ca	420	290	280	390	0·4
Mg	140	720	710	*940	0·2
Hardness (as $CaCO_3$)	1630	3680	3620	4840	2
Alkalinity	2·1	4·4	4·4	2·5	0·06
Cl	20250	10750	11150	15050	0
SO_4	3000	1500	1450	1950	1
Silica as SiO_2	0	16	12	5·8	0
Filterable organic carbon	12·5	14·5	17	11·5	5·8
Total phosphorus	0·028	0·023	0·02	0·019	0·045
Free reactive phosphorus	0·008	0·012	0·014	*0·019	0·011
Total Kjeldahl nitrogen	0·054	0·36	0·175	0·041	0·09
Nitrite as nitrogen	0·003	0·01	0·003	*0·007	0·004
Nitrate as nitrogen	0·019	1·65	0·015	*0·054	0·028
Ammonia as nitrogen	0·003	0·355	0·024	*0·017	0·02

papulosum (Wallr.) J. Gr. (Charophyta:Characeae), and the invertebrates ?Spionidae (Annelida:Polychaeta), *Halicyclops*, sp. nov. (Copepoda:Cyclopidae), ostracods, *Iravadia* sp., (Mollusca:Iravadiidae), girrids (Hemiptera) and *Kiefferulus intertinctus* Skuse (Diptera: Chironomidae).

The stygofauna of the Cape Range peninsula generally includes, in addition to *Stygiocaris stylifera* and *Milyeringa veritas*, the sympatric occurrence of a number of other taxa with Tethyan disjunct distributions including the genera *Haptolana* (Isopoda:Cirolanidae), *Halosbaena* (Thermosbaenacea), *Ophisternon* (Pisces:Synbranchiformes) and gammarid amphipods (Humphreys 1993*a*, 1993*b*; Knott 1993; Barnard and Williams 1995).

Biogeography

Remipedes are represented by 11 species belonging to six genera in two families (Table 2), the distributions of which are given in Figs 18–19. The discovery of *L. exleyi* is the first record of a remipede from the Indian Ocean and the Southern Hemisphere. No epigeal or open ocean species are known and only one other species (*Speleonectes tulumensis*) occurs on a continental landmass. Except for *L. exleyi*, sp. nov., only the genus *Speleonectes* is found off the Bahamas Bank (Table 2).

The hypogean restriction of remipedes suggests long isolation in cave habitats. Larval stages of remipedes have not been found but tiny juveniles with at least 14 trunk segments have been reported (Yager 1991*a*). It is not likely, therefore, that they disperse as larvae but instead have direct development. The environmental requirements for remipedes appear to be specific and this may also limit their dispersal.

Table 2.   List of known remipede species and type localities
Species occurring off the Bahamas Bank are marked with an asterisk

Type locality	Species	Family
Grand Bahama Island, Bahamas	*Speleonectes lucayensis* Yager, 1981	Speleonectidae
	Speleonectes benjamini Yager, 1987	Speleonectidae
	Godzilliognomus frondosus Yager, 1989	Godzilliidae
	Pleomothra apletocheles Yager, 1989	Godzilliidae
Abaco Island, Bahamas	*Cryptocorynetes haptodiscus* Yager, 1987	Speleonectidae
Providenciales, The Turks and Caicos	*Lasionectes entrichoma* Yager & Schram, 1986	Speleonectidae
North Caicos Island, The Turks and Caicos	*Godzillius robustus* Schram, Yager & Emerson, 1986	Godzilliidae
Quintana Roo, Mexico	**Speleonectes tulumensis* Yager, 1987	Speleonectidae
Lanzarote, Canary Islands	**Speleonectes ondinae* (Garcia-Valdecasas, 1984)	Speleonectidae
Matanzas Province, Cuba	**Speleonectes gironensis* Yager, 1994	Speleonectidae
Cape Range peninsula, Western Australia	**Lasionectes exleyi*, sp. nov.	Speleonectidae

The only other member of the genus, *L. entrichoma*, is known from three caves in the Turks and Caicos Islands in the south-western North Atlantic Ocean. The two disjunct species share many features, indicative of morphological conservation for a very long period of time, a characteristic also of the other genera in common between north-west Australia and the Caribbean: *Haptolana* (Bruce and Humphreys 1993), *Halosbaena* (Poore and Humphreys 1992) and *Danielopolina* (Baltanas and Danielopol 1995). This is also characteristic of many crustacean taxa thought to be ancient and widely separated relicts (Manning *et al.* 1986).

The origin of anchialine cave fauna is most likely to be from the continental margins (Stock 1986*a*, 1986*b*; Danielopol 1990) rather than, as proposed by Iliffe *et al.* (1984*b*), from the deep sea (Baltanas and Danielopol 1995). While inland populations of this Tethyan relict stygofauna have been explained using models involving isolation of fauna due to marine regression (Stock 1977, 1980), the wider distribution is explained by the Two-step Model (Boutin and Coineau 1990) which incorporates active marine dispersal of the genera followed by vicariance resulting from the movement of tectonic plates.

Recent investigations of the Cape Range cave fauna have revealed several crustacean genera that share disjunct distributions with *Lasionectes*. For example, the isopod *Haptolana* is found in Cuba, Somalia and Western Australia (Bruce and Humphreys 1993). The thermosbaenacean *Halosbaena* is known from north-west Australia, the Caribbean, and a marine lava cave in the Canary Islands (Poore and Humphreys 1992), also home to the remipede *Speleonectes* and the hadziid amphipod *Liagoceradocus* (Stock and Iliffe 1991).

These populations are considered to be relicts, that is, separated from a parent population by some vicariant event. Most Tethyan theories assume movement of ancestral marine fauna through the Tethys Seaway that separated the continents of Gondwana and Laurasia and which persisted from the Triassic until the late Eocene (200–40 million years ago) (Smith and Briden 1977).

The distribution of remipedes and their associated fauna can be explained by cave colonisation along the shores of Tethys during the Triassic and Jurassic 225–160 million years ago (Cals and Boutin 1985) and subsequent dispersal by the break-up of Pangea in the Mesozoic (Wilkens *et al.* 1986) through sea-floor spreading and continental drift (Stock and Longley 1981; Iliffe *et al.* 1984*b*; Hart *et al.* 1985; Wägele 1985). During the early Cretaceous the plate that is now Western Australia formed the eastern shore of Greater Tethys (Howarth 1981).

The age of the Cape Range (Late Oligocene to Middle Miocene) does not set a temporal limit to any element of the stygofauna. The fauna would have been widely dispersed across the North West Shelf at times of lower sea level, a shelf that abuts onto the Precambrian Pilbara Craton (Humphreys 1993*a*, 1993*b*). Consequently, the fauna could have spread widely through the crevicular habitat of the shelf at times of lower sea level and perhaps currently (some of the

stygofaunal species from the Cape Range peninsula occur on Barrow Island on the North West Shelf, 160 km to the north-east (Humphreys 1993a, 1993b).

Cladistic analysis of the nine known species of *Danielopolina* shows that the Australian species is the sister-group of the remaining eight species, which also refutes (Baltanas and Danielopol 1995) the supposed deep-sea ancestry of the genus. Similarly, *Halosbaena tulki* is the sister-group of the other two species in the genus (*H. fortunata* Bowman & Iliffe, 1986 from the Canary Islands, and *H. acanthura* Stock, 1976 from the Caribbean), all known from anchialine caves (Wagner 1994; H. P. Wagner, personal communication). Together these analyses indicate that the Australian populations underwent vicariance before those on either side of the Atlantic, which would support the proposed sequence in the break-up of Pangea as modelled by Howarth (1981). Eastern and western Gondwana had almost separated by the Upper Jurassic, 145 million years ago (Howarth 1981, fig. 13.9), were well separated by the Lower Cretaceous about 125 million years ago (Howarth 1981, fig. 13.12), and by the Upper Cretaceous about 80 million years ago were not even joined by epicontinental seas to landmasses other than Antarctica (Howarth 1981, fig. 13.15).

On either side of the Atlantic remipedes co-occur with other relictual crustacea (Newman 1991; Schram 1986) and their association with thermosbaenaceans and cirolanid isopods led specifically to the search for remipedes in Australia. As only a single deep anchialine cave has been examined, the prospects are good of finding additional genera currently known only from either side of the Atlantic Ocean.

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