Austral Ark

The State of Wildlife in Australia and New Zealand

Edited by

Adam Stow

Macquarie University, Ryde, Sydney, Australia

Norman Maclean

University of Southampton, U.K.

Gregory I. Holwell

University of Auckland, New Zealand

CHAPTER 24

Down under Down Under: Austral groundwater life

Grant C. Hose, Maria G. Asmyhr, Steven J. B. Cooper and William F. Humphreys

Summary

Aquifers of the Austral region are globally significant in terms of their biodiversity. They support a rich and unique fauna, specifically adapted to the harsh subterranean environment. In this chapter we review the nature and diversity of groundwater ecosystems across the Austral region. We consider first the global origins of the Australian groundwater fauna, and their distributions across Gondwana. As the Australian continent evolved, the western shield emerged from the sea during the Proterozoic, which has led to a distinct fauna in those ancient landscapes. In the 'newer' eastern Austral regions there has also emerged a rich groundwater fauna, and here we review the current knowledge of fauna in eastern Australia and New Zealand. Mining and agricultural development threaten groundwater ecosystems across the region, but perhaps the greatest threat is our current lack of knowledge of these unique and important ecosystems and their biota. New approaches for conservation planning provide hope for improved recognition and protection of groundwater ecosystems, but with relatively little surveying of groundwater fauna having been done across the region, much remains undiscovered.

24.1 Introduction

Being the driest inhabited continent on Earth, the availability of water has always been a critical factor shaping the evolution and distribution of species across Australia. So too, the availability of water is critical to the survival and prosperity of human populations across the broader region, from small outback towns to major capital cities. As human pressures increase demand for water, groundwater is increasingly being used to meet water needs of households, industries and farms. Groundwater use accounts for around 20% of the total water used across Australia, it is more than 50% in New Zealand (Fenwick *et al.* 2004), and in many areas it is the only reliable water supply.

Groundwater is essential to maintain a diverse range of groundwater-dependent ecosystems across Australia. These include some iconic and well-known surface

landscapes in which groundwater is surface expressed, or where surface biota can access the subterranean water (Eamus *et al*. 2006). Such ecosystems include the red gum forests of the Murray River flood plain in the south, the savanna of the Daly River floodplain in the north, the *Banksia* forests of the Gnangara Mound and swan coastal plain in the west, and the artesian mound springs as oases across the central arid zone. But groundwater itself is also an ecosystem. Water moving through the rocks and sediments at depth creates unique environments, inhabited by a distinct and diverse fauna, containing species not found in surface environments. Only in recent decades has the true biological diversity of aquifers begun to emerge. The diversity of Austral groundwater ecosystems is indeed comparable to that of other regions of the globe, yet we have only begun to scratch the subsurface. Since aquifers cover much of Australia and New Zealand, aquifers are perhaps the most widespread ecosystem type across the Austral region.

Groundwater biota is under threat from a range of pressures, some specific to the region, others of a more cosmopolitan nature. However, unlike other ecosystems, the conservation of groundwater ecosystems is limited and, indeed, difficult to achieve (Boulton 2009). This chapter examines the Australian groundwater fauna and considers first how processes of continental drift and sea level change have shaped the diversity across the Austral region and, second, the threats facing the groundwater ecosystems in the region, and the current and potential conservation strategies that can ensure the protection of aquifers in terms of both the water resource and biodiversity value.

24.2 Overview of groundwater ecosystems

Groundwater ecosystems differ greatly from surface environments, in terms of both biota and the key ecological variables and processes. There is no light underground and, consequently, there are usually no primary producers in groundwater ecosystems. The ecosystem is thus largely dependent on carbon that filters from the surface, through the soil to the groundwater. This carbon is used by bacteria and fungi and provides the basis of the rather simple aquifer food web (Humphreys 2006).

In many aquifers, where pore spaces are large enough, higher order micro- and meio-invertebrates such as Turbellaria, Rotifera, Nematoda and Protozoa (Humphreys 2006) and some larger invertebrates are also present. The meiofauna are predominantly crustaceans, such as Copepoda, Syncarida, Amphipoda, Isopoda and Ostracoda, but may include insects, nematodes, molluscs, oligochaetes and mites. Of the crustaceans, some groups are found exclusively in groundwater (Remipedia, Thermosbanacea and Speleaogriphacea), and it is common for crustaceans to make up more than 50% of the total species abundance and richness of the groundwater invertebrate community (Korbel & Hose 2011). Insects, in particular, are relatively uncommon in groundwater (Humphreys 2006) although diverse coleopteran assemblages are emerging in some areas (Cooper *et al*. 2002; Leys *et al*. 2003; Watts *et al*. 2007) and stream insects can migrate long distances to be found in alluvial aquifers remote from surface waters (e.g. Stanford & Ward 1988).

Overall, vertebrates are rare in groundwater both in Australia and globally, and because of their large size, tend to be limited to karst aquifers where large water-filled voids exist. There are only three species of groundwater-adapted vertebrates known in the region. These are the blind cave eel, *Ophisternon candidum* (Mees 1962)

(Synbranchiformes: Synbranchidae) and two species of cave gudgeon, *Milyeringa species* (Perciformes: Eleotridae). *Milyeringa veritas* (Whitley 1945) co-occurs with *O. candidum* in the karst of Cape Range, north-western Australia (Humphreys 2006), and a second species, *Milyeringa justitia* has been recently described from nearby Barrow Island, WA (Larson *et al.* 2013) .

Most biota found in groundwater ecosystems are highly evolved, obligate groundwater-dwelling animals (stygobites) not found in surface environments. The dark, nutrient- and space-poor aquifer environment has shaped the convergent evolution of groundwater fauna. Groundwater species from different biological groups have independently evolved the common morphological traits of lack of eyes, hardened body parts, lack of body pigments, worm-like body shapes and enhanced non-ocular sensory appendages (Humphreys 2006). As a result, many species are morphologically very similar, requiring specialist taxonomic expertise, or genetic analysis to distinguish different species. The conditions of the groundwater realm favour those organisms so adapted, so healthy groundwater ecosystems will have a relatively high proportion of stygobites in comparison to non-groundwater-adapted surface species (stygoxenes) (Malard 2001; Stein *et al.* 2010).

The supply of external carbon limits the productivity of groundwater ecosystems, usually constraining pristine groundwaters to be low-energy environments, with low biomass and abundance of microbial and invertebrate fauna. With the exception of the occasional chemoautotrophic Prokaryotes, groundwater ecosystems are generally devoid of primary producers (such as plants or algae that cannot grow in the dark). With the additional lack of vertebrates, groundwater ecosystems tend to be relatively simple systems (Humphreys 2006). However, despite the relatively stable temperature and water quality conditions, groundwater ecosystems are characterised by biotic heterogeneity, meaning that there is an uneven distribution of biota over space and time.

Microbial assemblages are the foundation of aquifer ecosystems (Gibert *et al.* 1994; Humphreys 2006). Through heterotrophic or chemotrophic pathways, they capture energy and form the basis of the aquifer food web, providing a food source for invertebrates (Novarino *et al.* 1997; Humphreys 2006). The majority of microbes are distributed sparsely within the aquifer matrix, occurring as single cells or small colonies attached to sediment surfaces; generally less than 1% of available sediment surfaces are colonised by bacteria (Griebler *et al.* 2002; Anneser *et al.* 2010). Healthy, undisturbed aquifers tend to have very low microbial diversity and activity relative to surface waters (Griebler & Lueders 2009), due mainly to naturally low concentrations of nutrients, carbon and oxygen (Gounot 1994). Most microbes inhabiting aquifers are attached rather than being free-living (Gounot 1994; Griebler & Lueders 2009; Anneser *et al.* 2010) although the ratio of attached to free-living bacteria can change with contamination (e.g. Griebler *et al.* 2002). See also Box 24.1.

In terms of meiofauna, groundwater ecosystems are typified by low α diversity (few species at any one locality), with a 'truncated' functional and taxonomic diversity (Gibert & Deharveng 2002). This creates a system with (generally) low horizontal (within trophic level) and vertical (between trophic level) diversity (*sensu* Duffy *et al.* 2007) in a given location, and short food chains. However, isolation has created a fauna dominated by short-range endemic species (Harvey 2002), providing high ß diversity (many species across localities) of invertebrates (Humphreys 2008). This trend is not evident in microbial assemblages which appear to be much more widely distributed (Griebler & Leuders 2009).

Box 24.1 Microbial assemblages

Like other elements of the groundwater environment, the microbial assemblages inhabiting aquifers in Australia have been poorly studied, with the exception of those organisms and assemblages used for the bioremediation of contaminated aquifers. The current paradigm of groundwater microbiology is that 'everything is everywhere' meaning that the microbial flora of groundwater is widespread, and comprises species commonly found in soil and surface water environments, with no endemic groundwater microbes yet recorded (Griebler & Leuders 2009).

Recent research in karst regions of the Nullabor and Cape Range (Seymour *et al.* 2007; Humphreys *et al.* 2012) suggest the potential for novel 'groundwater-only' species or at least specific assemblages may exist. The caves of the Nullabor host unique microbial biofilms, or 'cave slimes' that occur as dense 'mantles' or curtains that are suspended in the water column of the large water-filled limestone caverns (Holmes *et al.* 2001). In this environment, carbon for growth and metabolism is extremely limited. Accordingly, the microbes in the biofilm rely heavily on oxidation of nitrogen for energy. Detailed genetic screening of the biofilms identified many microorganisms known from other environments, but also identified several novel species which may well be endemic to these unique microbial communities (Tetu *et al.* 2013). Studies in Cape Range (Seymour *et al.* 2007; Humphreys *et al.* 2012) and in the Ashbourne aquifer, South Australia (Smith *et al.* 2012), have shown strong vertical stratification in microbial assemblages and are further evidence that groundwater assemblages are unique compared to those of other aquatic and terrestrial habitats.

In general, archaea and bacteria are diverse and abundant in groundwater communities, but the micro-eukaryotes, such as fungi, are relatively poorly studied. However, the little information available suggests that fungi are generally common but in lower abundance and diversity than they are in surface water ecosystems (Lategan *et al.* 2012). Indeed, fungi and yeasts made up less than 5% of the total abundance of cultivable heterotrophic microbiota in groundwater samples from aquifers across NSW (Lategan *et al.* 2012). Like bacterial assemblages, there is commonality of most taxa between aquifers at the genus level (Lategan *et al.* 2012), although some taxa were limited to specific wells or aquifers, particularly those that had been contaminated with chlorinated hydrocarbons. Indeed, low level contamination of groundwater by chlorinated hydrocarbons may stimulate the richness of fungi and yeasts. Highly chlorinated sites had few or no cultivable fungi and the uncontaminated reference sites were similar in richness and diversity to other aquifers across the state (Lategan *et al.* 2012).

24.3 Austral diversity

Just as in other ecosystems, and as evident in other chapters of this book, the biota of groundwater ecosystems reflects the unique history and evolution of the Australian continent and the region. Many groundwater species are relicts of once common surface species that sought refuge in the stable groundwater environment during times of past climate change. Consequently, the Austral groundwater fauna reflects the various stages of the evolution of the Austral region, starting with the break-up of Pangaea and

Gondwana, the drift north and the changing climate and aridity, the early and sustained emergence of large parts of the Australian continent from the sea during the Proterozoic, and the more recent evolution of the east coast landscapes and New Zealand. The evolution of the Austral landscape differed considerably from that of the Northern Hemisphere, particularly in that it lacked the Pleistocene glaciations that are considered to have been critical to the evolution of groundwater diversity in the Northern Hemisphere (Guzik *et al.* 2010). For this reason, and the extensive areas of saline groundwater and aridity across the region, Austral groundwater ecosystems were long considered to be depauperate of specialised groundwater fauna. However, since the 1990s, it has been established that the subterranean realm in Australia supports an enormous range of obligate subterranean animals in both terrestrial and aquatic habitats. Furthermore, as the species are typically endemic to very small areas, there is a very high biodiversity at both landscape and continental scales, a story that is still unfolding (Humphreys 2008, 2012; Guzik *et al.* 2010).

In 2000, there were, globally, over 7800 known stygofaunal species (Juberthie 2000). However, recent estimates will be far greater, due to large research efforts in Australian (see Guzik *et al.* 2010) and European karst regions. The growing interest in groundwater fauna across the Austral region is reflected in the recent growth in species descriptions, particularly arising from studies in the Yilgarn and Pilbara, but also further afield. In 2010, Guzik *et al.* reported some 770 stygofauna taxa known in the west of Australia. From this they predicted that around 80% of the groundwater fauna are unknown, and the true richness of the region may be as high as 4140 stygobitic species. With this high diversity, and the largely unexplored diversity of eastern Australia, it is clear that the Austral region is a biodiversity hotspot of global significance. In the next section we will consider the global origins of some elements of the groundwater fauna and the differences across the Austral region.

24.4 Global origins of Austral groundwater fauna

24.4.1 Tethyan connections

In a small area of north-western Australia, along the coast at Ningaloo Reef, Barrow Island and the adjacent Pilbara coast, the coastal groundwater in karst, though not directly connected with the sea, is affected by marine tides, is highly stratified with brackish water overlying sea water, and in total darkness (Jaume & Boxshall 2013). This anchialine habitat harbours a remarkable fauna largely comprising crustaceans restricted to anchialine systems the generic composition of which is predictable however far apart in the world they occur. This region of Australia abutted the Tethys, a shallow sea that spread between Africa and Europe into the opening Atlantic during the Jurassic as a result of the fragmentation of the supercontinents Pangaea and subsequently Gondwana. This connection has left a strong Tethyan signature in the fauna of these Australian anchialine habitats which are closely related to those inhabiting caves on either side of the Atlantic, in the Canary Islands and northern Caribbean. The marine part of the anchialine system includes many higher taxa that are new to the Southern Hemisphere including Remipedia, a new class described from the Caribbean as recently as 1981. Also copepods of the order Misophrioida and families Epacteriscidae and Ridgewayiidae, and the order Thermosbaenacea, tiny shrimp-like crustaceans that uniquely carry their eggs

and young in a dorsal rather than a ventral pouch (see Figure 24.2, Plate 57). One lineage, atyid shrimps of the genus *Stygiocaris* (see Figure 24.2, Plate 57), has been examined using molecular phylogenetics and found to be only distantly related to the other Australian atyid shrimps but which is the sister taxon to *Typhlatya* that occurs in similar habitats on either side of the North Atlantic (Page *et al*. 2008; von Rintelen *et al*. 2012). It has not yet been resolved whether this vicariant distribution resulted from fragmentation of continents, dispersal within Tethys or both (Bauzà-Ribot *et al*. 2012; Phillips *et al*. 2013).

24.4.2 Gondwanan connections: Phreatoicidea

Phreatoicidean isopods have a Gondwanan distribution and occur widely across southern Australia (and in tropical Arnhem Land and the Kimberley). Their distribution is strongly associated with the areas of the continent not submerged by Cretaceous seas. Five hypogean species are known from the Precambrian western shield where the family Hypsimetopidae is represented by the genera *Pilbarophreatoicus* in the Pilbara and *Hyperoedesipus* in the Yilgarn. These genera are closely related to the hypogean genera found in the Ganges Valley and from caves of Andrah Pradesh (India). These occurrences suggest that Hypsimetopidae were hypogean prior to the separation of Greater Northern India from the western shore of Australia (*c*. 130 My BP) (Wilson 2008).

Crenisopus, which is a stygobiont genus found in aquifers in the Kimberley region of Western Australia (Figure 24.1, Plate 56), is ancestral to most families in the Phreatoicidea, suggesting that the divergence between them occurred after they entered freshwater but prior to the fragmentation of East Gondwana during the Mesozoic era, this providing a link between African and Australasian lineages of phreatoicideans (Wilson & Keable 1999).

24.4.3 Gondwanan connections: Spelaeogriphacea

The crustacean order Spelaeogriphacea, which comprises four species of stygobionts, was described from a cave at an altitude of about 900 m up Table Mountain in South Africa, a feature pre-dating the separation of South America and Africa. A second species occurs in caves in Mato Grosso do Sul, western Brazil, these locations suggesting a split prior to the separation of Africa and South America, 110 Ma in the Early Cretaceous. The finding of two species in the Fortescue Valley, Pilbara, strengthens the Gondwana link. Living spelaeogriphaceans all occur in contact with geological contexts that are earliest Cretaceous or older. The colonisation of Gondwanan freshwater is likely to have occurred after the retreat of the Gondwanan ice sheet (after 320 Ma BP) and prior to the dissolution of Gondwana (142–127 Ma BP) (Jaume 2008).

24.4.4 Gondwanan connections: Bathynellacea

The tiny, vermiform and mostly interstitial stygobionts belonging to the Bathynellacea are another taxon suggesting links with other continents but these have yet to be tested using molecular phylogenetic methods. They are restricted to groundwater systems and occur throughout the world, suggesting that they are of Pangaean origin. However, most species are known only from their type locality and many belong to monotypic genera so that it is not surprising that their geographic distributions contain strong continental signatures. Some Australian parabathynellid genera have apparently clear affinities with
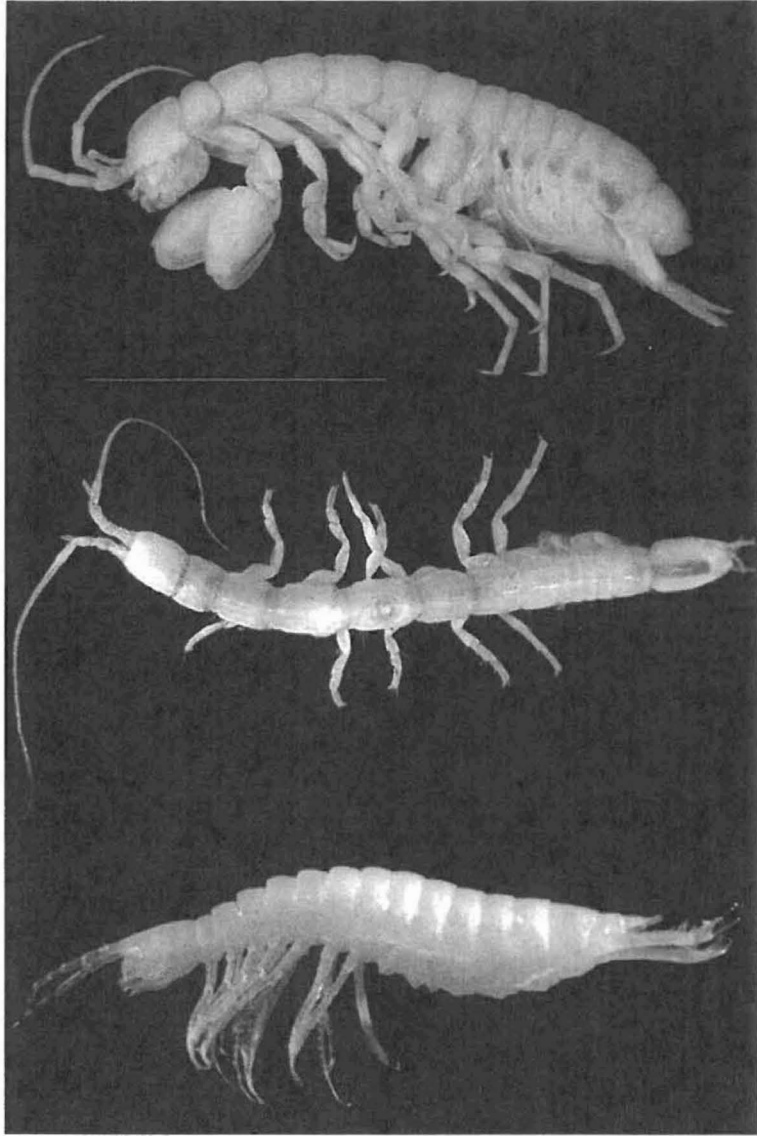
Figure 24.1 (Plate 56) Upper, *Crenisopus* sp. from Koolan Island, WA (photo George Wilson); middle, Phreatoicid isopod from WA (photo George Wilson); lower, *Brevisomabathynella* sp. (Parabathynellidae) from calcrete aquifer in Western Australia (photo Kym Abrams). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

eastern Gondwana; *Chilibathynella* and *Atopobathynella* are known from Chile and southeastern Australia, the latter also from India. *Notobathynella* also occurs in New Zealand while other Australian genera have a broader distribution with *Hexabathynella*, from eastern Australia, being found in New Zealand, southern Europe, Madagascar and South America. Conversely the genera *Kimberleybathynella*, *Brevisomabathynella*, *Billibathynellla* and *Octobathynella* are endemic to Australia (Schminke 2011).

The Australian fauna has turned up a paradox because the Parabathynellids are widely considered to have a freshwater origin and the species are typically from freshwater systems <500 mg l^{-1}. However, many of the species in Australia occur in brackish water

and *Brevisomabathynella clayi*, a large, free-swimming parabathynellid (Figure 24.1, Plate 56), occurs in arid Australia in water close to marine salinity (PSU 35.93) (Cho & Humphreys 2010) in the centre of the Western Shield, where it is associated with a number of maritime copepod lineages such as Ameiridae (Harpacticoida) and *Halicyclops* (Cyclopoida) (Humphreys 2008).

24.5 The arid interior of WA and SA

In the mid 1990s, following discoveries along coastal Western Australia of diverse crustacean fauna with Tethyan and Gondwanan connections, a diverse stygofauna was discovered in the arid Yilgarn and Pilbara regions of Western Australia (Humphreys 2001). These regions together form the Western Shield, a region of the Earth's crust that has remained emergent since the Paleozoic, and consequently containing an ancient history of freshwater habitats. The Western Shield is rich in mineral deposits and the requirement in Western Australia for mineral resource development projects to include subterranean fauna in environmental impact assessments resulted in widespread surveys that have shown that non-karst and non-alluvial substrates, such as pisolites and fractured rocks of the Pilbara region, also support diverse subterranean aquatic and terrestrial faunas. This survey effort has not been applied to many other areas of the Australian arid zone, with the exception of some recent work in South Australia (Flinders Ranges and Eyre Peninsula regions; Remko Leijs, personal communication).

Within the 220 000 km^2 Pilbara region, ~300 new species of troglobionts have been reported by consultancy companies, many of which appear to be short range endemics (SREs; Harvey 2002) and found in a variety of habitats, including pisolite, fractured rock, limestone karst and calcrete. These include diverse groups of arachnids, such as Schizomida, a tropical forest group that has survived the surface aridity in pesolitic iron ore mesas of the Pilbara region and humid caves in the arid Cape Range, and Palpigradi, with Australian native species only recently discovered in caves or boreholes in karst and fractured rock substrates from the Pilbara and calcretes of the Yilgarn region (Barranco & Harvey 2008). The Pilbara region is also known as a biodiversity hotspot for the crustacean order Ostracoda, with recent finds from the family Candonidae, representing 25% of the known genera in the world (Humphreys 2012; Karanovic 2012). Although the Pilbara and Yilgarn subterranean fauna regions are contiguous, they have radically different subterranean faunas with little overlap, even at the generic level (Table 24.1). The reason for this remarkable disjunction in the composition of the fauna is not understood and is difficult to reconcile with the Western Shield having been a single, continuously emergent land mass since the Paleozoic at least.

Within the Yilgarn region, the fauna, comprising diverse diving beetle species (Dytiscidae) and crustaceans, such as Amphipoda, Isopoda, Bathynellacea and Copepoda, was discovered in groundwater calcretes, shallow (10–20 m thick) carbonates formed by precipitation from groundwater, as a result of near-surface evaporation. Hundreds of isolated calcrete bodies exist in the region, deposited upstream of salt lakes (playas) along ancient palaeovalley systems. Groundwater flow and episodic surface recharge events, and presumably plant root systems, have resulted in numerous minor karst features within the calcretes, providing a suitable habitat for tiny invertebrates (<5 mm) within a groundwater environment that is the equivalent of a

Table 24.1   Overlap of stygal taxa between contiguous northern Yilgarn and Pilbara regions on the Western Shield of Australia. (Abstracted from Humphreys 2008 where the relevant references are given.) Shown are the number of species and genera of Copepoda, Candoninae (Candonidae: Podocopoda), oniscidean and tainisopidean Isopoda, and Dytiscidae (Coleoptera)

Stygal taxon	Unit	Yilgarn	Pilbara	Overlap %
Copepoda	species	30	43	4
Copepoda	genera	15	25	21
Podocopoda: Candoninae: Candonidae	species	5	58	0
Podocopoda: Candoninae: Candonidae	genera	1	13	8
Isopoda: Oniscidea, (stygobionts)	species	c. 20	0	0
Isopoda: Tainisopidea	species	1	5	17
Coleoptera: Dytiscidae	species	97	0	0

subterranean estuary (Humphreys *et al.* 2009). More recently, a diverse troglofauna, comprising taxa, such as oniscidean isopods, collembola, insects, diplurans, myriapods and arachnids (see Barranco & Harvey 2008) that would otherwise be at home in rainforest leaf litter, was also found to be associated with the groundwater calcretes.

Taxonomic treatment of much of the stygofauna and troglofauna is still in its infancy, but studies to date, including molecular phylogenetic and phylogeographic analyses of the stygobitic dytiscid beetles, amphipods and isopods, have shown that numerous species exist, the majority of which are restricted in their distribution to single calcrete bodies, leading to the description of the calcrete system as a subterranean archipelago (Cooper *et al.* 2002, 2007, 2008; Leys *et al.* 2003; Watts & Humphreys 2009). Molecular clock analyses suggest that subterranean lineages evolved 5–8 My ago, placing their evolutionary origins firmly in the period of spreading aridity on the Australian continent, following the drift northwards of the Indo-Australian plate to south-east Asia. This was a period, commencing in the late Miocene (~14 million years ago), of major climatic and environmental changes that resulted in the widespread disappearance of rainforest and permanent sources of water from the interior of Australia. It is likely that the groundwater calcretes acted as refugia for rainforest taxa that were able to adapt to life in darkness and track the water table underground. Notably, it is the groups of animals associated with rainforest leaf litter or capable of living in the hyporheic zone of creeks and rivers that comprise many of the taxa found in subterranean ecosystems. The species have subsequently survived in the calcretes for millions of years, despite considerable fluctuations in surface conditions resulting from ice age climatic changes during the Plio-Pleistocene, when the interior of Australia cycled from wet/warm to arid/cold climates (Byrne *et al.* 2008). They are thus living fossils of the Australian Miocene rainforest environment.

It has been recently discovered that many of the groups of aquatic organisms found in the Western Australian calcretes are also found in other Australian arid zone freshwater 'refugia'. These include the wetlands associated with isolated mound springs of the Great Artesian Basin (GAB: springs that formed by upwelling of groundwater from the GAB) in South Australia, which have provided refugia for a variety of aquatic organisms, including isopod and amphipod crustaceans that are related to species found in the calcretes (Murphy *et al.* 2009). Calcretes of the Ngalia basin, northwest of Alice Springs in the Northern Territory also harbour many of the taxa found in the Western Australian
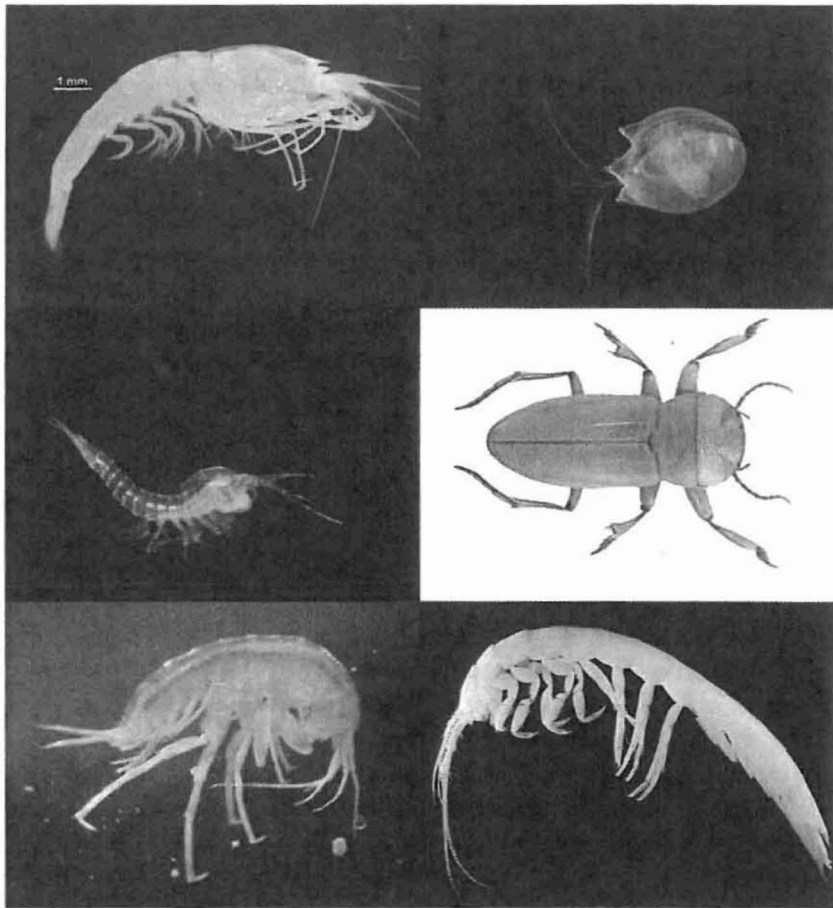
Figure 24.2 (Plate 57) Clockwise from upper left: *Stygiocaris* sp. (Atyidae) from anchialine waters of Ningaloo Coast World Heritage Area (photo Danny Tang); *Danielopolina baltanasi* from anchialine caves on Christmas Island, Indian Ocean (photo Ross Anderson); *Paroster byroensis* from calcrete aquifers, Gascoyne, WA (photo Chris Watts); *Pygolabis* humphreysi (Tainisopodidae) from the Pilbara, a family of isopods, also in the Kimberley, endemic to WA (photo George Wilson); Paramelitid amphipod from Cane River, WA (photo Remko Leijs); *Halosbaena tulki* (Thermosbaenacea), Ningaloo Coast World Heritage Area (photo Douglas Elford, Western Australian Museum). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

calcretes, including dytiscid beetle species (e.g. Balke *et al.* 2004; Figure 24.2, Plate 57) and a remarkably diverse *Haloniscus* isopod fauna (S. Taiti, unpublished data). These common elements further support the role of aridity in driving relatively widespread rainforest species underground or into isolated groundwater-dependent ecosystems on the surface.

Ongoing research of groundwater systems in the South Australian arid zone, also indicate that a diverse stygofauna exists in alluvial aquifers of the Flinders Ranges and Eyre Peninsula, including a dytiscid beetle (Leys *et al.* 2010) and parabathynellids (Abrams *et al.*, 2013). Amphipoda (family Chiltoniidae) are also particularly diverse in these groundwater systems, and again reveal the ancient connections between now isolated freshwater systems (R. King & R. Leijs, personal communication). Like the alluvial aquifers of eastern Australia there are many more subterranean species in the arid interior of Australia that await discovery.

24.6 The 'new' east

In their recent review, Guzik *et al.* (2010) predicted lower diversity in the newer landscapes of eastern Australia. The east of the continent is geologically younger, having had marine inundations through the Cretaceous period, and overall a much more dynamic geological history than parts of western Australia which have been emergent from the sea since the Proterozoic (BRM Palaoegeographic Group 1990).

Contemporary studies of groundwater biota in the east have focussed on applied ecology, with a focus to understand relationships to land use (Korbel *et al.* 2013), pollution impacts (Sinton 1984; Hartland *et al.* 2011; Stephenson *et al.* 2013), hydrology (Tomlinson 2008; Stumpp & Hose 2013), and aspects of groundwater sampling and assessment (Hancock & Boulton 2009; Hose & Lategan 2012; Korbel & Hose 2011). While some studies have compared the diversity of different aquifers and regions (Hancock & Boulton 2008) they have generally not been detailed, broad studies of phylogeography such as those undertaken in the Yilgarn and Pilbara (Guzik *et al.* 2008; Cooper *et al.* 2008), although some small-scale phylogenetic analyses have been done (Hose 2009; Cook *et al.* 2012).

The structure of groundwater assemblages in eastern Australia is similar to those in the west. Certainly the same higher taxa are present, although, as expected given the geographical separation, taxa collected from eastern Australia often form separate lineages within continental phylogenies (Leys & Watts 2008; Abrams *et al.*, 2013). Further, there appear differences in the relative abundances of different taxa. While amphipods and isopods are widespread across the west (e.g. Eberhard *et al.* 2009; Schmidt *et al.* 2007) they are encountered less frequently in the east (e.g. Hancock & Boulton 2008, 2009), which may reflect the history of marine inundations in the east, which elsewhere are considered to be responsible for the absence of some of the more ancient crustacean lineages of amphipods and isopods in the groundwater fauna (Bradbury 1999; Wilson & Johnson 1999). Instead, crustacean faunas are dominated by syncarids (Bathynellidae, Parabathynellidae and Psammaspididae) and Harpacticoid and Cyclopiod copepoda. Anaspidacea are only found in eastern Australia (Hobbs 2000), with several families found across the region (Serov 2002). Hancock & Boulton (2008) reported stygobitic elimid and dytiscid beetles from the Hunter and Peel River valleys, NSW (Watts *et al.* 2007, 2008), and these records remain the only examples of stygobitic beetles inhabiting alluvium in Australia. Although diverse dytiscid water beetle assemblages are present in the calcretes of the Yilgarn (Leys *et al.* 2003; Watts *et al.* 2008), such beetles are rare in the east.

Karstic and limestone habitats are traditionally the hotspots of groundwater diversity, and these habitats are somewhat rarer in eastern Australia than in the Western Shield and throughout Europe. However, much of the karst of New South Wales is impounded and as such is geologically isolated, and in some cases is of Devonian origin (Osborne *et al.* 2006) so there is great potential for these environments to support novel taxa through such long isolation. To date 82 stygobitic species have been recorded in the east coast karsts (summarised in Thurgate *et al.* 2001). Caves of Tasmania and New South Wales have the most diverse groundwater faunas (Thurgate *et al.* 2001), although this richness may also reflect the greater sampling effort in those states. The species richness of most cave and karst

regions in eastern Australia is low by world standards (Thurgate *et al.* 2001) but this may be a consequence of the small, impounded nature of these features.

The deep alluvial deposits of the east coast have yielded a rich fauna. Hancock & Boulton (2008) examined parts of the Peel and Hunter Valley alluviums in NSW, and the Burnett and Pioneer Valley alluviums in Queensland. The study recorded 87 taxa, with seven to 33 taxa per aquifer. Tomlinson (2008) expanded on Hancock & Boulton's (2008) survey of the Peel alluvium and reported 54 taxa of which 33 were obligate groundwater inhabitants. More recent surveys of the alluvial aquifers associated with inland rivers have yielded similar richness, with 20 taxa in the Gwydir (Korbel *et al.* 2013), 15 in the Namoi (Korbel 2013), and ten taxa in a small area of the Macquarie River alluvium (Hancock & Boulton 2009). Similar higher taxa were recorded across all studies, but it was often the Acarina that were the most (morpho)species-rich group. Although detailed species-level taxonomy has not been performed on the specimens collected in these studies, it is likely that each taxon represents a new species, with perhaps the exception of potential hydrologic connectivity and hence species overlap between the Peel and Namoi Rivers.

Upland swamps are distinctive features of low-relief plateau areas in eastern Australia (Young 1986; Dodson *et al.* 1994). They form in shallow depressions in the landscape and, fed by rainfall and regional groundwater, provide a unique, shallow groundwater ecosystem. Sampling of swamps in the Southern Highlands and Blue Mountains of NSW has identified assemblages variably dominated by harpacticoid and cyclopoid copepods, nematodes and ostracods, but also containing syncarids, mites and amphipods. While not all species are likely to be stygobitic, these systems are potentially a diverse source of fauna. Initial studies show particularly fine-scale endemism, with swamps in the Southern Highlands separated by only several hundred metres containing genetically distinct harpacticoid copepod populations (Hose 2009). Similar patterns of endemism are likely in Blue Mountains swamps as seen in other taxa (Dubey & Shine 2010).

The fractured rock systems of eastern Australia appear somewhat less diverse than those of the west (e.g. Eberhard *et al.* 2005), but nevertheless, stygofauna have been recorded in the fractured Triassic Hawkesbury sandstone to the north (11 stygobitic taxa; Hose & Lategan 2012) and south of Sydney (three stygobitic taxa; Hose 2008, 2009), with the likelihood that each area contains locally endemic taxa. The assemblages are dominated by copepods (Harpacticoida and Cyclopoida), but syncarids are also common in some areas. The fauna appears spatially limited within the aquifers, and constrained to shallow water bearing zones (Hose, personal observation). There is a clear need to extend the taxonomy of these surveys to better describe and contextualise the diversity of this region.

The coastal sand aquifers are a common feature of the east coast of Australia. They are an important water source for local communities, but given the high population density on the east coast, the integrity of these aquifers is under threat. For example, the Botany sands aquifer in Sydney is perhaps the most contaminated groundwater site in Australia, with contamination from industrial chlorinated hydrocarbons that began in the 1940s (Acworth 2001). The site is now one of Australia's largest groundwater clean-up projects. While sampling of the aquifer did not reveal meiofauna, diverse prokaryote and eukaryote assemblages were evident, with changes in assemblage structure evident and associated with the contamination gradient (Stephenson *et al.* 2013). The pore space provided by sand aquifers is generally too small to permit stygofauna, although sampling

in the coastal sands of the Tomago-Tomaree and Woy Woy and Umina sandbeds on the NSW central coast region of the NSW central coast has revealed three stygobitic taxa (Hose, unpublished data).

Some of the earliest records of stygofauna in the Austral region emanated from the rich alluvial aquifers of the Canterbury plains (Chilton 1882). This region, and indeed the rest of the New Zealand islands have proved a rich source of stygofauna with over 160 known groundwater taxa (Fenwick & Scarsbrook 2004), but the true richness is likely to exceed several hundred taxa (Fenwick *et al.* 2004).

As seen in Western Australia over the past decade, the intensity of mineral resource exploration and extraction has fuelled the search for stygofauna as part of environmental impact assessments and mine approvals. Following the lead of the west, new approvals for coal and coal seam gas extraction are also requiring assessments of groundwater ecosystems. To date this has been largely *ad hoc*, and done by environmental consultants as needed on a site-specific basis. There is a clear need for a comprehensive survey of groundwater ecosystems in eastern Australia, supported by government agencies to examine the diversity of these ecosystems before more regions are developed for mineral exploitation.

24.7 Threats to groundwater ecosystems

The greatest threat facing groundwater ecosystems both in the Austral region and globally, is the current lack of understanding of structure, functioning and diversity of these systems. Indeed, many topics that are well studied in other branches of ecology are essentially unexplored in groundwater (Larned 2012). In particular, little is known of the ecology, distribution and life history of groundwater taxa, which makes conservation efforts particularly challenging (see also Box 24.2).

Box 24.2 Ecosystem services of groundwater ecosystems

Ecosystem goods and services (collectively 'ecosystem services') are natural products and ecological functions that are of benefit to humans (Millennium Ecosystem Assessment 2005). Groundwater ecosystems provide a number of such services (Table 24.2) which include water storage and transport, water purification, and the support of groundwater-dependent ecosystems (Haack & Bekins 2000; Herman *et al.* 2001; Murray *et al.* 2006; Boulton *et al.* 2008).

Table 24.2 Ecosystem services provided by groundwater (from Tomlinson & Boulton 2008)

Type of service	Examples
Provisioning	Water for drinking, irrigation, stock and industrial uses
Supporting	Bioremediation (water purification), ecosystem engineering (flow maintenance), nutrient cycling, sustaining linked ecosystems, providing refugia
Regulating	Flood control and erosion prevention
Cultural	Religious and scientific values, tourism

Perhaps the most critical of these services is the provision of water for human consumption, industry and agriculture. Currently, aquifers provide 600–700 km^3 of water annually, making it the world's most extracted raw material (Zektser & Everrett 2004). In many developing countries it is the most important and safest source of drinking water, yet it is equally important in developed countries, providing nearly 70% of the piped water supply in EU countries (Zektser & Everrett 2004).

The capacity for water quality improvements in aquifers, such as the removal of nitrogen, breakdown of organic contaminants and the assimilation of DOC, is determined largely by the microbial assemblages within an aquifer (Gounot 1994; Chapelle 2001; Griebler 2001; Haack & Bekins 2000, Griebler & Lueders 2009). Under anaerobic conditions, denitrifying bacteria can oxidise nitrate to gaseous nitrogen which is then removed from the groundwater (Gounot 1994). Similar microbial-mediated processes are responsible for the breakdown of organic chemicals; however, the exact mechanisms remain unclear (Chapelle 2001; Goldscheider et al. 2006).

Stygofauna contribute to water quality improvement by grazing on microbial biofilms which in turn promotes biofilm activity and hence purification capacity (Chapelle 2001; Gounot 1994). The burrowing activity of macroinvertebrates and the biofilm grazing may help maintain the porosity of the aquifer matrix, thereby maintaining flow and the movement of nutrients through the aquifer (Boulton et al. 2008; Danielopol et al. 2000; Haack & Bekins 2000; Des Châelliers et al. 2009). There is evidence that macroinvertebrate burrowing enhances flow in benthic and hyporheic environments and although likely to occur, it remains untested in aquifers (Boulton et al. 2008).

The economies of Australia and New Zealand are both dependent on primary production and, particularly for Australia, mineral exports. Unfortunately, both of these major industries pose a threat to groundwater ecosystems (e.g. Korbel et al. 2013). Physical threats to groundwater ecosystems arise through changes in the groundwater regime, such as changes in the availability of groundwater in terms of its flow, depth and timing, and the quality of the water.

With groundwater ecosystems heavily dependent on carbon and oxygen infiltration from surface environments, changes to the rate and volume of groundwater moving through an aquifer can alter the distribution of such nutrients, and consequently impact significantly on fauna. Reductions in flow and the resupply of oxygen can lead to anoxia and limited carbon availability. Natural patterns of decreasing nutrients with depth limit most groundwater fauna to shallow depths (Danielopol et al. 2000), and changing the groundwater regime further exacerbates this limitation to fauna distributions. Such changes may occur by way of reduced groundwater recharge, such as interception of run-off by impervious surfaces, or groundwater abstraction leading to changes in the natural hydraulic gradient and flow. Lowering of the watertable in the Jewel Cave Karst system has led to drying of cave root mat habitats and the loss of fauna (Eberhard & Davies 2011).

Lowering of groundwater tables is a common consequence of over-abstraction of groundwater or reduced groundwater recharge, such that the rate at which water is

extracted exceeds the rate at which water recharges the aquifer. Fauna are able to tolerate small changes in groundwater levels, but ongoing declines in water levels reduce the volume of accessible habitats for stygofauna and can disconnect groundwater from surface waters (Hancock 2009). Rapid declines in groundwater may lead to stranding of organisms in layers above the water table (Tomlinson 2008; Stumpp & Hose 2013), but the mobility of the taxa is important in enabling their survival. Stygofauna may not survive 48 h in drying sediments (Tomlinson 2008; Stumpp & Hose 2013).

Anthropogenic activities have impacted the quality of groundwater the world over, reducing its suitability for human use and as a habitat for groundwater biota. In the Austral region, increasing concentrations of dissolved ions (salinity), nutrients (particularly carbon and nitrogen) such as from sewage contamination (Sinton 1984; Hartland *et al.* 2011), metals and organic chemicals (Stephenson *et al.* 2013) all threaten groundwater biota and can lead to changes in groundwater assemblages. Unfortunately, changes associated with groundwater quality and contamination are difficult to fix, and if possible, remediation is a long and costly process. Changes to groundwater quality can be directly toxic to biota (e.g. Hose 2005, 2007; Humphreys 2007), or through changes, facilitate the establishment of stygoxenes that may be better able to tolerate the new conditions. Even though direct impacts of stygoxenes on groundwater assemblages may not be evident (Jasinska *et al.* 1993), exotic species pose a considerable threat to fauna (Proudlove 2001), often leading to shifts in ecosystem structure and function.

Dryland and irrigation salinity threatens large areas of productive agricultural lands in Australia and New Zealand. In such cases, the rise of water tables through saline sediments increases the salinity of the groundwater. Similarly, the extraction of fresh groundwater in coastal areas can permit intrusion of sea water into otherwise freshwater aquifers as hydraulic gradients are changed. With many stygofauna having marine ancestry, it is likely that stygofauna have some capacity to tolerate small increases in salinity. Indeed, crustaceans from surface waters tend to be relatively tolerant to increases in salinity relative to other taxa (Kefford *et al.* 2003). Generally stygofauna are rarely found at salinities above 3000 µS/cm (Hancock & Boulton 2008) although in the Yilgarn this condition is commonly and greatly exceeded (Humphreys *et al.* 2009). The threat of saline groundwater is not limited to the aquifer ecosystem but extends to adjoining surface waters (Halse *et al.* 2003).

24.8 Conservation strategies, issues and priorities for groundwater ecosystems

With most groundwater species known from only one or two sites, the majority of them could potentially be classified as vulnerable or endangered taxa (Gibert & Deharveng 2002; Humphreys 2006). Indeed, some of the most defining characteristics of subterranean fauna are their seemingly narrow distributions and extreme endemism over short geographical ranges (short-range endemics, *sensu* Harvey 2002). However, lack of formal species descriptions and reliable data on distribution for the majority of stygofauna in the Austral region would result in them being classified as data deficient in the IUCN Red List of threatened species (International Union for Conservation of Nature). Given this lack of data, the wiser approach is to protect entire habitats and their surface recharge areas (Boulton *et al.* 2003). Two global agreements are in place for protecting subterranean

habitats; the Ramsar Convention (Ramsar Convention on Wetlands 1971) a global treaty on conservation and the sustainable use of wetlands including subterranean wetlands, and the UNESCO world heritage list (Culver & Pipan 2009). Although not the main focus of these lists, some stygofauna hotspots have been included and are protected under these agreements (Culver & Pipan 2009).

The field of conservation biology of stygofauna is in its infancy across the world, and concerted surveys of biodiversity on a large scale are not common. An exception, however, is in Europe, where great progress has been made towards elucidating biodiversity and developing conservation strategies as a result of the large-scale subterranean biodiversity survey project PASCALIS (Protocol for the ASsessment and Conservation of Aquatic Life In the Subsurface) (Gibert *et al*. 2005). This project sampled a variety of groundwater habitats across several European countries and the results that emerged from it were used to aid the selection of sites for a groundwater reserve network (Michel *et al*. 2009).

'There are simply too many subterranean species at risk to deal with them one at the time' (Culver *et al*. 2000), thus designing reserve networks to protect all species may be impractical. However, because subterranean species are geographically concentrated in a small percentage of the landscape, the geographical extent of a reserve does not have to take up large areas. Based on grid cells containing stygofauna across Belgium, France, Italy, Portugal, Slovenia and Spain, Michel *et al*. (2009) found that by conserving as little as 10% of the landscape containing groundwater the majority of the species (73.8%) were included in the reserve network. In France, Ferreira *et al*. (2007) found that less than 2% of the landscape was needed to capture 60% of known groundwater species.

In contrast to Europe (PASCALIS project) and parts of the USA (see Culver *et al*. 2000), for Australian aquifers, where very little stygofaunal sampling has occurred, integrated plans for groundwater use and conservation remain non-existent or limited (Boulton 2009). Given the short duration of research targeting these ecosystems in Australia (the past two decades), the amount of biodiversity that remain undiscovered is likely to be enormous. With the majority of subterranean groundwater ecosystems in Australia occurring in areas of high and competing demands for water and mineral resources – such as the Pilbara and Yilgarn regions of Western Australia and the Hunter Valley in NSW – it is urgent to develop efficient conservation strategies for these ecosystems.

So far, the majority of groundwater surveys in Australia have been fuelled by industrial interests, and have not been integrated into groundwater management. Water resource legislation in most Australian states provides for an assessment of the environmental impact of water extraction; however, the focus is generally on groundwater-dependent ecosystems (GDEs) on the surface (Tomlinson *et al*. 2007). Only in Western Australia are there specific requirement for stygofauna surveys before development assessments (Tomlinson *et al*. 2007). Albeit a few Australian subterranean species and several groundwater-dependent communities are listed under biodiversity protection legislation, such listings are only applicable to species and communities under a demonstrable threat (Tomlinson & Boulton 2010).

There is an almost complete lack of information on the basic biology and ecology of the Australian subterranean fauna (Humphreys 2008), but this is not a local phenomenon (Larned 2012). Virtually no data exist on life-cycles, reproduction or population size or genetic structure. As such, groundwater fauna are not applicable for inclusion in

endangered species lists (e.g. the Red List or The Endangered Species Act). Moreover, the creation of national parks based on subterranean value seems unlikely in Australia; given that most subterranean ecosystems exist in areas of considerable economic interest (Boulton 2009).

A few authors have put forward possible approaches towards stygofauna conservation (see Tomlinson et al. 2007; Tomlison & Boulton 2008; Boulton 2009). In a review, Tomlinson & Boulton (2008) suggest taking an ecohydrological approach for management of groundwater. Groundwater habitat type is a key determinant of biodiversity, and combined with ecologically relevant aspects such as resource supply (via hydrological connectivity) and living space (aquifer void characteristics), and can together with distributional data be used to guide conservation efforts (Tomlinson & Boulton 2008). A DNA-based approach to rapid biodiversity assessment was proposed by Asmyhr & Cooper (2012). DNA sequences can serve as surrogates for species diversity, an approach that is particularly useful for ecosystems comprising a high number of cryptic species in which morphological identification is difficult (Bradford et al. 2010; Asmyhr & Cooper 2012). Although not proposed as a way of discouraging traditional taxonomic surveys, molecular methods may be used as an initial screening, allowing systems to be preserved while awaiting formal descriptions.

There is great potential in combining these two approaches for designing groundwater reserve networks in Australia. The level of genetic divergence among stygofauna samples from different sites may serve as the basis for selection of sites comprising the most evolutionary distinct taxa (Asmyhr et al. unpublished). A habitat typology, as proposed by Tomlinson & Boulton (2008) can be used to predict possible stygofauna hotspots, and serve as a surrogate for groundwater biodiversity in areas of high anthropogenic pressure. Although still at an early stage, the use of surrogates for groundwater biodiversity has been explored by a few authors (indicator species: Stoch et al. 2009; aquifer type: Linke et al., unpublished).

Finally, considering that aquifers are not stand-alone ecosystems, rather they are an essential part of a wide range of surface freshwater GDEs, there is a need for a holistic approach towards freshwater conservation. Without a significant increase in reserve cost, aquifers can be included in a broader freshwater conservation network, such as, for example, together with rivers and wetlands (Linke et al., unpublished).

REFERENCES

Abrams, K. M., King, R. A., Guzik, M. T., Cooper, S. J. B., Austin, A. D. (2013) Molecular phylogenetic, morphological and biogeographic evidence for a new genus of parabathynellid crustaceans (Syncarida: Bathynellacea) from groundwater in an ancient southern Australian landscape. *Invertebrate Systematics*, 27, 146–172.

Acworth, R. I. 2001. Physical and chemical properties of a DNAPL contaminated zone in a sand aquifer. *Quarterly Journal of Engineering, Geology and Hydrogeology*, 34, 85–98.

Anneser, B., Pilloni, G., Bayer, A., et al. (2010) High resolution analysis of contaminated aquifer sediments and groundwater – what can be learned in terms of natural attenuation? *Geomicrobiology Journal*, 27, 130–142.

Asmyhr, M. G., Cooper, S. J. B. (2012). Difficulties barcoding in the dark: the case of crustacean stygofauna from eastern Australia. *Invertebrate Systematics*, **26**(6), 583–591. doi:10.1071/IS12032

Balke, M., Watts, C. H. S., Cooper, S. J. B., Humphreys, W. F., Vogler, A. P. (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.

Barranco, P. Harvey, M. S. (2008) The first indigenous palpigrade from Australia: a new species of *Eukoenenia* (Palpigradi: Eukoeneniidae). *Invertebrate Systematics*, **22**, 227–234.

Bauzà-Ribot, M. M., Juan, C., Nardi, F., *et al.* (2012) Mitogenomic phylogenetic analysis supports continental-scale vicariance in subterranean thalassoid crustaceans. *Current Biology*, **22**, 2069–2074

Boulton, A. J. (2009) Recent progress in the conservation of groundwaters and their dependent ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 731–735.

Boulton, A. J., Fenwick, G., Hancock, P., Harvey, M. (2008) Biodiversity, functional roles and ecosystem services of groundwater invertebrates. *Invertebrate Systematics*, **22**, 103–116.

Boulton, A. J., Humphreys, W. F., Eberhard, S. M. (2003). Imperilled subsurface waters in Australia: biodiversity, threatening processes and conservation. *Aquatic Ecosystem Health and Management*, **6**, 37–41. doi:10.1080/14634980390151565

Bradbury, J. H. (1999). The systematics and distribution of Australian freshwater amphipods: a review. In: *Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands*, Schram, F. R., von Vaupel Klein, J. C. (eds.). Leiden, The Netherlands, Brill, pp. 533–540.

Bradford, T., Adams, M., Humphreys, W. F., Austin, A. D., Cooper, S. J. B. (2010) DNA barcoding of stygofauna uncovers cryptic amphipod diversity in a calcrete aquifer in Western Australia's arid zone. *Molecular Ecology Resources*, **10**, 41–50. doi:10.1111/j.1755-0998.2009.02706.x

BMR Palaeogeographic Group (1990) *Australia, Evolution of a Continent*. Canberra, Australia: Australian Government Publishing Service.

Byrne, M., Yeates, D. K., Joseph, L., *et al.* (2008) Birth of a biome: synthesizing environmental and molecular studies of the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398–4417.

Chapelle, F. H. (2001) *Groundwater Microbiology and Geochemistry*. New York, John Wiley & Sons.

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

Cho, J.-L., Humphreys, W. F. (2010) Ten new species of the genus *Brevisomabathynella* Cho, Park and Ranga Reddy, 2006 (Malacostraca, Bathynellacea, Parabathynellidae) from Western Australia. *Journal of Natural History*, **44**, 993–1079.

Cook, B. D., Abrams, K. M., Marshall, J. *et al.* (2012) Species diversity and genetic differentiation of stygofauna (Syncarida : Bathynellacea) across an alluvial aquifer in north-eastern Australia. *Australian Journal of Zoology*, **60**, 152–158.

Cooper, S. J. B., Hinze, S., Leys, R., Watts, C. H. S., Humphreys, W. F. (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.

Cooper, S. J. B., Bradbury, J. H., Saint, K. M., *et al.* (2007) Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from central Western Australia. *Molecular Ecology*, 16, 1533–1544.

Cooper, S. J. B., Saint, K. M., Taiti, S., Austin, A. D., Humphreys, W. F. (2008) Subterranean archipelago: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea:Haloniscus) from the Yilgarn region of Western Australia. *Invertebrate Systematics*, 22, 195.

Culver, D. C., Pipan, T. (2009) *The Biology of Caves and Other Subterranean Habitats*, 1st edn. New York, Oxford University Press.

Culver, D. C., Master, L. L., Christman, M. C., Hobbs III, H. H., (2000). Obligate cave fauna of the 48 Contiguous United States. *Conservation Biology*, 14, 386–401.

Danielopol, D. L., Pospisil, P., Rouch, R. (2000) Biodiversity in groundwater: a large-scale view. *Trends in Ecology & Evolution*, 15, 223–224.

Des Châtelliers, M. C., Juget, J., Lafont, M, Martin, P. (2009) Subterranean aquatic Oligochaeta. *Freshwater Biology*, 54, 678–690. doi: 10.1111/j.1365-2427.2009.02173.x

Dodson, J. R., Roberts, F. K., DeSalis, T. (1994) Palaeoenvironments and human impact at Burraga Swamp in montane rainforest, Barrington Tops National Park, New South Wales, Australia. *Australian Geographer*, 25, 161–169.

Dubey, S., Shine, R. (2010) Restricted dispersal and genetic diversity in populations of an endangered montane lizard (*Eulamprus leuraensis*, Scincidae). *Molecular Ecology*, 19, 886–897.

Duffy, J. E., Cardinale, B. J., France, K. E. *et al.* (2007) The functional role of biodiversity in food webs: Incorporating trophic complexity. *Ecology Letters*, 10, 522–538.

Eamus, D., Froend, R., Murray, B. R., Hose, G. C. (2006) A functional methodology for determining the groundwater regime needed to maintain health of groundwater dependent ecosystems. *Australian Journal of Botany*, 54, 97–114.

Eberhard, S. M., Davies, S. (2011) Impacts of drying climate on aquatic cave fauna in Jewel Cave and other caves in southwest Western Australia. *Journal of the Australasian Cave & Karst Management Association*, 83, 6–13.

Eberhard, S. M., Halse, S. A., Humphreys, W. F. (2005) Stygofauna in the Pilbara region, north-west Western Australia: a review. *Journal of the Royal Society of Western Australia*, 88, 167–176.

Eberhard, S. M., Halse, S. A., Williams, M. *et al.* (2009) Exploring the relationship between sampling efficiency and short-range endemism for groundwater fauna in the Pilbara region, Western Australia. *Freshwater Biology*, 54, 885–901.

Fenwick, G. D. & Scarsbrook, M. (2004) Lightless, not lifeless: New Zealand's subrerranean biodiversity. *Water & Atmosphere*, 12(3). Accessed 12/04/13, www.niwa.co.nz/sites/default/files/import/attachments/lightless.pdf

Fenwick, G. D., Thorpe, H. R., White, P. A. (2004) Groundwater systems. In *Freshwaters of New Zealand*, Harding, J., Mosley, P., Pearson, C., Sorrell, B. (eds.). Christchurch: New Zealand Hydrological Society and New Zealand Limnological Society, pp. 291–298.

Ferreira, D., Malard, F., Dole-Olivier, M.-J., Gibert, J. (2007). Obligate groundwater fauna of France: diversity patterns and conservation implications. *Biodiversity and Conservation*, 16, 567–596. doi:10.1007/s10531-005-0305-7

Gibert, J. (2001) *Protocols for the Assessment and Conservation of Aquatic Life in the Subsurface (PASCALIS): a European Project (EVK2-CT-2001–00121)*. Available at www. pascalis-project.com. Accessed 1/5/13./

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

Gibert, J., Stanford, J. A., Dole-Oliver, M. J., Ward, J. (1994). Basic attributes of groundwater ecosystems and prospects for research. In *Groundwater Ecology*, Gibert, J., Danielopol, D., Stanford, J., (eds.). California, Academic Press, pp. 7–40.

Gibert, J., Brancelj, A., Camacho, A. *et al.* (2005) Groundwater biodiversity, Protocols for the ASsessment and Conservation of Aquatic Life In the Subsurface (PASCALIS): overview and main results. In: *Proceedings of an International Symposium on World Subterranean Biodiversity*, Gibert, J. (ed.). University of Lyon, Lyon, Villeurbanne, 8–10 December 2004, pp. 39–52.

Goldscheider, N., Hunkeler, D., Rossi, P. (2006) Review: microbial biocenoses in pristine aquifers and an assessment of investigative methods. *Hydrogeology Journal*, 14, 926–941.

Gounot, A. M. (1994) Microbial ecology of ground waters. In *Groundwater Ecology*, Gibert, J., Danielopol, D., Stanford, J., (eds.). San Diego, California, Academic Press, pp. 189–215.

Griebler, C. (2001) Microbial ecology of subsurface ecosystems. In: *Groundwater Ecology: A Tool for Management of Water Resources*, Griebler, C., Danielopol, D., Gibert, J., Nachtnebel, H. P., Notenboom, J. (eds.). Official Publication of the European Communities, Luxembourg, pp. 81–108.

Griebler, C., Lueders, T. (2009) Microbial biodiversity in groundwater ecosystems. *Freshwater Biology*, 54, 649–677.

Griebler, C., Mindl, B., Slezak, D., Geiger-Kaiser, M. (2002) Distribution patterns of attached and suspended bacteria in pristine and contaminated shallow aquifers studied with an *in situ* sediment exposure microcosm. *Aquatic Microbial Ecology*, 28, 117–129.

Guzik, M. T., Cooper, S. J. B., Humphreys, W. F., Cho, J.-L., Austin, A. (2008). Phylogeography of the ancient Parabathynellidae (Crustacea: Bathynellacea) from the Yilgarn region of Western Australia. *Invertebrate Systematics*, 22, 205–216. doi:10.1071/IS07040

Guzik, M. T., Austin, A. D., Cooper, S. J. B., *et al.* (2010) Is the Australian subterranean fauna uniquely diverse? *Invertebrate Systematics*, 24, 407–418. doi:10.1071/IS10038

Haack, S. K., Bekins, B. A. (2000) Microbial populations in contaminant plumes. *Hydrogeology Journal*, 8, 63–76.

Halse, S. E., Ruprecht, J. K., Pinder, A. M. (2003) Salinisation and prospects for biodiversity in rivers and wetlands of south-west Western Australia. *Australian Journal of Botany*, 51, 673–688.

Hancock, P. J. (2009) *Alluvial Aquifer Fauna During and Following Drought*. Groundwater in the Sydney Basin Symposium, Sydney, August 4–5.

Hancock, P. J., Boulton, A. J. (2008) Stygofauna biodiversity and endemism in four alluvial aquifers in eastern Australia. *Invertebrate Systematics*, 22, 117–126.

Hancock, P. J., Boulton, A. J. (2009) Sampling groundwater fauna: efficiency of rapid assessment methods tested in bores in eastern Australia. *Freshwater Biology*, 54, 902–917.

Hartland, A., Fenwick, G. D., Bury, S. J. (2011) Tracing sewage derived organic matter into a shallow groundwater food web using stable isotope and fluorescence signatures. *Marine and Freshwater Research*, 62, 119–129.

Harvey, M. S. (2002) Short-range endemism in the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics*, 16, 555–570.

Herman, J. S., Culver, D. C., Salzman, J. (2001) Groundwater ecosystems and the service of water purification. *Stanford Environmental Law Journal*, 20, 479–495.

Hobbs III, H. H. (2000) Crustacea. In: *Ecosystems of the World 30. Subterranean Ecosystems*, Wilkens, H., Culver, D. C., Humphreys, W. F. (eds.). Amsterdam, Elsevier.

Holmes, A. J., Tujula, N. A., Holley, M. *et al.* (2001) Phylogenetic structure of unusual aquatic microbial formations in Nullarbor caves, Australia, *Environmental Microbiology*, 3, 256–264.

Hose, G. C. (2005) Assessing the need for groundwater quality guidelines using the species sensitivity distribution approach. *Human and Ecological Risk Assessment*, 11, 951–966.

Hose, G. C. (2007) A response to comments on assessing the need for groundwater quality guidelines using the species sensitivity distribution approach. *Human and Ecological Risk Assessment*, 13, 241–246.

Hose, G. C. (2008) *Stygofauna Baseline Assessment for Kangaloon Borefield Investigations – Southern Highlands, NSW*. Report to Sydney Catchment Authority, Access Macquarie Ltd, North Ryde.

Hose, G. C. (2009) *Stygofauna Baseline Assessment for Kangaloon Borefield Investigations – Southern Highlands, NSW*. Supplementary Report – Stygofauna molecular studies. Report to Sydney Catchment Authority, Access Macquarie Ltd, North Ryde.

Hose, G. C., Lategan, M. J. (2012) *Sampling Strategies for Biological Assessment of Groundwater Ecosystems*. CRC CARE Technical Report no. 21, CRC for Contamination Assessment and Remediation of the Environment, Adelaide, Australia.

Humphreys, W. F. (2001). Groundwater calcrete aquifers in the Australian arid zone: The context to an unfolding plethora of stygal biodiversity. *Records of the Western Australian Museum*, (Supplement 64), 63–83.

Humphreys, W. (2006) Aquifers: the ultimate groundwater dependent ecosystem. *Australian Journal Botany*, 54, 115–132.

Humphreys, W. F. (2007) Comment on: Assessing the need for groundwater quality guidelines for pesticides using the species sensitivity distribution approach by Hose. *Human and Ecological Risk Assessment*, 13, 236–240. doi:10.1080/10807030601107551

Humphreys, W. F. (2008) Rising from Down Under; Developments in subterranean biodiversity in Australia from groundwater fauna perspective. *Invertebrate Systematics*, 22, 85–101.

Humphreys, W. F. (2012) Diversity patterns in Australia. In *Encyclopedia of Caves*, 2nd edn, Culver, D., White, W. (eds.). San Diego, Academic Press, pp 203–219.

Humphreys, W. F., Watts, C. H. S., Cooper, S. J. B., Leijs, R. (2009) Groundwater estuaries of salt lakes: buried pools of endemic biodiversity on the western plateau, Australia. *Hydrobiologia*, 626, 79–95.

Humphreys, W., Tetu, S., Elbourne, L., *et al.* (2012) Geochemical and microbial diversity of bundera sinkhole, an anchialine system in the eastern Indian ocean. *Natura Croatica*, 21, 59–63.

Jasinska, E. J., Knott, B., Poulter, N. (1993) Spread of the introduced yabby, *Cherax* sp (Crustacea: Decapoda: Parastacidae), beyond the natural range of freshwater crayfishes in Western Australia. *Journal of the Royal Society of Western Australia*, 76, 67–69.

Jaume, D. 2008 Global diversity of spelaeogriphaceans & thermosbaenaceans (Crustacea; Spelaeogriphacea & Thermosbaenacea) in freshwater. *Hydrobiologia*, 595, 219–224

Jaume, D., Boxshall, G. A. (2013) Life in extreme environments: anchialine caves. *Marine Ecology. Encyclopedia of Life Support Systems (EOLSS)*.

Juberthie, C. (2000) The diversity of the karstic and pseudokarstic hypogean habitats in the world. In *Ecosystems of the World 30. Subterranean Ecosystems*, Wilkens, H., Culver, D. C., Humphreys, W. F. (eds.). Amsterdam, Elsevier, pp. 17–39.

Karanovic, I. (2012) *Recent Freshwater Ostracods of the World: Crustacea, Ostracoda, Podocopida*. Berlin, Springer-Verlag.

Kefford, B. J., Papas, P. J., Nugegoda, D. (2003) Relative salinity tolerance of macroinvertebrates from the Barwon River, Victoria, Australia. *Marine and Freshwater Research*, 54, 755–765.

Korbel, K. (2013) Robust and sensitive indicators of groundwater health and biodiversity. Unpublished PhD Thesis. University of Technology, Sydney, Australia.

Korbel, K. L., Hose, G. C. (2011) A tiered framework for assessing groundwater ecosystem health. *Hydrobiologia*, 661, 329–349.

Korbel, K. L., Hancock, P. J., Serov, P., Lim, R. P., Hose, G. C. (2013) Groundwater ecosystems change with landuse across a mixed agricultural landscape. *Journal of Environmental Quality*, 42, 380–390.

Larned, S. T. (2012) Phreatic groundwater ecosystems: research frontiers for freshwater ecology. *Freshwater Biology*, 57, 885–906.

Larson, H. L., Foster, R., Humphreys, W. F., Stevens, M. I. (2013). A new species of the blind cave gudgeon *Milyeringa* (Gobioidei, Eleotridae, Butinae) from Barrow Island, Western Australia, with a redescription of *M. veritas* Whitley. *Zootaxa*, 3616(2), 135–150.

Lategan, M. J., Torpy, F., Newby, S., Stephenson, S., Hose, G. C. (2012) Fungal communities vary among aquifers, providing potential indicators of groundwater contamination. *Geomicrobiology Journal*, 29, 352–361.

Leys, R., Watts, C. H. S. (2008) Systematics and evolution of the Australian subterranean hydroporine diving beetles (Dytiscidae), with notes on *Carabhydrus*. *Invertebrate Systematics*, **22**, 217–225.

Leys, R., Watts, C. H., Cooper, S. J., Humphreys, W. F. (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution*, **57**, 2819–2834.

Leys, R., Roudney, B., Watts, C. H. S. (2010) *Paroster extraordinarius* sp. nov., a new groundwater diving beetle from the Flinders Ranges, with notes on other diving beetles from gravels in South Australia (Coleoptera: Dystiscidae). *Australian Journal of Entomology*, **49**, 66–72.

Malard, F. (2001) Groundwater contamination and ecological monitoring in a Mediterranean karst ecosystem in southern France. In *Groundwater Ecology: A Tool for Management of Water Resources*, Griebler, C., Danielopol, D., Gibert, J., Nachtnebel, H. P., Notenboom, J. (eds.). Official Publication of the European Communities, Luxembourg, pp. 183–194.

Michel, G., Malard, F., Deharveng, L. *et al.* (2009) Reserve selection for conserving groundwater biodiversity. *Freshwater Biology*, **54**, 861–876. doi:10.1111/j.1365-2427.2009.02192.x

Millennium Ecosystem Assessment, (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. Washington, DC, World Resources Institute.

Murphy, N. P., Adams, M., Austin, A. D. 2009. Independent colonization and extensive cryptic speciation of freshwater amphipods in the isolated groundwater springs of Australia's Great Artesian Basin. *Molecular Ecology*, **18**, 109–122.

Murray, B. R., Hose, G. C., Lacari, D., Eamus, D. (2006) Valuation of groundwater dependent ecosystems: a functional methodology incorporating ecosystem services. *Australian Journal of Botany*, **54**, 221–229.

Novarino, G., Warren, A., Butler, H. *et al.* (1997) Protozoan communities in aquifers: a review. *FEMS Microbiology Review*, **20**, 261–275.

Osborne, R. A. L., Zwingmann, H., Pogson, R. E., Colchester, D. M. (2006) Carboniferous clay deposits from Jenolan Caves, New South Wales: implications for timing of speleogenesis and regional geology. *Australian Journal of Earth Sciences*, **53**, 377–405. doi:10.1080/ 08120090500507362

Page, T. J., Humphreys, W. F., Hughes, J. M. (2008) Shrimps Down Under: Evolutionary relationships of subterranean crustaceans from Western Australia (Decapoda: Atyidae: *Stygiocaris*). *PLoS ONE*, **3**, e1618, 1–12.

Phillips, M. J., Page, T. J., de Bruyn, M. *et al.* (2013) The linking of plate tectonics and evolutionary divergences (Reply to Bauzà-Ribot et al.). *Current Biology*, **23**, 603–605.

Proudlove, G. S. (2001) The conservation status of hypogean fishes. *Environmental Biology of Fish*, **62**, 239–249.

Schmidt, S., Hahn, H. J., Hatton, T., Humphreys, W. F. (2007) Do faunal assemblages reflect the exchange intensity in groundwater zones? *Hydrobiologia*, **583**, 1–19.

Schminke, H. K. (2011) Arthropoda: Crustacea: Malacostraca: Bathynellacea Parabathynellidae In: *Invertebrate Fauna of the World*, Vol. 21. Incheon, Republic of Korea: National Institute of Biological Resources.

Serov, P. A. (2002) *A Preliminary Identification of Australian Syncarida (Crustacea)*. CRC Freshwater Ecology, Albury.

Seymour, J., Humphreys, W. F., Mitchell, J. G. (2007). Stratification of the microbial community inhabiting an anchialine sinkhole. *Aquatic Microbial Ecology*, 50, 11–24.

Sinton, L. W. (1984) The macroinvertebrates of a sewage polluted aquifer. *Hydrobiologia*, 119, 161–169.

Smith, R. J., Jeffries, T. C., Roudnew, B. *et al.* (2012) Metagenomic comparison of microbial communities inhabiting confined and unconfined aquifer ecosystems. *Environmental Microbiology*, 14, 240–253.

Stanford, J. A., Ward, J. V. (1988) The hyporheic habitat of river ecosystems. *Nature*, 335, 64–66.

Stein, H., Kellermann, C., Schmidt, S. I. *et al.* (2010) The potential use of fauna and bacteria as ecological indicators for the assessment of groundwater quality. *Journal of Environmental Monitoring*, 12, 242–254.

Stephenson, S., Chariton, A., O'Sullivan, M. *et al.* (2013) Changes in microbial assemblages along a gradient of hydrocarbon contamination in a shallow coastal sand aquifer. *Geomicrobiology Journal*, in press.

Stoch, F., Artheau, M., Brancelj, A., Galassi, D. M. P., Malard, F. (2009). Biodiversity indicators in European ground waters: towards a predictive model of stygobiotic species richness. *Freshwater Biology*, 54, 745–755. doi:10.1111/j.1365–2427.2008.02143.x

Stumpp, C., Hose, G. C. (2013) Impact of water table drawdown and drying on subterranean aquatic fauna in in-vitro experiments. *PLoS ONE*, 8(11), e78502. doi: 10.1371/journal.pone.0078502

Tetu, S. G., Breakwell, K., Elbourne, L. D. H. *et al.* (2013) Life in the dark: metagenomic evidence that a microbial slime community is driven by inorganic nitrogen metabolism. *ISME Journal*, in press.

Thurgate, M. E., Gough, J. S., Clarke, A. K., Serov, P., Spate, A. (2001) Stygofauna diversity and distribution in eastern Australian caves and karst areas. *Records of the Western Australian Museum Supplement*, 64, 49–62.

Tomlinson, M. (2008) A framework for determining environmental water requirements for alluvial aquifer ecosystems. PhD thesis. Armidale, Australia: University of New England.

Tomlinson, M., Boulton, A. (2008) Subsurface groundwater dependent ecosystems: a review of their biodiversity, ecological processes and ecosystem services. Waterlines Occasional Paper No. 8, National Water Commission, Canberra, Australia.

Tomlinson, M., Boulton, A. J. (2010) Ecology and management of subsurface groundwater dependent ecosystems in Australia: a review. *Marine and Freshwater Research*, 61, 936–949.

Tomlinson, M., Boulton, A. J., Hancock, P. J., Cook, P. G. (2007) Deliberate omission or unfortunate oversight: should stygofaunal surveys be included in routine

groundwater monitoring programs? *Hydrogeology Journal*, **15**, 1317–1320. doi:10.1007/s10040-007-0211-z

von Rintelen, K., Page, T.J., Cai, Y. *et al.* (2012) Drawn to the dark side: a molecular phylogeny of freshwater shrimps (Crustacea: Decapoda: Caridea: Atyidae) reveals frequent cave invasions and challenges current taxonomic hypotheses. *Molecular Phylogenetics and Evolution*, **63**, 82–96.

Watts, C. H. S., Humphreys, W. F. (2009) Fourteen new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot, *Paroster* Sharp and *Exocelina* Broun, from underground waters in Australia. *Transactions of the Royal Society of South Australia*, **133**, 62–107.

Watts, C. H. S., Hancock, P.J., Leys, R. (2007) A stygopitic *Carabhydrus* Watts (Dytiscidae, Coleoptera) from the Hunter Valley in New South Wales, Australia. *Australian Journal of Entomology*, **46**, 56–59.

Watts, C. H. S., Hancock, P.J., Leys, R. (2008) *Paroster peelensis* sp. nov.: a new stygobitic water beetle from alluvial gravels in northern New South Wales (Coleoptera: Dytiscidae). *Australian Journal of Entomology*, **47**, 227–231.

Wilson, G. D. F. (2008) Gondwanan groundwater: subterranean connections of Australian phreatoicidean isopods to India and New Zealand. *Invertebrate Systematics*, **22**, 301–310.

Wilson, G. D. F., Johnson, R. T. (1999) Ancient endemism among freshwater isopods (Crustacea, Phreatoicidea). In *The Other 99%. The Conservation and Biodiversity of Invertebrates*, Ponder, W., Lunney, D. (eds.). Transactions of the Royal Zoological Society of New South Wales. Mosman, Australia, Royal Zoological Society of New South Wales, pp. 264–268.

Wilson, G. D. F., Keable, S.J. (1999). A new genus of phreatoicidean isopod (Crustacea) from the North Kimberley Region, Western Australia. *Zoological Journal of the Linnean Society, London*, **126**, 51–79.

Young, A. R. (1986) The geomorphic development of dells (Upland Swamps) on the Woronora Plateau, N. S. W., Australia. *Zeitschrift for Geomorphologie*, **30**, 317–327.

Zektser, I. S. and Everett, L. G. (eds.) 2004. *Groundwater Resources of the World and Their Use*, UNESCO IHP-VI Series on Groundwater No. 6. Paris, France, UNESCO.

Chapter 17, **Plate 55 (Figure 17.2)** In some cases it may be necessary to restrict access to endangered reptile populations. For full caption text see page [361].
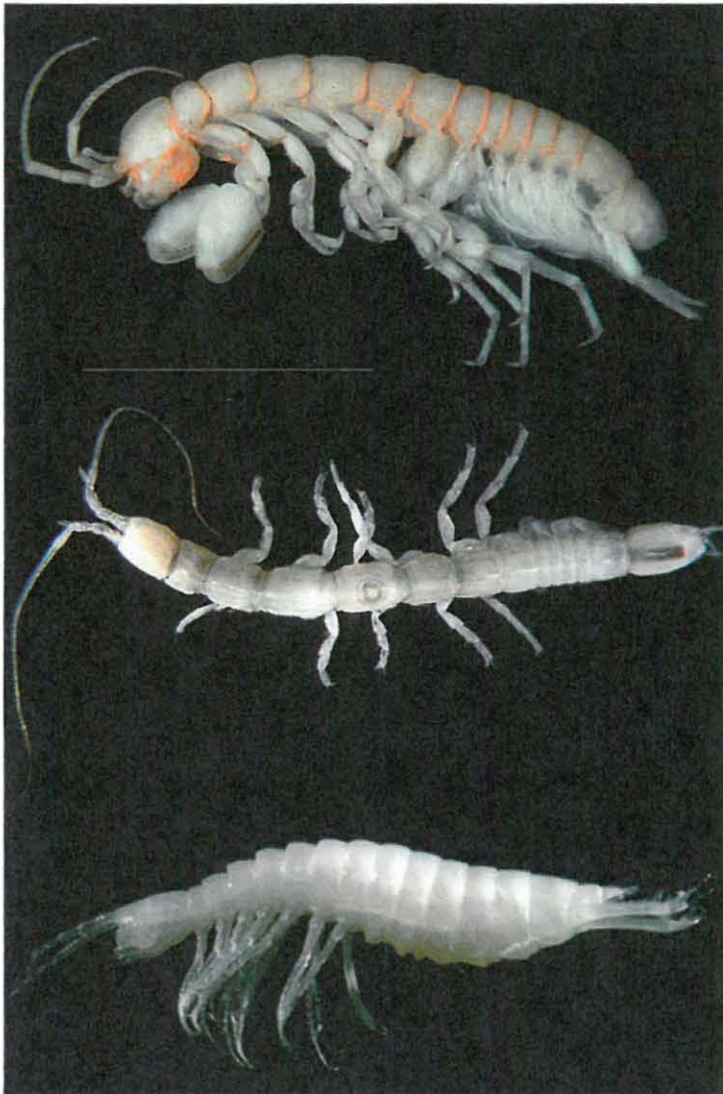
Chapter 24, **Plate 56 (Figure 24.1)** Upper, *Crenisopus* sp. from Koolan Island, WA; middle, Phreatoicid isopod from WA; lower, *Brevisomabathynella uramurdahensis* (Parabathynellidae) from calcrete aquifer in Western Australia. For full caption text see page [518].
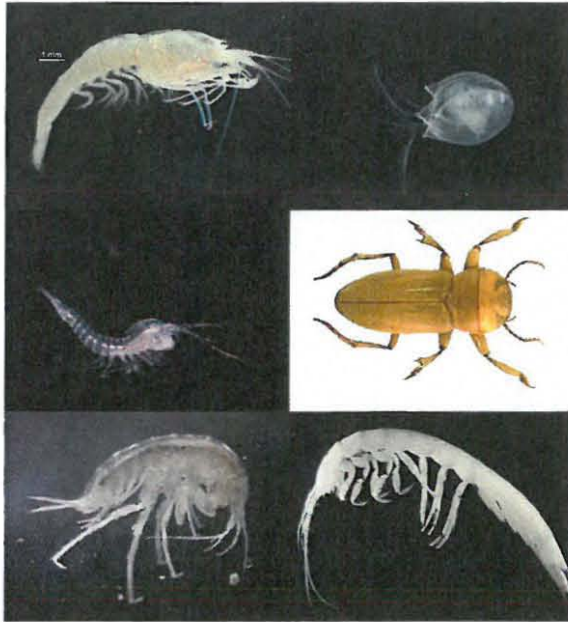
Chapter 24, **Plate 57 (Figure 24.2)** Clockwise from upper left: *Stygiocaris* sp. (Atyidae); *Danielopolina baltanasi, Paroster byroensis, Pygolabis* sp. Tainisopodidae); Paramelitid amphipod; *Halosbaena tulki* (Thermosbaenacea). For full caption text see page [521].

Chapter 12, **Plate 58 (Figure 12.3)** The shrubby tororaro (*Muehlenbeckia astonii*), a species Nationally Endangered, has become a popular garden plant and is now commonly seen in traffic islands.