RUNNING HEADER: **Diversity in Australian subterranean ecosystems**

WHERE DOES THE FAUNA LIE: THE DIVERSITY OF AUSTRALIAN SUBTERRANEAN ECOSYSTEMS

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ABSTRACT

Limestone caves that people can enter are the familiar site of subterranean ecosystems (SEs) and some are significant tourist sites largely on account of their fauna. But subterranean fauna is much more widespread and diverse, occurring in both the air-filled and water filled voids in a wide variety of geological settings. In typical limestone karst the main ecosystem may be in the finer solution channels and cavities inaccessible to people. SEs occur widely in pseudokarst substrates such as lava tubes (Undara) and sandstone (e.g. Proterozoic Pentecost Sandstone), and in groundwater deposits such as calcretes and pisolites, and in alluvial and colluvial deposits ranging from sands to boulder, and in fractured rock aquifers. They occur from temperate to tropical climates, from rainforest to desert, in unconfined and confined aquifers to a kilometre depth, in freshwater, and in the subterranean estuaries of salt lakes and oceans. Many taxa, with both terrestrial and aquatic lifestyles, became subterranean when the surface became unsuitable owing to the onset of aridity in the Tertiary; they are especially diverse in arid areas, and the terrestrial taxa found there are of groups typical of the rainforest floor are moisture dependent and occur only where cave air is nearly saturated with water. Some groundwater animals (stygofauna) belong to more ancient lineages that were already in groundwater when the super continents fragmented. In consequence there are close relatives inhabiting groundwater in other continents, especially in the fragments of Gondwana. Such faunas have persisted despite global climatic and geological changes of great magnitude, through ice ages and the transition of rainforest to deserts. The movement of animals into the subterranean realm has resulted in samples of the fauna from different geological eras being preserved as a living zoo, and, because it is entrapped in place, the subterranean fauna tells us about Earth's deep history.

I. INTRODUCTION

As most (97%) of the world's liquid freshwater occurs as groundwater (Gibert et al. 1994), it is not odd that this subterranean world is the largest terrestrial biome (Gold 1992). Life forms may occur several kilometres below the Earth's surface and specialised invertebrate, and occasional vertebrate, aquatic species occurs to depths of at least 1000 m (Morocco: Essafi *et al.* 1998) and 800 m (Texas: Longley 1992) respectively. While groundwater and surface water are now recognised as a single interconnected resource, it still comes as a surprise, even to many environmental professionals (Boulton et al. 2003), that aquifers are ecosystems, often in close continuity with surface waters — they are the ultimate groundwater dependent ecosystem (Humphreys 2006). Changes at the surface, to the groundwater and the aquifer matrix itself may affect these systems, potentially after long delays (Humphreys 2002).

The diversity of subterranean life in Australia has really only started to be appreciated only over the last two decades and it is continuing to surprise variously through its diversity, taxonomic composition, apparent age, the types of habitats and the water quality in which it occurs. This paper provides a brief background to the nature, significance and distribution of subterranean aquatic faunas and the habitats they occupy in Australia. Most of the literature pertaining to this issue can be accessed through the works cited in Humphreys (2006) and I will cite works here only where necessary. While this paper focuses on the aquatic component of this fauna, the stygofauna. It needs to be mentioned here, that an equally remarkable subterranean fauna inhabits the air-filled voids, the troglofauna (Humphreys 2000, 2004; Wilkens et al. 2000; Eberhard & Humphreys 2003). Troglofauna can also be accessed through bores if the casing is slotted above the water table (known in this way from Cape Range, Barrow Island, Yilgarn, Pilbara, east and west Kimberley but barely studied) and typically comprise short range endemic species, often belonging to relictual rainforest lineages (Humphreys 1993, 2000b).

2 GENERALITIES

2.1 Stygofauna

Stygofauna are animals inhabiting groundwater which, except in karst areas, are invertebrates. They have various lifestyles and many animals occur in groundwater either accidentally (termed stygoxenes) or with varying degrees of affinity for groundwater, inhabiting it on a permanent or a temporary basis (termed stygophiles), but only stygobites are obligate inhabitants of groundwater. Animals in these several ecological types collectively comprise the stygofauna (Gibert et al. 1994: 12). As elsewhere, Australian stygofauna predominantly comprise various groups of crustaceans (51 of the 61 families: especially amphipods, isopods, copepods, ostracods and bathynellaceans) but also present are various types of worms (e.g. turbellaria, nematodes, oligochaetes, polychaetes), gastropods (especially Hydrobiidae), water mites, insects (notably Dytiscidae in arid Western Australia) and fish (in Australia only Cape Range and Barrow Island). There is a diverse microbiota that is largely unstudied with few exceptions (Humphreys, 1999; Holmes et al. 2001; Hancock & Steward 2004, Hancock this volume; J. Seymour and W.F. Humphreys, unpublished data).

Stygobitic macrofauna have a convergent morphology (Fig. 1) exhibiting a reduction or loss of eyes, pigments and hardened body parts — they are characteristically translucent — and they have enhanced non-optic sense organs (Culver *et al.* 1995). Those species inhabiting interstitial spaces are often elongate, even vermiform, thus facilitating their movement between particles (Figure 2). They typically lack resting stages, have few young and arte long lived relative to their surface relatives, attributes considered adaptations to the low energy environment they inhabit (Coineau 2000). These attributes make them very efficient bio-accumulators (Plénet *et. al.* 1992), slow to recover from reductions in their populations and difficult to study. Owing to these biological characteristics, the species inhabiting groundwater ecosystems are often locally endemic, that is, they are restricted to a small geographic area.

2.2 Biodiversity

Over the last decade it has become increasing recognised that groundwater ecosystems are not semi-deserts, occupied by rare, effete lineages, but are dynamic systems comparable in complexity to surface ecosystems (Rouch 1977, Gibert *et al.* 1994) but lacking primary producers (Gibert & Deharveng 2002), except in the special case of chemosynthesis (Poulson & Lavoie 2000). The magnitude of the biodiversity present in subterranean waters globally has only recently been given prominence (e.g. Rouch and Danielopol 1997; Sket

1999; Culver and Sket 1999; Wilkens *et al.,* 2000; Danielopol et al. 2000; Danielopol and Pospisal 2001).

Australia, especially the western and south-eastern parts, has unexpectedly come to the attention of stygobiologists and systematists on account of their diverse regional groundwater faunas (stygofauna). These include a number of higher order taxa variously new to science (WA endemic Tainisopidea), new to the southern hemisphere (Thermosbaenacea, Remipedia, Epacteriscidae), or new to Australia (Spelaeogriphacea, Pseudocyclopiidae). Else, they are the first living relatives of lineages otherwise known from the fossil record as long ago as the early Cretaceous, such as the ostracods *Microceratina* (Namiotko et al. 2004) and *Vestalenula* Martens & Rossetti (Martens & Rossetti 2002).

2.3 Regional diversity

As knowledge of the stygofauna of Australia is increasing at such a rate, any estimate of the biodiversity it contains is premature. However, it is already apparent that Australia contains a stygofauna of global significance. The only regional survey of stygofauna in Australia has been conducted in the Pibara where ca. 350 species have been recorded, predominantly ostracods (S. Halse, CALM Pilbara Stygofauna Survey, pers. comm.). The next best worked area is the central and northern Yilgarn where c 210 species are known, predominantly Dytiscidae. There are an estimated 82 stygobites and 34 stygophiles from SE Australia karst (Thurgate et al. 2001a) and 43 from alluvial aquifers (Hancock, this volume). Various other smaller, but highly significant faunas are known from the Carnarvon Basin (c 35 species in karst: relictual tethyan fauna containing higher taxa not elsewhere known in the Southern Hemisphere), Perth Basin (karst and alluvial), Leeuwin Naturaliste (karst), Kimberley (karst, sandstone and alluvia), Ngalia Basin, NT (calcrete), NT and Far North Queensland (karst and pseudokarst), and Christmas Island (karst anchialine), and diverse stygofauna is emerging in South Australia (R. Leijs, pers. comm.). At a very conservative estimate at least 750 species have been recorded, mostly in the last 10 years, more than 500 of which are in the mineraliferous Pilbara and Yilgarn.

To place this in perspective, some of the major karst areas of the northern hemisphere have been research intensively by generations of researchers. The best worked and richest region is the Balkan Peninsula where >650 stygobite species have been recorded (plus 975 species of troglofauna: Sket et al. 2004); 114 species of stygobionts are known from the Slovenian karst, where stygal taxonomy started in 1768, which has the highest density of aquatic subterranean biodiversity (Culver et a, 2004). In the 48 contiguous states of USA about 1000 obligate cave species are known, of which 269 are stygobites (Culver et al 2003) with no more than 80 species in any region.

Many regions of Australia remain entirely unexplored for stygofauna largely owing to the recent nature of such enquiry, but often owing to their remoteness and /or lack of access to groundwater, For a number of reasons all the areas that have been examined are expected to yield considerably greater diversity when adequately surveyed for stygofauna. Firstly, even within the sampled areas the sampling density is low. For example, even within the pastoral areas of the Yilgarn, groundwater access it typically one well per paddock, commonly 100 km^2, while large swathes of the desert, even where there is prospective stygofauna habitat, lack access to groundwater. Secondly, sample sites typically yield additional taxa because species accumulation curves do not reach an asymptote even after a great number of sampling occasions (Hancock, this vol.; S. Halse and S.M. Eberhard, pers. comm.; W.F. Humphreys et al., unpublished data), which implies that most species are rare, as in other ecosystems (May 1976). The significance of this in the context of subterranean fauna is that most species have quite restricted ranges, are 'short range endemics' to use the current catchphrase. Finally, stygofauna includes many cryptic species so that as taxonomic understanding emerges, both by detailed morphological studies and by molecular (largely DNA) studies, the resolution of the species boundaries is improved and the recognised diversity will increase, substantially in some linegaes. It is being found commonly that isolated populations of stygofauna, especially amongst the various amphipod families, show deep phylogenetic divergences although they cannot be separated easily using morphological criteria.

Australia probably has the phylogenetically most diverse stygofauna globally.

2.4 Origins

Groundwater ecosystems may be very persistent through geological time (review Humphreys 2000a) and many of the lineages present in Australia's groundwaters have ancient origins (discussion in Humphreys 2002). There are those whose origins are related to the Tethys (e.g., anchialine fauna of both north-western Australia and Christmas Island: several lineages from the former have congeneric species which are known elsewhere only from subterranean waters on either side of the North Atlantic), Pangaea (e.g., Bathynellacea, crangonyctoid amphipods) and Gondwana (e.g., phreatoicidean isopods, Spelaeogriphacea). Others, from their distribution, provide information on eustatic changes (*Milyeringa*: Humphreys 2001; *Norcapensis*: Bradbury & Williams 1997b; *Stygiocaris*: Humphreys & Adams 2001; *Halosbaena*: Humphreys 2001) and the spreading aridity of central Australia during the Miocene (Leys et al. 2003). While a pattern of repeated colonisation—even recolonisation of surface habitats—may an active process in some regions (Culver *et al.* 1995), much of the Australian stygofauna appears to have been isolated underground in the geological past. For example, following a long period of invasion of calcrete systems, colonisation seems to have abated over the subsequent several million years (Leys et al 2003).

2.6 Species extent

Those stygofauna confined to subterranean life (stygobites) are typically restricted in extent to a single aquifer. If there is a linear aquifer, such as along a river valley, then a species may potentially occupy a substantial geographic range. However, the data available indicates that most stygobites in Australia are short range endemic species, confined to a single aquifer, such as the groundwater of a given tributary (T. Finston, pers. comm. 2006), or a discrete aquifer such as an isolated karst (Thurgate et al. 2001b) or a given body of groundwater calcrete (Watts & Humphreys 2003; Cooper et al. 2002; Leys et al. 2003). These conclusions are largely derived from studies on the Western Plateau of Australia, both in WA and NT. The younger topography of the eastern seaboard and the impact in the south of Pleistocene glaciations, could have produced more integrated aquifers containing wide ranging stygal species, but studies there are still at too early a stage to draw any general conclusion as to whether these eastern seaboard stygal communities differ in this way, as well as in their composition.

2.7 Water quality

Stygofauna globally have been considered to be restricted to freshwater, rarely slightly brackish, except in the special case of those inhabiting anchialine ecosystems (see below). The Western Shield, however, which comprises amongst the oldest emergent landscapes on earth, contains groundwaters ranging at the surface from fresh to hypersaline and often with a marked halolcline. These far-inland aquifers (e.g. calcretes associated with Lake Way) may contain a mix of near-marine lineages (e.g., Cyclopidae, *Halicyclops,* and hyalid and melitid amphipods) alongside ancient freshwater lineages (*Parastenocaris*, Parastenocarididae, Fig. 2; crangonyctoid amphipods). Furthermore, Bathynellacea, a stygal lineage with global freshwater distribution, occur there in waters of marine salinity. The presence of diverse stygofauna in waters of marine salinity in groundwater estuaries of far inland salt lakes (Humphreys et al. submitted) is unknown outside the Western Plateau of Australia.

Anchialine ecosystems are salinity stratified coastal aquifers affected by marine tides but with no surface connection with the sea, namely they are subterranean marine estuaries. Globally, anchialine ecosystems contain a distinct and remarkable fauna whose general composition is predictable, often at the generic level, however far apart in the world they occur. The fauna comprises numerous anchialine endemic higher taxa that display remarkably disjunct global distributions; Cape Range (north-western Australia) has the only example of remipede-type (Humphreys and Danielopol 2006) anchialine community known outside the North Atlantic. Element of this fauna also occur on Barrow Island and on the Pilbara coast (deltas of the Robe and Fortescue Rivers). Christmas Island also contains a significant, but entirely different anchialine fauna (procaridid-type: Humphreys and Danielopol 2006), the general composition of which is also predictable, often at the generic level, however far apart in the world they occur (known also from Bermuda, Ascension Island, Hawai'i).

2.8 Broad distribution patterns

Several parts of Australia, including the cratons and associated orogens that comprise the 'Western Shield', have been emergent above sea level since the Proterozoic (Fig. 3). These long emergent areas are home to many ancient freshwater lineages such as the Bathynellacea, phreatoicidean and tainisopidean isopods, crangonyctoid amphipods and candonine ostracods (Bradbury 1999; Bradbury & Williams 1997a; Humphreys 2001a; Karanovic & Marmonier 2003; Wilson 2001, 2003 Wilson and Johnson 1999). Species belonging to ancient freshwater lineages have been recovered from Proterozoic Pentecost Sandstone aquifers in the Kimberley (*Crenisopus*: Wilson & Keable 1999) and on small continental islands (Koolan Island), including one with an anchialine system (*Atopobathynella*: Barrow Island).

The areas inundated by the sea in the Cretaceous and more recently, particularly the Eocene inundation, are largely devoid of these more ancient lineages but there is some invasion in both directions. For example, hyalid amphipods have deeply invaded the palaeovalleys of the Yilgarn, Thermosbaenacea reach 300 m altitude in the Robe River, about the height of the Eocene high stand, and crangonyctoid amphipods occur on the narrow coastal plain of the Perth Basin. Marine waters penetrated deeply the palaeovalleys of the southern Yilgarn, increasing substantially potential sites of invasion of groundwaters by marine lineages. Along all the boundaries of former high sea level stands there are likely sites for relictual marine fauna, and former islands are likely sites for ancient freshwater taxa limited to small areas.

In addition to distribution patterns dictated by marine influences, there are regional patterns of obscure origin. The most remarkable is the difference between the Yilgarn and the Pilbara, both apparently part of the same long emergent land mass, which, while each has a diverse fauna, have almost no genera in common and major differences in higher taxa. For example, stygal diving beetles (Dytiscidae) and Oniscidea, which are so diverse in the Yilgarn, are absent from the Pilbara, although present in the Northern Territory at the same latitude. The isopod family Tainisopidae present in the Kimberley and Pilbara, is absent from the Yilgarn.

3 TYPES AND DISTRIBUTION OF SUBSTRATES AND FAUNA

3.1 Karst

Subterranean faunas are typically to be found wherever there is adequate void space in aquifers (Fig. 4). Most notably such voids are associated with carbonate karst (soluble rock landscapes) because it is possible, on visiting tourist or wild caves, for people to see the groundwater, either static or flowing, and to envisage the complexity and the hydraulic integration of the groundwater system. Similar large voids may be found in sandstone karst and pseudokarst such as lava tubes. However, even in such setting, most of the biological action occurs in the finer voids, far too small for people to enter.

Australia, as with other parts of Gondwana, has much smaller area of carbonate deposits (Fig. 5) than other parts of the world. Nonetheless, the Nullarbor is the largest area of exposed karst in the world. Despite this and its age and mixed water types, it is remarkable for its lack of stygofauna: only two species being known, both melitid amphipods, one of which is described (Bradbury and Eberhard 2000). Australia has extensive areas of soft rock (non-metamorphosed carbonates predominantly in the south and west of the continent) and hard rock karst (metamorphosed carbonates mostly in the east and north), as well as areas of volcanic pseudokarst (south and north) and groundwater calcrete karst in the arid centre. While some of these contain rich stygofaunas (calcretes, Cape Range, some impounded karst of NSW), others, notably the Nullarbor (two species known) and Chillagoe (one species known), appear to be almost devoid of stygofauna.

3.2 Fractured rock

Fractured rock aquifers occur wherever voids are created beneath the piezometric surface by fracturing of the native rock, including in karst. Whereas in the latter voids are often common through solution effects, in non-karstic systems fracturing may be the only mechanism of void formation. While carbonate karst typically produces a water chemistry benign for stygofauna (slightly alkaline pH), water in igneous and metamorphic sedimentary rocks may be acidic and less suitable for stygofauna.

3.3 Colluvium and Alluvium

The breakdown of parent rock in the regolith may be transported and fractionated by gravity and water to yield sediments with graded particle size in space and through time. Hence, the characteristic void space varies with depth and geographic position, and characteristic void space may vary at a given position through time. As the characteristic void size may determine the nature of the possible stygofauna, both space and time may be of interest to an evolutionary biologist, but it is the spatial dimension that is pertinent to those wishing to understand the contemporary distribution and composition of the stygofauna in an area and the likely impacts of certain activities on the stygofauna.

The thin colluvial and alluvial deposits in Kimberley head waters contain a surprising array of stygofauna (meiofauna) with at least 17 species known from around Argyle Diamond mine with up to 7 species per site.

The deep alluvial deposits of the eastern seaboard (Hancock & Steward 2004; Hancock et al 2005) contrast sharply with the thin regolith of the Western Shield. Recent work is revealing rich stygofaunas in these alluvial deposits, especially close to rivers, with 43 taxa recorded and from 11 to 22 taxa per aquifer (Hancock, this volume). This will add a new dimension and further invigorate work on stygal ecosystems in Australia because it is in such settings that the that surface water / groundwater interaction is most dynamic (Hancock, 2002, 2004) and the fauna quite distinct (Thurgate et al 2001a, 2001b; Hancock, this volume) from those found in the west, central and northern Australia.

4 WATER ATTRIBUTES

4.1 Spatial scale

Subterranean waters may conveniently be separated into groundwater and the hyporheic waters that occur below river channels (Jones and Mulholland 2000) and which form a broad ecotone between surface water and groundwater. Animals are mostly restricted to the upper parts of subterranean ecosystems, nonetheless, diverse stygofaunas may be found at great depth in karst systems; vertebrates to 800 m in the Edwards Aquifer, Texas (Longley 1992), and macro invertebrates at depths of up to one kilometre in Morocco (Essafi *et al.* 1998). Groundwater ecosystems occur at a range of spatial scales, from the boundary layer of the biofilm on sedimentary particles, through reach, tributary, and catchments (Boulton, 2001). In general, it appears that the greater the distance of the groundwater habitat from epigean influence the greater is the affinity of the fauna to the groundwater. This "distance" occurs in four dimensions, as vertical depth in groundwater, distance from the bank in parafluvial aquifers, and distance or time along groundwater hyporheic flowpaths (Dole-Olivier et al. 1994). Indeed, there is a thesis that through time the sedimentary systems globally are interconnected along the hyporheic corridor providing a dispersal route for meiobenthic taxa along a continuous alluvial aquifer system (Stanford and Ward, 1993), which in the long term is probably interconnected with other catchments (Ward and Palmer, 1994).

4.2 Hydrogeochemical evolution.

Groundwater may have a prolonged residence time and undergo profound hydrogeochemical evolution. This may affects the suitability of the water for particular stygofauna, particularly through a reduction in organic matter and the associated reduction in dissolved oxygen, and by the increase in dissolved solids (higher salinity). While such change may occur over a protracted temporal scale (10^3 -10^4 years), the spatial scale may be quite constrained (10^0 - 10^1 km), as for example in the groundwater estuaries of salt lakes (Humphreys et al. submitted).

4.3 Groundwater deposits

The hydrogeochemical evolution of groundwater may result in the deposition of minerals in a physical form that makes them highly suitable habitats for subterranean fauna in sites where suitable habitats were not previously available. For example, groundwater calcretes of the arid zone (Fig. 5, denoted as numerous small unfilled sites in inlands) and pisolites deposits associated, for example, with drainage from the Pilbara. The calcretes are associated with the hydrogeochemical cycles in the palaeodrainage systems in the Yilgarn, WA and Ngalia Basin, NT, and for which the salt lakes (playas) represent the groundwater base level,

4.4 Epikarst

Globally, there is a significant aquatic fauna in the epikarst (the region between the soil and the groundwater) that is dependent on the vadose water and is not groundwater dependent in the strict sense in that removal of groundwater would not necessarily influence the fauna, but, many things that way affect groundwater may also impact on the epikarst. Epikarst fauna has been examined in Europe (Pipan 2005) and is known to occur in Australia (Eberhard 2004) and where it may be expected to be diverse, especially in more humid climates.

5 CONCLUSIONS

Australia has a species rich and phylogenetically diverse stygofauna of very varied origins, and which occurs over a wide range of both substrates and water quality. In each respect, it is shaping up to become the global leader in the diversity of each of these attributes. The recent recognition of this fauna, and the rapid response of granting agencies, researchers, regulators and land managers, means that Australia can also take the lead in tackling the management issues that have arisen.

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FIGURE CAPTIONS

Fig. 1: Subterranean animals, clockwise from upper left: 1, the phreatoicidean isopod *Phreatoicoides gracilis* Sayce, 1900; 2, the melitid amphipod *Norcapensis mandibulis* from caves in Cape Range; 3, *Tjirtudessus eberhardi* (Dytiscidae), one of 50 species of blind diving beetles from calcretes aquifers in the Australian arid zone; 4, the atyid shrimp *Stygiocaris stylifera* from the Cape Range anchialine ecosystem. Photos by: 1, GDF Wilson Australian Museum; 2-4, W.F. Humphreys; 3, from painting by Elyse O'grady.

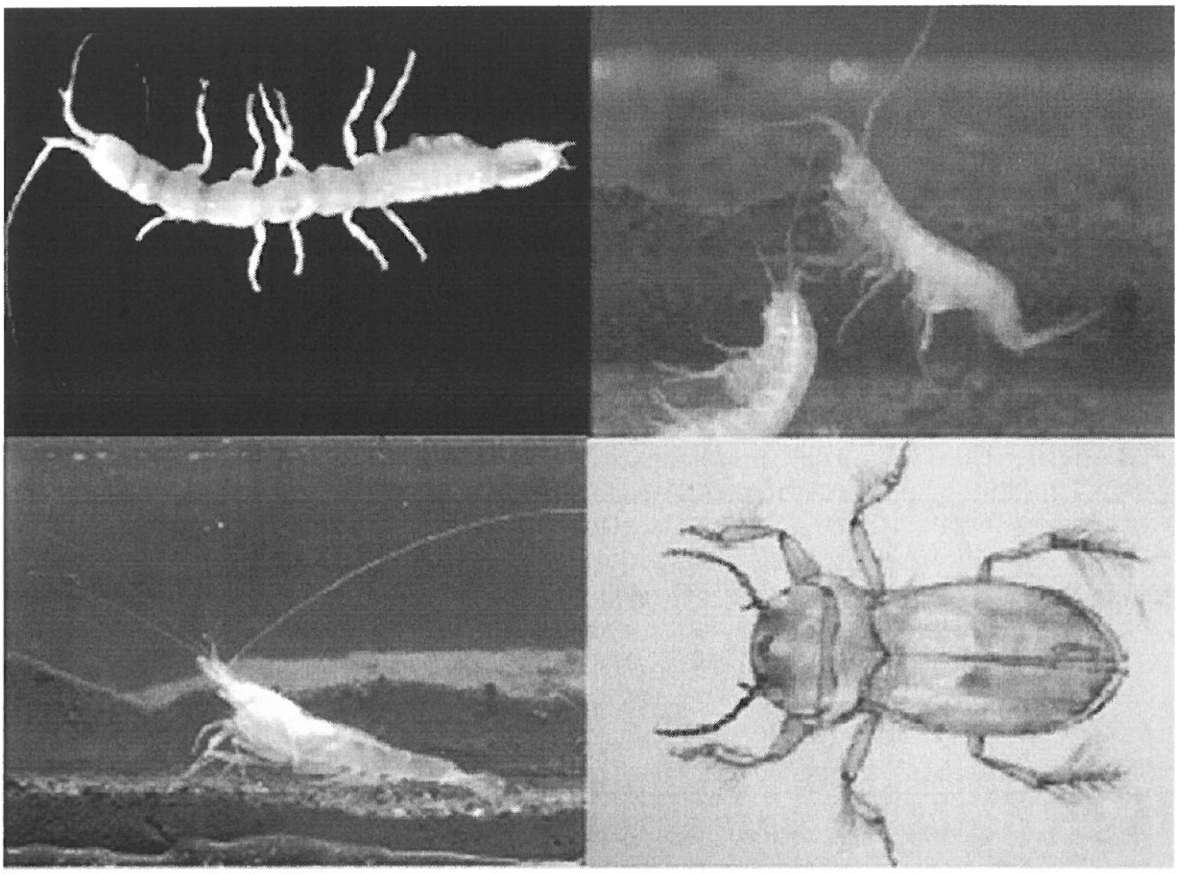
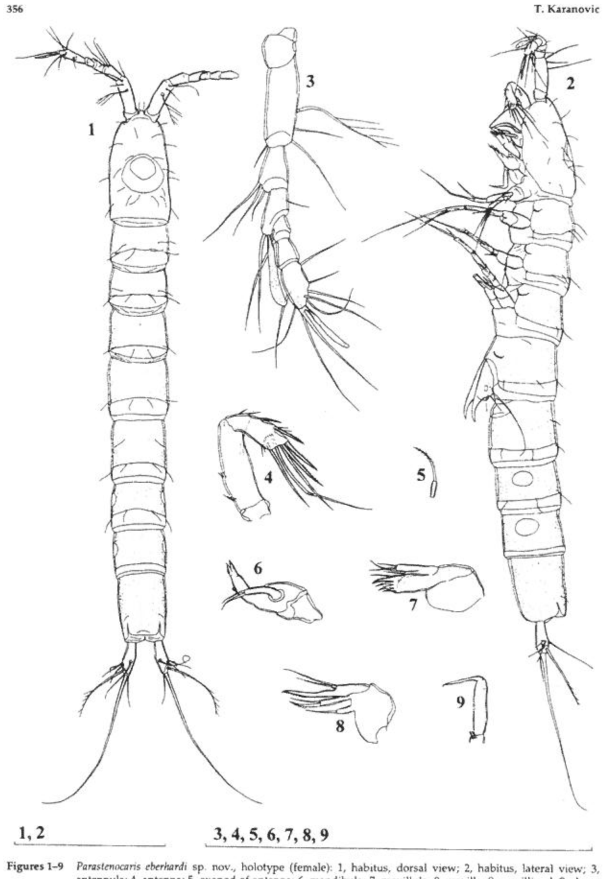


Fig. 2: *Parastenocaris eberhardi* from caves on the Leeuwin-Naturaliste ridge, WA, showing the vermiform body form typical of interstitial stygofauna (image from Karanovic 2005).



Figures 1–9 *Parastenocaris eberhardi* sp. nov., holotype (female): 1, habitus, dorsal view; 2, habitus, lateral view; 3, antennula; 4, antenna; 5, exopod of antenna; 6, mandibula; 7, maxillula; 8, maxilla; 9, maxilliped. Scales = 0.1 mm.

Fig. 3: The current outline of Australia superimposed on the areas continually emergent (brown) since the Proterozoic. The remainder (light blue) was inundated by the Cretaceous oceans and partly during the Eocene. Derived from data in BMR Palaeogeographic Group (1990). Ancient freshwater lineages of stygofauna may be expected in the continuously emergent areas but they will largely have been eliminated from the regions immersed in the sea. The palaeoshorelines are likely places to locate relictual marine taxa.

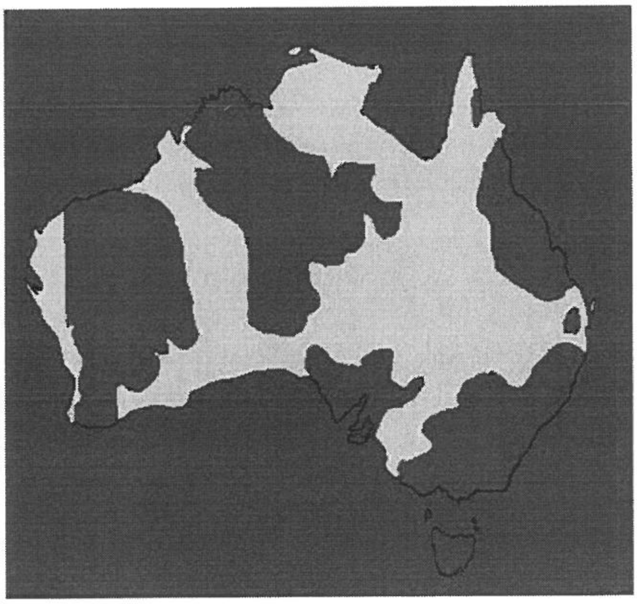


Fig. 4: Schematic section of karst showing how the subterranean voids are variously interconnected both internally and externally facilitating or impeding the movement of energy, materials and organisms. Other subterranean habitats have similar attributes working at different temporal and spatial scales but largely kacking open conduit flow. Figure from: Eberhard & Humphreys. 2003. The crawling, creeping and swimming life of caves. *In* Finlayson & Hamilton-Smith (eds). *Beneath the surface: a natural history of Australian caves.* UNSW Press, Sydney.

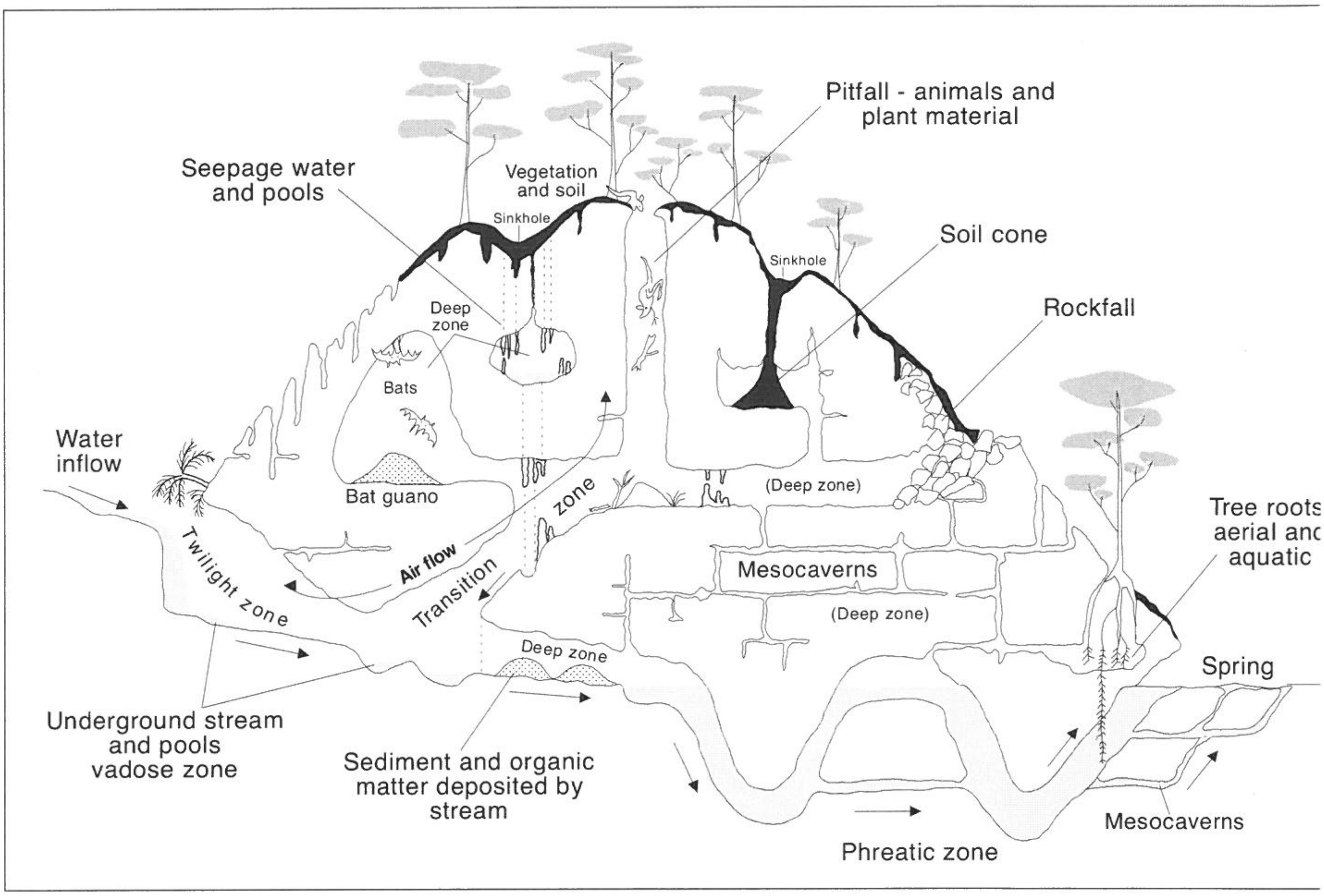


Fig. 5: Karst areas of Australia. Graphic by K.G. Grimes.