Aquifers: the ultimate groundwater-dependent ecosystems

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Abstract. Australian aquifers support diverse metazoan faunas comprising obligate groundwater inhabitants, largely crustaceans but also including insects, worms, gastropods, mites and fish. They typically comprise short-range endemics, often of relictual lineages and sometimes widely vicariant from their closest relatives. They have been confined to subterranean environments from a range of geological eras and may contain information on the deep history of aquifers. Obligate groundwater fauna (stygobites) occurs in the void spaces in karst, alluvial and fractured rock aquifers. They have convergent morphologies (reduction or loss of eyes, pigment, enhanced non-optic senses, vermiform body form) and depend on energy imported from the surface except in special cases of *in situ* chemoautotrophic energy fixation. In Australia, many stygofaunas in arid areas occur in brackish to saline waters, although they contain taxa from lineages generally restricted to freshwater systems. They may occur alongside species belonging to taxa considered typical of the marine littoral although far removed in space and time from marine influence. The ecological attributes of stygofauna makes them vulnerable to changes in habitat, which, combined with their taxonomic affinities, makes them a significant issue to biodiversity conservation. The interaction of vegetation and groundwater ecosystems is discussed and, in places, there are conservation issues common to both.

Introduction

Over the last decade it has become increasingly recognised that the groundwater ecosystems of Australia contain a highly diverse fauna comprising groundwater-inhabiting metazoans (Humphreys and Harvey 2001), referred to as stygofauna. This mirrors the situation for European groundwaters, which have been studied in much greater detail and for much longer (Botosaneanu 1986). In Europe, it has been recognised that groundwaters 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). Notwithstanding that, aquifers may be living museums containing a sample of the lineages that comprised the faunas from various geological periods. While a pattern of repeated colonisation, even recolonisation of surface habitats (Culver *et al*. 1995), may be an active process, some stygal lineages were apparently isolated underground in the Miocene (24–5 million years ago) by the onset of aridity in Australia (Humphreys 1993*a*; Cooper *et al*. 2002; Leys *et al*. 2003), or by orogenic and eustatic events (Stock 1980; Boutin and Coineau 1990; Notenboom 1991), processes that may have given rise to endemic higher taxa. Other lineages have become separated from their relatives by the movement of continental plates, before or after their isolation underground (Schminke 1974; Poore and Humphreys 1992, 1998; Wilson and Keable 1999; Humphreys 2000*a*, 2000*b*),

and, as with some epigean aquatic crustaceans (Daniels *et al*. 2004), have Gondwanan, even Pangaean affinities, or with distributions that clearly mirror the Greater Tethys (Boxshall and Jaume 2000; Humphreys 2000*b*, 2000*d*; Jaume and Humphreys 2001; Jaume *et al*. 2001; Namiotko *et al*. 2004). Hence, groundwater ecosystems may be very persistent through geological time (review Humphreys 2000*d*) owing to their obligatory subterranean biology, the fauna remain *in situ* in their original context and are consequently important subjects in unravelling deep history.

In the 19th and early 20th century, Australasia was at the forefront of research on aquifer organisms (Chilton 1882, 1882, 1883, 1884, 1894, 1918, 1925; reviewed Hurley 1990) but since then has lagged in the international league. Australia is not alone and 'Only very recently has the existence of groundwater animals ... on this continent [North America] been recognised to represent a largely unappreciated reservoir of biodiversity' (Ward *et al*. 1992). Within the last decade, major conferences and reports in Australia failed to encompass groundwater ecosystems or their fauna (Australian Water Resources Council 1992; Australian Geological Survey Organisation 1993). Thus, as recently as 1994, it was possible to write 'Recognition ... of the biodiversity inherent in the fauna ... of groundwaters, their vulnerability to groundwater

contamination, their functional role and their potential utility to hydrogeological investigations remains, in practice, unrecognised in Australia' (Humphreys 1994). Even as late as 1998, a lack of appreciation of the diversity and extent of aquifer ecosystems (Hatton and Evans 1998) led to the severe underestimation of the extent and significance of groundwater dependent ecosystems in Australia, a dismissal now firmly rejected (T. Hatton and R. Evans, pers. comm.). Only recently has subterranean fauna been included as a requirement for some environmental impact assessment (Western Australia—Hamilton-Smith *et al.* 1996; Environmental Protection Authority (EPA) 1998; Tasmania—Eberhard 1995, 1999; Tasmanian WHA 1999), and is now routine in Western Australia (EPA 2003). The application of fauna protection legislation to several stygal species and communities (Western Australia: Conservation and Land Management (CALM) 2001; Commonwealth Environmental Protection and Biological Conservation (EPBC) Act 1999), has raised considerably awareness of stygofauna to a broader public (Playford 2001).

Groundwater ecology is a young subject globally and the last decade saw the first international conference of groundwater ecology (Stanford and Simons 1992) and a major textbook on the subject (Gibert *et al.* 1994). Internationally, groundwater ecosystems, especially those in karst, have gained recognition by the Council of Europe (Council of Europe 1992; Juberthie 1995; PASCALIS Project under the *Fifth Framework Programme*, European Commission), the World Bank (Vermeulen and Whitten 1999), and under the Ramsar Convention—*Convention on Wetlands of International Importance especially as Waterfowl Habitat, Ramsar, Iran, 1971*—(resolved at Brisbane meeting, 1996; Humphreys 2000*b*). Whereas, in Australasia,

> '... *given their high conservation value, the groundwater upon which* [underground aquatic ecosystems and their novel fauna] ... *depend should be given the highest level of protection*' [emphasis added] (ANZECC ARMCANZ 2000).

As this paper is destined for a botanical journal, I focus, where possible, on botanical links with groundwater systems. There is clear and well established coupling of groundwater ecosystems and vegetation through the provision of allochthonous energy from plants to the groundwater, and conversely, by the provision of water to the vegetation. Here, in part, I attempt to identify and discuss other types of association between vegetation and groundwater ecosystems. It is also appropriate to provide some references to facilitate the reader's access to the broader literature on groundwater ecosystems. The best general text is Gibert *et al.* (1994) and other important international sources may be gleaned from Griebler *et al.* (2001) and Wilkens *et al.* (2000). Much of the Australian literature, not addressed directly here, can be recovered from papers in

Boulton (2000), Boulton and Hancock (2006), Boulton *et al.* (2003), Hancock *et al.* (in press), Humphreys (1993*a*); Humphreys and Harvey (2001), and from some less widely available texts (Humphreys 2000*c*, 2002*a*; Eberhard 2004).

Classification

Except in karst areas, where vertebrates may occur, groundwater animals are invertebrates, which display various degrees of dependence on subterranean existence. They range from occasional inhabitants to species totally dependent on groundwater. Some animals occur in groundwater either by chance (termed *stygoxenes*), while others have varying degrees of affinity for groundwater, inhabiting it on a permanent or a temporary basis (termed *stygophiles*). Only *stygobites* are obligate inhabitants of groundwater. Stygoxenes, stygophiles and stygobites collectively comprise the stygofauna (following Gibert *et al.* 1994). Deeper groundwater ecosystems are largely inhabited by stygobites that comprise elements of the ultimate groundwater dependent ecosystem. Stygobites are overwhelmingly crustaceans that belong to many higher taxa. However, in Australia, the stygofauna may include stygobitic species of worms, snails, mites, insects and fish (Humphreys 2000*a*, 2002*b*; Humphreys and Harvey 2001) (e.g. Fig. 1).

Stygobites have convergent morphologies, exhibiting a reduction or loss of eyes, pigments and hardened body parts, they are commonly translucent, and they have enhanced non-optic sense organs. Conversely, the relaxation of constraints on epigean lifestyles may release unexpected morphological diversity, as seen, for example, in stygobitic diving beetles (Dytiscidae; Watts and Humphreys 1999, 2000, 2001, 2003, 2004). Smaller members are often characteristically vermiform which aids their movement within the alluvium (Coineau 2000). Stygobites are in intimate contact with their milieu, generally have no resting or dispersal stages, are slow-growing, long-lived, have few young and often sparse populations. These attributes make them suitable bioindicators, efficient bioaccumulators, slow to recover from reductions in their populations and difficult to study. Owing to these biological characteristics, the species inhabiting groundwater ecosystems are commonly short-range endemics (Cooper *et al.* 2002; Leys *et al.* 2003); that is, they are restricted to a small geographic area, are vulnerable to change and are a significant issue for biodiversity conservation.

Surface waters and groundwater may interact in an ecotone beneath and alongside surface waters, referred to as the hyporheic and parafluvial zones respectively. Greatest interaction occurs in zones of downwelling and upwelling water and such zones can be identified by piezometric measurements and because of the partial imposition of their chemical and biological signature on the receiving zone. This important ecotone, between surface and groundwater,
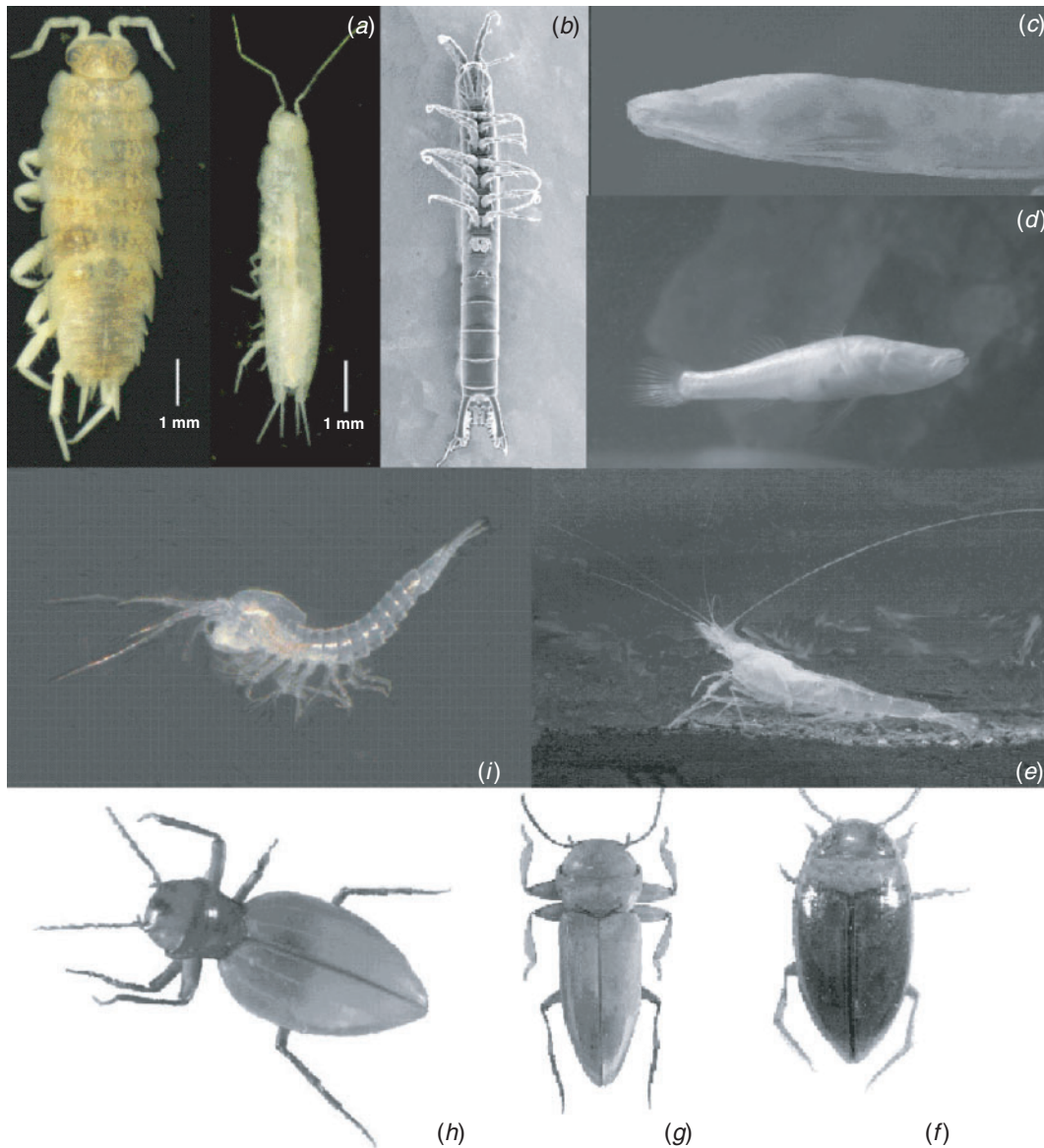
Fig. 1. Groundwater animals (sb) and surface relatives (epi). Clockwise from upper left. (*a*) *Haloniscus searlei* Chilton (epi) and *Haloniscus* sp. nov. (sb); (*b*) Bathynellidae, Bathynellacea, ventral view, collage from scanning electron microscope images by J-L Cho; (*c*) *Ophisternon candidum*, blind cave eel, head (sb); (*d*) *Milyeringa veritas*, cave gudgeon (sb); (*e*) *Stygiocaris stylifera* Holthuis, Atyidae (sb); (*f*) *Limbodessus compactus* (Clark) (epi); (*g*) *Limbodessus macrotarsus* (Watts & Humphreys) (sb); (*h*) *Nirripirti arachnoides* Watts & Humphreys (sb); (*i*) *Halosbaena tulki* Poore & Humphreys, Thermosbaenacea, anchialine, (sb). Images: Douglas Elford, Western Australian Museum (*c–f, i*); Joo-Lae Cho (*b*); Stefano Taiti (*a*); Chris Watts (*f–h*).

is discussed by Boulton and Hancock (2006), whereas my purpose here is to discuss the proper groundwater ecosystem, a zone largely inhabited by stygobites (obligate groundwater fauna) and which has a much less intimate connection to the epigean world.

Where

Subterranean ecosystems are most diverse in areas where subterranean voids are well developed and these areas typically are in classic karst, such as Tertiary (65–1.8 million years ago) orogenic karst, and the Dinaric karst of the Balkans. Cape Range, Western Australia, is the only Australian example of such Tertiary orogenic karst (Fig. 2). However, non-carbonate karst and pseudokarst such as lava tubes may also harbour diverse subterranean faunas. Recently, groundwater calcrete aquifers that are associated with the chains of salt lakes in the palaeovalleys of the Australian arid zone have been recognised to contain diverse stygofaunas typically comprising short-range endemic species (Humphreys 1999*a*, 2001*a*; Cooper *et al*. 2002).
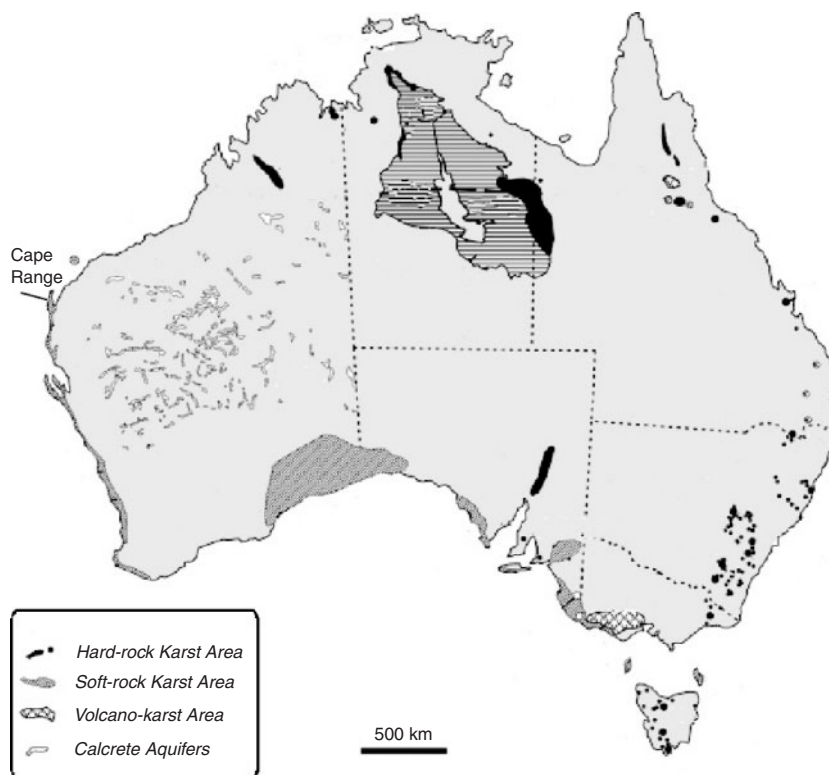
Fig. 2. Karst areas of Australia. The areas in non-coastal parts of Western Australia are groundwater calcretes. Graphic courtesy of K. G. Grimes with modification.

The calcretes are discrete, shallow and thin (10–20 m thick) carbonates deposited from the groundwater flow in palaeovalleys immediately upstream of the salt lakes (playas) that represent the groundwater base level (Humphreys 1999*a*, 2001*a*) and as such often support phreatophytic vegetation. However, stygofaunas comprising taxa of appropriate size to the voids are found in fractured rock aquifers (Pilbara), thin regoliths (Kimberley), and coarse (Caranarvon Basin) and fine alluvia (Perth Basin). Whereas stygofauna in groundwater were originally accessed largely by sampling cave waters, in recent decades the research has increased in scope by accessing groundwater through artificial access points such as bore holes (tube wells) and hand-dug wells. This has permitted a wider range of karst to be sampled and allowed groundwater ecosystems to be accessed from alluvial and fractured rock aquifers.

Coarse alluvial deposits are also important areas for subterranean ecosystems (e.g. in Australia the Robe and Fortescue deltas, Pilbara) but the distinction between hyporheic (see Boulton and Hancock 2006) and groundwater systems is not yet well established in such areas in Australia. As alluvial deposits become finer they become more restrictive for subterranean life (Pospisil 1994), not only by limiting the size of individuals and so the range of taxa that can occur within the voids, but also because

as sediments become finer so water flow is impeded. This, in turn, limits the flux of water and its contained oxygen and nutrients, especially organic carbon, to act as an energy source for the ecosystem (see descriptions in Boulton 2001; Humphreys 2002*a*).

The ^{36}Cl isotopic data suggest that substantial recharge of the superficial aquifers in the Ngalia Basin, Northern Territory, occurs only during favourable interglacial climatic regimes. The indicated groundwater residence time near the playa lakes is often considerably in excess of 80 kyr and consequently dominated by sulfate and chloride, reflecting the long residence times in the groundwater flow (Jacobson and Wischusen 2001). Despite these long temporal flowpaths, these groundwaters contain a rich stygofauna bordering the playas (Taiti and Humphreys 2001; Balke *et al*. 2004; W. F. Humphreys and C. H. S. Watts, unpubl. data).

Habitat characteristics

Perpetual darkness is the most obvious characteristic of subterranean life, one shared with life in abyssal depths. However, groundwater systems often exhibit large, even sharp, gradients of organic carbon, oxygen, salinity, Eh, pH and water chemistry both along the groundwater flowpath (which, importantly, also represents a temporal gradient), and with depth within the aquifer. The establishment of the gradients may reflect organic matter respiration in the

groundwater flow, or abiotic reactions resulting from the characteristics of the aquifer matrix (Griebler 2001).

Anchialine habitats are coastal mixohaline groundwaters affected by marine tides, usually with a reduced subaerial exposure (Stock *et al*. 1986) (analogous to groundwater estuaries; Moore 1999). They are circum-globally distributed in tropical/subtropical latitudes, mostly in arid coastal areas. They have a stable water column but with sharp physico–chemical gradients and typically have freshwater layered over seawater (Sket 1981, 1996). Analogous haloclines are also found in some arid-zone aquifers of the continental interior (Watts and Humphreys 2003). In the arid-zone anchialine ecosystem at Bundera Sinkhole, Cape Range, the gradient with depth goes from about half seawater at the surface to seawater at depth. The halocline is associated with sharp changes in Eh, oxygen, water chemistry and hydrogen sulfide (Fig. 3) which is associated with chemoautotrophic bacteria (Humphreys 1999*b*). Below this layer occurs a unique ecosystem of relictual higher orders of crustaceans, elsewhere known only from anchialine caves of the North Atlantic (Humphreys 2000*a*, 2002*b*). On the arid interior plateaux, calcrete aquifers occur near salt lakes and have surface water ranging from freshwater to seawater salinities. Whereas in the Pilbara water typically remains fresh throughout the depth profile, in the Yilgarn strong salinity gradients may occur reaching several times seawater salinity at depth (W. F. Humphreys, unpubl. data; Watts and Humphreys 2004) (Fig. 4).

Biodiversity

Groundwaters comprise complex ecosystems interacting with surface systems in a manner pertinent to both groundwater and surface-water quality, but in ways as yet poorly understood (Gibert *et al*. 1994; Boulton 2000). As such, the groundwater fauna may maintain ecosystem function to protect groundwater quality (Murray *et al*. 2006);
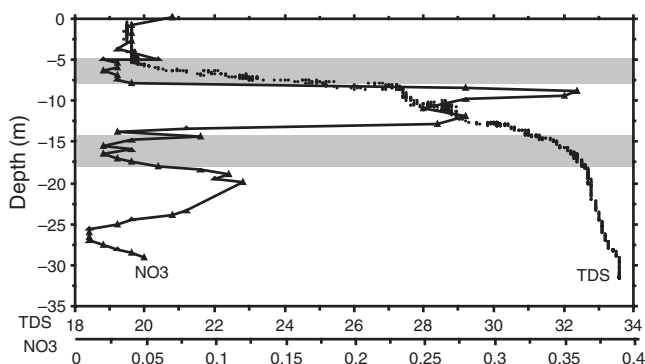
this is the rationale behind the global effort to conserve biodiversity. In recent years stygofauna (groundwater animals) and groundwater (or aquifer) ecosystems have become the focus of much attention, owing to both the biodiversity they contain and their functional properties (Botosaneanu 1986; Gibert *et al*. 1994; Juberthie and Decu 1994, 1998, 2002; Culver *et al*. 1995; Wilkens *et al*. 2000). Globally, subterranean fauna comprises a significant component of biodiversity (Rouch and Danielopol 1997; Sket 1999) and particularly biodiverse areas have been referred to as 'hot-spots' of subterranean biodiversity (Rouch and Danielopol 1997; Culver and Sket 1999*b*; Danielopol *et al*. 2000*b*; Danielopol and Pospisil 2001). Certain areas in Australia also contain particularly diverse stygofaunas (Bradbury and Williams 1997*a*, 1997*b*; Humphreys 2001*a*; papers in Humphreys and Harvey 2001; Cooper *et al*. 2002; Boulton *et al*. 2003; Karanovic 2003*a*, 2004; Karanovic and Marmonier 2003).

Despite numerous isolated karsts on the humid eastern seaboard of Australia, it is the arid zone that is yielding some of the most interesting and more diverse groundwater faunas (Humphreys 2001*a*; Watts and Humphreys 1999, 2000, 2001, 2003, 2004; Taiti and Humphreys 2001; Cooper *et al*. 2002; Leys *et al*. 2003). As elsewhere, however, great diversity is also found in classical karst (Thurgate *et al*. 2001*a*, 2001*b*), anchialine (Humphreys 1999*b*, 2000*a*, 2000*c*; Jaume and Humphreys 2001; Jaume *et al*. 2001) and alluvial settings (Boulton *et al*. 1998; Hancock *et al.* in press).

Globally, stygal biodiversity overwhelmingly comprises crustaceans belonging to many higher taxa, and this is true in Australia. A partial list of Australian higher taxa containing stygal representatives indicates the dominance of crustaceans in the stygofauna; 82% of the 55 higher taxa listed in Table 1 are crustaceans that belong to many
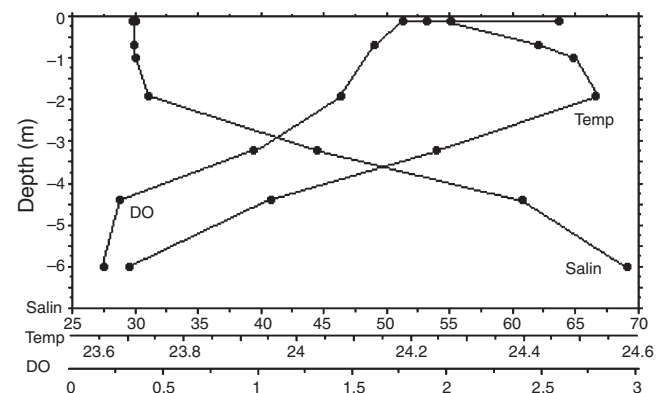

Fig. 3. Changes in water quality with depth (0–33 m) in Bundera Sinkhole, an anchialine ecosystem (original data). Other parameters may be seen in Humphreys 1999*b*. Stippled bars denote elevated hydrogen sulfide layers; fine line, NO3; heavy line, salinity as total dissolved solids (g L^{-1}).

Fig. 4. Vertical profile of salinity (mg L^{-1}), temperature (°C) and DO (mg L^{-1}) in saline bore in the centre of the Western Shield at Lake Way. Despite having sea water salinity at the surface, this site supports stygal oniscideans, bathynellaceans, harpacticoid copepods, amphipods and dytiscid diving beetles.

Table 1. The distribution of 55 families of stygofauna amongst higher taxa in Australia, of which 82% of families are crustaceans

Taxon	No. of families	Notes
Platyhelminthes: Turbellaria	1	
Annelida: Polychaeta	1	First record of a cavernicolous spionid
Annelida: Oligochaeta	2	
Mollusca: Gastropoda	1	
Syncarida	4	Basal Parabathynellidae
Remipedia: Nectiopoda	1	One species in Southern Hemisphere
Copepoda: Calanoida	3	Copepod affinities—freshwater: generally with Gondwana or Eastern Gondwana; marine origin generally with Tethyan connections
Copepoda: Cyclopoida	1	
Copepoda: Harpacticoida	7	
Copepoda: Misophrioida	1	Tethyan affinities
Ostracoda: Myodocopida	1	One species in Southern Hemisphere
Ostracoda: Podocopida	5	
Peracarida: Spelaeogriphacea	1	Two species in Australia
Peracarida: Thermosbaenacea	1	One species in Southern Hemisphere
Amphipoda	9	
Isopoda	8	Endemic order & Gondwanan affinities
Decapoda	3	
Arachnida: Acarina	2	Gondwanan affinities
Insecta: Coleoptera	1	Globally richest GW beetle fauna by factor of 10
Vertebrata: Pisces	2	

lineages. Particularly diverse are Amphipoda (Perthiidae, Neoniphargidae, Paramelitidae, Eusiridae, Paracalliopiidae, Melitidae, Hyalidae and Bogidiellidae), Isopoda (Oniscidea, Asellota, Phreatoicidea, Cirolanidae and the Australian endemic Tainisopidea) and Ostracoda. Globally, Candoninae (Candonidae) ostracods are common elements of stygofauna and recent finds from the Pilbara have resulted in the description of ~25% of the world's genera. These new genera are more closely related to the South American and African Candoninae than to European ones (I. Karanovic, pers. comm.; Karanovic 2003*a*, 2003*b*; Karanovic and Marmonier 2002, 2003). Other significant stygal ostracods from Australian groundwaters include Darwinulidae (Martens and Rossetti 2002), *Microceratina* (Namiotko *et al.* 2004) and *Danielopolina* (Thaumatocypridoidea). Numerous new species of groundwater copepods are being described from Australia, largely from the Western Shield, including five new genera of Cyclopoida and Harpacticoida, and several genera are reported for the first time from Australia (*Nitocrella* Ameiridae (Eurasia), *Parapseudoleptomesochra* (global), *Haifameira* Ameiridae (depth of Mediterranean Sea) and the family Parastenocarididae (Pangaea, freshwater)) (T. Karanovic, pers. comm., Karanovic 2003, 2004; Karanovic *et al.* 2001; Pesce *et al.* 1996*a*, 1996*b*). The Syncarida are also proving to be diverse with several stygal Anaspidacea (Zeidler 1985) and a great diversity of the stygobitic Bathynellacea (both Parabathynellidae and Bathynellidae) are being recognised, including new genera and species with unique lifestyles and unexpectedly saline habitats (Cho 2005; Cho *et al.* 2005; W. F. Humphreys, unpubl. data; J.-L. Cho, pers. comm. 2004).

The only two species of vertebrate stygobites known from Australia, which occur in sympatry in the Cape Range karst, north-western Australia, are the blind cave eel, *Ophisternon candidum* (Mees 1962) (Synbranchiformes: Synbranchidae), the world's longest stygobitic animal, and the cave gudgeon, *Milyeringa veritas* Whitley 1945 (Perciformes: Eleotridae). In the same anchialine systems several higher taxa occur that are mostly unknown elsewhere in the Southern Hemisphere, with their closest relatives, commonly congeneric species, being known from similar ecosystems on either side of the North Atlantic. They include Thermosbaenacea, Remipedia, thaumatocypridid ostracods, epacteriscid and pseudocyclopiid calanoid copepods, speleophriid misophrioid copepods, hadziid amphipods and atyid decapods, together largely comprising a relict tethyan fauna (Humphreys 2000*a*; Jaume and Humphreys 2001; Jaume *et al.* 2001). Elements of this tethyan fauna also occur on Christmas Island, Indian Ocean (Namiotko *et al.* 2004; Kornicker *et al.* in press), otherwise considered to support a distinct procaridid decapod anchialine community (Humphreys and Danielopol 2006) restricted to three other seamount islands around the globe (Ascension Island, Bermuda, Hawai'i: Humphreys and Eberhard 2001).

Several of these Australian stygobites are members of crustacean higher taxa belonging to lineages that globally are entirely stygal, such as Spelaeogriphacea (known from only four species, Pilbara (2 species), Brazil (1),

South Africa (1)), Thermosbaenacea, Remipedia (tethyan anchialine), Bathynellacea, and the Australian endemic Tainisopidea. As such, with their restricted powers of dispersal and typically short-range endemic status, they are especially useful to untangle deep biogeographical history.

Less common components known from the groundwater fauna include gastropod molluscs (especially Hydrobiidae), Oligochaeta (especially Phreodrilidae: Pinder and Brinkhurst 1997), momonid and mideopsid Acarina (Harvey 1998; M. S. Harvey, pers. comm. 2004), Insecta (especially Coleoptera: Dytiscidae of more than 80 species occur in groundwater calcretes in the arid zone, all being short-range endemic species; Watts and Humphreys 1999, 2001, 2003, 2004). There are, of course, numerous meiofauna groups and minor elements of the groundwater fauna that are even more poorly understood, including microturbellarians, rotifers, nematodes and protozoa. Finally, and whatever the energy source, microorganisms (mostly bacteria and fungi) capture the energy (Findlay and Sobczak 2000), utilising either heterotrophic or chemotrophic pathways, and the resulting biofilms are grazed by the stygal animals, thus supporting the groundwater ecosystem, *sensu lato*.

Several parts of Australia, including the cratons and associated orogens that comprise the 'Western Shield' (Hocking *et al*. 1987), have been emergent above sea level since the Proterozoic (Fig. 5), although the extreme longevity of the cratonic interiors of Australia has been challenged

Fig. 5. The current outline of Australia superimposed on the areas (dark) continually emergent since the Proterozoic, of which, to the left, is the Western Shield, comprising the Pilbara and Yilgarn cratons and associated orogens (shaded area to left: west). Derived from data in BMR Palaeogeographic Group (1990).

(Belton *et al*. 2004). Amongst these is the Western Shield, which, nevertheless, must rank amongst the oldest non-marine landscapes on Earth and as such it supports many of the ancient freshwater lineages, including the phreatoicidean isopods, crangonyctoid amphipods and candonine ostracods (Bradbury 1999; Wilson and Johnson 1999; Humphreys 2001*a*; Wilson 2001). However, as discussed above, waters on the central parts of the Western Shield have different salinities, ranging from fresh to hypersaline, and this is reflected in the fauna found there. Some ecosystems contain a mix of near-marine lineages (e.g. Cyclopidae, *Halicyclops* and ceinid and melitid amphipods) alongside ancient freshwater lineages (*Parastenocaris*, Parastenocarididae and crangonyctoid amphipods). Furthermore, Bathynellacea, a stygal lineage with global freshwater distribution, occurs there in waters of marine salinity alongside taxa in freshwater (W. F. Humphreys, unpubl. data). This circumstance may reflect that the salinity is stratified, sometimes with hypersaline groundwater in these palaeodrainage systems, as well as the ancient origins of the fauna. The occurrence of ancient lineages, with brackish water ancestry, in shallow aquifers within the palaeovalleys of the Western Shield, and elsewhere (e.g. Ngalia Basin, Northern Territory: Balke *et al*. 2004; W. F. Humphreys and C. H. S. Watts, unpubl. data) suggests, independent of evidence derived from salt lakes (De Deckker 1983), that such saline conditions have a long history in the Australian landscape.

Processes

Many species that belong to lineages that are predatory in epigean environments are found to be omnivorous or polyphagous in subterranean environments. Thus, in addition to the general lack of primary production (acknowledging occasional chemoautotrophy), there are few top predators and consequently subterranean ecosystems have a truncated functional biodiversity (Gibert and Deharveng 2002).

By analogy with surface ecosystems, invertebrates have numerous potential functional roles in groundwater systems, but as yet experimental evidence is largely lacking. These roles include the maintenance of voids, suggested also for protozoa (Haack and Bekins 2000), the alteration of redox gradients, enhancing the release of organic carbon and the cycling of nutrients (which often limit bioremediation processes: Haack and Bekins 2000), promotion of biofilm activity (*inter alia* through grazing, nutrient cycling and improved hydraulic flow paths), the provision of favourable sites for microbial activity (see also Gebruk *et al*. 1997 below), the acceleration of cycling, movement and mass transfer of energy and materials through the sediments, alteration of population size and community structure through predation ('top-down' effects) and as prey ('bottom-up' effects). These issues are discussed and referenced more fully by Boulton (2000: table 2). Although it is recognised that consortia of microorganisms can work, by mechanisms

yet to be identified, to breakdown contaminant plumes (Haack and Bekins 2000), it has yet to be recognised whether stygofauna 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 2000*a*).

The greater the distance of the groundwater habitat from epigean influence the greater 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: fig. 9). Concomitantly, biological activity decreases as a result of the depletion of organic matter and oxygen through ecosystem respiration. In consequence, changes to the near-surface groundwater are likely to have the greatest impact on energy flux within the ecosystem. Depending on the nature of the aquifer, changes to the groundwater elevation may move its upper layers into or out of layers suitable to support the stygal ecosystem, either with respect to the matrix void space or with respect to physicochemical composition. Such changes may enhance or diminish the suitability of the ecosystem to support a given stygal assemblage. Conversely, Simon (2000) has shown that regular changes in water level may be important in maintaining the trophic dynamics of some karst aquifers.

Removal of oxygen in confined or semi-confined aquifers, where replenishment of dissolved oxygen (DO) is not possible, occurs over time in the order of 10^1 to 10^5 years, largely depending on organic carbon content of sediment (Malard and Hervant 1999). Consequently, the addition of organic carbon, which is typically very low in groundwater ($<1\,\mathrm{mg\,L^{-1}}$ in pristine aquifers: Gounot 1994), will deplete DO in such aquifers and may severely alter the ecosystem. One method by which DO may inadvertently be reduced in such situations is by the intrusion of tree roots and organic matter through anthropogenic openings. Mineral exploration bores are typically abandoned, plugged only superficially and left uncased and these can form conduits for roots and organic detritus to enter the groundwater. It is not known whether this has an impact on any stygal ecosystem in Australia and primary research would be required to determine whether the guidelines governing mineral exploration drilling should be given the force of the regulations governing water bore drilling (MPR 2002).

Even in unconfined karst aquifers, sewage-polluted sites have been shown to exhibit large changes to species composition and relative abundance with respect to uncontaminated sites (Lez karst system, Hérault, France: Malard *et al.* 1996). Contamination from sewage (Sinton 1984; Malard *et al.* 1994; Simon and Buikema 1997), metals (Plénet *et al.* 1992), inorganic chemicals (Mösslacher *et al.* 2001) and pesticides (Notenboom *et al.* 1994) have

been found to reduce diversity in stygofaunal communities. Organic pollution can extirpate stygofauna and lead to its replacement by epigean fauna (Malard *et al.* 1994; Notenboom *et al.* 1994). For example, septic effluent in Banners Corner Cave stream increased the food supply for the stygofauna but damaged the ecosystem (Simon and Buikema 1997) and Culver *et al.* (1992) recorded the loss of cave isopods and amphipods in Cedars karst system, Virginia, as a result of organic pollution.

Food (energy)

Caves and groundwater are typically low in sources of energy (Huppop 2000). Subterranean biota principally rely on energy from exogenic (allochthonous) organic matter that is derived from surface plants and transported to subterranean habitats by water flow, percolation, gravity or animals in the form of coarse and fine particles (Deharveng and Bedos 2000). The respiration of roots, rootmat communities, and within biofilms and decaying organic matter, cause a reduction in dissolved oxygen in groundwater, which already is typically low (Coineau 2000). In consequence, DO is increasingly depleted the further the groundwater is removed in distance, or in time, along the flowpath from the point of acquisition of the energy by the groundwater. This may serve to exclude epigean taxa from groundwater and benefit stygobites, many of which are very tolerant of very low DO concentrations and adapted to this low-energy environment (Malard and Hervant 1999; Hervant *et al.* 1998*a*, 1998*b*, 1998*c*).

As groundwater ecosystems are perpetually dark, bacteria are dependent on the fluxes of organic carbon and on the availability of imported labile organic compounds (see Danovaro *et al.* 2001) for their energy (except in the special case of chemoautotrophic energy fixation: Fisher and Likens 1973). Whatever the energy source, microorganisms (mostly bacteria and fungi) capture the energy (utilising either heterotrophic or chemotrophic pathways) and the resulting biofilms are grazed by the stygal animals, thus supporting the groundwater ecosystem, *sensu lato*. Energy is largely derived from the downward movement of photosynthetically derived particulate or dissolved organic carbon (DOC) reaching the water table through the overlying matrix, or transported laterally within the groundwater flow. The DOC in groundwater is generally low (median $0.7\,\mathrm{mg\,L^{-1}}$ DOC in 100 samples from 27 USA States: Leenheer *et al.* 1974 cited in Malard and Hervant 1999) and is often limiting to microbial activity (Anderson and Lovley 1997) and ecosystem metabolism (e.g. Baker *et al.* 2000). However, phreatic biofilm, a potential food source for interstitial animals (Bärlocher and Murdoch 1989), may be adapted to low carbon availability as it did not respond to additional DOC (Craft *et al.* 2002). In the Organ Cave streams of West Virginia, dissolved organic matter (DOM) originating from soils fuelled bacterial production that was then used by higher trophic levels (Simon *et al.* 2003). This

cave-stream food web has three trophic levels (Simon 2000) which is typical of subterranean ecosystems and is truncated relative to surface ecosystems both at the base (no primary production) and at the top (few strict predators) (Gibert and Deharveng 2002).

Direct inputs of food into groundwater systems may occur from root exudates (Howarth 1983), or from chemoautotrophic bacteria. Recent work has shown that a variety of stygal ecosystems may also be dependent on energy derived *in situ* along chemoautotrophic pathways, being fixed, for example, by methanogens and sulfur bacteria. In the artesian Edwards Aquifer in Texas (Longley 1992) and in Movile Cave in Romania (Sarbu 2000), sulfides of petroleum and magmatic origin respectively, support chemoautotrophic ecosystems (Poulson and Lavoie 2000). These ecosystems are analogous to those associated with deep-sea cold seeps and hydrothermal vents, respectively, (Gebruk *et al*. 1997). Chemoautotrophy has also been implicated in anchialine systems of Mexico and Australia (Humphreys 1999*b*, Pohlman *et al*. 2000) and in Frasassi Cave in Italy (Sarbu *et al*. 2000). Chemoautotrophs derive their energy from hydrocarbons or sulfates entrained in the groundwater flow, either from basaltic origin (Poulson and Lavoie 2000), or in the case of anchialine systems, probably from the sea. With these few exceptions, subsurface rates of chemoautotrophic primary production are generally lower than those of surface environments (Chapelle and Lovley 1990; Jones *et al.* 1995).

Subterranean food-web research is sparse globally and almost non-existent in Australia. The Cape Range subterranean waterways (Humphreys 2000*b*) occur beneath a diverse arid-zone vegetation comprising mostly *Eucalyptus* scrub, *Ficus* and, on the plain, principally *Triodia* grassland and chenopods (Keighery and Gibson 1993). Stable isotope composition shows that the energy utilised by the stygofauna in the deep aquifer to the east of the range is predominantly derived from deeper-rooting C_3 plants, but with a significant contribution from C_4 plants (Davies 1996). On the west coast of Cape Range, and on nearby Barrow Island, the stygofauna are known to utilise energy derived from both C_3 and C_4 photosynthetic pathways and to have a chemoautotrophic signature (Humphreys 1999*b*, 2002*b*) but with the same stygal species apparently fulfilling very different ecological roles in different parts of the ecosystem (Humphreys 2002*b*). While both the terrestrial and aquatic components feed on the specialised subterranean fauna, they also make opportunistic use of epigean fauna entering the stygal realm through surface openings, both natural and artificial (Humphreys and Feinberg 1995).

Interactions of plants and groundwater ecosystems

Humphreys (2002*a*) addressed the three major components that are essential to the functioning of groundwater ecosystems, a place to live (including the presence of water),

oxygen and food (energy), categories that will serve to focus this discussion on the interactions of vegetation and groundwater ecology, both directly and indirectly, and in overt and more subtle ways.

A place to live

Plants may provide a substrate for stygofauna to live on (such as root mats and associated mycorrhiza) or within (e.g. decaying coarse organic matter) (Jasinska and Knott 2000; Simon and Benfield 2001; Eberhard 2004). In addition, as roots may penetrate to depths of 50 m or more (Gillieson 1996), they may act as agents, producing subterranean voids and channelling water and humic substances to the groundwater. This occurs through the physical action and respiration of roots and the decay of organic matter in soil and water, causing the elevation of carbon dioxide, which produces carbonic and humic acids. This accelerates karst processes, particularly in limestone environments.

In tropical, temperate and arid climates roots may penetrate deeply into fissured substrates such as karsts (Jasinska *et al*. 1996; Deharveng and Bedos 2000), calcretes (W. F. Humphreys, unpubl. data) and lava tubes (Howarth 1987) to access groundwater. They penetrate cave streams and lakes, shallow aquifers and anchialine waters (groundwater estuaries). In several caves in Australia, roots may form mats in the surface layers of phreatic waters. Whereas these have been studied only in south-western Australia (Eberhard 2004), root mats associated with groundwaters have been reported widely in Australia (Poore and Humphreys 1992; Jasinska and Knott 2000) and Christmas Island (Humphreys and Eberhard 2001). Root mats are an important source of energy, through grazing, death and exudates, as well as nutrients and habitats in cave ecosystems (Howarth 1983).

Vegetation effects on groundwater

Whereas it is well known that groundwater affects vegetation (e.g. Groom *et al*. 2000*a*, 2000*b*; Groom 2003), it is less well recognised that vegetation may have direct and indirect affects on groundwater ecosystems. Floristic (Commander 1994*a*), structural and density changes in surface vegetation may have a direct impact on the groundwater level, its dynamics and quality by changing the rate of either recharge or utilisation of groundwater. This has been observed in both karst areas (Hamilton-Smith and Eberhard 2000) and in alluvial aquifers. For example, the establishment of exotic plantations (*Pinus radiata* D.Don) on karst in South Australia resulted in a 1-m reduction of water level over 5 years, and in nearby Mount Burr Cave, a rise in the water table of similar magnitude, followed their removal by wildfire (Grimes *et al*. 1995).

The characteristics and amount of vegetation cover may have important implications for subterranean ecosystems solely because of its effect on the seasonal variation in the

level of the groundwater, either by changing infiltration rates or from direct withdrawal of water by phreatophytes. The dynamics of groundwater recharge and withdrawal directly affect the local groundwater level, and possibly the downflow, and thus the vertical extent of the phreatic zone. Potential effects are seen, for example, in the Dorvan-Cleyzieu karst aquifer in France, where the temporal sequence of flooding and drying appear to play an important role in the maintenance of biofilms which should be important energy sources for higher trophic levels in the aquifer (Simon 2000).

In alluvial areas, extensive salinisation followed removal of the natural vegetation for arable agriculture in Western Australia and Victoria, owing to increased groundwater recharge (Hart *et al*. 1991; Salama *et al*. 1993). The resulting rise in the watertable mobilises the salts stored in this ancient landscape, forming saltlakes where it has intercepted the surface, and with saline discharges resulting in widespread salinisation of the river systems. Groundwater upwelling may prevent penetration of salt water into the hyporheos (Boulton *et al*. 1999); however, the recharging of aquifers during river spates by this salinised water may be expected to have an impact on groundwater ecosystems and on phreatophytes remote from the point of saline discharge.

The direct use of the groundwater by phreatophytic vegetation may have a large impact on local hydrology, an effect strikingly illustrated by mesquite (*Prosopis juliflora* (Sw.) DC.), a species introduced for stock feeding. This weed consumed the entire groundwater flow (Tromble 1977) within the calcrete estuarine fan associated with a major tropical episodic river, the Fortescue, Pilbara, Western Australia. The location and form of the seawater wedge within this groundwater estuary (Commander 1994*b*) is likely to change profoundly in response to this interception of groundwater flow (Moore 1999) and have a major impact on the location and extent of the contained anchialine fauna which, in addition to unique components, also contains elements of the broader Cape Range/Barrow Island anchialine fauna.

More subtle effects may also occur within natural vegetation. In the Jewel Cave karst system, south-western Australia, Eberhard (2004) found that declining groundwater levels persisted over several years to a decade, despite above average rainfall, and that this coincided with a reduced frequency of burning within the catchment. The reduction in fire frequency (from an average of 2.4 fires per decade to <0.5 fires per decade) allowed an increased density of shrub cover and ground litter in the understorey of the tall eucalypt forest. Eberhard considered this has limited the groundwater recharge, as a result of increased interception of rainfall and evapotranspiration of rainfall, and he is currently testing this hypothesis with an experimental burn and before–after measurement of rainfall, leaf area index, soil moisture infiltration and groundwater levels.

Roots as food

In south-western Australia the rootlets in rootmats are in eco-endomycorrhizal association with several fungi, including Zygomycetes, Ascomycetes and Basidomycetes. Although this assemblage is grazed by cavernicolous stygofauna, it is not known whether fungivore specialists exist in association with the root mats (Jasinska and Knott 2000).

Eberhard (2004) found that cave waters containing rootmats contained many more species of stygofauna (7–22 species per cave) than caves where rootmats were absent (3 or 4 species per cave). However, in Lake Cave, south-western Australia, for example, 17 of 22 species (77%) were not confined to rootmat habitats and 14 species were not at all associated with the root mats. Hence, Eberhard's (2004) work shows that rootmats provide habitat, but are not a necessary condition, for the occurrence of most of the species.

The absence of allogenic sinking streams in the Augusta watertable caves results in groundwaters that contain little coarse, particulate organic matter. However, root mats represent a rich alternative food resource that may permit the survival of facultative cave dwellers, which comprised 31 of 46 species recorded in his study, that otherwise could not survive in the food-poor groundwaters (Eberhard 2004). This interpretation is supported by the high proportion of stygophilic species collected only from rootmats and not collected in habitats where rootmats were absent.

Stygobites appear to be adapted to low-energy environments typical of groundwater (Poulson and Lavoie 2000) and the advantages stygobitic animals have over their surface counterparts may be eliminated if the energy level increases as a result, for example, of organic pollution (Malard and Hervant 1999) and thus be displaced by epigean invaders (Malard 1995). This may be the case in these rootmat ecosystems which provide an abundance of energy in the upper layers of the phreatic waters, and where relatively few of the species are stygobitic. This is in contrast to many other groundwater ecosystems in Australia in which most of species occurring there are strongly stygobitic (Humphreys 1993*a*, 1993*b*, 1999*a*, 2000*a*, 2000*b*).

Age and stability of groundwater fauna

Taxa may become restricted to subterranean habitats at different times, as a result of climatic change, vicariance or speciation. Therefore, any stygal assemblage may contain representative taxa associated with different geological eras. Consequently, subterranean faunas preserve deep historical information in relative geographical location, owing to the evolutionary and environmental entrapment of the fauna in subterranean voids. Many elements of the troglobite and stygobite fauna of Australia are relicts from the fauna of more humid climates, both temperate and tropical (Humphreys 1993*a*, 1993*b*, 2000*a*). For example, the calcretes of the Yilgarn, WA, contain diving beetles

(Cooper *et al*. 2002; Leys *et al*. 2003) and Oniscidea (Taiti and Humphreys 2001; S. Taiti, W. F. Humphreys, S. J. B. Cooper, K. Saint and R. Leijs, unpubl. data) which became stygal in the late Tertiary, as well as much more ancient freshwater lineages such a crangonyctoid Amphipoda and Bathynellacea (Syncarida). Similarly, the Pilbara contains ancient freshwater lineages (Tainisopidea, Phreatoicidea, Paramelitidae, Spelaeogriphacea), together with more recent marine derivatives (Melitidae) (Bradbury and Williams 1997*a*, 1997*b*; Humphreys 1999*a*, 2001*a*). It is surprising that the Yilgarn and Pilbara, which have comprised a single emergent landmass since the Proterozoic (Hocking *et al*. 1987), have very different stygofaunas.

The combination in Australia of long-emergent landmasses and areas of Cretaceous marine inundation are considered broadly to determine the distribution of ancient freshwater lineages (Bradbury 1999; Humphreys 1999*a*; Wilson 2001), such as Bathynellacea, crangonyctoid amphipods, phreatoicidean isopods and more recent marine derivatives (e.g. ceinid and melitid amphipods). Humphreys (2001*a*) suggested that some taxa may have migrated coastward and inland, respectively, along palaeovalleys.

Various lineages support clear connections with Pangaea (Bathynellacea; Camacho 2003), Gondwana (the crustacean lineages Spelaeogriphacea; Poore and Humphreys 1998, 2003) and Phreatoicidea (Wilson and Keable 1999) and the water mites *Tiramideopsis*, Mideopsellinae: Arrenuroidea: Mideopsidae (Harvey 1998) and Tethys (Danielopol *et al*. 2000*a*; Jaume *et al*. 2001; Namiotko *et al*. 2004), with some lineages inhabiting groundwater before the dissolution of the supercontinents (Wilson 2001). For example, the presence of stygobitic sister taxa of hypsimetopodid phreatoicidean isopods in the Ganges Valley, and the Pilbara and Yilgarn, Australian Western Shield (respectively *Nichollsia*, *Pilbaraphreatoicus* and *Hyperoedesipus*) (G. D. F. Wilson, pers. comm.; Wilson 2001) would indicate a particularly ancient phylogeny. Similarly, the presence of a series of syntopic stygobitic lineages, largely comprising congeneric species of several crustacean higher taxa, that are found widely vicariant in anchialine ecosystems of north-western Australia and the North Atlantic. The inferred ages of the faunas suggest that not only was rafting on tectonic plates a major vicariant process, but that some faunas have remained geographically *in situ* while denudation processes removed ∼5 km of cover rock (Kohn *et al*. 2000, 2002), forcing a radical change in geological context from that originally colonised from the surface. This apparent discordance between the inferred age of stygofauna and the current geological context is not an uncommon theme in stygal systems (Poore and Humphreys 1998; Humphreys 2004).

Management and conservation

Australia is the driest inhabited continent, with two-thirds lying within the arid zone, and it has the most unpredictable rainfall. Against this background, groundwater systems are remarkably stable and the presence of obligate groundwater inhabitants that are short-range endemics (Cooper *et al*. 2002) indicates that it is very persistent through geological time. However, owing to global climatic changes of the order of 10^3–10^5 years, the groundwater systems in semi-arid Australia are in almost universal hydrologic disequilibrium, that is they are in a state of net discharge (Hatton 2001). As such, they, and the groundwater-dependent ecosystems they support, are exceptionally vulnerable to hydrological misinterpretation and to changes in recharge and in the exploitation of the groundwater resource, as well as to the removal of the aquifer matrix.

Boulton *et al*. (2003) advocated protection aimed at the habitat or ecosystem scale and identified the following three common themes in particular reference to Australian subsurface biodiversity: (1) an ignorance of the invertebrate biodiversity of the various groundwater environments (2) a high degree of small-range endemics (Cooper *et al*. 2002) in the Australian stygobites and (3) the intimate link between surface and subsurface aquatic ecosystems, the latter two themes being common world-wide (e.g. Danielopol *et al*. 1997, Danielopol *et al*. 2000*b*; Marmonier *et al*. 1997; Sket 1999*a*; and reviews in Gibert *et al*. 1994; Winter *et al*. 1998).

There is a synergy in some areas between issues of conservation of phreatophytic vegetation and groundwater ecosystems. For example, water mining from deep palaeochannel sand aquifers, with a residence time of the water in the order of 10^5 years (Johnson *et al*. 1999), is becoming a widespread practice in arid Australia, especially in the mineraliferous areas. The deep sand aquifers are coupled, *inter alia*, with the overlying phreatic calcrete aquifers in a manner not understood (S. Johnson, Water and Rivers Commission, pers. comm.; R. Martin, Anaconda Nickel Ltd, pers. comm.). The latter are a source of water for pastoral, human and industrial consumption and support rich and diverse groundwater ecosystems comprising short-range endemics and phreatophytic vegetation.

In borefields the groundwater surface may be dimpled both spatially and temporally by drawdown cones of adjacent wells. Concomitantly, any interface with underlying sea water will be similarly dimpled in mirror image to that of the groundwater surface (Humphreys 2002*a*) but magnified about forty-fold owing to the Ghyben–Herzberg effect (Ford and Williams 1989). This expresses the relationship which occurs in near-coastal porous aquifers where fresh water overlies sea water; the depth below sea level of the fresh water–salt water interface is *c*. 40 times the height of the water table above sea level. Thus, a minor drawdown of the groundwater can lead to a major intrusion of sea water into an aquifer where it may impinge on stygofauna as well as overlying or downstream groundwater-dependent ecosystems. Similar effects will be seen in salinity-stratified

inland waters, the magnitude of the saline water mounding being dependent on the relative densities of the saline and overlying fresh water. Hence, hydrogeological research and modelling are needed of the separate aquifer dynamics, and of their coupling, to assess and to manage those impacts that may result from the abstraction of water from deep palaeochannel sands.

Strong advocacy, the requirement to include stygofauna in some environmental impact assessment, and the application of fauna protection legislation to some stygal species and communities in Australia, have raised considerably the awareness of groundwater ecosystems to a broader public. More formally, the Council of Australian Governments (COAG) Water Reform Agenda (a major national strategy formalised by a COAG Agreement in 1994) lists ecological sustainability as a central element of the agenda. Nationally in Australia, there is an agreement to manage groundwater better (COAG Task Force on Water Reform 1996) and among the key principles are that natural ecological processes and biodiversity are sustained (i.e. ecological values are sustained) and that all water uses are managed in a manner that recognises ecological values (ANZECC ARMCANZ 1996). The ecosystems most clearly dependent on groundwater are those comprising obligate subterranean aquatic species (stygobites) (Hatton and Evans 1998). As part of the COAG water reform agenda, all Australian States have revised, or are revising, water legislation. The agenda stresses, *inter alia*, that issues of sustainability and the environmental needs of rivers, must be taken into account in planning water infrastructure developments, and that the environmental requirements of the river systems would be adequately met before any harvesting of the water resource occurs. Thus, there is a clear need for better integration of hydrogeological and groundwater ecology research programs. In a post-COAG era, provision needs to be made for the water requirements of groundwater-dependent ecosystems. Informed management of these will require a greatly increased understanding of the faunistic diversity and the ecological processes occurring in order to maintain the health of groundwater ecosystems.

The obligate groundwater faunas of Australia contain numerous geographic and phyletic relict species, as well as of higher taxa (Wilson and Johnson 1999; Wilson 2001, 2003) typically comprising short-range endemic species (Cooper *et al.* 2002; Leys *et al.* 2003). Many species and communities, probably a majority, would fulfil IUCN criteria for listing as vulnerable or endangered on account of aerial extent alone, or because they exist as a single restricted entity.

There are several distinct conservation elements amongst the stygofauna of Australia, including (1) lineages of marine origin with tethyan affinities (e.g. anchialine fauna), (2) ancient freshwater lineages of the continental regions (e.g. phreatoicidean and tainisopidean isopods,

crangonyctoid amphipods, candonine ostracods, bathynellaceans) and (3) Tertiary invaders of inland groundwaters (e.g. dytiscid diving beetles, oniscidean isopods). Each contains relict faunas captured in the groundwater, with many now exhibiting broadly disjunct distributions with the fragments of Gondwana or Tethys, and some, notably Bathynellacea, with Pangaea. As such, they are of great scientific and conservation significance, comprising living communities of genetic diversity isolated underground during different geological periods.

Acknowledgments

References

Anderson RT, Lovley DR (1997) Ecology and Biogeochemistry of *in situ* groundwater bioremediation. *Advances in Microbial Ecology* **15**, 289–350.

ANZECC ARMCANZ (1996) 'National Principles for the provision of water for ecosystems.' Occasional paper SWR no. 3. (Agriculture and Resource Management Council of Australia and New Zealand and Australian and New Zealand Environment and Conservation Council, Sustainable Land and Water Resources Management Committee, Subcommittee on Water Resources: Canberra)

ANZECC ARMCANZ (2000) 'Australian and New Zealand guidelines for fresh and marine water quality.' National water quality management strategy paper no. 4. (Australian and New Zealand Environment and Conservation Council and Agriculture and Resource Management Council of Australia and New Zealand: Canberra)

Australian Geological Survey Organisation (1993) Aquifers at risk: towards a national groundwater quality perspective. *AGSO Journal of Australian Geology & Geophysics* **14**, 99–318.

Australian Water Resources Council (1992) 'National water quality management strategy draft guidelines for groundwater protection.' (Australian Water Resources Council: Melbourne)

Baker MA, Valett HM, Dahm CN (2000) Organic carbon supply and metabolism in a shallow groundwater ecosystem. *Ecology* **81**, 3133–3148.

Balke M, Watts CHS, Cooper SJB, Humphreys WF, Vogler AP (2004) A highly modified stygobitic diving beetle of the genus *Copelatus* (Coleoptera, Dytiscidae): taxonomy and cladistic analysis based on mtDNA sequences. *Systematic Entomology* **29**, 59–67. doi: 10.1111/j.1365-3113.2004.00229.x

Bärlocher F, Murdoch JH (1989) Hyporheic biofilms—a potential food source for interstitial animals. *Hydrobiologia* **184**, 61–67.

Belton DX, Brown RW, Kohn BP, Fink D, Farley KA (2004) Quantitative resolution of the debate over antiquity of the central Australian landscape: implications for the tectonic and geomorphic stability of cratonic interiors. *Earth and Planetary Science Letters* **219**, 21–34. doi: 10.1016/S0012-821X(03)00705-2

BMR Palaeogeographic Group (1990) 'Australia, evolution of a continent.' (Australian Government Publishing Service: Canberra)

Botosaneanu L (1986) 'Stygofauna Mundi: a faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial).' (E.J. Brill: Leiden, The Netherlands)

Boulton AJ (2000) River ecosystem health Down Under: assessing ecological condition in riverine groundwater zones in Australia. *Ecosystem Health* **6**, 108–118. doi: 10.1046/j.1526-0992.2000.00011.x

Boulton AJ (2001) Twixt two worlds: taxonomic and function biodiversity at the surface water/groundwater interface. In 'Subterranean biology in Australia 2000'. (Eds WF Humphreys, MS Harvey) *Records of the Western Australian Museum* **64**(Suppl.), 1–13.

Boulton AJ, Hancock PJ (2006) Rivers as groundwater-dependent ecosystems: a review of degrees of dependency, riverine processes and management implications. *Australian Journal of Botany* **54**, 133–144.

Boulton AJ, Marmonier P, Davis JA (1999) Hydrological exchange and subsurface water chemistry in streams varying in salinity in south-western Australia. *International Journal of Salt Lake Research* **8**, 361–382. doi: 10.1023/A:1009060912470

Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM (1998) The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* **29**, 59–81. doi: 10.1146/annurev.ecolsys.29.1.59

Boulton AJ, Humphreys WF, Eberhard SM (2003) Imperilled subsurface waters in Australia: biodiversity, threatening processes and conservation. *Aquatic Ecosystem Health & Management* **6**, 41–54. doi: 10.1080/14634980301475

Boutin C, Coineau N (1990) Regression model 'Modèle Biphase' d'évolution et origine des micro-organismes stygobies interstitiels continentaux. *Revue de Micropaléontologie* **33**, 303–322.

Boxshall GA, Jaume D (2000) Discoveries of cave misophrioids (Crustacea: Copepoda) shed new light on the origin of anchialine faunas. *Zoologischer Anzeiger* **239**, 1–19.

Bradbury JH (1999) The systematics and distribution of Australian freshwater amphipods: a review. In 'Crustaceans and the biodiversity crisis.' (Eds FR Schram, JC von Vaupel Klein). Proceedings of the fourth international crustacean congress, Amsterdam, The Netherlands, 20–24 July 1998 (Brill: Leiden, The Netherlands)

Bradbury JH, Williams WD (1997*a*) Amphipod (Crustacea) diversity in underground waters in Australia: an Aladdin's Cave. *Memoirs of the Museum of Victoria* **56**, 513–519.

Bradbury JH, Williams WD (1997*b*) The amphipod (Crustacea) stygofauna of Australia: description of new taxa (Melitidae, Neoniphargidae, Paramelitidae), and a synopsis of known species. *Records of the Australian Museum* **49**, 249–341.

CALM (2005) 'Threatened species and ecological communities.' (Department of Conservation and Land Management: Perth) www.naturebase.net/plants_animals/watscu/index.html

Camacho AI (2003) Historical biogeography of *Hexabathynella*, a cosmopolitan genus of groundwater Syncarida (Crustacea, Bathynellacea, Parabathynellidae). *Biological Journal of the Linnean Society* **78**, 457–466. doi: 10.1046/j.0024-4066.2002.00149.x

Chapelle FH, Lovley DR (1990) Rates of microbial metabolism in deep coastal plain aquifers. *Applied and Environmental Microbiology* **56**, 1865–1874.

Chilton C (1882) On some subterranean Crustacea. *Transactions and Proceedings of the New Zealand Institute* 14, 174–180.

Chilton C (1883) Notes on and a new species of subterranean Crustacea. *Transactions and Proceedings of the New Zealand Institute* **15**, 87–92.

Chilton C (1884) Subterranean Crustacea. *New Zealand Journal of Science* **2**, 89.

Chilton C (1894) The subterranean Crustacea of New Zealand: with some general remarks on the fauna of caves and wells. *Transactions of the Linnean Society, London* **6**, 163–284.

Chilton C (1918) A fossil amphipod belonging to the freshwater genus Phreatoicus. *Journal and Proceedings of the Royal Society of New South Wales* **51**, 365–388.

Chilton C (1925) A new blind freshwater amphipod (genus Neoniphargus) from Western Australia. *Journal and Proceedings of the Royal Society of Western Australia* **11**, 81–84.

Cho J-L (2005) A primitive representative of the Parabathynellidae (Bathynellacea, Syncarida) from the Yilgarn Craton of Western Australia. *Journal of Natural History* **39**, 3423–3433.

Cho J-L, Park J-G, Humphreys WF (2005) A new genus and six new species of the Parabathynellidae (Bathynellacea, Syncarida) from the Kimberley Region, Western Australia. *Journal of Natural History* **39**, 2225–2255.

COAG Task Force on Water Reform (1996) 'Groundwater allocation and use: a national framework for improved groundwater management in Australia.' Occasional paper no. 2. (Council of Australian Government: Canberra)

Coineau N (2000) Adaptions to interstitial groundwater life. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 189–210. (Elsevier: Amsterdam)

Commander DP (1994*a*) 'Interaction of landuse, water supply and geology on the Swan Coastal Plain.' Excursion guidebook no. 9. (Geological Society of Australia (WA Division): Perth)

Commander DP (1994*b*) Hydrogeology of the Fortescue River alluvium, Ashburton Plain, Carnarvon Basin. *Geological Survey of Western Australia Professional Papers, Report* **37**, 101–124.

Cooper SJB, Hinze S, Leys R, Watts CHS, Humphreys WF (2002) Islands under the desert: molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics* **16**, 589–598. doi: 10.1071/IT01039

Council of Europe (1992) 'Convention on the conservation of the wildlife and natural environment of Europe Criteria for the selection of subterranean habitat of biological interest.' Recommendation no. 36 (1992) on the conservation of subterranean habitats, Annexe 1 to the recommendation. (Council of Europe: Bruxelles)

Craft JA, Stanford JA, Pusch M (2002) Microbial respiration within a floodplain aquifer of a large gravel-bed river. *Freshwater Biology* **47**, 251–262. doi: 10.1046/j.1365-2427.2002.00803.x

Culver DC, Jones WK, Holsinger JR (1992) Biological and hydrological investigations of the Cedars, Lee County, Virginia: an ecologically significant and threatened karst area. In 'Proceedings of the first international conference on groundwater ecology'. (Eds JA Stanford, JJ Simons) pp. 281–290. (American Water Resources Association: Bethesda, ML)

Culver DC, Sket B (1999) Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies* **62**, 11–17.

Culver DC, Kane TC, Fong DW (1995) 'Adaptation and natural selection in caves: the evolution of *Gammarus minus*.' (Harvard University Press: Cambridge, MA)

Danielopol DL, Pospisil P (2001) Hidden biodiversity in the groundwater of the Danube Flood Plain National Park (Austria). *Biodiversity and Conservation* **10**, 1711–1721. doi: 10.1023/A:1012098706986

Danielopol DL, Claret C, Marmonier P, Pospisil P (1997) Sampling in springs and other ecotones. In 'Conservation and protection of the biota of karst symposium, Nashville, Tennessee, 13–16 February 1997'. (Eds ID Sasowsky, DW Fong, EL White) pp. 8–14. Special Publication No. 3. (Karst Waters Institute: Charles Town, WV)

Danielopol DL, Baltanás A, Humphreys WF (2000*a*) *Danielopolina kornickeri* sp. n. (Ostracoda: Thaumatocypridoidea) from a western Australian anchialine cave—morphology and evolution. *Zoologica Scripta* **29**, 1–16. doi: 10.1046/j.1463-6409.2000.00027.x

Danielopol DL, Pospisil P, Rouch R (2000*b*) Biodiversity in groundwater: a large-scale view. *Trends in Ecology & Evolution* **15**, 223–224. doi: 10.1016/S0169-5347(00)01868-1

Daniels SR, Hamer M, Rogers C (2004) Molecular evidence suggests an ancient radiation for the fairly shrimp genus *Streptocephalus* (Branchiopoda: Anostraca). *Biological Journal of the Linnean Society* **82**, 313–327. doi: 10.1111/j.1095-8312.2004.00359.x

Danovaro R, Dell'Anno A, Fabiano M, Pusceddu A, Tselepides A (2001) Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. *Trends in Ecology & Evolution* **16**, 505–510. doi: 10.1016/S0169-5347(01)02215-7

Davies PM (1996) Appendix 1: stable isotope analyses of food-webs associated with stygofauna of Exmouth borefield. In 'Supplementary investigation of the effect of public water supply abstraction on the stygofauna and aquifer of the Cape Range. An addendum to extensions to Exmouth water supply borefield'. *Carta Economica Regional* (June), 1995. (Water Authority of Western Australia: Perth)

De Deckker P (1983) Australian salt lakes: their history, chemistry and biota—A review. *Hydrobiologia* **105**, 231–244. doi: 10.1007/BF00025191

Deharveng L, Bedos A (2000) The cave fauna of Southeast Asia: origin, evolution and ecology. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 603–632. (Elsevier: Amsterdam)

Dole-Olivier M-J, Marmonier P, Creuzé des Châtelliers M, Martin D (1994) Interstitial fauna associated with the alluvial floodplains of the Rhône Rover (France). In 'Groundwater ecology'. (Eds J Gibert, DL Danielopol, JA Stanford) pp. 313–346. (Academic Press: London)

Eberhard SM (1995) Impact of a limestone quarry on aquatic cave fauna at Ida Bay in Tasmania. In 'Proceedings of the 11th Australasian cave and karst management association conference, Tasmania, May 1995'. pp. 125–137.

Eberhard SM (1999) Cave fauna management and monitoring at Ida Bay Tasmania. *Nature Conservation Report* **99**, 1–37 (Parks and Wildlife Service: Hobart)

Eberhard SM (2004) Ecology and hydrogeology of a threatened groundwater-dependent ecosystem: The Jewel Cave karst system in Western Australia. PhD Thesis, Murdoch University, Perth.

EPA (1998) 'Environmental protection of Cape Range Province Preliminary Position Statement No. 1. Bulletin 905.' (Environmental Protection Authority: Perth)

EPA (2003) Consideration of subterranean fauna in groundwater and caves during environmental impact assessment. In 'Guidance statement for the assessment of environmental factors no. 54'. (Environmental Protection Authority: Perth)

EPBC Act (1999) Environmental Protection and Biological Conservation Act 1999. http://www.deh.gov.au/biodiversity/threatened/index.html.

Findlay S, Sobczak WV (2000) Microbial communities in hyporheic sediments. In 'Streams and ground waters.' (Eds JB Jones, PJ Mulholland) pp. 287–306. (Academic Press: San Diego, CA)

Fisher SG, Likens GE (1973) Energy flow in Bear Brook New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**, 421–439.

Ford DC, Williams PW (1989) 'Karst geomorphology and hydrology.' (Unwin Hyman: London)

Gebruk AV, Galkin SV, Vereshchaka AL, Moskalev LI, Southward AJ (1997) Ecology and biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge. *Advances in Marine Biology* **32**, 93–130.

Gibert J, Deharveng L (2002) Subterranean ecosystems: a truncated functional biodiversity. *Bioscience* **52**, 473–481.

Gibert J, Danielopol DL, Stanford JA (1994) 'Groundwater Ecology.' (Academic Press: London)

Gillieson D (1996) 'Caves: processes, development and management.' (Blackwell: Oxford)

Gounot AM (1994) Microbial ecology of groundwaters. In 'Groundwater ecology'. (Eds J Gibert, DL Danielopol, JA Stanford) pp. 189–215. (Academic Press: London)

Griebler C (2001) Microbial ecology of subsurface ecosystems. In 'Groundwater ecology—a tool for management of water resources'. (Eds C Griebler, DL Danielopol, J Gibert, HP Nachtnebel, J Notenboom) pp. 81–108. (Office for Official Publications of the European Communities: Luxembourg)

Griebler C, Danielopol DL, Gibert J, Nachtnebel HP, Notenboom J (Eds) (2001) 'Groundwater ecology: a tool for management of water resources.' (Office for Official Publications of the European Communities: Luxembourg)

Grimes KG, Hamilton-Smith E, Spate AP (1995) South east karst province of South Australia. Report on behalf of the Australasian cave and karst management association for the National Parks and Wildlife Service of South Australia, Adelaide.

Groom PK (2003) Groundwater-dependency and water relations of four Myrtaceae shrub species during a prolonged summer drought. *Journal of the Royal Society of Western Australia* **86**, 31–40.

Groom PK, Froend RH, Mattiske EM (2000*a*) Impact of groundwater abstraction on a *Banksia* woodland, Swan Coastal Plain, Western Australia. *Ecological Management & Restoration* **1**, 117–124. doi: 10.1046/j.1442-8903.2000.00033.x

Groom PK, Froend RH, Mattiske EM, Koch BL (2000*b*) Myrtaceous shrub species respond to long-term decreasing groundwater levels on the Gnangara Groundwater Mound, northern Swan Coastal Plain. *Journal of the Royal Society of Western Australia* **83**, 75–82.

Haack SK, Bekins BA (2000) Microbial populations in contaminant plumes. *Hydrogeology Journal* **8**, 63–76. doi: 10.1007/s100400050008

Hamilton-Smith E, Eberhard SM (2000) Conservation of cave communities in Australia. In 'Ecosystems of the World, vol. 30: dubterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 647–664. (Elsevier: Amsterdam)

Hamilton-Smith E, Kiernan K, Spate A (1996) 'Karst management considerations for the Cape Range karst province, Western Australia'. (Department of Environmental Protection: Perth)

Hancock PJ, Boulton AJ, Humphreys WF (2005) Aquifers and hyporheic zones: towards an ecological understanding of groundwater. The future of hydrogeology. *Hydrogeology Journal* **13**, 98–111.

Hart BT, Bailey P, Edwards R, Hortle K, James K, McMahon A, Meredith C, Swadling K (1991) A review of the salt sensitivity of the Australian freshwater biota. *Hydrobiologia* **210**, 105–144.

Harvey MS (1998) Unusual new water mites (Acari: Hydracarina) from Australia, Part 1. *Records of the Western Australian Museum* **19**, 91–106.

Hatton T (2001) Land use and catchment water balance. CSIRO Land and Water Technical Report 18/01, Canberra.

Hatton T, Evans R (1998) Dependence of ecosystems on groundwater and its significance to Australia. Land and Water Resources Research and Development Corporation, Occasional Paper 12/98, Canberra.

Hervant F, Mathieu J, Barre H, Simon K (1998a) Long-term starvation and re-feeding in hypogean and epigean crustaceans: survival, locomotory and respiratory adaptations. *Memoires de Biospeologie* **25**, 15–23.

Hervant F, Mathieu J, Messana G (1998b) Oxygen consumption and ventilation in declining oxygen tension and posthypoxic recovery in epigean and hypogean crustaceans. *Journal of Crustacean Biology* **18**, 717–727.

Hervant F, Mathieu J, Messana G, Bou C (1998c) Severe hypoxia and subsequent recovery in the hypogean isopod *Stenasellus virei*. *Memoires de Biospeologie* **25**, 7–13.

Hocking RM, Moors HT, van de Graaff WJE (1987) Geology of the Carnarvon Basin, Western Australia. *Geological Survey of Western Australia, Bulletin* **133**, 1–289.

Howarth FG (1983) Ecology of cave arthropods. *Annual Review of Entomology* **28**, 365–389.
doi: 10.1146/annurev.en.28.010183.002053

Howarth FG (1987) The evolution of non-relictual tropical troglobites. *International Journal of Speleology* **16**, 1–16.

Humphreys WF (1993a) The biogeography of Cape Range, Western Australia. *Records of the Western Australian Museum* **45**(Suppl.), 1–248.

Humphreys WF (1993b) The significance of the subterranean fauna in biogeographical reconstruction: examples from Cape Range peninsula, Western Australia. *Records of the Western Australian Museum* **45**(Suppl.), 165–192.

Humphreys WF (1994) The subterranean fauna of the Cape Range coastal plain, northwestern Australia. Report to the Australian Heritage Commission and the Western Australian Heritage Committee. (Western Australian Museum: Perth)

Humphreys WF (1999a) Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In 'The other 99%. The conservation and biodiversity of invertebrates'. (Eds W Ponder, D Lunney) pp. 219–227. (Transactions of the Royal Zoological Society of New South Wales: Sydney)

Humphreys WF (1999b) Physico-chemical profile and energy fixation in Bundera Sinkhole, an anchialine remiped habitat in north-western Australia. *Journal of the Royal Society of Western Australia* **82**, 89–98.

Humphreys WF (2000a) The hypogean fauna of the Cape Range peninsula and Barrow Island, northwestern Australia. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 581–601. (Elsevier: Amsterdam)

Humphreys WF (2000b). Karst wetlands biodiversity and continuity through major climatic change—an example from arid tropical Western Australia. In 'Biodiversity in wetlands: assessment, function and conservation, vol. 1'. (Eds B Gopal, WJ Junk, JA Davis) pp. 227–258. (Backhuys Publishers: Leiden, The Netherlands)

Humphreys WF (2000c) First in, last out: should aquifer ecosystems be at the vanguard of remediation assessment? In 'Contaminated site remediation: from source zones to ecosystems, vol. 1'. (Ed. CD Johnston) pp. 275–282. (Centre for Groundwater Studies: Perth)

Humphreys WF (2000d) Relict faunas and their derivation. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 417–432. (Elsevier: Amsterdam)

Humphreys WF (2001a) Groundwater calcrete aquifers in the Australian arid zone: the context to an unfolding plethora of stygal biodiversity. In 'Subterranean biology in Australia 2000'. (Eds WR Humphreys, MS Harvey) *Records of the Western Australian Museum* **64**(Suppl.), 63–83.

Humphreys WF (2001b) *Milyeringa veritas* Whitley 1945 (Eleotridae), a remarkably versatile cave fish from the arid tropics of northwestern Australia. *Environmental Biology of Fishes* **62**, 297–313. doi: 10.1023/A:1011880726946

Humphreys WF (2002a) Keynote address: groundwater ecosystems in Australia: an emerging understanding. In 'Proceedings of the International Association of Hydrogeologists conference, Darwin, Australia, 12–17 May 2002'. [CD-ROM]

Humphreys WF (2002b) The subterranean fauna of Barrow Island, northwestern Australia, and its environment. *Memoires de Biospeologie* **28**, 107–127 [International Journal of Subterranean Biology].

Humphreys WF (2004) Diversity patterns in Australia. In 'Encyclopedia of Caves'. (Eds DC Culver, W White) pp. 183–196. (Academic Press: San Diego, CA)

Humphreys WF, Danielopol DL (2006) *Danielopolina* (Ostracoda, Thaumatocyprididae) on Christmas Island, Indian Ocean, a sea mount island. *Crustaceana* **78** (11), in press.

Humphreys WF, Eberhard S (2001) Subterranean fauna of Christmas Island, Indian Ocean. *Helictite* **37**, 59–74.

Humphreys WF, Feinberg MN (1995) Food of the blind cave fishes of northwestern Australia. *Records of the Western Australian Museum* **17**, 29–33.

Humphreys WF, Harvey MS (Eds) (2001) Subterranean Biology in Australia 2000. *Records of the Western Australian Museum* **64**(Suppl.), 1–242.

Huppop K (2000) How do cave animals cope with food scarcity in caves? In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 159–188. (Elsevier: Amsterdam)

Hurley DE (1990) Charles Chilton: the Phreatoicoidea and other interests of a phreatic pioneer from down under. *Bijdragen tot de Dierkunde* **60**, 233–238.

Jacobson G, Wischusen J (2001) Groundwater for Aboriginal communities in central Australia: the Western Water Study (Wiluraratja Kapi), Northern Territory. In 'Gondwana to greenhouse: Australian environmental geoscience'. (Ed. VA Gostin) pp. 171–178. Geological Society of Australia Special Publication 21. (Blackwell Science Ltd: Melbourne)

Jasinska EJ, Knott B (2000) Root-driven faunas in cave waters. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 287–307. (Elsevier: Amsterdam)

Jasinska EJ, Knott B, McComb AJ (1996) Root mats in ground water: a fauna-rich habitat. *Journal of the North American Benthological Society* **15**, 508–519.

Jaume D, Humphreys WF (2001) A new genus of epacteriscid calanoid copepod from an anchialine sinkhole in northwestern Australia. *Journal of Crustacean Biology* **21**, 157–169.

Jaume D, Boxshall GA, Humphreys WF (2001) New stygobiont copepods (Calanoida; Misophrioida) from Bundera sinkhole, an anchialine cenote on north-western Australia. *Zoological Journal of the Linnean Society* **133**, 1–24. doi: 10.1006/zjls.2000.0288

Johnson SL, Commander DP, O'Boy CA (1999) Groundwater resources of the Northern Goldfields Western Australia. Hydrological records series report HG 2. Water and Rivers Commission, Perth.

Jones JB Jr, Fisher SG, Grimm NB (1995) Vertical hydrological exchange and ecosystem metabolism in a Sonoran Desert Stream. *Ecology* **76**, 942–952.

Juberthie C (1995) 'Underground habitats and their protection.' (Council of Europe Press: Strasbourg)

Juberthie C, Decu V (Eds) (1994) 'Encyclopedia Biospeleologica, vol. 1.' (Société de Biospéologie: Moulis and Bucarest)

Juberthie C, Decu V (Eds) (1998) 'Encyclopedia Biospeleologica, vol. 2.' (Société de Biospéologie: Moulis and Bucarest)

Juberthie C, Decu V (Eds) (2002) 'Encyclopedia Biospeleologica, vol. 3.' (Société de Biospéologie: Moulis and Bucarest)

Karanovic I (2003*a*) Towards a revision of Candoninae (Crustacea: Ostracoda): Descriptions of two new genera from Australian groundwaters. *Species Diversity* **8**, 353–383.

Karanovic I (2003*b*) A new genus of Candoninae (Crustacea, Ostracoda, Candonidae) from the subterranean waters of southwestern Western Australia. *Records of the Western Australian Museum* **21**, 315–332.

Karanovic I, Marmonier P (2002) On the genus *Candonopsis* (Crustacea: Ostracoda: Candoninae) in Australia, with a key to the world recent species. *Annals of Limnology* **38**, 199–240.

Karanovic I, Marmonier P (2003) Three new genera and nine new species of the subfamily Candoninae (Crustacea, Ostracoda, Podocopida) from the Pilbara region (Western Australia). *Beaufortia* **53**, 1–51.

Karanovic T (2003) First representative of the genus *Allocyclops* Kiefer, 1932 (Crustacea, Copepoda, Cyclopoida) from the Australian subterranean waters. *Annales de Limnologie* **39**, 141–149.

Karanovic T (2004) Subterranean copepods (Crustacea: Copepoda) from arid Western Australia. *Crustaceana* **3**(Suppl.), 1–366.

Karanovic T, Pesce GL, Humphreys WF (2001) Copepods from groundwaters of Western Australia, V. *Phyllopodopsyllus wellsi* sp. nov. (Crustacea: Copepoda: Harpacticoida) with a key to world species. *Records of the Western Australian Museum* **20**, 333–344.

Keighery G, Gibson N (1993) Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. *Records of the Western Australian Museum* **45**(Suppl.), 51–85.

Kohn BP, O'Sullivan PB, Gleadow AJW (2000) Phanerozoic denudation history of southwest Australian crystalline terranes inferred from apartite fission track thermochronology. *Geological Society of Australia. Abstracts* **58**, 213–215.

Kohn BP, Gleadow AJW, Brown RW, Gallagher K, O'Sullivan PB, Foster DA (2002) Shaping the Australian crust over the last 300 million years: insights from fission track thermotectonic imaging and denudation studies in key terranes. *Australian Journal of Earth Sciences* **49**, 697–717.
doi: 10.1046/j.1440-0952.2002.00942.x

Kornicker LS, Danielopol DL, Humphreys WF (in press) Description of anchialine ostracode *Danielopolina* sp. cf. *D. kornickeri* from Christmas Island, Indian Ocean, *Crustaceana*.

Leys R, Watts CHS, Cooper SJB, Humphreys WF (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution* **57**, 2819–2834.

Longley G (1992) The subterranean aquatic ecosystem of the Balcones Fault Zone Edwards Aquifer in Texas—threats from overpumping. In 'Proceedings of the first international conference on groundwater ecology'. (Eds JA Stanford, JJ Simons) pp. 291–300. (American Water Resources Association: Bethesda, MD)

Malard F (1995) Contribution à l'étude biologique de la qualité des eaux souterraines karstiques: application à un site atelier Nord-Montpelliérain (bassin de la source du Lez). Thesis, Université Claude Bernard, Lyon.

Malard F, Hervant F (1999) Oxygen supply and the adaptations of animals in groundwater. *Freshwater Biology* **41**, 1–30.
doi: 10.1046/j.1365-2427.1999.00379.x

Malard F, Reygrobellet J-L, Mathieu J, Lafont M (1994) The use of invertebrate communities to describe groundwater flow and contaminant transport in a fractured rock aquifer. *Archiv fur Hydrobiologie* **131**, 93–110.

Malard F, Mathieu J, Reygrobellet JL, Lafont M (1996) Biomonitoring groundwater contamination: application to a karst area in southern France. *Aquatic Sciences* **58**, 158–187.
doi: 10.1007/BF00877113

Marmonier P, Ward JV, Danielopol DL (1997) Round table 2 biodiversity in groundwater/surface water ecotones: central questions. In 'Groundwater/surface water ecotones: biological and hydrological interactions and management options'. (Eds J Gibert, J Mathieu, F Fournier) pp. 231–235. (Cambridge University Press: Cambridge, UK)

Martens K, Rossetti G (2002) On the Darwinulidae (Crustacea: Ostracoda) from Oceania. *Invertebrate Systematics* **16**, 195–208.
doi: 10.1071/IT01022

Moore WS (1999) The subterranean estuary: a reaction zone of ground water and sea water. *Marine Chemistry* **65**, 111–125.
doi: 10.1016/S0304-4203(99)00014-6

Mösslacher F, Griebler C, Notenboom J (2001) Biomonitoring of groundwater systems: methods, applications and possible indicators among the groundwater biota. In 'Groundwater ecology—a tool for management of water resources'. (Eds C Griebler, DL Danielopol, J Gibert, HP Nachtnebel, J Notenboom) pp. 173–182. (Office for Official Publications of the European Communities: Luxembourg)

MPR (2002) 'Guidelines for the protection of surface and groundwater resources during exploration drilling.' (Department of Minerals and Energy: Perth)

Murray BR, Hose GC, Eamus D, Licari D (2006) Valuation of groundwater-dependent ecosystems: a functional methodology incorporating ecosystem services. *Australian Journal of Botany* **54**, 221–229.

Namiotko T, Wouters K, Danielopol DL, Humphreys WF (2004) On the origin and evolution of a new anchialine stygobitic *Microceratina* species (Crustacea, Ostracoda) from Christmas Island (Indian Ocean). *Journal of Micropalaeontology* **23**, 49–60.

Notenboom J (1991) Marine regressions and the evolution of ground dwelling amphipods (Crustacea). *Journal of Biogeography* **18**, 437–454.

Notenboom J, Plénet S, Turquin M-J (1994) Groundwater contamination and its impact on groundwater animals and ecosystems. In 'Groundwater ecology'. (Eds J Gibert, DL Danielopol, JA Stanford) pp. 477–504. (Academic Press: London)

Pesce GL, De Laurentiis P, Humphreys WF (1996*a*) Copepods from ground waters of Western Australia. I. The genera *Metacyclops*, *Mesocyclops*, *Microcyclops* and *Apocyclops* (Crustacea Copepoda: Cyclopidae). *Records of the Western Australian Museum* **18**, 67–76.

Pesce GL, De Laurentiis P, Humphreys WF (1996*b*) Copepods from ground waters of Western Australia. II. The genus *Halicyclops* (Crustacea Copepoda: Cyclopidae). *Records of the Western Australian Museum* **18**, 77–85.

Pinder AM, Brinkhurst RO (1997) Review of the Phreodrilidae (Annelida: Oligochaeta: Tubificida) of Australia. *Invertebrate Taxonomy* **11**, 443–523. doi: 10.1071/IT95025

Playford PE (2001) Subterranean biotas in Western Australia. Report for the EPA. Environmental Protection Authority, Perth.

Plénet S, Marmonier P, Gibert J, Stanford JA, Bodergat A-M, Schmidt CM (1992) Groundwater hazard evaluation: a perspective for the use of interstitial and benthic invertebrates as sentinels of aquifer metallic contamination. In 'Proceedings of the first international conference on groundwater ecology'. (Eds JA Stanford, JJ Simons) pp. 319–329. (American Water Resources Association: Bethesda, MD)

Pohlman JW, Cifuentes LA, Iliffe TM (2000) Food web dynamics and biogeochemistry of anchialine caves: a stable isotope approach. In 'Ecosystems of the Wworld, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 345–357. (Elsevier: Amsterdam)

Poore GCB, Humphreys WF (1992) First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. *Invertebrate Taxonomy* **6**, 719–725. doi: 10.1071/IT9920719

Poore GCB, Humphreys WF (1998) First record of Spelaeogriphacea from Australasia: a new genus and species from an aquifer in the arid Pilbara of Western Australia. *Crustaceana* **71**, 721–742.

Poore GCB, Humphreys WF (2003) Second species of *Mangkurtu* (Spelaeogriphacea) from north-western Australia. *Records of the Western Australian Museum* **22**, 67–74.

Pospisil P (1994) The groundwater fauna of a Danube aquifer in the 'Lobau' Wetland in Vienna Austria. In 'Groundwater ecology'. (Eds J Gibert, DL Danielopol, JA Stanford) pp. 347–366. (Academic Press: London)

Poulson TL, Lavoie KH (2000) The trophic basis of subsurface ecosystems. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 231–249. (Elsevier: Amsterdam)

Rouch R (1977) Considérations sur l'écosystème karstique. *Comptes Rendus Hebdomadaires des Seances. Academie des Sciences. Serie D. Sciences Naturelles* **284**, 1101–1103.

Rouch R, Danielopol DL (1997) Species richness of microcrustacea in subterranean freshwater habitats. Comparative analysis and approximate evaluation. *Internationale Revue gesamten Hydrobiologie* **82**, 121–145.

Salama RB, Farrington P, Bartle GA, Watson GD (1993) The role of geological structures and relict channels in the development of dryland salinity in the wheatbelt of Western Australia. *Australian Journal of Earth Sciences* **40**, 45–56.

Sarbu SM (2000) Movile Cave: a chemoautotrophically based groundwater ecosystem. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 319–343. (Elsevier: Amsterdam)

Sarbu SM, Galdenzi S, Menichetti M, Gentile G (2000) Geology and biology of Frasassi Caves in Central Italy: an ecological multidisciplinary study of a hypogenic underground karst system. In 'Ecosystems of the World, vol. 30: subterranean ecosystems'. (Eds H Wilkens, DC Culver, WF Humphreys) pp. 359–378. (Elsevier: Amsterdam)

Schminke HK (1974) Mesozoic intercontinental relationships as evidenced by bathynellid crustacea (Syncarida: Malacostraca). *Systematic Zoology* **23**, 157–164.

Simon KS (2000) Organic dynamics and trophic structure in karst groundwater. PhD Thesis. Faculty of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Simon KS, Benfield EF (2001) Leaf and wood breakdown in cave streams. *Journal of the North American Benthological Society* **20**, 550–563.

Simon KS, Buikema AL Jr (1997) Effects of organic pollution on an Appalachian cave: changes in macroinvertebrate populations and food supplies. *American Midland Naturalist* **138**, 387–401.

Simon KS, Benfield EF, Macko SA (2003) Food web structure and the role of epilithic biofilms in cave streams. *Ecology* **84**, 2395–2406.

Sinton LW (1984) The macroinvertebrates in a sewage-polluted aquifer. *Hydrobiologia* **119**, 161–169. doi: 10.1007/BF00015207

Sket B (1981) Fauna of anchialine (coastal) cave waters, its origin and importance. 'Proceedings of the eighth international congress of speleology'. (National Speleological Society: Huntsville, AL)

Sket B (1996) The ecology of anchihaline caves. *Trends in Ecology & Evolution* **11**, 221–255. doi: 10.1016/0169-5347(96)20031-X

Sket B (1999*a*) High biodiversity in hypogean waters and its endangerment—the situation in Slovenia, the Dinaric Karst and Europe. *Crustaceana* **72**, 767–780. doi: 10.1163/156854099503951

Sket B (1999*b*) The nature of biodiversity in hypogean waters and how it is endangered. *Biodiversity and Conservation* **8**, 1319–1338.

Stanford JA, Simons JJ (Eds) (1992) 'Proceedings of the first international conference on groundwater ecology.' (American Water Resources Association: Bethesda, MD)

Stock JH (1980) Regression model evolution as exemplified by the genus Pseudoniphargus (Amphipoda). *Bijdragen tot de Dierkunde* **50**, 105–144.

Stock JH, Iliffe TM, Williams D (1986) The concept 'anchialine' reconsidered. *Stygologia* **2**, 90–92.

Taiti S, Humphreys WF (2001) New aquatic Oniscidea (Crustacea, Isopoda) from groundwater calcretes of Western Australia. In 'Subterranean biology in Australia 2000'. (Eds WF Humphreys, MS Harvey) *Records of the Western Australian Museum* **64**(Suppl.), 133–151.

Tasmanian WHA (1999) 'Tasmanian Wilderness World Heritage Area Management Plan.' (Tasmanian Parks and Wildlife Service: Hobart)

Thurgate ME, Gough JS, Clarke AK, Serov P, Spate A (2001*a*) Stygofauna diversity and distribution in Eastern Australian caves and karst areas. *Records of the Western Australian Museum* **64**(Suppl.), 49–62.

Thurgate ME, Gough JS, Spate A, Eberhard SM (2001*b*) Subterranean biodiversity in New South Wales: from rags to riches. *Records of the Western Australian Museum* **64**(Suppl.), 37–48.

Tromble JM (1977) Water requirements of mesquite (*Prosopis juliflora*). *Journal of Hydrology* **34**, 171–179. doi: 10.1016/0022-1694(77)90069-5

Vermeulen J, Whitten T (1999) 'Biodiversity and cultural property in the management of limestone resources: lessons from East Asia.' (The World Bank: Washington, DC)

Ward JV, Voelz NJ, Marmonier P (1992) Groundwater faunas at riverine sites receiving treated sewage effluent. In 'Proceedings of the first international conference on groundwater ecology'. (Eds JA Stanford, JJ Simons) pp. 351–364. (American Water Resources Association: Bethesda, MD)

Watts CHS, Humphreys WF (1999) Three new genera and five new species of Dytiscidae (Coleoptera) from underground waters in Australia. *Records of the South Australian Museum* **32**, 121–142.

Watts CHS, Humphreys WF (2000) Six new species of *Nirridessus* and *Tjirtudessus* (Dytiscidae; Coleoptera) from underground waters in Australia. *Records of the South Australian Museum* **33**, 127–144.

Watts CHS, Humphreys WF (2001) A new genus and six new species of Dytiscidae (Coleoptera) from underground waters in the Yilgarn palaeodrainage system of Western Australia. *Records of the South Australian Museum* **34**, 99–114.

Watts CHS, Humphreys WF (2003) Twenty-five new Dytiscidae (Coleoptera) of the genera *Tjirtudessus* Watts and Humphreys, *Nirripirti* Watts and Humphreys and *Bidessodes* Regimbart, from underground waters in Australia. *Records of the South Australian Museum* **36**, 135–187.

Watts CHS, Humphreys WF (2004) Thirteen new Dytiscidae (Coleoptera) of the genera *Boongurrus* Larson, *Tjirtudessus* Watts & Humphreys and *Nirripirti* Watts & Humphreys, from underground waters in Australia. *Transactions of the Royal Society of South Australia* **128**, 99–129.

Wilkens H, Culver DC, Humphreys WF (Eds) (2000) 'Ecosystems of the World, vol. 30. subterranean ecosystems.' (Elsevier: Amsterdam)

Wilson GDF (2001) Australian groundwater-dependent isopod crustaceans. In 'Subterranean biology in Australia 2000'. (Eds WR Humphreys, MS Harvey) *Records of the Western Australian Museum* **64**(Suppl.), 239–240.

Wilson GDF (2003) A new genus of Tainisopidae fam. nov. (Crustacea: Isopoda) from the Pilbara, Western Australia. *Zootaxa* **245**, 1–20.

Wilson GDF, Johnson RT (1999) Ancient endemism among freshwater isopods (Crustacea, Phreatoicidea). In 'The other 99% the conservation and biodiversity of invertebrates'. (Eds W Ponder, D Lunney) pp. 264–268. (Transactions of the Royal Zoological Society of New South Wales: Sydney)

Wilson GDF, Keable SJ (1999) A new genus of phreatoicidean isopod (Crustacea) from the north Kimberley Region, Western Australia. *Zoological Journal of the Linnean Society* **126**, 51–79. doi: 10.1006/zjls.1998.0180

Winter TC, Harvey JW, Franke OL, Alley WM (1998) Ground water and surface water—a single resource. Circular 1139. United States Geological Survey, Denver, CO.

Zeidler W (1985) A new species of crustacean (Syncarida: Anaspidacea: Koonungidae), from sinkholes and caves in the south-east of south Australia. *Transactions of the Royal Society of South Australia* **109**, 63–75.