

Rising from Down Under: developments in subterranean biodiversity in Australia from a groundwater fauna perspective

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Abstract. Over the last two decades, Australia has undergone a renaissance in studies of subterranean biology. This paper sets these recent developments into context from the perspective of groundwater fauna. Owing to its obligate subterranean life, typical local endemism and the geological persistence of subterranean habitats, stygofauna is an excellent subject for biogeographic study. Groundwater containing diverse faunas range from freshwater to marine salinities in both coastal and continental locations. They occur in typical karst, alluvial, and fractured rock aquifers, but also in novel matrices formed during the hydrogeochemical evolution of groundwater (goethite pisolites and groundwater calcretes) in the Tertiary. This range of habitats, water quality and the diverse origins of the fauna (Gondwanan, Pangaeon and Tethys) support a phylogenetically highly diverse fauna. Several taxa, notably among the Podocopa, Bathynellacea, Amphipoda, and Dytiscidae show remarkable species diversity. Typically there is fine spatial scale endemism of species associated with local aquifers, but there are inexplicable regional differences, such as the change of fauna between the Yilgarn and Pilbara, contiguous areas on the long emergent Western Shield. The anchialine taxa representing higher taxa are highly disjunct from their congeners in the North Atlantic. The emerging species richness, the fine scale patchwork of endemism, and the distinct regional differences, respectively, contribute to a substantial increase in α , β and γ diversity of the aquatic fauna, especially in arid Australia. This diversity is posing challenging issues for proponents and regulators of mineral development because much of this diversity has emerged in the two most mineraliferous provinces of Australia. The scientific capacity to respond is challenged by the sheer scale of the emerging issues.

Additional keywords: anchialine, calcrete, Gondwana, Pangaea, salt lake, stygofauna, Tethys, troglifauna.

Introduction

Although some pioneering work on subterranean fauna was undertaken in Australasia (Higgins and Petterd 1883; Chilton 1894; Hurley 1990), until quite recently Australia was long considered to have an impoverished cave fauna, a condition variously attributed to a lack of karst, aridity, the global lack of tropical troglobites and the absence of widespread Pleistocene glaciation (Moore 1964; Hamilton-Smith 1967; Barr, 1973). These arguments would also have applied to stygofauna, the inhabitants of underground waters in both karstic and alluvial aquifers, had their widespread occurrence been recognised at that time (Humphreys 2004). Concomitantly, there was perceived to be a high proportion of animals found only in caves but not specialised for cave life, i.e. lacking overt troglomorphy (Hamilton-Smith 1971; Humphreys 1995).

Groundwater and surface water are now recognised as a single interconnected resource (Boulton *et al.* 2003) but it continues to surprise many that aquifers are ecosystems, often in close association with surface waters – they are the ultimate groundwater-dependent ecosystems (Humphreys 2006). Changes at the surface may affect groundwater and the subterranean matrix, potentially after long delays (Humphreys 2002a). Most (97%) of the world's liquid freshwater occurs as groundwater (Gibert *et al.* 1994) making this subterranean world the largest 'terrestrial' biome (Gold 1992). Life forms

may occur several kilometres below the Earth's surface and specialised invertebrate, and the occasional vertebrate, aquatic species occur to depths of at least 1000 m (Essafi *et al.* 1998 (1000 m in Morocco); Longley 1992 (800 m in Texas)).

The dependence on groundwater of a wide variety of ecosystems is an increasing focus of research, policy, and management. These issues in Australia have most recently been examined in Eamus and Farrer (2006). The more overt impacts of changing groundwater dynamics are manifest on surface groundwater-dependent ecosystems, especially phreatophytic vegetation, and springs such as those emanating from the Great Artesian Basin (Noble *et al.* 1998; Habermehl, 2001).

Only in the last two decades has the diversity of subterranean life in Australia been appreciated (Humphreys *et al.* 2005). The fauna is continuing to surprise, variously through its diversity, taxonomic composition and apparent age, and by the types of habitats and the water quality in which it occurs (Humphreys 2004). This paper provides a brief background to the nature, significance, and distribution of subterranean aquatic faunas and the habitats they occupy in Australia with some comment on terrestrial subterranean fauna. Most of the literature pertaining to this issue can be accessed through the works cited in Culver *et al.* (2000), the Australian literature in Humphreys (1993, 2000b) and Humphreys and Harvey (2001), and stygofauna

particularly in Humphreys (2006). Although this paper focuses on the aquatic component of this fauna, the stygofauna, an equally remarkable subterranean fauna, the troglifauna, inhabits air-filled voids (Humphreys 2000b, 2004; Wilkens *et al.* 2000; Eberhard and Humphreys 2003; Harvey *et al.* 2008; Barranco and Harvey 2008). Although troglifauna is typically studied by entering caves, it can also be accessed through bores, as in the case of stygofauna, if they are unlined, or if the lining (casing) is slotted above the water table (e.g. Cape Range, Barrow Island, Yilgarn, Pilbara, east and west Kimberley (but barely studied); see Barranco and Harvey 2008; Harvey *et al.* 2008). Troglifauna typically comprise small range endemic species, possibly relictual rainforest lineages (Harvey *et al.* 1993; Humphreys 1990, 1993, 2000b).

Stygofauna

Stygofauna are animals inhabiting groundwater and they are largely invertebrates except in some karst areas where stygal vertebrates are found. Animals occur in groundwater either accidentally (termed stygoxenae) 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 of these ecological types collectively comprise the stygofauna (Gibert *et al.* 1994: 12). As elsewhere, Australian stygofauna predominantly comprise numerous crustacean families (51 of the 61 families (updated from Humphreys 2006) 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 parts of arid Australia) and fish (in Australia only in Cape Range and Barrow Island). The diverse microbial communities, particularly in biofilms are, with few exceptions (Humphreys, 1999b; Holmes *et al.* 2001; Hancock and Steward 2004; Seymour *et al.* 2007; Hancock and Boulton 2008), largely unstudied in Australia other than in the context of bioremediation (Critchley *et al.* 2003). While it is recognised that consortia of microorganisms can work (by mechanisms yet to be identified) to break down contaminant plumes (Haack and Bekins 2000), stygofauna may be expected similarly to interact with biofilms, and other expressions of microbial diversity, so as to promote or to restrict their activity and the community diversity in groundwaters (Humphreys 2000c). By analogy with surface ecosystems, invertebrates have numerous potential functional roles in groundwater systems, including the promotion of biofilm activity (*inter alia* through grazing, nutrient cycling, and improved hydraulic flow paths), but as yet experimental evidence is largely lacking. This issue is addressed extensively by Boulton *et al.* (2008).

Stygobitic animals have a convergent morphology (Fig. 1) exhibiting a reduction or loss of eyes, pigments (they are characteristically translucent) and hardened body parts, 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 (Fig. 2). Convergent physiological adaptations also occur, notably a lower metabolic rate and loss of circadian periodicity (Langecker 2000). They typically lack resting stages, have few

young and are long-lived relative to their surface relatives, attributes considered adaptations to the low energy environment they inhabit (Coineau 2000). For example, embryonic development in the single egg of the bathynellacean *Antrobathynella stammeri* Schminke, 1982 takes nine months, while the life-span of *Iberobathynella* exceeds 2.5 years (Coineau 2001). These attributes make them very efficient bio-accumulators (Plénet *et al.* 1992), slow to recover from reductions in their populations and difficult to study. By virtue of these biological characteristics and because many are small range endemics (Leys *et al.* 2003; Finston *et al.* 2007; Cooper *et al.* 2007), the species inhabiting subterranean ecosystems are often considered intrinsically vulnerable to anthropogenic effects (Humphreys 2002b), despite evidence of exceptionally long persistence through geological eras in subterranean habitats subjected to massive geological and climatic change (e.g. Longley 1981, 1992 (USA); Poore and Humphreys 1998; Humphreys 2000a (Australia)).

Biodiversity

Recently, groundwater ecosystems have been recognised as dynamic systems comparable in complexity to surface ecosystems (Rouch 1977; Gibert *et al.* 1994) but their trophic structure is truncated owing to the lack of primary producers (Gibert and Deharveng 2002), except in the special case of chemosynthesis (Sarbu *et al.* 1996; Poulson and Lavoie 2000). Globally, it is only in the last decade that the magnitude of biodiversity present in subterranean waters has been accepted and given prominence (e.g. Rouch and Danielopol 1997; Sket 1999; Culver and Sket 2000; Danielopol *et al.* 2000; Wilkens *et al.* 2000; Danielopol and Pospisil 2001).

Australia, especially the western and south-eastern parts, has unexpectedly come to the attention of stygobiologists and systematists globally on account of the recently discovered diverse regional groundwater faunas (stygofauna). These include several higher order taxa, many of which are new to science. Examples include the Western Australian endemic Tainisopidae (Brandt and Poore 2003; Wilson 2003), new to the southern hemisphere, and new to Australia, the widely vicariant Epacteriscidae (Jaume and Humphreys 2001), Pseudocyclopiidae (Jaume *et al.* 2001), Remipedia (Yager and Humphreys 1996), Spelaeogriphacea (Poore and Humphreys 1998, 2003) and Thermosbaenacea (Poore and Humphreys 1992). Others represent basal taxa of more widespread lineages, for example, Parabathynellidae (Cho 2005) and Phreatoicidea (Wilson and Keable 1999). Others are the first living relatives of lineages previously known from the subfossil and fossil record as long ago as the Late Cretaceous, such as the ostracod genera *Microceratina* (Cytheruridae) (Namiotko *et al.* 2004) and *Vestalenula* (Darwinulidae) (Martens and Rossetti 2002). Over the same period the non-aquatic subterranean (troglitic) fauna has yielded the first known subterranean spiroboloid millipede (Hoffman 1994), and the first described Australian representatives of the orders Schizomida (Harvey 1988) and Palpigradi (Barranco and Harvey 2008).

Regional diversity in Australia

Knowledge of the stygofauna of Australia is increasing at such a rate that any estimate of the biodiversity it contains is prema-

ture. For example 83 of 84 described species of Candonini have been described since 2002 (Karanovic and Marmonier 2002, 2003; I. Karanovic 2003a, 2003b; 2004, 2005a, 2005b, 2007), 61 of 65 species of stygal Copepoda have been described since 1996 (Nicholls 1945a, 1945b; Pesce *et al.* 1996a, 1996b; Pesce and De Laurentiis 1996; De Laurentiis *et al.* 1999, 2001; T. Karanovic *et al.* 2001; Karanovic and Pesce 2002; T. Karanovic 2003, 2004a, 2004b, 2005, 2006), and all 83 species of stygal Dytiscidae have been described since 1999 (Watts and Humphreys 1999, 2000, 2001, 2003, 2004, 2006; Balke *et al.* 2004). 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 Pilbara where *c.* 350 species (predominantly ostracods (I. Karanovic 2007)) have been recorded (Department of Environment and Conservation Pilbara Stygofauna Survey, S. Halse, pers. comm.). The next best sampled area is the central and northern Yilgarn where *c.* 210 species, predominantly

Dytiscidae, are known. There are an estimated 82 stygobites and 34 stygophiles from southeastern Australian karst (Thurgate *et al.* 2001b) and 52 from alluvial aquifers (Hancock and Boulton 2008). Various other smaller, but significant, faunas are known from the Carnarvon Basin (*c.* 35 species in karst). These include relictual tethyan fauna containing higher taxa not known elsewhere in the southern hemisphere. Examples include the Perth Basin (karst and alluvium) Humphreys (2000b), Leeuwin-Naturaliste (karst: Jasinska *et al.*, 1996; Eberhard 2004), Kimberley (karst, sandstone and alluvia: Wilson and Ponder 1992; Cho *et al.* 2005), Ngalia Basin, NT (calcrete: Balke *et al.* 2004; Taiti and Humphreys 2001; Watts and Humphreys 2006), far north Queensland (karst and pseudo-karst: Howarth 1987), and Christmas Island (karst anchialine: Humphreys and Eberhard 2001; Namiotko *et al.* 2004; Humphreys and Danielopol 2005; Kornicker *et al.* 2006), and a diverse stygofauna is emerging in South Australia (R. Leijds, pers. comm.).

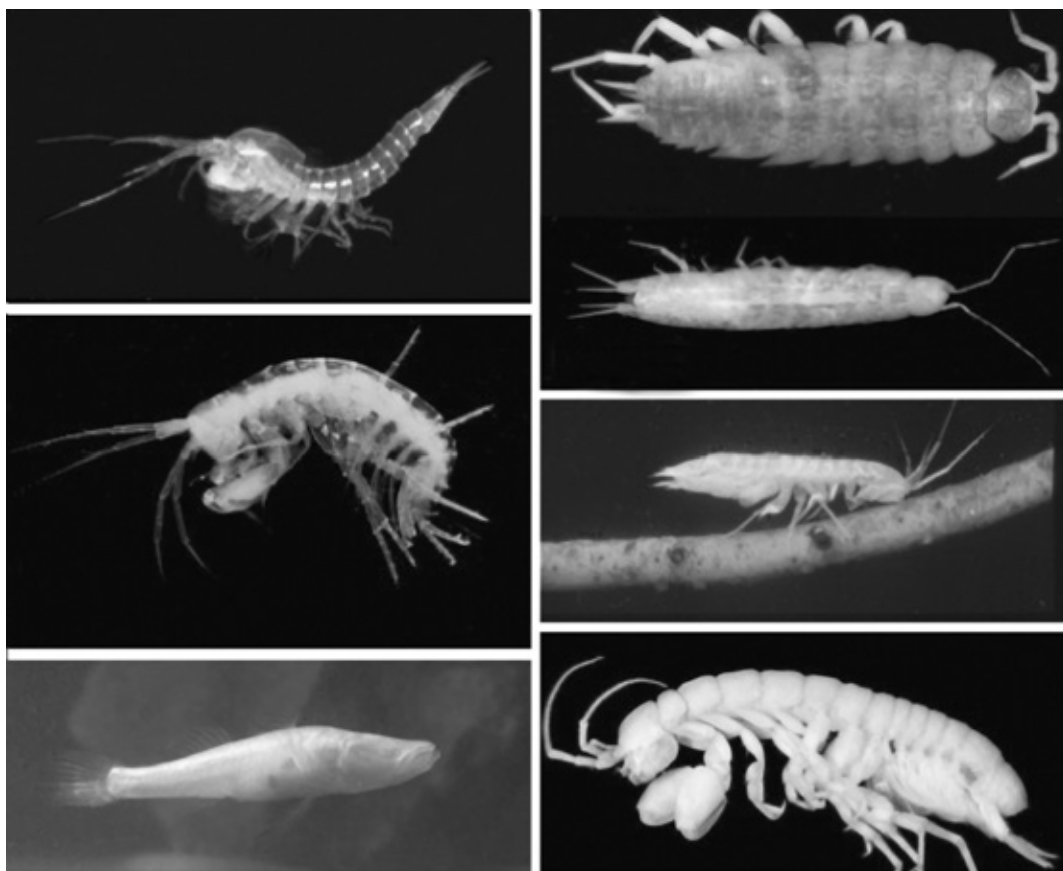


Fig. 1. Subterranean animals, clockwise from upper left: 1, *Halosbaena tulki* Poore & Humphreys (Halosbaenidae: Thermosbaenacea) inhabits anchialine and inland groundwater of north-western Australia, and is congeneric with anchialine species of north Atlantic shores; 2a, *Haloniscus searlei* Chilton, 1920 (Scyphacida: Oniscidea) inhabits salt lakes across southern Australia, while 2b, *Haloniscus* sp. 12 is a stygal species restricted to a single calcrete aquifer in the Carnegie palaeodrainage, WA; 3, *Tainisopus fontinalis* Wilson & Ponder, 1992 (Tainisopodidae: Tainisopidea: Isopoda), an isopod sub-order endemic to north-western Australia; 4, an undescribed species in the genus *Crenisopus* (Amphisopodidae: Phreatoicoidea) from Koolan Island, Kimberley; 5, *Milyeringa veritas* (Mees) (Eleotridae) from anchialine waters of north-western Australia, one of two cave fish species in Australia; 6, *Nurina poulteri* Bradbury & Eberhard, 2002 (Melitidae: Amphipoda) from the Nullarbor karst. Images: 3 and 6, S. M. Eberhard; 2, S. Taiti; 1, 5, D. Elford, WA Museum; 4, G. Wilson, Australian Museum (some images have been manipulated to monochrome and background detail adjusted).

At a very conservative estimate at least 750 species have been recorded from Australia, mostly in the last 10 years. This value represents 22% of the 3410 described species in 13 large higher taxa of freshwater stygobites that were enumerated by Scarsbrook and Fenwick (2003) from the world synopsis (Botosaneanu 1986); more than 500 of which are in the mineraliferous Pilbara and Yilgarn. While these figures are now dated, Australia, which comprises ~7% of the Earth's land area, would appear to exceed the world average density (species per unit area) of stygal species. By comparison, those major drainage systems that have been well studied in the northern hemisphere, have between 35 and 90 stygobite species (Dole-Olivier *et al.* 1994; Stanford *et al.* 1994; Ward and Palmer 1994). In their review of especially diverse stygal communities, Culver and Sket (2000) reported between seven and 48 species in non-porous aquifers or karst drainages. To place this in a broader perspective, some of the major karst areas of the northern hemisphere have been studied 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 troglifauna (Sket *et al.* 2004)). Slovenia, where stygal taxonomy started in 1768, has the highest density (114 species of stygobionts) of aquatic subterranean biodiversity (Culver *et al.* 2004). From six European countries (Belgium, France, Italy, Portugal, Slovenia, Spain) 1059 stygobiotic species have been recorded (Michell *et al.* in press). In the 48 contiguous states of USA ~1000 obligate cave species are known, of which 269 are stygobites (Culver *et al.* 2003) with no more than 80 species in any karst region.

Many regions of Australia remain entirely unexplored for subterranean fauna largely on account of the recent nature of

such enquiry, but often owing to their remoteness and/or the lack of access to the air and water filled voids of the subterranean habitat. For several reasons all the areas that have been examined are expected to yield considerably greater diversity when they have been adequately sampled. Firstly, the sampling density (sample sites area⁻¹) is low even within the better sampled regions; in the only regional survey (Eberhard *et al.* in press) sample site density was 0.0022 km⁻² (one site 460 km⁻²) while even within the pastoral areas of the arid Yilgarn, groundwater access is typically one shallow pastoral well (in themselves poor sites for stygofauna sampling) per four paddocks, a sample site density of 0.0025 km⁻² (one site 400 km⁻²), while large swathes of the deserts, even where there is prospective stygofauna habitat, lack entirely access to groundwater. Those regions more widely sampled for stygofauna have not been similarly sampled for troglifauna, although they are commonly present, including Palpigradi, Pseudoscorpionida, Schizomida, Meenoplidae (Homoptera: Fulgoroidea), Curculionidae, Araneae (several families). Secondly, species diversity will be under represented because most sites have been sampled on few occasions, frequently just once, and we know that species accumulation curves do not reach a plateau over many sampling occasions (Hancock and Boulton 2008; S. Halse and S. Eberhard, pers. comm.; W. F. Humphreys, S. J. B. Cooper, R. Leys and C. H. S. Watts, unpubl. data). This also implies that most species are rare (May 1976). Thirdly, as most species of stygobites appear to have very restricted ranges (e.g. Taiti and Humphreys 2001; Cooper *et al.* 2002; Leys *et al.* 2003; Watts and Humphreys 2006, and the 'short range endemics' of Harvey (2002)) infill sampling is likely to expose additional areas of endemism, such as discrete calcrete aquifers (Cooper *et al.* 2007), or groundwater tributaries

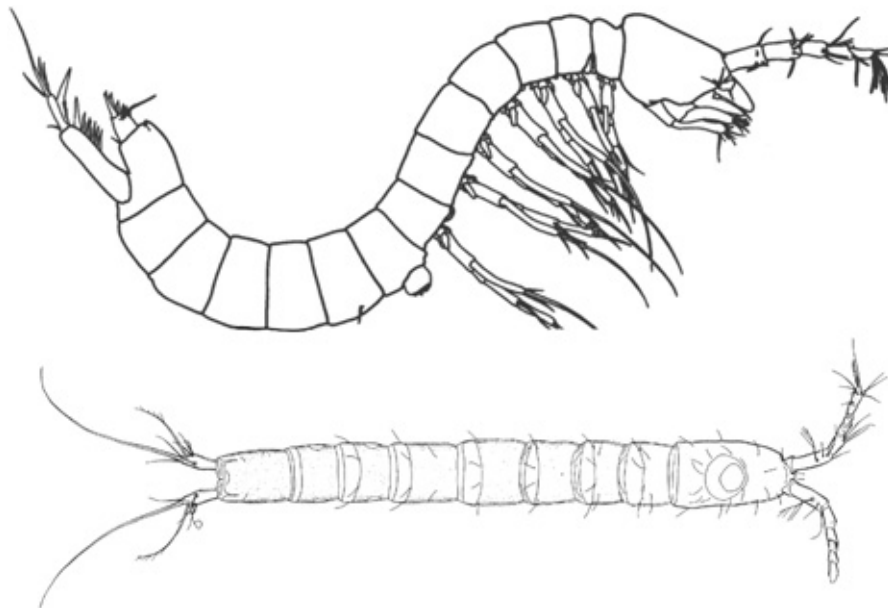


Fig. 2. Interstitial stygal species are typically vermiform. Upper: *Kimberleybathynella mandorana* (Cho, Park & Humphreys, 2005) (Parabathynellidae: Bathynellacea: Syncarida). Lower: *Parastenocaris eberhardi* Karanovic, 2005 (Parastenocarididae: Copepoda). Reproduced with permission. *Journal of Natural History* (<http://www.informworld.com>) and *Records of the Western Australian Museum*.

(Finston *et al.* 2007). Finally, the Australian stygofauna includes many cryptic species, for example, *Stygiocaris*, Decapoda: Atyidae (Knott 1993; Page *et al.* 2008), and amphipods (Finston *et al.* 2004, 2007; Cooper *et al.* 2007), as has been found to be the case in other stygofauna (Goricki and Trontelj 2006; Lefébure *et al.* 2006a, 2006b, 2007; Trontelj *et al.* 2007) and more generally (Bickford *et al.* 2007). Consequently, as taxonomic understanding emerges, both through detailed morphological and molecular studies (largely DNA but also allozymes: Humphreys and Adams 1991), the resolution of species boundaries will improve, and the recognised biodiversity will undoubtedly increase, substantially so in some lineages. For example, it is commonly found that isolated populations of stygofauna, especially amongst the various amphipod families, show deep phylogenetic divergences although they cannot easily be separated using morphological criteria (Finston *et al.* 2004, 2007; Cooper *et al.* 2007). Cryptic species generally are increasingly being exposed with the aid of molecular methods (Bickford *et al.* 2007) and this also occurs with some Australian troglifauna (cave dwelling animals) (Humphreys and Shear 1993; Humphreys and Adams 2001).

Owing to the wide latitudinal range (from tropical to temperate), climatic variety (desert to rainforest, coast to montane), the diversity of subterranean habitats within the Australian continent and its oceanic islands, and the diverse origins of the fauna, Australia arguably has the phylogenetically most diverse stygofauna globally. These habitats include typical terrestrial and freshwater aquatic karst (Humphreys and Adams 1991; Wilson and Ponder 1992; Thurgate *et al.* 2001b; Eberhard 2004), pseudokarst (Undara lava tube, sandstone, Humphreys 1995; Wilson and Keable 1999) and alluvial habitats (eastern Australia: Hancock and Boulton 2008), but phylogenetically significant stygofaunas also inhabit inland saline waters (Taiti and Humphreys 2001; Humphreys 2006), and anchialine ecosystems of both epicontinental (Humphreys 2000b, 2002b) and oceanic types (Humphreys and Danielopol 2005).

Origins

Subterranean habitats can be very persistent and cave soil from Jenolan Caves, New South Wales, has been dated to the Devonian (375 Mya) Osborne *et al.* (2006). Consequently many such habitats have been present throughout the formation and dissolution of Pangaea and the fragmentation of Gondwana. Similarly, aquifers may persist through geological eras. For example, the Edwards Aquifer, Texas, supports a diverse subterranean community derived from the Cretaceous marine inundation of the area (Holsinger and Longley 1980; Longley 1981, 1986, 1992). As subterranean communities may comprise lineages isolated underground in different geological eras they have the potential to yield information on past geological and climatic events in deep history, that is, to serve as 'living fossils' of certain provenance. This is especially the case for those higher taxa, largely Crustacea, the entire membership of which is confined to subterranean systems, as, for example, Bathynellacea, Thermosbaenacea and Spelaeogriffacea. Such taxa, isolated underground and producing no dispersive phase, potentially provide the most robust subjects for testing biogeographic hypotheses (especially Bathynellacea, largely confined to freshwater stygal habitats with a Pangaeian distribution).

graphical hypotheses (especially Bathynellacea, largely confined to freshwater stygal habitats with a Pangaeian distribution).

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 (Humphreys 2002a; Wilson 2008). There are those whose origins are related to the former extent of Tethys and represented by the anchialine fauna of both north-western Australia and Christmas Island. Several lineages from the former have congeneric species known elsewhere only from subterranean waters on either side of the North Atlantic, and the latter from comparable faunas on Hawaii, Ascension Island and Bermuda. Other lineages have affinities with Pangaea (e.g. Bathynellacea, and crangonyctoid amphipods) and Gondwana (e.g. phreatoicidean isopods, Spelaeogriffacea, and Candoninae ostracods).

The ostracod fauna of Western Australian continental subterranean waters is extremely diverse and almost exclusively comprises very old lineages within the subfamily Candoninae (Candonidae: Podocopida) that have clear Gondwanan affinities (Table 1). Others, from their distribution, provide information on eustatic changes, for example, *Milyeringa*, Pisces, Eleotridae (Humphreys 2001b); *Norcapensis*, Amphipoda, Melitidae (Bradbury and Williams 1997b); *Stygiocaris*, Decapoda, Atyidae (Humphreys and Adams 2001); *Halosbaena*, Thermosbaenacea (Humphreys 2001a), and the troglobite *Draculoides bramstokeri* Schizomida, Hubbardiidae (Harvey and Humphreys 1995), and the spreading aridity of central Australia during the Miocene (Leys *et al.* 2003). Although some regions may show repeated and continuing colonisation of groundwater, and even recolonisation of surface habitats (Culver *et al.* 1995), much of the Australian stygofauna appears to have been isolated underground in the geological past. For example, following a period of invasion of calcrete systems by dytiscid beetles, colonisation appears to have abated over the subsequent several million years (Leys *et al.* 2003), while the molecular phylogenies of several amphipod lineages show deep divisions between adjacent tributaries or calcretes (Cooper *et al.* 2007; Finston *et al.* 2007).

Based on the Pilbara environmental conditions (Eberhard *et al.* 2005), Humphreys (2001a) hypothesised that isolated headwater stygal communities would occur as a result of the reduced flow and consequent upstream progression of salinity

Table 1. The number of genera in each of three tribes of Candoninae (Candonidae: Podocopida) from the Western Shield of Australia and their continental distribution

(I. Karanovic 2004, 2005a; I. Karanovic, pers. comm.) Most genera are endemic to the northern part of the Western Shield and these Pilbara endemics are denoted by brackets. The continental distribution of these stygal ostracods is indicative of the Gondwanan affinities of these ancient lineages.

Tribe	Pilbara	South America	Africa	% genera Pilbara endemics
Candonopsini	2 (1)	2	0	50
Danielocandonini	3 (3)	1	1	100
Humphreyscandonini	8 (8)	0	0	100
Total	13 (12)	3	1	92

as the arid conditions intensified through the Tertiary. This hypothesis was first tested, and was found wanting, when applied to the stygal communities that inhabit calcretes found in palaeovalleys of the Yilgarn and that are deposited near salt lakes from the groundwater flow. There, molecular phylogenies of stygal dytiscid beetles do not map the drainage pattern but rather support multiple independent invasions of calcretes across a wide region (Cooper *et al.* 2002; Leys *et al.* 2003), a history also consistent with that of stygal oniscidean isopods (Taiti and Humphreys 2001; Cooper *et al.* 2008). Conversely, in the Pilbara, where rivers are still active, if episodic, the phylogeny of stygal amphipods in isolated headwater aquifers largely match the drainage pattern (Finston *et al.* 2007), consistent with the original hypothesis.

Species extent

Those stygofauna confined to subterranean life (stygobites) are typically restricted to a single aquifer. If there is a linear aquifer, such as along a river valley, then a species potentially may have a substantial geographic extent (Dole-Olivier *et al.* 1994) but as morphologically cryptic species of stygofauna occur commonly (see page 89), these more extensive species ranges may need to be reassessed. However, the data available indicate that most stygobites in Australia are indeed small range endemic species, confined to a single aquifer, such as the groundwater of a given headwater (theory: Humphreys 1999a; data: Finston *et al.* 2007), impounded karst (Thurgate *et al.* 2001a) or a groundwater calcrete (Humphreys 1999a; Taiti and Humphreys 2001; Cooper *et al.* 2002; Leys *et al.* 2003; Watts and Humphreys 2003). These conclusions are largely derived from studies on the Western Plateau of Australia, both in Western Australia and the Northern Territory. The younger topography of the Great Dividing Range near the eastern seaboard of Australia, and the impact to the south of Pleistocene glaciations (Eberhard *et al.* 1991), may have resulted in aquifers better connected both hydrologically and by substrates suitable for stygofaunal dispersal, and so containing wide-ranging stygal species, as reported from such landscapes in the northern hemisphere (Stanford and Ward 1993; Dole-Olivier *et al.* 1994; Stanford *et al.* 1994; Ward and Palmer 1994). However, the information relating to stygal systems of the eastern seaboard of Australia is largely derived from impounded karsts (Thurgate *et al.* 2001b), which, by definition, are isolated geologically. Studies of stygal communities in alluvial systems found on the eastern seaboard (e.g. Hancock and Boulton 2008) are still at too early a stage to draw any general conclusion as to whether the species have wider ranges than is typical of the western plateau.

Water characteristics

Stygofauna globally have been considered to be restricted to freshwater, rarely mildly brackish, except in the special case of those inhabiting anchialine ecosystems (see below). However, the Western Shield of Australia, which comprises amongst the oldest emergent landscapes on earth, contains groundwaters ranging, at the water table, from fresh to hypersaline, the latter commonly with a marked halocline. These far-inland aquifers (e.g. calcretes associated with Lake Way: T. Karanovic 2004b; W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper, unpubl.

data) may contain a mix of near-marine lineages (e.g. *Halicyclops*, Cyclopidae and hyalid amphipods) alongside ancient freshwater lineages (*Parastenocaris*, Parastenocarididae, Fig. 2; crangonyctoid amphipods). Furthermore, Bathynellacea, a largely freshwater stygal lineage with a global distribution, occur there in waters with salinity of oceanic levels. Such diverse stygofauna in continental waters of marine salinity (unknown outside the Western Plateau of Australia) occur in the context of the groundwater estuaries of far-inland salt lakes. In such situations the hydrogeochemical evolution of the groundwater, which has both spatial and temporal dimensions, causes the deposition of calcretes in which the void space develops that forms the stygal habitat.

Anchialine (or anchihaline) ecosystems occur in salinity-stratified coastal aquifers affected by marine tides but with no surface connection with the sea (Sket 1981, 1996; Stock *et al.* 1986), that I interpret as subterranean marine estuaries (Moore 1999; Humphreys *et al.* 2006). They are noted both for their relict faunas and their high species richness (Sket 1981, 1996), support an anchialine–endemic class (Remipedia) and at least ten new families of crustaceans have been described from anchialine systems in the last two decades. Globally, epicontinental 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 (Jaume *et al.* 2001). The fauna comprises numerous anchialine endemic higher taxa that display remarkable and extreme disjunct global distributions. Cape Range (north-western Australia) has the only example of a remipede-type (Humphreys and Danielopol 2005) anchialine community known outside the north Atlantic (Table 2). Elements of this fauna also occur on Barrow Island and on the Pilbara coast (Robe and Fortescue River deltas). Christmas Island, an isolated seamount in the Indian Ocean, also contains a significant, but entirely different anchialine fauna (procaridid-type: Humphreys and Danielopol 2005), the general composition of which is also predictable, often at the generic level, however far apart in the world they occur (they are also known from Bermuda, Ascension Island, Hawaii: Humphreys and Danielopol 2005).

While this discussion has focused on salinity, other physicochemical correlates may be important in influencing the distribution of groundwater fauna (Hose 2005, 2007; Humphreys 2007) but they will be mentioned here only in passing. Stygofauna are rich in calcareous systems where the pH is typically between 7.2–8.2. In the Pilbara, where there is a great diversity of groundwater Ostracoda (Karanovic 2007), the presence of 102 species was predominantly determined by pH and carbonate saturation. Water of low pH, with Eh values indicating a reducing environment, or with a total nitrogen concentration in excess of 10 mg l⁻¹ rarely contained Ostracoda (Reeves *et al.* 2007). However, even with these strong associations, ostracods were found in waters varying from pH 4.40–8.69, Eh -558 to +837 mV, TDS 54–13000 mg L⁻¹; %Ca²⁺ saturation 0.22–68.46. In contrast, *Danielopolina* (Ostracoda, Thaumatoocyprididae) occurs in anchialine systems of brackish to marine salinity (Humphreys and Danielopol 2005) and may be found below multiple layers of hydrogen sulphide in 100% seawater (Humphreys 1999b).

Many stygobitic animals are highly resistant to low levels of dissolved oxygen, some only being known from oxygen deficient waters (<0.5 mg L⁻¹ DO), and may sometimes rapidly switch between areas of low and high pO₂ (Hervant *et al.* 1998; Malard and Hervant 1999) and many hypogean species survive anoxia for much longer than their surface relatives (Hervant and Mathieu 1995; Hervant *et al.* 1995). In an Australian context stygofauna are commonly, perhaps typically, associated with suboxic waters in both anchialine (Humphreys 1999b; Seymour *et al.* 2007) and continental groundwaters (Watts and Humphreys 2004, 2006) with dissolved oxygen levels well below 1 mg L⁻¹.

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 and Williams 1997a; Bradbury 1999; Wilson and Johnson 1999; Humphreys 2001a; Wilson 2001, 2003; Karanovic and Marmonier 2003). Species belonging to ancient freshwater lineages have also been recovered from Proterozoic Pentecost Sandstone aquifers in the Kimberley (*Crenisopus*, Tainisopidae: Wilson and Keable 1999) and on small continental islands (Koolan Island, G. D. F. Wilson, pers. comm.), including Barrow Island that has an anchialine system (Humphreys 2002b; Cho *et al.* 2006a).

Those areas inundated by the sea in the Cretaceous and more recently, particularly the Eocene inundation, are largely devoid of these more ancient lineages (Bradbury 1999; Wilson and Johnson 1999) confined to the former 'islands', but there

is some intrusion of each fauna across the inundated/emergent 'divide'. For example, hyalid amphipods have deeply invaded the palaeovalleys of the Yilgarn, melitid amphipods are isolated in caves at *c.* 200 m altitude in Cape Range (Adams and Humphreys 1993) and Thermosbaenacea reach 300 m altitude in the Robe River, about the height of the Eocene high sea level stand (Humphreys 2001a), and crangonyctoid amphipods, a freshwater lineage, occur on the narrow coastal plain of the Perth Basin. Marine waters deeply penetrated the palaeovalleys of the southern Yilgarn (Jones, 1990; Worrall, (CRCAMET, CSIRO) pers. comm.), substantially increasing potential sites of invasion of groundwaters by marine lineages. The shores of former high sea level stands are likely sites for relictual marine fauna, while former islands are likely sites for ancient freshwater taxa restricted to small areas.

In addition to distribution patterns that have resulted from marine influences, there are regional patterns of obscure origin. The most remarkable is the difference between the northern Yilgarn and Pilbara regions of the Western Shield, which have formed a single emergent land mass since the Proterozoic (Fig. 3: BMR Palaeogeographic Group 1990). While each region has a diverse fauna, they have almost no genera in common and exhibit major differences in higher taxa (Table 3) including the globally spectacular diversity of Podocopida in the Pilbara (Table 1: Karanovic 2007), particularly in the endemic tribe Humphreyscandonini.

Biogeographic indicators

While obligate subterranean fauna as a class may be good candidates as historical biogeographic indicators, there is probably none more so than Bathynellacea (Syncarida). Bathynellacean ancestors inhabited tropical seas in the Carboniferous and Permian (Schminke 1973) but have long been mainly restricted

Table 2. Some major disjunctions of higher taxa restricted to subterranean systems

Taxon	Ordinal level	Australia	Elsewhere (lead in references)
Remipedia	Class	1 species: Anchialine Cape Range, single location. <i>Lasionectes exleyi</i> Yager & Humphreys, 1996	Caribbean (14 species), Canary Islands (1 species) (Koenemann <i>et al.</i> 2004)
Thermosbaenacea	Order	1 species: adjacent North West Shelf to 300 m AHD on Robe River; anchialine and freshwater. <i>Halosbaena tulki</i> Poore & Humphreys, 1992	Thirty-three species – amphi-Atlantic plus Mediterranean, Somalia, Cambodia (Wagner 1994)
<i>Speleophria</i> : Misophriodidea	Genus	1 species: Cape Range peninsula anchialine. <i>Speleophria bunderae</i> Jaume, Boxshall & Humphreys, 2001	Bermuda, Palau archipelago anchialine (Jaume <i>et al.</i> 2001)
Spelaeogriphacea	Order	2 species: Fortescue Valley, Pilbara. <i>Mangkurtu mityula</i> Poore & Humphreys, 1998; <i>M. kutjarra</i> Poore & Humphreys, 2003	Two species: Table Mountain, South Africa; Mato Grosso, Brazil (Poore and Humphreys 1998)
Tainisopidea	Sub-order (Brandt and Poore 2003)	<i>Tainisopus</i> : 2 species: Kimberley (Wilson and Ponder 1992) plus undescribed species (WFH, unpubl. data). <i>Pygolabis</i> : 6 species: Pilbara and Lyons River valley (Wilson, 2003)	Unknown outside north-western Australia
<i>Haptolana</i>	Genus	Several species adjacent North West Shelf. <i>Haptolana pholeta</i> Bruce & Humphreys, 1993; 2 spp. from Pilbara (N. Bruce, pers. comm.)	One species in each of Cuba and Somalia (Bruce and Humphreys 1993)
Procarididae	Family	One species Christmas Island, Indian Ocean. <i>Procaris noelensis</i> Bruce & Davie, 2006	Four species in two genera from anchialine waters of Hawaii, Ascension Island, Bermuda (Bruce and Davie 2006; Humphreys and Danielopol 2006)
Synbranchidae	Family	One of only two stygal species. <i>Ophisternon candidum</i> (Mees, 1962)	Stygal species Yucatan, epigean species Indian Ocean shores (Rosen and Greenwood 1976).

to interstitial groundwater (a few species occur deep in Lake Baikal, *Bathynella baicalensis* Bazikalova, 1954 and *Baicalobathynella magna* Bazikalova, 1954). This habitat and lifestyle severely limits their potential for wide scale dispersal and as such they are potentially supreme indicators for historical biogeography. This is supported by the distribution of several taxa (Table 4). While many genera have distributions suggesting a clear Pangaean or Gondwanan heritage (or some subset thereof), cladistic analysis of *Atopobathynella* species reveals a much more complex history (Cho *et al.* 2006a), as is being found in some surface taxa within Australia (Giribet and Edgecombe 2006). In addition there seems to be many short range endemic species within Bathynellacea (Spain, Camacho *et al.* 2006; Australia, Cho 2005; Cho *et al.* 2006a, 2006b; Guzik *et al.* 2008). From the evidence of *Billibathynella*, which closely resembles the hypothetical stem species of Parabathynellidae (Schminke 1973), it has been suggested that Parabathynellidae made the transition to groundwater in Notogaea and that this transition was made from freshwater (Cho 2005).

Types and distribution of substrates and fauna

Karst

Subterranean faunas are being found widely in Australia where there is adequate connected void space below ground, and groundwater faunas commonly occur where these voids are water filled. Most notably such voids are generally 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 (Fig. 4). Similar large voids may be found in sandstone karst and pseudokarst such as lava tubes. However, even in such settings, most of the fauna may be expected to occur in the finer voids, the mesocaverns, far too small for people to enter. Australia (Humphreys 2006: Fig. 2), as with other parts of Gondwana, has much smaller area of carbonate deposits than other parts of the world. Nonetheless, the Nullarbor is the largest area of exposed karst in the world – the Nullarbor is remarkable for the poverty of its stygofauna, despite its size, Tertiary age and mixed water

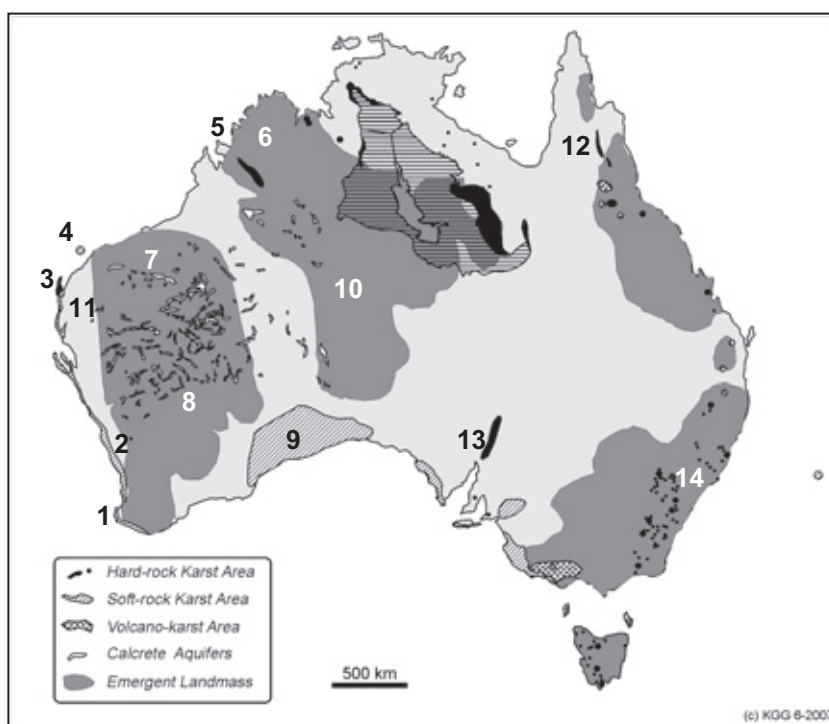


Fig. 3. Karst areas and areas continually emergent (pale shading) since the Palaeozoic on the current outline of Australia. Karst areas, especially Tertiary orogenic karst, are often rich in subterranean fauna. The non-emergent areas (derived from data in BMR Palaeogeographic Group, 1990) were inundated by the Cretaceous oceans and partly during the Eocene. 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. Graphic by K. G. Grimes. Inset: The general position of Australian locations referred to in the text. 1, Leeuwin–Naturaliste; 2, Perth Basin; 3, Cape Range; 4, Barrow Island; 5, Koolan Island; 6, Kimberley; 7, Pilbara, the location of the Robe River; 8, Hinkler Well calcrete drains towards Lake Way in the central Yilgarn; 9, Nullarbor; 10, Lake Lewis is in the Ngalia Basin, Northern Territory; 11, Carnarvon Basin; 12, Far North Queensland and Undara Lava Tube; 13, South Australia; 14, New South Wales and Jenolan Caves in the Great Dividing Range. Christmas Island (in the Indian Ocean, south of Java) is not shown.

Table 3. Overlap of stygal taxa between contiguous northern Yilgarn and Pilbara regions on the Western Shield of Australia

Shown are the number of species and genera of Copepoda, Candoninae (Candonidae: Podocopida), oniscidean and tainisopidean Isopoda, and Dytiscidae (Coleoptera)

Stygal taxon	Unit	Yilgarn	Pilbara	Overlap %	Reference
Copepoda	species	30	43	4	T. Karanovic 2004a, 2006
Copepoda	genera	15	25	21	As above
Podocopoda: Candoninae: Candonidae	species	5	58	0	I. Karanovic 2003a, 2003b, 2004, 2005a, 2005b, 2007; Karanovic and Marmonier 2002, 2003.
Podocopoda: Candoninae: Candonidae	genera	1	13	8	As above
Isopoda: Oniscidea	species	c. 20	0	0	Taiti and Humphreys 2001; Cooper <i>et al.</i> 2008, S. Taiti, pers. comm.
Isopoda: Tainisopidea	species	1 ^A	5	17 ^A	Wilson 2003
Coleoptera: Dytiscidae	species	97	0	0	Watts and Humphreys 1999, 2000, 2001, 2003, 2004, 2006

types, only one species is described, a melitid amphipod (Bradbury and Eberhard 2000), although three families of amphipod are reported to be present (S. Eberhard, pers. comm.). 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) (Hamilton-Smith and Eberhard 2000) and groundwater calcrete karst in the arid centre (Humphreys 2001a). While some of these contain rich stygofaunas (e.g. calcretes in Cape Range, and some impounded karst of NSW), others, notably the Nullarbor and Chillagoe (one species known), appear to have a sparse stygofauna (Humphreys and Harvey 2001).

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, solution by the groundwater develops an integrated subterranean drainage, in non-karstic systems fracturing may be the only mechanism of void formation and that may remain as open fractures to depths of at least 120 m in the Yilgarn (Dames and Moore 1993, cited in Johnson *et al.* 1999).

While carbonate karst typically produces a water chemistry benign for stygofauna (due to its slightly alkaline pH), water in igneous and metamorphic sedimentary rocks may be acidic and less suitable for stygofauna. This is probably the case in palaeovalleys to the south of the mulga–eucalypt line (or south of 29°S) in Western Australia where carbonaceous deposits from Eocene marine inundation of the southern palaeochannels

resulted in the reduction of sulfur, extensive anoxic conditions, and consequently a lack of calcrete (Morgan 1993). Nonetheless, stygofauna are found in areas inundated by the Eocene marine transgression near the south coast.

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 may also vary at a given position through time. As the characteristic void size may determine its suitability for colonisation by different 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 immediate likely impacts of anthropogenic activities on the stygofauna.

The thin colluvial and alluvial deposits in Kimberley headwaters contain a surprising array of stygofauna (meiofauna) with at least 17 species known from around Argyle Diamond mine with up to seven species per site (I. Karanovic 2004; T. Karanovic 2004b; Cho *et al.* 2005; W. F. Humphreys, unpubl. data).

The deep alluvial deposits of the eastern seaboard (Hancock and 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 and Boulton 2008). This will add a new dimension and further invigorate work on stygal ecosystems in Australia

Table 4. The continental distribution of various genera of Bathynellacea arranged in order of increasingly restricted endemism defined by increasingly restricted distribution amongst or within continents

Genus	No. species	Distribution	Source
<i>Hexabathynella</i>	23	Americas, Europe, Australia, New Zealand, Africa, Madagascar	Camacho 2006
<i>Chilibathynella</i>	3	South America, India, Australia, New Zealand	Camacho 2006
<i>Atopobathynella</i>	10	South America, Australia, New Zealand	Cho <i>et al.</i> 2006
<i>Ctenibathynella</i>	7	Africa, Middle East, S. America	Camacho 2006
<i>Thermobathynella</i>	2	South America, Africa	Camacho 2006
Gen. nov.	12	Western plateau, Australia	Guzik <i>et al.</i> 2008 (this issue)
<i>Kimberleybathynella</i>	6	north-western Australia	Cho <i>et al.</i> 2005

because the fauna is quite distinct (Thurgate *et al.* 2001a, 2001b; Hancock and Boulton 2008) from those found in the west, central and northern Australia, and it is in such settings that the surface water/groundwater interaction is most dynamic (Hancock 2002, 2004). Investigation of alluvial deposits will yield much information regarding surface impacts on groundwater, as well as the changing quality of surface waters as a result of their temporary membership as groundwater.

Habitat attributes

Spatial scale

Subterranean waters may conveniently be separated into groundwater and the hyporheic waters that occur below river channels (Jones and Mulholland 2000) and that 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 have been found to 800 m depth in an artesian system (Longley 1992) and invertebrates to a 1 km depth (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 epigeal 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 and hyporheic flowpaths (Dole-Olivier *et al.* 1994). Indeed, there is a thesis that sedimentary systems globally are interconnected along the hyporheic corridor providing a dispersal route for meiobenthic taxa along a spatio-temporally continuous alluvial aquifer system (Stanford and Ward 1993) that in the long-term is interconnected with other catchments (Ward and Palmer 1994). This is analogous to the global connectivity suggested to occur along the mid-oceanic ridges (Hart *et al.* 1985) or through the deep sea (Boxshall and Jaume 1999).

Hydrogeochemical evolution

Groundwater may have a prolonged residence time and undergo profound hydrogeochemical evolution (e.g. Hinkler Well: Mann and Deutscher 1978; Mann and Horwitz 1979, and Lake Lewis: Arakel 1986; English *et al.* 2001). This may affect the suitability of the water for particular stygofauna through a reduction in organic matter and the associated reduction in dissolved oxygen, and by the increase in dissolved solids (higher salinity). Although such change may occur over a protracted temporal scale (10000–100000 years), the spatial scale may be quite constrained (1–10 km), as for example in the groundwater estuaries of salt lakes (W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper, unpubl. data).

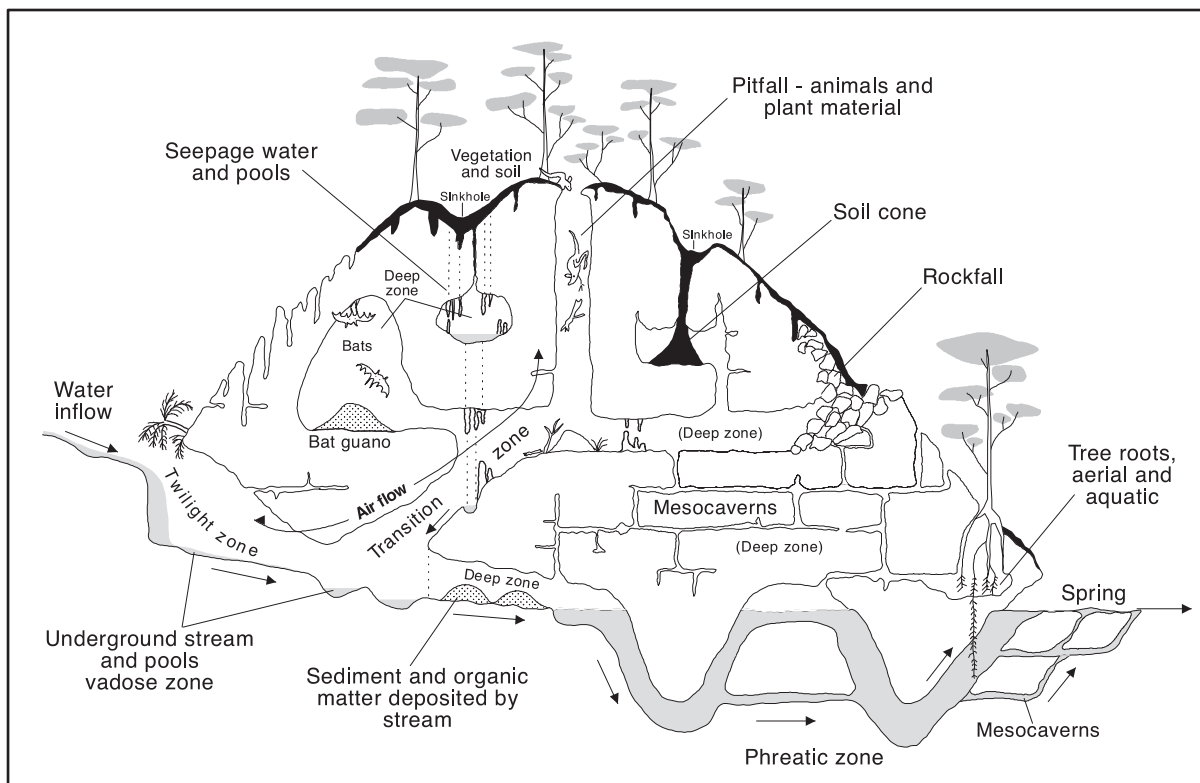


Fig. 4. Schematic section of karst showing how the subterranean voids are variously interconnected both internally and externally facilitating or impeding the movement of energy, materials and organisms. Other subterranean habitats have similar attributes working at different temporal and spatial scales but largely lacking open conduit flow. Figure from: Eberhard and Humphreys (2003). Reproduced with permission from University of New South Wales Press, Sydney.

Other groundwater habitats

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 and goethite pisolite deposits associated, for example, with westerly drainage from the Pilbara (Heim *et al.* 2006), are habitat for a rich troglobitic fauna (Harvey *et al.* 2008). The calcretes are associated with the hydrogeochemical cycles (Morgan 1993) in the palaeodrainage systems in the Yilgarn, WA and Ngalia Basin, NT, and for which the salt lakes (playas) represent the groundwater base level. Interestingly, both appear to have an inverted temporal profile owing to the mode of formation: pisolites because they form at the groundwater surface as water level declines over geological time (Heim *et al.* 2006), and calcrete because it is displaced upward from its formation at the groundwater surface (Mann and Deutscher 1978).

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. However, many things that affect groundwater may also impact on the epikarst. The study of epikarst fauna was pioneered in Europe by the extensive and elegant studies of B. Delay and R. Rouch (e.g. Delay and Juberthie-Jupeau 1976; Rouch and Carlier 1985) and more recently by Pipan (2005) in Slovenia and USA (T. Pipan, pers. comm.) and is known to occur in Australia (Eberhard 2004) where it may be expected to be diverse, especially in more humid climates.

Conclusions

Bradbury and Williams' (1997a) description of the emerging amphipod diversity in Australia's underground water as an Aladdin's Cave is clearly applicable generally to Australian stygofauna. Australia has a species rich and phylogenetically diverse stygofauna of very varied origins and occurs over a wide range of both substrates and water quality. In each respect, Australia is shaping up to become a 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 has the potential to emerge as a leading centre for tackling the management and conservation issues that have arisen and are present globally.

The renaissance of subterranean biology in Australia is youthful but there has emerged a vigorous and exciting research output in taxonomy and systematics, phylogeography, genetics, and evolutionary and conservation biology. This will surely progress, as it has in those regions of the world with a more mature heritage of subterranean biology, into ethology, neuroscience, physiology, evolution and development. But, unlike these regions with a long established tradition of research in subterranean biology, particularly southern Europe and North America, in Australia there is no background in the basic biology and ecology of the subterranean fauna, no knowledge of life cycles or reproductive information, and almost no population ecology or toxicology information (Hose 2005, 2007;

Humphreys 2007). This will seriously impede the development of subterranean biology in Australia, more so than on the other Gondwanan fragments, owing to a prevailing scientific culture that does not favour the study of basic biology. Significant resources are being devoted to assessing development projects for subterranean fauna, especially at mine sites in Western Australia. These need to be channelled appropriately so that they contribute properly to the understanding of this wealth of biodiversity and the ecological processes that support it and which it provides. Monitoring requirements need to extend beyond mere surveillance (Nichols and Williams 2006) so as to contribute to this broader understanding.

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