Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages

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Arid northwestern Australia contains one of the world's more diverse subterranean faunas including many relict obligate groundwater (stygo-) faunas in karst and calcrete aquifers, principally crustaceans, with affinities pertinent to Tethys, and to Pangaea and its derived landmasses. Higher order taxonomic groups are present that are elsewhere unknown in Australia (order Spelaeogriphacea) or in the southern hemisphere (class Remipedia, order Thermosbaenacea), as well as a number of genera ancestral to the main Australian diversification. Many are found in aquifers that are the principal water supply in this arid region and are vulnerable to pollution, water abstraction and dewatering operations.

INTRODUCTION

Northwestern Australia contains one of the world's more diverse subterranean faunas including a series of relict stygofaunas — obligate inhabitants of subterranean waters — principally Crustacea, with affinities pertinent to the biogeography of Australia, Eastern Gondwana, Gondwana, Pangaea and Tethys (Holthuis 1960; Poore and Humphreys 1992, 1998; Wilson and Ponder 1992; Bartsch 1993; Humphreys 1993a,b,c,d, 1994, 1995, in press a,b; Bruce and Humphreys 1993; Harvey *et al.* 1993; Aubrecht and Kozur 1995; Baltanas and Danielopol 1995; Yager and Humphreys 1996; Bradbury and Williams 1996a,b, 1997a,b; Harvey 1998; Wilson and Keable, in press).

In this paper I discuss biological diversity in the subterranean realm, in particular the presence of rich relictual subterranean faunas being found in northwestern Australia, especially in aquatic systems. The subterranean system is the largest terrestrial biome (Gold 1992; Juberthie, in press), but is difficult to explore as access depends on scarce natural and artificial holes. It contains a specialized macrofauna restricted to the air-filled and water-filled voids within the subterranean realm, and which are referred to respectively as troglofauna comprising troglobites, and stygofauna comprising stygobites — the term troglobites is sometimes used generally to encompass all hypogean fauna. Such faunas can be highly diverse and are typically locally endemic (e.g., papers in Humphreys 1993a,b, in press b).

Subterranean fauna may occur in any subterranean void ranging from the interstices of alluvial deposits, particularly gravels, and in boulder deposits such as screes, but especially in the crevices, caves, sinkholes and conduits characteristic of karstlands that develop on soluble rock terrains, principally limestones. Globally, many biologically interesting karsts are associated with mountains formed during the Tertiary — Cape Range, which lies on the western shoulder of Australia, is the only such limestone karst in Australia.

Arid zones (Peck 1978; Howarth 1980), the tropics (Vandel 1965; Barr 1968; Mitchell 1970) and Australia (Moore 1964; Hamilton-Smith 1967; Barr 1973) have all been considered to have poor prospects for supporting specialized subterranean faunas. Hence the arid north-west of Australia should be peripheral to debates on the origin and evolution of subterranean faunas in either aquatic or terrestrial habitats. Knowledge of this region, however, has developed substantially in the last decade such that it is now recognized to include one of the world's more diverse and notable subterranean faunal provinces.

Similarly, this far flung province of Tethys (Fig. 1) — the ocean that formed between the continents of Gondwana and Laurasia following the fragmentation of Pangaea during the Triassic (*c.* 200 Ma) and which persisted, in various guises, until the late Eocene (*c.* 40 Ma: Smith and Briden 1977) — might be considered peripheral to understanding the development of the Tethys biota or the origin of its aquatic fauna. Yet a picture is emerging that the region may be pivotal to understanding not only the evolution of Australian fauna, but also to the development of the tethyan fauna.

Anchialine habitats consist of near coastal water bodies of variable salinity, restricted exposure to open air, some subterranean

Pp. 219–27 in *The Other 99%. The Conservation and Biodiversity of Invertebrates* ed by Winston Ponder and Daniel Lunney, 1999. Transactions of the Royal Zoological Society of New South Wales, Mosman 2088.

connection to the sea, and showing noticeable marine as well as terrestrial influences (Stock *et al.* 1986) — they typically occur in volcanic or limestone bedrock. In this paper I consider principally the stygofauna contained in freshwater and anchialine aquifers, mainly in karstic limestones and calcretes — carbonate deposits forming near the water table in arid lands as a result of concentration processes by near-surface evaporation (Jacobson and Arakel 1986) — in three areas of northwestern Australia, namely the Cape Range peninsula/ Barrow Island, Pilbara and Kimberley (Fig. 2).

SEA SALT AND KARST — CAPE RANGE PENINSULA AND BARROW ISLAND

The Cape Range peninsula and Barrow Island karstlands — karst is a soluble rock landscape typified by limestone — include a variety of habitats which together contain at least 66 species of troglobites endemic at the species, generic or family level. These include at least 41 species (31 genera) of troglobites — representing a relictual rainforest fauna with both temperate and tropical affinities and many gondwanan connections (Harvey *et al.* 1993; Humphreys 1993a,b,c,d) and at least 22 species (12 genera) of stygobites including the only two vertebrate stygobites in Australia, two species of blind cave fish (Humphreys 1994, in press a) (Table 1). The exceptional diversity of this region (Bradbury and Williams 1997a,b) contrasts with other coastal karsts in Australia, such as the Eucla Basin (Nullarbor) and the Gambier Sunklands, that are notable for the sparsity of their stygofauna.

This concentration of subterranean fauna probably owes its existence to the close proximity of variably brackish water, freshwater and terrestrial subterranean habitats. Additional to it having been the eastern seaboard of the developing Tethys waterway, the area has been in close proximity to the edge of the tectonically stable Pilbara region — emergent above the sea since the Precambrian — and which, since the Cretaceous (Fig. 1), has been continually juxtaposed to the edge of the continental shelf in a carbonate depositional environment (Hocking *et al.* 1987).

The most notable fauna is that inhabiting the anchialine system of the Cape Range peninsula and Barrow Island (Humphreys

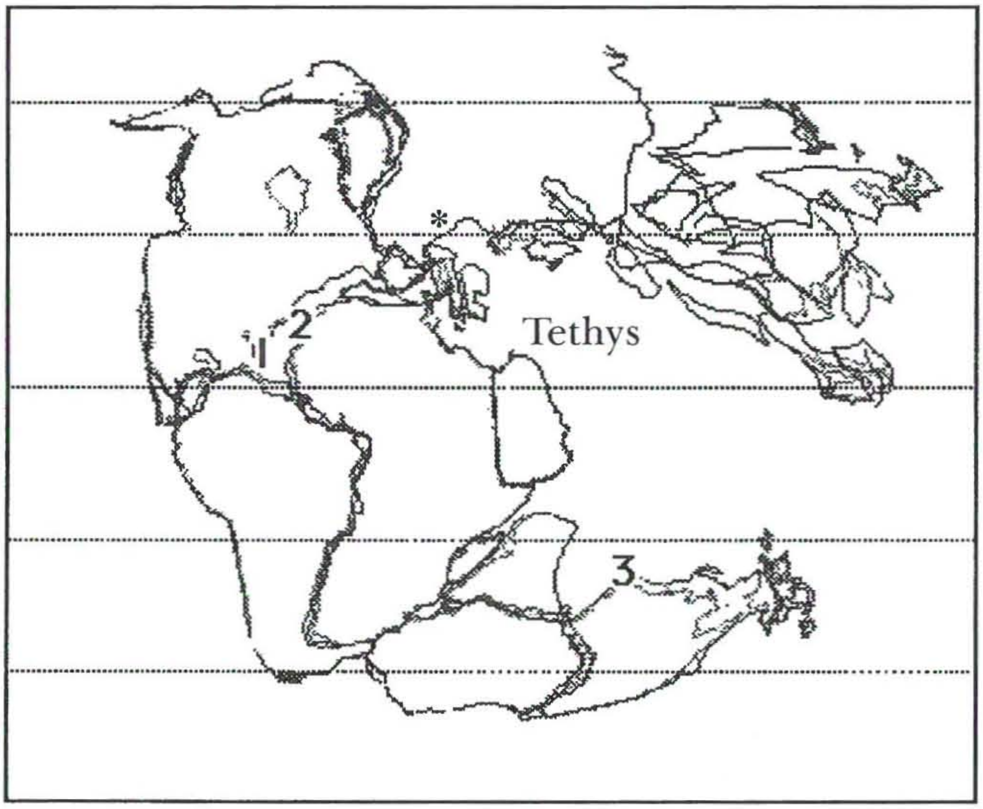

Figure 1. The location of the continental plates in the Jurassic (165 Ma). Points denote 1. Caribbean, 2. Canary Islands, 3. Cape Range peninsula. The plate map was produced using Scotese and Denham (1988) and then simplified. Tethys is developing westwards into the proto-Mediterranean and proto-Atlantic. * denotes location of fossil ancestors of *Danielopolina* — extant on the Cape Range peninsula — from marine caves deposits of Jurassic age in the Czech Republic (Aubrecht and Kozur 1995).

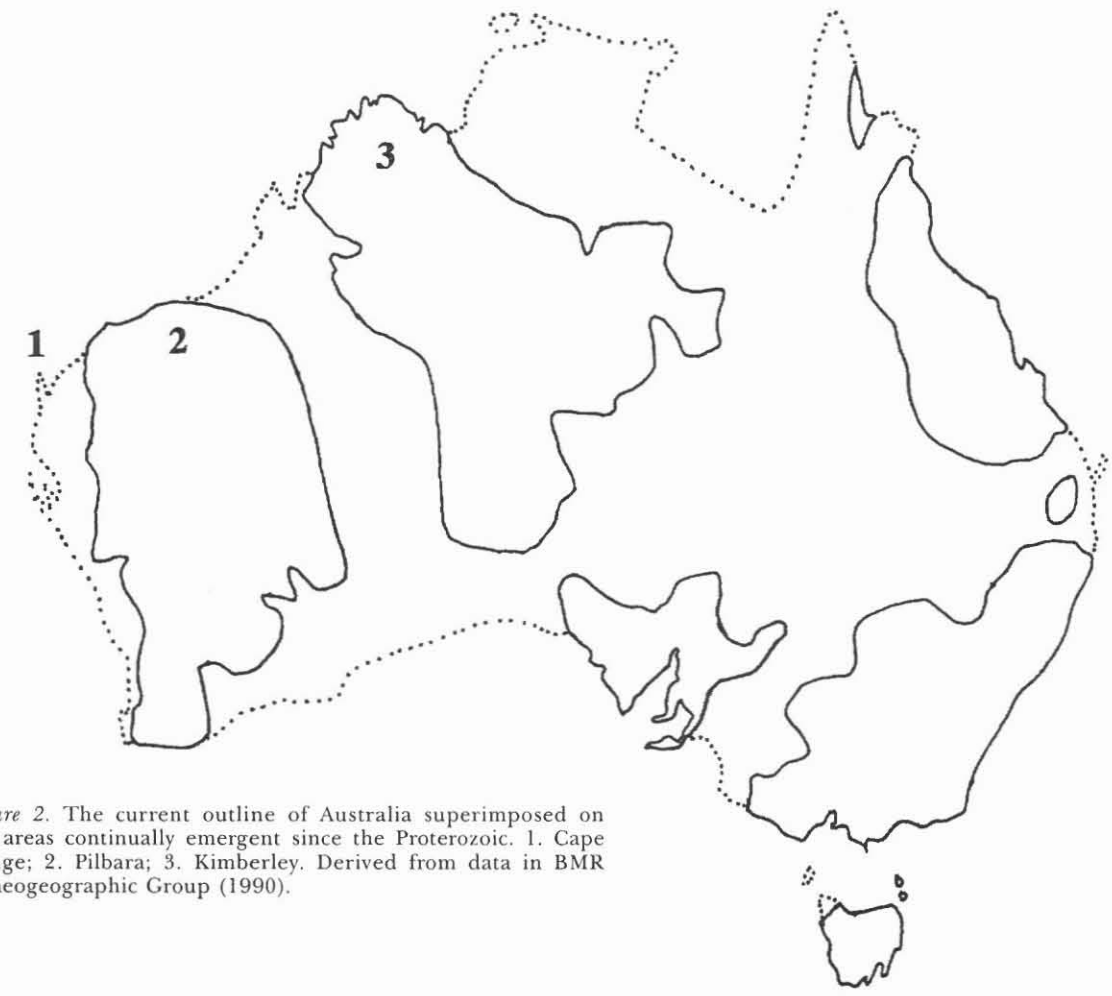

Figure 2. The current outline of Australia superimposed on the areas continually emergent since the Proterozoic. 1. Cape Range; 2. Pilbara; 3. Kimberley. Derived from data in BMR Palaeogeographic Group (1990).

1994), the only such system described from the southern hemisphere. It supports a diverse subterranean fauna, principally of crustaceans, and includes the only members of the class Remipedia and the order Thermosbaenacea known from the southern hemisphere.

This fauna has clear affinities with the Tethys (Poore and Humphreys 1992; Humphreys 1993b; Knott 1993; Yager and Humphreys 1996). It contains species congeneric with those inhabiting caves on either side of the North Atlantic (*Halosbaena,* Canaries and Caribbean), or with otherwise widely disjunct distributions (*Haptolana,* Cuba, Somalia; *Lasionectes,* Turks and Caicos; *Liagoceradocus* (Bradbury and Williams 1996b), Canaries and Pacific; *Danielopolina* (Baltanas and Danielopol 1995), North Atlantic and eastern Pacific). Cladistic analyses of two of these lineages suggest that, in each case, the Australian species is the sister group to the remaining world species (*Halosbaena,* Wagner 1994; H. P. Wagner, pers. comm. 1995; *Danielopolina,* Baltanas and Danielopol 1995). The ancestors of one lineage (*Danielopolina*) were already present in marine caves in the Late Jurassic (Aubrecht and Kozur 1995) at the earliest stages of the opening of the Tethys between the Old and New Worlds (Fig. 1). Hence these distributions are consistent with the hypothesis that the tethyan fauna invaded the developing Tethys from the eastern Tethys with an early invasion of the subterranean habitat and that the current discontinuous distribution resulted from tectonic plate rafting.

CALCRETES AND KARST — PILBARA FRESHWATER

Recent sampling has been undertaken of the northwestern stygofauna which lie on the cratons themselves — parts of the Earth's crust little deformed for a prolonged period — which have been emergent and hence freshwater systems since the Precambrian. Cratons may seem unlikely places to search for ancient relictual stygofauna owing to the lack of many suitable sites for karst development. However, carbonate deposits are widespread throughout the arid zone both as soil and groundwater calcretes (Arakel 1996). They are especially important in the Australian

Table 1. Some stygofauna genera of northwestern Australia — mostly found in the last seven years — with their probable affinities and the authority for the genera or for their affinities. CRP, Cape Range peninsula; BI, Barrow Island; T, Tethys; P, Pangaea; G, Gondwana. • Denotes endemic genus.

Major taxon	Genus	Locality	Affinities	Authority
Tethyan genera with North Atlantic affinities				
Ostracoda: Halocyprida	*Danielopolina*	CRP	T	Baltanas and Danielopol 1995
Remipedia: Nectiopoda	*Lasionectes*	CRP	T	Yager and Humphreys 1996
Isopoda: Cirolanidae	*Haptolana*	CRP/BI	T	Bruce and Humphreys 1993
Amphipoda: Hadziidae	*Liagoceradocus* [2 spp.]	CRP/BI	T	Bradbury and Williams 1996b
Thermosbaenacea	*Halosbaena*	CRP/BI	T	Poore and Humphreys 1992
Copepoda: Cyclopidea	*Halicyclops* n. sp.	Philbara coast	T	De Laurentis, Pesce and Humphreys, in press
Probable freshwater linages				
Syncarida: Bathynellacea: Parrabathynellidae	*Atopobathynella*,	CRP/BI Kimberley	G/P	H. K. Sminke, pers. comm. 1994
Syncarida: Bathynellacea: Bathynellidae	gen. indet.	CRP/BI Kimberley Pilbara	P	H. K. Sminke, pers. comm. 1994; W. F. Humphreys, unpubl.
Isopoda: Flabellifera: n. fam.	•*Tainisopus* [2+ spp.]	Kimberley	•	Wilson and Ponder 1992
Isopoda: Flabellifera: n. fam.	*n. gen. [2+ spp.]	Pilbara	•	G. F. Wilson, pers. comm. 1997
Isopoda: Phreatoicidea: Amphisopidae	*n. gen.	Kimberley	G	Wilson and Keable, in press
Isopoda: Phreatoicidea: Amphisopidae	*n. gen.	Pilbara	G	Knott and Halse, pers. comm. 1998
Isopoda: Phreatoicidea: Amphisopidae	*Hyperoedesipus*	Pilbara	G	G. F. Wilson, pers. comm. 1997
Oligochaeta: Phreodrilidae	gen. indet.	Pilbara	G	A. Pinder, pers. comm. 1997
Chelicerata: Acarina: Hydracarina	*Tiramideopsis*	Pilbara	India	Harvey 1998
Spelaeogriphacea	*n. gen.	Pilbara	G/P	Poore and Humphreys 1998
Amphipoda: Bogidiellidae	**Bogidomma*	BI	T	Bradbury and Williams 1996a
Decapoda: Atyidae	**Stygiocaris* [2 spp.]	CRP/BI	Madagascar	Holthuis 1960
?Lineages				
Pisces: Eleotridae	**Milyeringa*	CRP	•	Whitley 1945
Pisces: Synbranchiformes	*Ophisternon*	CRP	T	Mees 1962
Ostracoda: Cypridacea: Candoninae	*?Caribecandona*	Pilbara	Haiti	K. Wouters, pers. comm. 1997
Amphipoda: Melitidae	**Nedsia* [8+ spp.]	CRP/BI	T	Barnard and Williams 1995; Bradbury and Williams 1996a
Amphipoda: Melitidae	**Norcapensis*	CRP	•	Bradbury and Willaims 1997b

context (Fig. 2) as they form in arid climates (annual rainfall <200 mm) with high potential evaporation (>3 000 mm per year: Mann and Horwitz 1979). Groundwater calcretes often develop typical karst features which are suitable for stygofauna sampling, as shown in the Millstream aquifer in the western Fortescue Valley, Pilbara (Fig. 3) (Barnett and Commander 1985; Poore and Humphreys 1998).

The Millstream aquifer on the Fortescue River (Fig. 3) contains a rich relict fresh-water stygofauna with clear gondwanan (W. F. Humphreys, unpubl. 1996), probably Pangaean affinities. It includes the crustacean order Spelaeogriphacea, known previously only from two caves in South Africa and Brazil (Poore and Humphreys 1998). The associated fauna includes phreodrilid oligochaetes that generally have a cool climate Gondwanan distribution (Pinder and Brinkhurst 1997), phreatoicid isopods (?closest to *Hyperoedesipus*: G. F. Wilson, pers. comm. 1996), a diverse amphipod fauna including crangonyctoid amphipods that do not align with known groups (J. Bradley, pers. comm. 1996), syncarids (Bathynellacea), the ostracod *?Caribecandona* (K. Wouters, pers. comm. 1997), the water mite genus *Tiramideopsis* previously known only from India (M. S. Harvey, pers. comm. 1996; Harvey 1998), plus at least another 10 species of ostracods, copepods and amphipods.

Further sampling in the Pilbara in 1997 showed that the stygal community varies both along the length of the Fortescue River, from its headwaters to the coast, and from that in the adjacent catchments of the Robe and Hardey Rivers, the latter being a tributary of the Ashburton River. These faunas were mainly found in calcretes but also in river gravels, especially those deposited below water gaps downstream of Millstream where a tethyan fauna predominates.

Groundwater calcretes occur widely in Australia but in isolated, though sometimes extensive, pockets usually associated with palaeodrainage lines (Fig. 3). As the sampling to date suggests that these pockets may

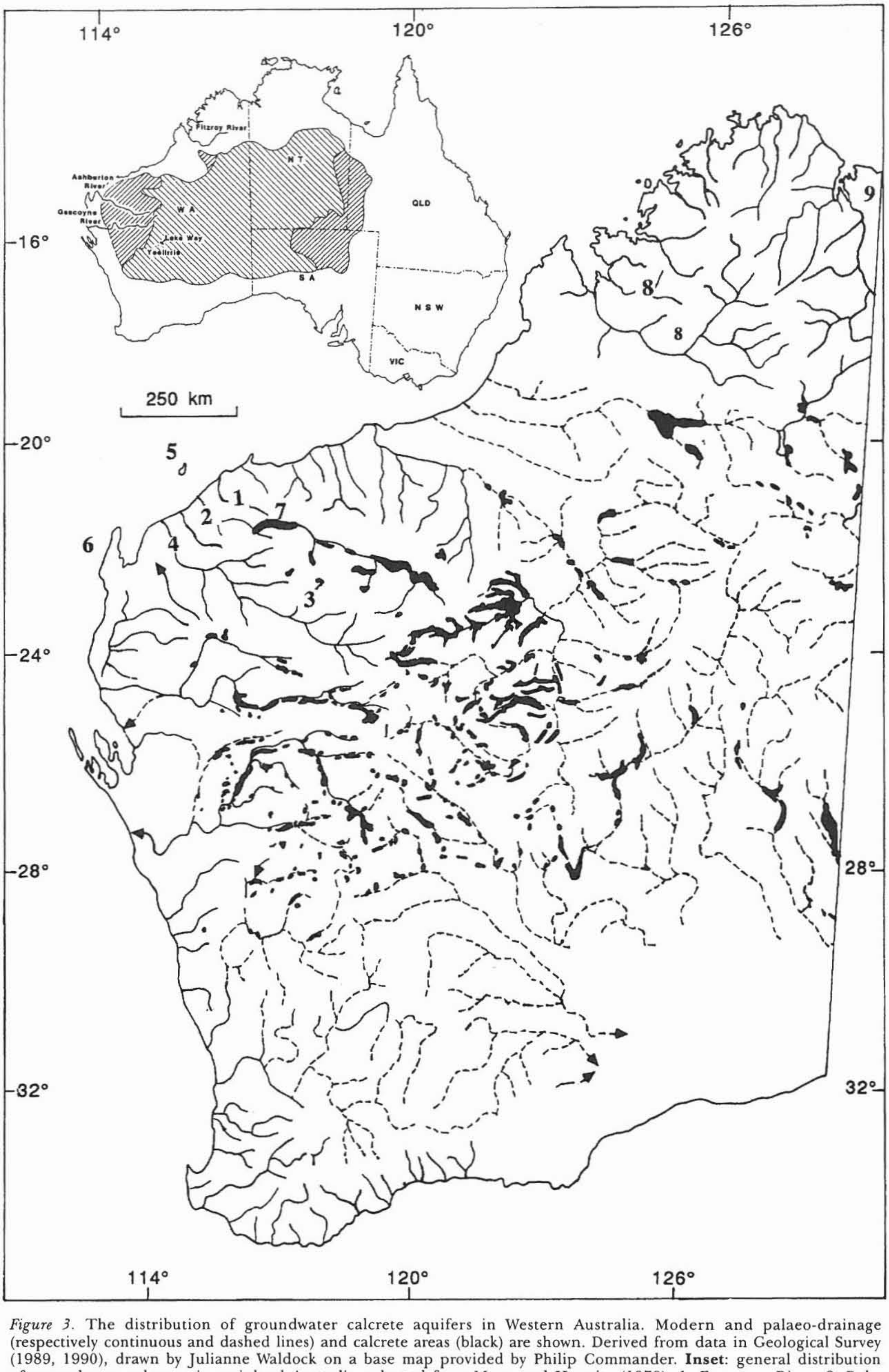

Figure 3. The distribution of groundwater calcrete aquifers in Western Australia. Modern and palaeo-drainage (respectively continuous and dashed lines) and calcrete areas (black) are shown. Derived from data in Geological Survey (1989, 1990), drawn by Julianne Waldock on a base map provided by Philip Commander. **Inset**: general distribution of groundwater calcretes in mainland Australia, adapted from Mann and Horwitz (1979). 1, Fortescue River; 2, Robe River; 3, Hardey River; 4, Ashburton River; 5, Barrow Island; 6, Cape Range; 7, Millstream; 8, Devonian reef system between the 8's; 9, Ningbing Range, an outlier of 8.

contain distinct faunas, then these calcrete aquifers have potential to contain substantial reservoirs of hidden biodiversity. Hence, the stygal communities in the calcretes of Australia — and probably other arid regions — are of considerable interest both as regards the biogeography of the faunas themselves and for their potential in the study of landscape change.

FRESHWATER KARST — KIMBERLEY

As parts of the southern Kimberley are arid I provide brief comment on the findings from the sparse stygofauna collecting that has been conducted there but which has revealed important and unexpected stygal groups.

Bathynellid syncarids occur in both the northern and southern Kimberley (Humphreys 1995; W. F. Humphreys, unpubl.). Syncarids are considered to have entered freshwater in the Carboniferous and so have a Pangaean distribution (Schminke 1974).

A new family of flabelliferan isopod that has speciated within the northern Devonian reef system (Fig. 3) of the west Kimberley (Wilson and Ponder 1992); the family is found throughout the western parts of the same system (W. F. Humphreys, unpubl. 1997; S. M. Eberhard, unpubl. 1998) as well as in remote outcrops of the reef in the north-east Kimberley (Fig. 3: Ningbing Range; S. M. Eberhard, unpubl. 1998). Cladistic analysis suggests that this family is related to the cosmopolitan marine Limnoriidae and Sphaeromatidae, but at a basal level, suggesting it is much older than the more derived families like the Cirolanidae (G. D. F. Wilson, pers. comm. 1997). A separate clade (G. D. F. Wilson, pers. comm. 1997) of this family has recently been found in the Pilbara calcretes in the upper Fortescue and the Hardey Rivers (W. F. Humphreys, unpubl.). Finally, a hypogean phreatoicid is found in sandstones in the north Kimberley (Humphreys 1995). The phreatoicid is basal to the Phreatoicidea suggesting divergence after they entered fresh water but prior to the fragmentation of East Gondwana during the Mesozoic era (G. D. F. Wilson, pers. comm. 1997; Wilson and Keable, in press).

CONSERVATION

The subterranean ecosystem is the world's most extensive terrestrial ecosystem, occurring in all climatic zones and ranging from the tops of mountains to 120 m below sea level (Juberthie, in press), and yet it is largely ignored in planning the conservation estate. It contains 97% of the world's freshwater (UNESCO 1986) and is exceptionally vulnerable to the ingress of pollutants (Notenboom *et al.* 1994). The contained fauna is largely ignored in quality assessment and monitoring — it is not mentioned in Australian conferences (AGSO 1993), policy documents (Australian Water Resources Council, 1992) or strategic resource assessment of groundwater, despite discussion of ecologically sustainable development (Allen 1997).

The biodiversity present in underground waters is considerable and has only recently started to be examined as an ecological system (Marmonier *et al.* 1993; Gibert *et al.* 1994) containing specialized faunas and unique lineages. Groundwater systems offer opportunities for empirical testing of ecological hypotheses in simpler and less variable conditions than are present at the surface. But, more importantly, as many aquifers are still in pristine condition, the faunas they contain offer scope for monitoring human impacts on these systems.

These relictual lineages are best conserved by protecting their habitat and its associated water flows. In this arid area, however, karst (Cape Range) and calcretes (Pilbara) often constitute the principal water supply for human activities. We need to recognize that surface operations (sealing or clearing), as well as those below ground (water abstraction, mine dewatering) have considerable potential to hazard these ancient relictual communities. These effects may be direct, through pollution of the groundwater — nutrient enrichment may lead to the invasion of subterranean systems by surface dwelling species (Malard 1995) — and by intercepting environmental flows of energy and water — phreatophytic weeds may account for most of the groundwater flow through an aquifer (Commander 1994).

These ecosystems are facing significant risks resulting from the lowering of the water table below ecologically appropriate levels. Such processes may result in the physical modification or loss of subterranean environments through general surface slumping in flood-plain calcrete aquifers resulting from the withdrawal of supporting water.

PROSPECTS

The biodiversity discussed here represents the barest glimpse at the stygofauna of northwestern Australia, an especially suitable location for ancient lineages as much of the area has not been inundated by the sea since the Precambrian (Fig. 2). This paper was written to serve as an exemplar of the diversity yet to be found in this region and its potential to aid our understanding of the

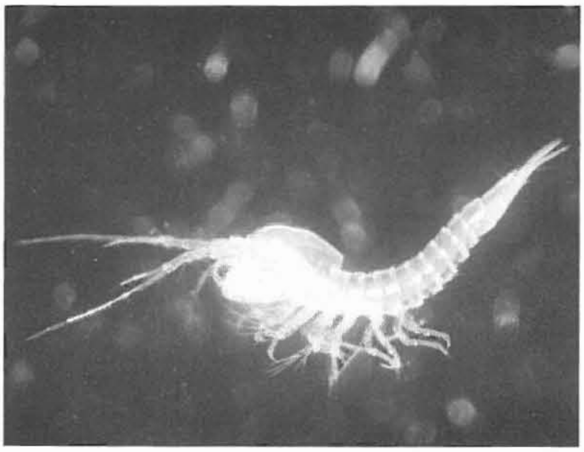

Figure 4a. Halosbaena tulki Poore and Humphreys (Crustacea: Thermosbaenacea): freshwater cave. Length *c.* 2 mm.

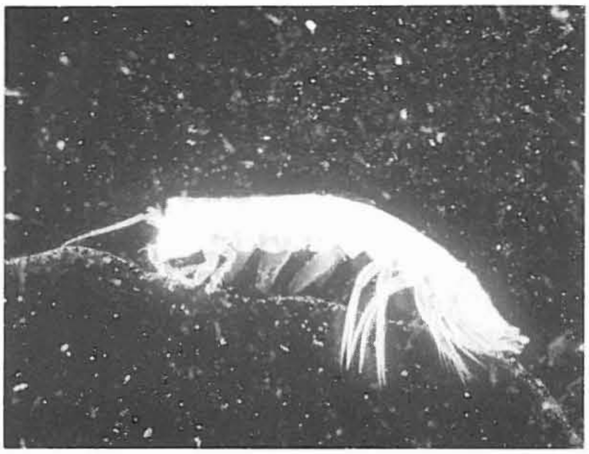

Figure 4b. Liagoceradocus branchialis Bradbury and Williams (Amphipoda: Hadziidae): anchialine cave, below pycnocline in very low oxygen tension. Length *c.* 4 mm.

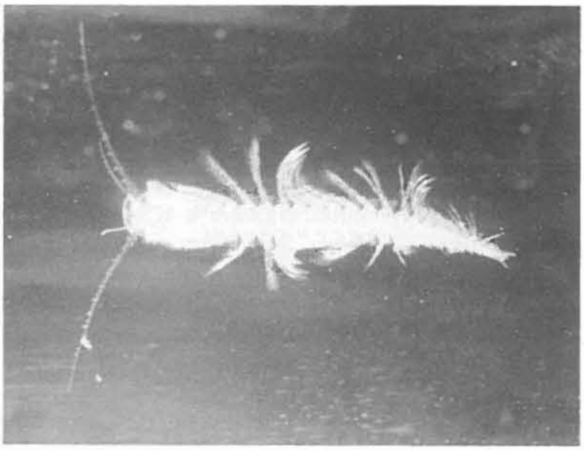

Figure 4c. Lasionectes exleyi Yager and Humphreys (Crustacia: Remipedia): anchialine cave, below pycnocline in very low oxygen tension. Length *c.* 10 mm.

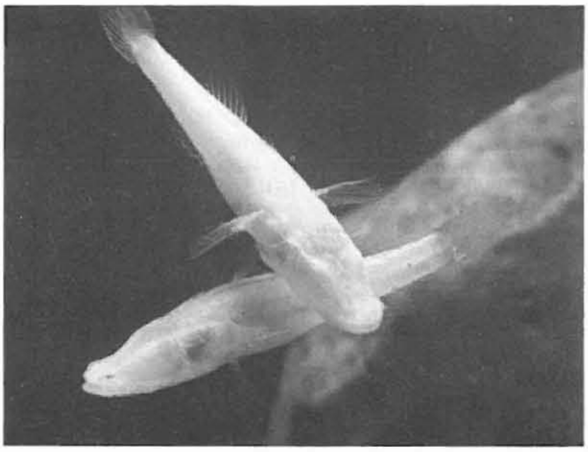

Figure 4d. Milyeringa veritas Whitley (Pisces: Eleotridae). Length *c.* 45 mm. The blind cave eel *Ophisternon candidum* (Mees) (Synbranchiformes) is sympatric. Fresh to brackish.

evolution of lineages, both within Australia and Gondwana. In addition, it may help our understanding of the evolution of tethyan stygofaunas and the colonization of Tethys as its development progressively separated the Old World from the New (Fig. 1). The newly discovered and isolated stygofauna communities in calcrete deposits offer exciting possibilities in the realms of exploring the development of drainage patterns and in the development of landscapes.

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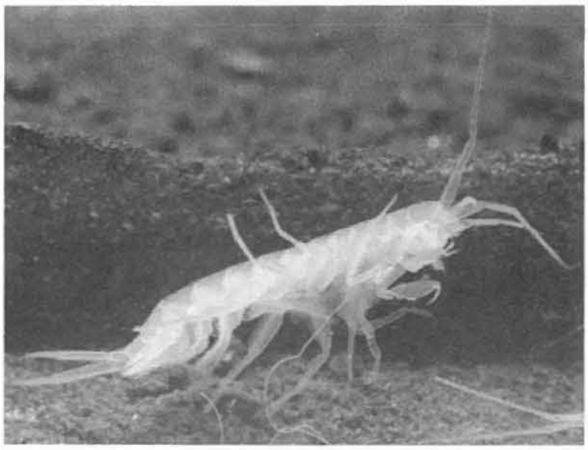

Figure 4e. Norcapensis mandibulis Bradbury and Williams (Amphipoda: Melitidae): freshwater cave. Length *c.* 10 mm. All photographs Douglas Elford, Western Australian Museum.

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