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# *Australasian Subterranean Biogeography*

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They are found ... in the dark recesses of caverns and of the waters under the earth, where no storm ruffles the everlasting stillness, no light illuminates the thick darkness, and no sound breaks the eternal silence.

–Charles Chilton (1894: p. 273), a pioneer student of groundwater fauna

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# Introduction

‘We did not during our voyage pass a more dull and uninteresting time’ (Darwin 1839: 432). Charles Darwin was unimpressed with the natural history of Western Australia, a misconception gained during a brief visit by HMS *Beagle* to Albany in 1836, an area now recognised as a biodiversity hotspot. Nearly 180 years later a similar misconception is being revealed, in that Western Australia in particular, but Australia more broadly, is a biodiversity hotspot for the obligate subterranean species (Guzik *et al.* 2011a). Such species, typified as cave inhabitants, have long been recognised as important subjects in evolutionary studies – including by Darwin (1872) himself – by biospeleologists and increasingly by contemporary evolutionary biologists (Wilkens 2010; Leijs *et al.* 2012; Vergnon *et al.* 2013; Jeffery 2005). This awakening is surprising because Australia was long considered to be a poor prospect for those obligate subterranean species – troglobionts – that inhabit the subterranean voids.

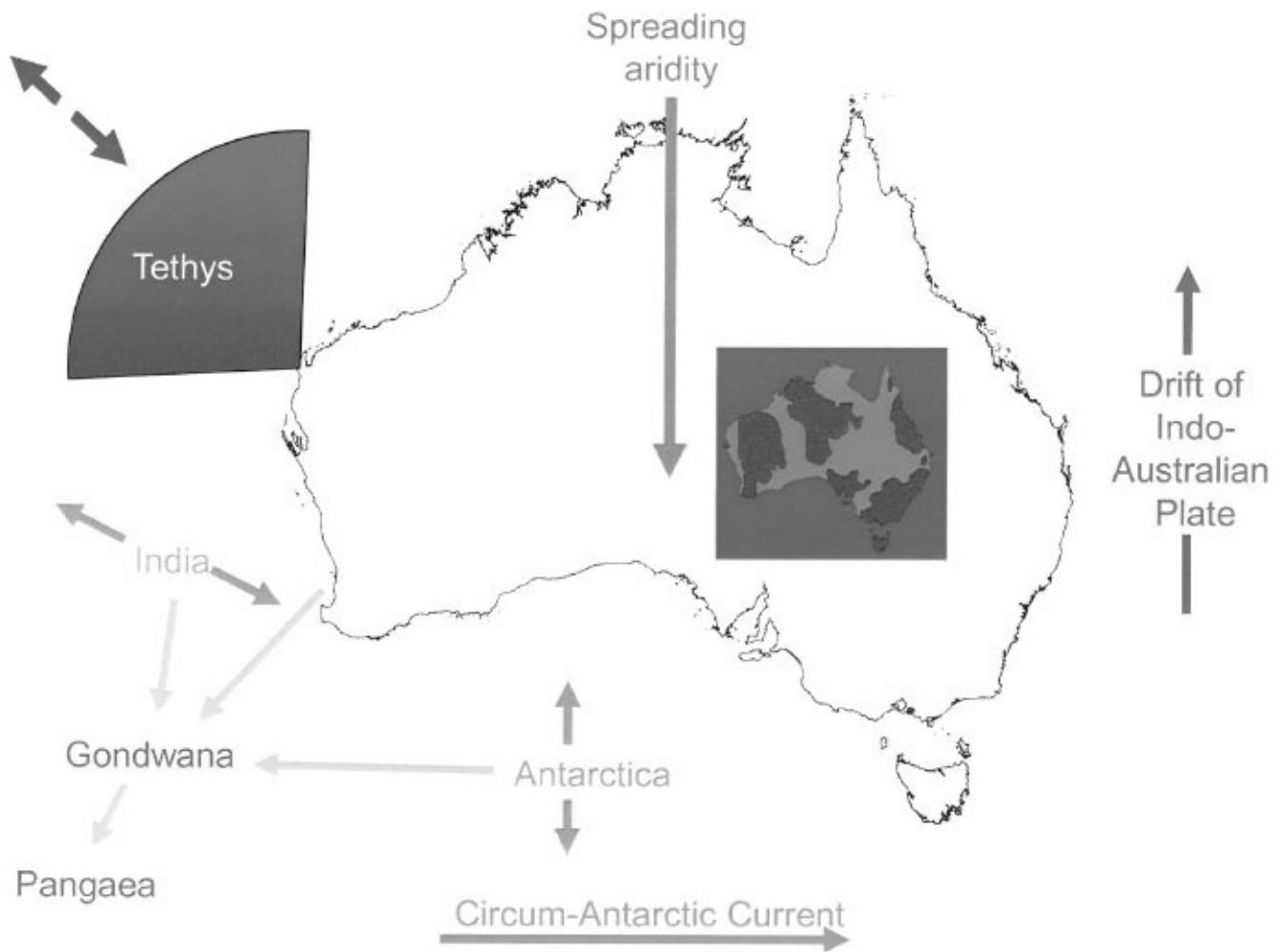
This misconception was on account of the relative scarcity of carbonate karst in Australia and the widespread aridity of its climate compared with the better-studied and biospeleologically diverse areas of the Northern Hemisphere, especially the Dinaric karst. Globally, research on subterranean biology has overwhelmingly been centred on carbonate karst, in which solutional processes create an interconnected hydrogeological network. Such systems may expand to form caves by further solution or by collapse, and changes in hydrology may leave air-filled voids suitable for colonisation by lineages of terrestrial troglobionts, especially insects, myriapods and arachnids, while the flooded voids serve as a habitat for lineages of aquatic troglobionts, which overwhelmingly comprise crustaceans. The aridity of Australia was considered unfavourable for a diverse troglobiont fauna because abundant water was considered necessary both for cave formation and for the maintenance of humidity-dependent troglobionts. Finally, subterranean faunas were thought not to be favoured by small climatic variation – in the north, as one-third of the continent lies in the tropics, and in the south by the absence of widespread phases of glaciation during the Pleistocene – which was considered to be a major driver of troglobiont evolution in the Northern Hemisphere (Holsinger 2000). It is not surprising, therefore, that troglobiont species were initially recorded in the humid, cold south of Australasia, in Tasmania and New Zealand (Hurley 1990). Tasmania, now known to have a troglobiont diversity comparable to some areas in the Northern Hemisphere, is both humid (annual rainfall 1458–2690 mm) and the only area of Australia that was subjected to repeated episodes of glaciation during the Pleistocene. Moderately diverse troglobiont faunas were reported from the more humid areas of New South Wales, such as the Jenolan Caves (mean annual rainfall 968 mm) (Thurgate *et al.* 2001). In the 1980s, diverse troglobiont faunas were found in tropical Queensland (Chillagoe, rainfall 850 mm) (Howarth 1988; Howarth and Stone 1990) and in central Queensland (Undara lava tube, rainfall 789 mm) (Gray 1989; Hoch and Howarth 1989a–c). Since about 1990 it has been recognised that there is a great diversity of subterranean fauna in arid and semiarid parts of Australia (Guzik *et al.* 2011a), occurring in typical Tertiary karst areas such as the Nullarbor karst and Cape Range, as well as in alluvial aquifers (Humphreys 2000a). However, an ever-increasing biodiversity is being discovered in atypical substrates, such as groundwater

calcretes in the Yilgarn (Humphreys 2008; Leijs *et al.* 2012) and the Northern Territory (Cho *et al.* 2006; Watts and Humphreys 2009), lacustrine and groundwater calcretes in the Pilbara (Poore and Humphreys 1998; Finston *et al.* 2009), and in the fractured rock and pisolites associated with Precambrian banded iron formations (BIFs) and their derivatives (Halse and Pearson 2014).

It is notable that the great diversity of troglobionts now known in Australia has emerged in the last two decades, in atypical habitats, many of which are in the tropics and/or arid areas, including Cape Range (median rainfall 210 mm), Barrow Island (median rainfall 280 mm) and Christmas Island (median rainfall 2011 mm), Pilbara (spatially averaged median rainfall 298 mm), and in the monsoonal Kimberley region (spatially averaged median rainfall – Northern, Central and Dampierland IBRA bioregions – 515–939 mm) (Humphreys 1991, 1993a, 1995; Humphreys *et al.* 2013; Humphreys and Eberhard 2001; Eberhard *et al.* 2005; reviews: Humphreys 2008, 2012).

## Background to Chapter

A series of deep history events have been hypothesised to have significantly influenced the biogeography of the subterranean fauna of Australia. These fall into a number of discrete areas: the tectonic stability of the continent, the absence of widespread glaciation since the Permian, the latitudinal extent of Australia, the spreading aridity since the opening of the Drake Passage allowed the establishment of the Antarctic Circumpolar Current, the scarcity of karst relative to Laurasian continents, past connections with Gondwana and the close connection of the North West Shelf area with Tethys. These are summarised in the schema in [Figure 11.1](#), which is built around our current understanding of the historical biogeography of the subterranean fauna (Humphreys 2012). As knowledge of the subterranean fauna of Australia is so incomplete, I want to set the discussion of the biogeography of the better-known higher taxonomic groups of subterranean fauna against this schema. This may provide a research framework against which more refined hypotheses may emerge, and which may itself be refuted in whole or in part as a consequence of such studies.



**FIGURE 11.1** Schematic diagram depicting various effects resulting from plate tectonic and eustatic events over geological time that are hypothesised to have influenced the biogeography and evolution of the Australian subterranean fauna. The inset map depicts the extent of marine inundation during the Cretaceous. (After Humphreys, W.F., *Encyclopedia of Caves*, Academic Press, San Diego, CA, 2012.)

## Characteristics of Obligate Subterranean Animals

Animals have different degrees of affinity with subterranean environments: in this Chapter I am going to deal particularly with obligate subterranean animals that inhabit air-filled or water-filled voids and which are termed *terrestrial troglobionts* and *aquatic troglobionts*, respectively. Owing to their evolutionary adaptations to the subterranean life, such species are incapable of existing in the surface environment in which the lineage evolved, and so they complete their entire life cycle in the subterranean realm. These evolutionary changes include a broad range of morphological, behavioural and physiological adaptations but they are manifest overtly by the characteristic reduction or loss of eyes, the reduction or loss of body pigment, the loss of wings where relevant, the elongation of appendages and the enhancement of

nonoptic senses, or, in the case of minute interstitial lineages, by a vermiform body shape, the better to move within sediments (Langecker 2000; Coineau 2000).

Troglobionts were traditionally considered to be the inhabitants of caves – voids large enough for people to enter – largely in carbonate karst terranes where solution processes form a network of voids for colonisation by surface lineages. It was later recognised that subterranean habitats occur also in fissure systems, in lava fields and in nonconsolidated granular sediments (Sket 2008). As foreshadowed in the introduction, in Australia it seems that troglobionts may occur wherever interconnected voids of appropriate size and habitat (aquatic or air) are found, and that inland aquatic troglobionts – elsewhere known from freshwater – may occur in inland waters up to at least typical marine levels of salinity (Humphreys *et al.* 2009).

Troglobionts evolved from surface lineages, and so the integrated study of both the surface and subterranean members of the lineage is essential to understand the nature, degree and rate of the evolutionary changes leading to the troglobiont habit (Leijs and Watts 2008) and may provide a time frame useful for biogeographic analysis. This is commonly not possible in Australia, where surface ancestors are absent and thought often to have been ablated by surface aridity. However, this is not the particular subject of this chapter, which will be restricted to elucidating what is known of the biogeographical affinities of troglobionts that inhabit Australia.

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## Troglobionts and Biogeography

Troglobionts have evolved, ultimately, from surface lineages and become trapped by their evolution within a given geological context, after which their biogeography is at the whim of geological rather than biological processes and events. This is because troglobionts typically develop a suite of morphological, developmental, behavioural and physiological changes, termed *trogglomorphies*, that are considered to be adaptive to their obligate subterranean life – although this is still a major research area and focus of debate – and which make them unable to survive in their ancestral surface habitats. Speciation may occur in situ of the troglobiont habitat through microallopatric vicariance as a result of the changes through time in the continuity of subterranean voids, which may become more integrated, for example, by solution effects in karst or fragmented owing to changing water tables, landscape evolution or infill by siltation and collapse. The net effect is that hypogean lineages commonly have very small geographic extent, what are termed *short-range endemics* – limited to a cave or a part of an aquifer – placing them at high risk in terms of conservation. As they are locked into their geological context they are powerful instruments in historical biogeography, the more so because subterranean habitats can be very persistent, with caves in the European Alps dated at least to the Miocene (Audra *et al.* 2007), while clay from the Jenolan Caves, New South Wales, has been dated to the Early Carboniferous (ca. 340 Ma; Osborne 2010). These processes are, however, dynamic and may not indicate the continuous presence of troglobiont habitat because, for example, the Devonian reef complex in the Kimberley was planed off by

the Permian ice sheet, during which the giant grike landscape formed by water flow beneath the ice sheet and was subsequently infilled by sediments. The present cave systems are still being exposed by the erosion of these infill sediments (Playford *et al.* 2009). Consequently, many such habitats may have been present throughout the formation and dissolution of Pangaea and the fragmentation of Gondwana, but each case needs careful scrutiny. Aquifers, similarly, may persist through geological eras, and the Edwards Aquifer, Texas, for example, supports a diverse subterranean community derived from the Cretaceous marine inundation of the area (Holsinger and Longley 1980; Longley 1986).

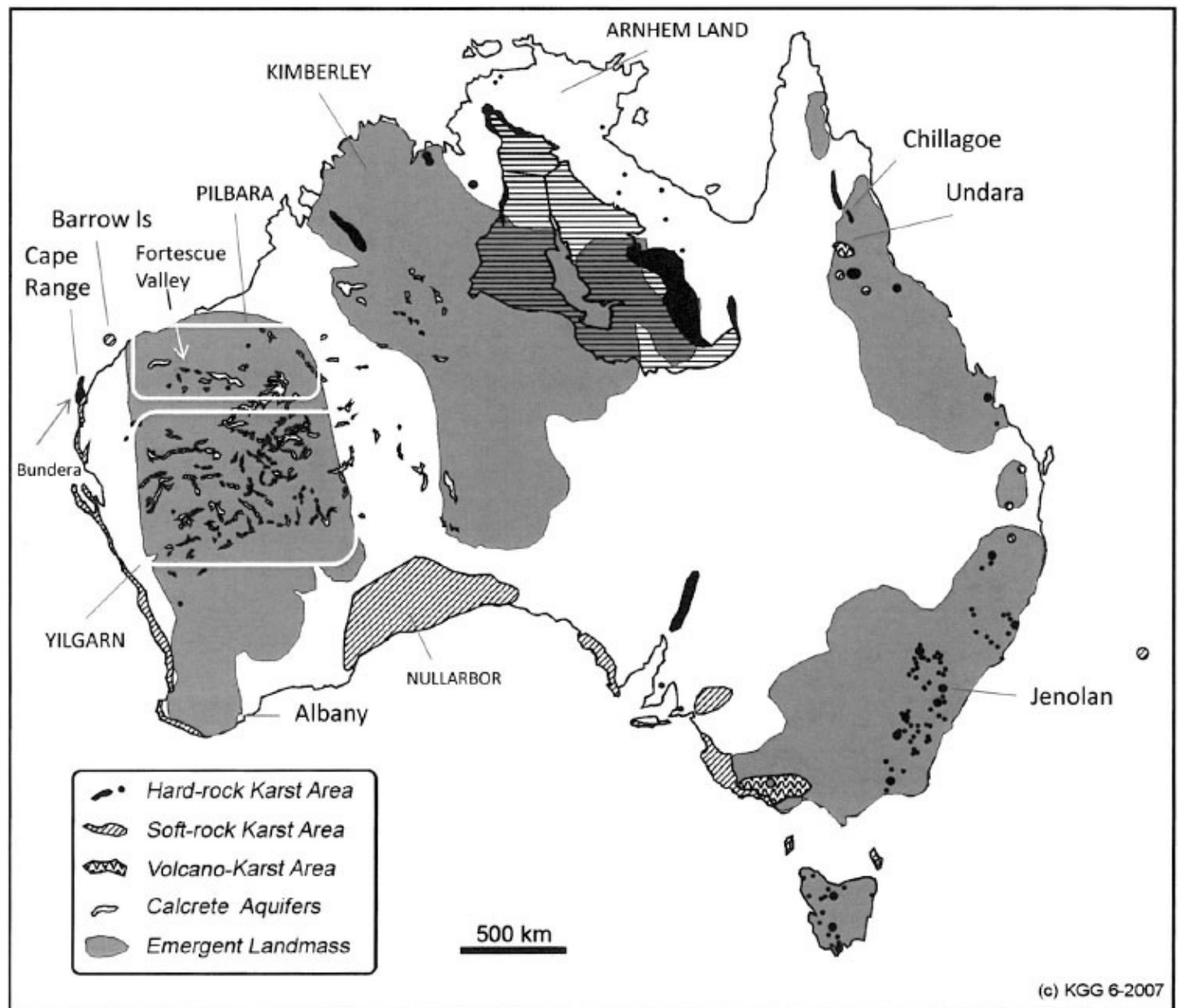
As subterranean communities may comprise lineages isolated underground in different geological eras, they have the potential to yield information on past geological and climatic events in deep history – that is, to serve as ‘living fossils’ of certain provenance. This is particularly the case in Australia owing to the widespread tectonic stability and consequent integrity of the geomorphology of the continent, with its extensive shield regions long emergent from the sea. Key lineages are represented in those higher taxa, largely Crustacea, the entire membership of which is confined to subterranean freshwater systems – for example, Bathynellacea and Spelaeogriphacea, which are well represented in Australia (Humphreys 2012). Such taxa, isolated underground and producing no dispersive phase, have the potential to provide the most robust subjects for testing biogeographic hypotheses. Some of the lineages present in Australia’s groundwaters are purported to have persisted through geological time (Humphreys 2000b,c; Wilson 2008). There are those whose origins are related to the former extent of Tethys and represented by the anchialine fauna of both northwestern Australia and Christmas Island. Several lineages from the former – remipede-type anchialine fauna (Humphreys and Danielopol 2006) – have congeneric species known elsewhere only from subterranean waters on either side of the North Atlantic, and the latter – procarid-type anchialine fauna – from comparable faunas on Hawaii, Ascension Island and Bermuda. Other lineages have affinities with Pangaea (e.g. Bathynellacea and crangonyctoid amphipods) and Gondwana (e.g. phreatoicidean isopods, Spelaeogriphacea and Candoninae ostracods).

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## Geological and Climatic Settings

Geologically, large parts of Australia have been stable, especially the *Western Shield* (Hocking *et al.* 1987), and lacking major tectonic uplift save in the eastern highlands and along the western margin with its gently folded anticlines of Tertiary carbonates in the northern Carnarvon Basin, with Cape Range and Barrow Island (Figure 11.2) notable for troglobionts. The Western Shield of Australia comprises the Pilbara and Yilgarn cratons and the related orogens, and lies at the western rim of the western plateau of Australia. Having been emergent above the sea since at least the Palaeocene, it ranks among the oldest non-marine landmasses on Earth. This must be interpreted carefully because the erosion surface means the landscape is younger (Vasconcelos *et al.* 2008) and may have had a very different geology and geomorphology at the relevant period to be considered. The degree of erosion is examined using the age and distribution of detrital zircons, the volume of deep basin deposits, and

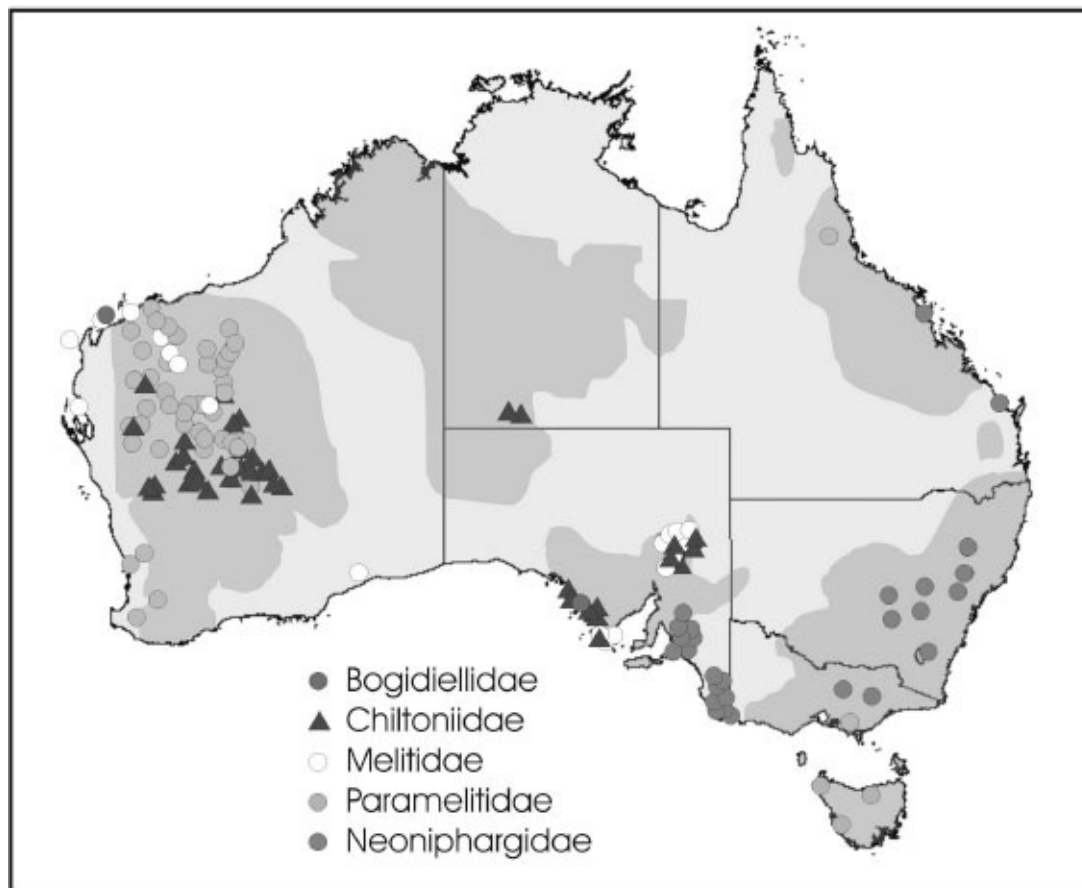
palaeothermal and present-day geothermal gradients. Such studies indicate that there has been massive erosion of the cratonic areas, where several kilometres of cover rock was removed from the Yilgarn Craton in the Permian to Early Cretaceous, and ~4.09 km of basement was removed from the Western Shield between the Early Ordovician and the end of the Cretaceous, an average rate of  $8.87 \text{ m Ma}^{-1}$  ( $0.009 \text{ mm year}^{-1}$ ). The minimum denudation rate for the Yilgarn Craton was  $4.5\text{--}5.0 \text{ m Ma}^{-1}$  in the Mesozoic and  $1.5\text{--}2.0 \text{ m Ma}^{-1}$  during the Late Cretaceous– Early Tertiary (reviewed by Kohn *et al.* 2002). However, owing to isostatic adjustment these massive bulk losses would have made little difference to the altitude of emergence of the landscape above sea level.



**FIGURE 11.2** Australian karst and locations. Black and hashed areas denote karst area of differing types (inset key). The extensive shaded areas denote those plateau areas that were not inundated by the sea during the Cretaceous. The rectangle outlines in white denote the

approximate extent of the Pilbara and Yilgarn regions as discussed in the text. (Developed from a base map drawn for me by Ken Grimes.)

This landscape supports many of the higher taxa considered to be ancient fresh groundwater lineages, such as bathynellaceans, tainisopidean and phreatoicidean isopods, crangonyctoid amphipods and candonine ostracods (Bradbury 1999; Wilson and Johnson 1999; Humphreys 2001; Wilson 2001; I. Karanovic 2003). Denudation, combined with plate tectonic movement and climate change, means that these ancient Gondwanan lineages could have, and in some caves seem to have (Wilson 2008), evolved into troglobionts in a very different zoogeographic and ecophysiological context and in a geological and geomorphological context quite different from that prevailing today. Trapped in their subterranean realm, they may have predominantly moved vertically, up to several kilometres, through the landscape as the geology changed around them by erosion (surface ablation), solution (karstification; Humphreys and Adams 2001), accretion (groundwater calcretes and pisolites, Spelaeogriphacea; Poore and Humphreys 1998; Schizomida, Harvey *et al.* 2008) and deposition (alluvial interstitial; Boulton 2001), and been progressively isolated by landscape evolution (Humphreys and Adams 2001; Harvey *et al.* 2008).



**FIGURE 11.3 (See colour insert.)** The distribution of five families of troglobiont amphipods overlain on a base map of Australia depicting the distribution of long emergent land areas



(deeper shading). Map by Remko Leijes. (From Humphreys, W.F., *Encyclopedia of Caves*, Academic Press, San Diego, CA, 2012.)

These long-emergent areas are home to many ancient freshwater lineages that are dominated by subterranean crustaceans, including Bathynellacea, Spelaeogriphacea, phreatoicidean and tainisopidean isopods, crangonyctoid amphipods (Figure 11.3) and candonine ostracods (Bradbury and Williams 1997; Bradbury 1999; Wilson and Johnson 1999; Poore and Humphreys 1998, 2003; Humphreys 2001; Wilson 2001, 2003; I. Karanovic and Marmonier 2003). Species belonging to ancient freshwater lineages have also been recovered from Proterozoic Pentecost sandstone aquifers in the Kimberley (*Crenisopus*, Tainisopidae; Wilson and Keable 1999) and on small continental islands (Kimberley, Koolan Island; G.D.F. Wilson, pers. comm.), including Barrow Island, which has an anchialine system (Humphreys 2002; Cho *et al.* 2006; Humphreys *et al.* 2013). These lineages have clear Gondwanan connections, but the historical biogeography has yet to be supported using molecular phylogeographic analysis.

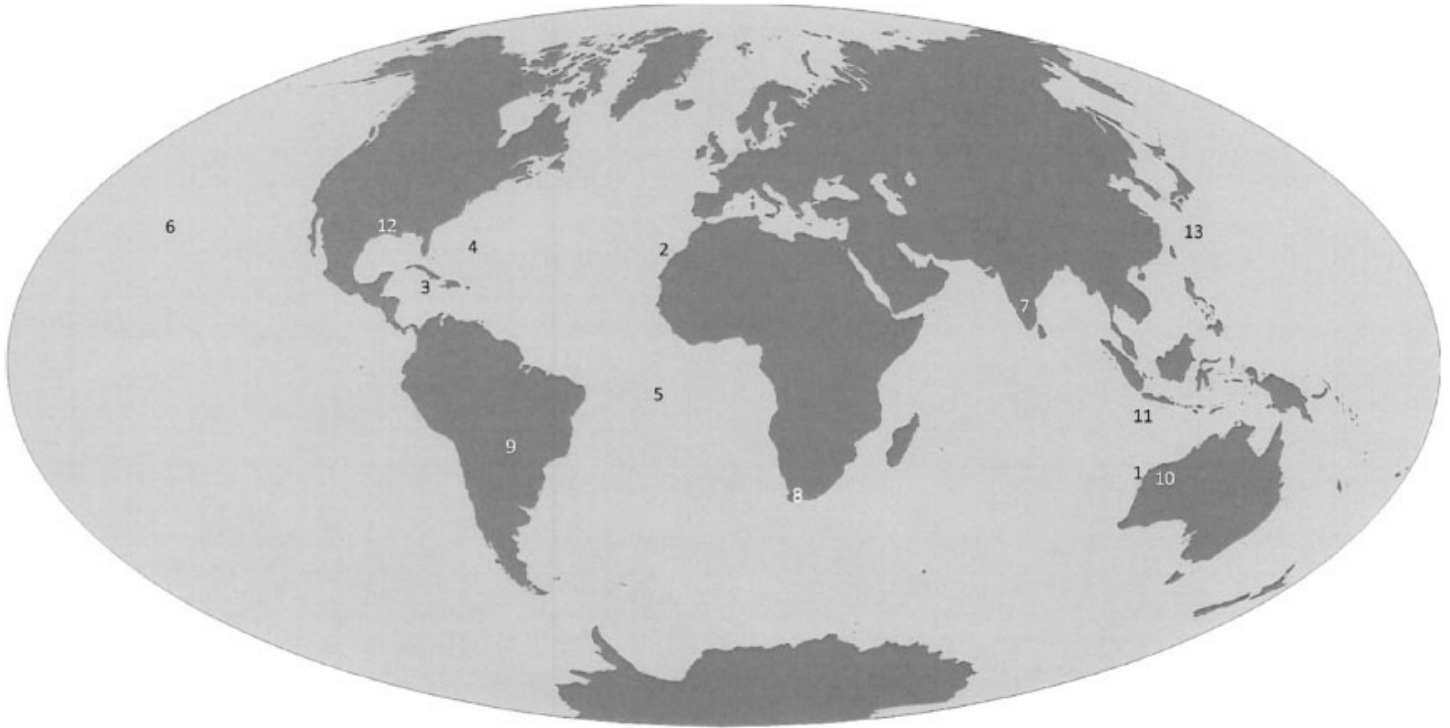
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## Intercontinental Connections

The crustacean order Spelaeogriphacea is known from only four species worldwide, all in freshwater, two of which occur in calcrete aquifers in the Fortescue Valley, Pilbara. The type species occurs in fractured sandstone on the top of Table Mountain, South Africa, and the final species occurs in karst in the western Mato Grosso, Brazil (Figure 11.4). The location of one species atop Table Mountain, a site that has not been near sea level since before the separation of Africa and South America, indicates a Gondwanan origin for this fauna (Poore and Humphreys 1998), but no molecular phylogenetic analysis has been conducted that may support this interpretation. The alternative hypothesis, suggested by the South American and Australian locations, could be dispersion through Tethys (Poore and Humphreys 2003), but this is contraindicated by the Table Mountain location.

Phreatoicidean isopod crustaceans live in freshwater, usually associated with groundwater, in India, South Africa, New Zealand and across southern Australia (and in tropical Arnhem Land and the Kimberley). This current Gondwanan distribution belies their origin, as fossils attributable to this order are cosmopolitan. Their Australian distribution is strongly associated with the areas of the continent not submerged by Cretaceous seas, and about 10 species in eight genera are hypogean (cavernicolous or spring emergents). In the Kimberley the stygobiont genus *Crenisopus* is phylogenetically basal to most families in the Phreatoicidea, suggesting divergence after they entered freshwater but prior to the fragmentation of East Gondwana during the Mesozoic era, and so provides a link between African and Australasian lineages of phreatoicideans (Wilson and Keable 1999). Five hypogean species occur on the Precambrian Western Shield, where the family Hypsimetopidae is represented by the genera *Pilbarophreatoicus* in the Pilbara and *Hyperoedesipus* in the Yilgarn regions (separate cratons of the Western Shield). These genera are closely related to the hypogean genus *Nichollsia*

found in the Ganges Valley of India and a new genus from caves of Andhra Pradesh (east-central India). Wilson and Keable (2001) contend that as *Nichollsia* is nested phylogenetically within the Australian Hypsimetopodinae, this troglobiont clade has a minimum age of 130 Ma, the timing of the separation of Greater India from Australia. They used this information to propose that a high conservation value should be placed on this group owing to its great phylogenetic age, endemism and localised diversity.



**FIGURE 11.4** Worldwide locations mentioned in the text: (a) Cape Range + Bundera, Australia; (b) Canary Islands, Spain; (c) Caribbean; (d) Bermuda; (e) Ascension Island; (f) Hawaii, United States; (g) Andhra Pradesh, India; (h) Table Mountain, South Africa; (i) Mato Grosso del Sul, Brazil; (j) Fortescue Valley, Australia; (k) Christmas Island, Australia; (l) Edwards Aquifer, TX, United States; (m) Minamidaito-jima, Okinawa, Japan. (Base map adapted from <http://www.freeworldmaps.net>.)

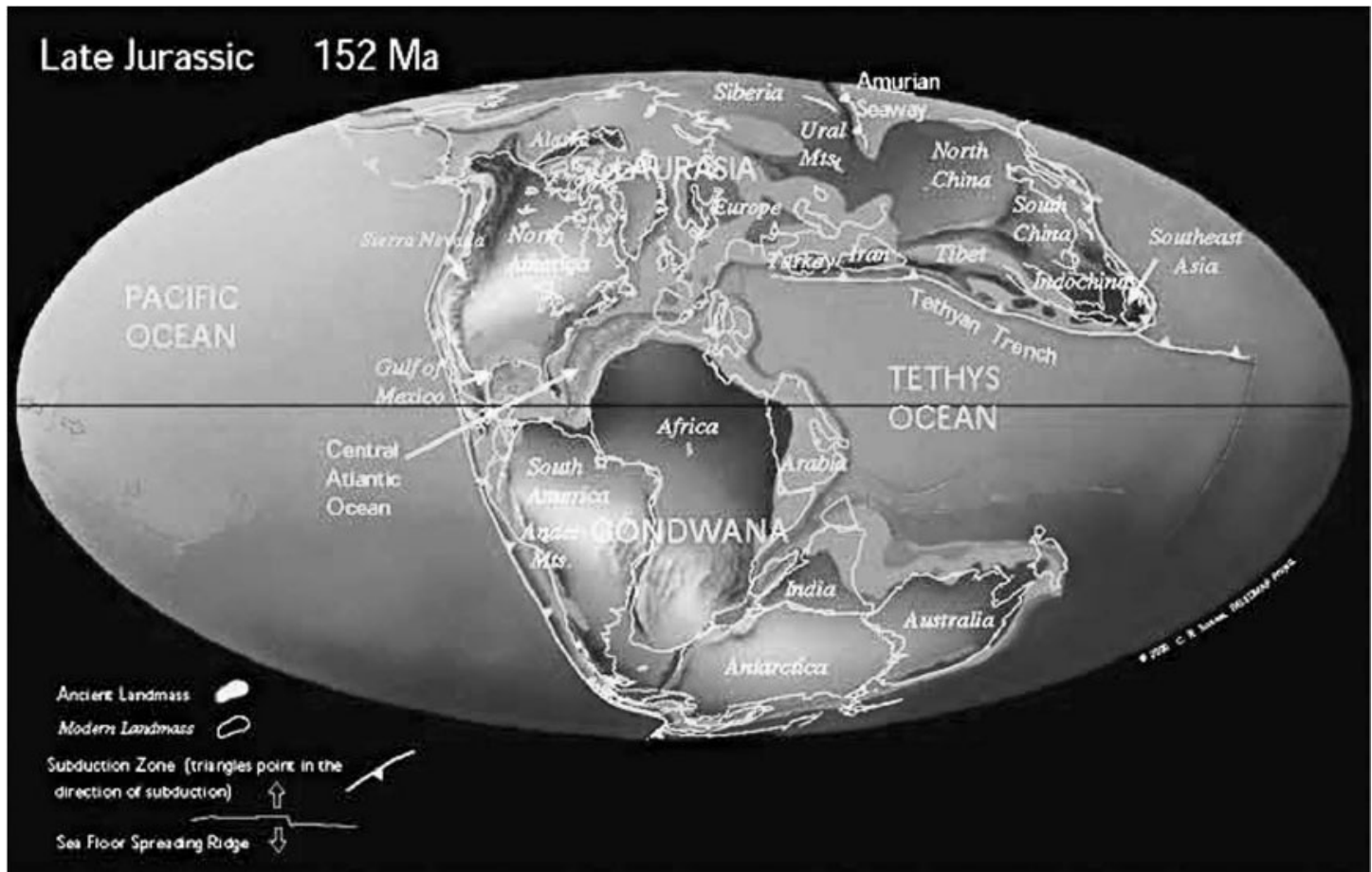
## Tethyan Connections

Anchialine systems are inland groundwater near the ocean that are influenced by marine tides but have no surface connection to the ocean – subterranean estuaries – and which exhibit marked hydrogeochemical stratification with marine waters separated from the overlying freshwater by a marked density gradient and layer(s) of hydrogen sulphide. The seawater layer supports a diverse fauna of aquatic troglobionts predominantly comprising higher taxa of crustacean (classes, orders and families) that are endemic to anchialine habitats and typically comprise biogeographic and/or phylogenetic relicts. The general composition of anchialine

fauna is predictable however far apart in the world they occur (mainly the Caribbean, the Canary Islands, Cape Range in northwestern Australia; [Figure 11.4](#)). The Australian anchialine fauna occurs on the coast fringing the North West Shelf – Cape Range, Barrow Island and the Pilbara coast south of the Fortescue River – but it is fully expressed outside the North Atlantic only in Bundera sinkhole in the Ningaloo Coast World Heritage Area. This fauna comprises atyids, thermosbaenaceans, hadziid amphipods, cirolanid isopods, remipeds, thaumatocypridid ostracods *Humphreysella* (formerly *Danielopolina*) and an array of copepods, including ridgewayid, epacteriscid and pseudocyclopiid calanoids, and speleophriid misophrioids. The fauna includes the only known representative of the class Remipedia in the Southern Hemisphere, and several genera, until reassigned in 2013, were known elsewhere from anchialine systems on either side of the North Atlantic (*Lasionectes*, *Halosbaena*, *Speleophria*, *Danielopolina*). At the larger scale there are a number of troglobiont higher taxa with major disjunctions in their distributions, indicative of vicariant events ([Table 11.2](#) in Humphreys 2008). However, recent study has resolved some higher taxa to be Bundera endemics but closely related to the other anchialine lineages – namely, the remipede family Kumongidae (Hoenemann *et al.* 2013) and genera *Welesina* (thaumatocypridid ostracod; Iglukowska and Boxshall 2013) and *Bunderia* (epacteriscid calanoid copepod; Jaume and Humphreys 2001). *Halosbaena*, however, the predictor for the presence of Remipedia in Australia (Poore and Humphreys 1992), is indicated by molecular phylogenetic analysis, to be a relatively late (Eocene) arrival in continental Australia where it has diversified (Page *et al.* 2016).

Being troglobionts, these anchialine lineages are thought to have poor capability or opportunities for dispersal, particularly across the deep ocean, and this attribute, combined with their distributions, which closely match areas covered by the sea in the Late Mesozoic, suggest that their present distributions may have resulted by vicariance as a result of the movement of tectonic plates. The epicontinental Tethys spread westwards between the fragmenting Pangaeon terranes (now the Mediterranean area) into the opening North Atlantic in the Jurassic ([Figure 11.5](#)), and it is suggested that anchialine precursors spread through and colonised the shores of these epicontinental seas before being separated by the development of the deep ocean. Thus, the current vicariant distributions have resulted through migration of the tectonic plates. Alternatively, the lineages may have dispersed broadly across Tethys before the closure of the Mediterranean in the Middle Miocene (ca. 14 Ma) constrained distribution. The timing of the diversification of these lineages is crucial to interpreting the current distribution of the anchialine faunas, independently of plate tectonic evidence, using a molecular clock approach. It is possible that both processes have been involved at various temporal and spatial scales, and that different lineages have different origins, although this is belied by the coherent composition and habitat of anchialine faunas. At some stage the fauna became restricted to anchialine habitats, and the presence of a close fossil relative of thaumatocypridid *Welesina* in a crevicular context in Jurassic age rocks in the Czech Republic – then a northern arm of Tethys – suggests an early troglobiont transition in at least one element of the anchialine fauna. Conversely, the atyid shrimp genus *Stygiocaris*, endemic to the Australian anchialine system, is sister to the amphi-Atlantic genus *Typhlatya* (Page *et al.* 2008), from which it appears to have diverged in the Palaeogene (Botello *et al.* 2012) and thus

suggests dispersal through the ocean. The present data are inadequate to test hypotheses on the origin of the anchialine fauna using molecular phylogenetics (von Rintelen *et al.* 2012; Botello *et al.* 2012; Hoenemann *et al.* 2013), and testing even the more straightforward hypothesis of trans-ocean basin plate tectonic vicariance (Atlantic, Bauzà-Ribot *et al.* 2012; Indian Ocean, Chakrabarty *et al.* 2012; Parenti and Ebach 2013) has been strongly contested (de Bruyn *et al.* 2013; Phillips *et al.* 2013) due to the claimed use of inappropriate molecular calibration.



**FIGURE 11.5** (See colour insert.) Position of tectonic plates in the Late Jurassic showing the link between northwest Australia, the Canary Islands and Caribbean regions through the westward expansion of Tethys into the developing Atlantic Ocean as Pangaea fragmented. (From Scotese, C.R., PALEOMAP, 2002. <http://scotese.com/late1.htm>. With permission.)

While the epicontinental anchialine habitats are characterised by the remipedes, those occurring on isolated seamounts support a distinct anchialine fauna, characterised by the presence of the primitive shrimp *Procaris* (Procarididae) occurring with alpheid, hippolytid and atyid shrimps, an assemblage that is also predictable however far apart they occur. Seamount anchialine faunas are known from all tropical oceans, occurring on Hawaii, Christmas Island, Ascension Island and Bermuda. Recently, two elements of the epicontinental anchialine system have been found on isolated seamounts: the thaumatocypridid *Humphreysella* and the thermosbaenacean *Halosbaena* have been found on Christmas Island, and the latter also on Minamidaito-jima, Okinawa (Shimomura and Fujita 2009; Page *et al.*



2016), which, given the likely age of the islands, suggests the oceanic dispersal (Humphreys and Danielopol 2006) of these two iconic anchialine taxa, although there is no coherent theory to account for this, nor for the occurrence of the anchialine copepod *Speleophria* in the Nullarbor (Karanovic and Eberhard 2009).

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## Discordant Geological Setting

There are a number of troglobiont lineages that, on the basis of other evidence, inhabit geological settings that are discordant with their phylogenetic age, occurring in geomorphological settings that are too young. Among these are the spelaeogriphacean *Mangkurtu* and the remipedean *Kumonga*. *M. mityula* inhabits a freshwater aquifer in the Millstream Dolomite that probably formed in the Middle-to-Late Tertiary in the Fortescue Valley (Figure 11.4), the latter formed by the Late Jurassic in the Proterozoic Hamersley Group, including the Wittenoom Dolomite. The distribution of the four extant spelaeogriphaceans in South America, Africa and Australia (Figure 11.4) could have resulted from Gondwanan vicariance or Tethyan dispersal (see section Tethyan Connections in this chapter), but either theory would place *M. mityula* in a discordant geological setting. This discordance was explained by the continuity of the habitat with the underlying cavernous Wittenoom Dolomite of Proterozoic age, allowing the troglobiont fauna to migrate up through the developing geology (Poore and Humphreys 1998), but the denudation processes, discussed previously, would provide a means by which the fauna could also have migrated downwards through the landscape as it eroded, coming to occupy the de novo aquifer.

By contrast, *Kumonga*, which belongs to the monotypic crustacean family Kumongidae, is a basal member of the lineage of remipedia found in anchialine systems in parts of the former Tethys – the Canary Islands and some Caribbean islands on the North American Plate, especially the Bahamas – and is hypothesised to have dispersed either on the tectonic plates as Gondwana fragmented, or else through the Tethys sea as it spread into the developing North Atlantic in the Jurassic (Figures 11.4 and 11.5). The current geological setting in Tertiary carbonate karst is discordant with either hypothesis and suggests the lineage (Hoenemann *et al.* 2013) has moved through geological settings as they formed. That the fauna can move through developing landscape is supported by the nature of their habitat – anchialine systems occur where freshwater and seawater form a salinity-stratified subterranean estuary – which will move laterally and vertically to accommodate changing sea levels. The present habitat was only flooded by the sea in the Holocene and for most of the Pleistocene would have been many kilometres seawards and at up to 140 m lower altitude. However, the principle hypothesis of the origin of this fauna – which awaits testing using molecular phylogenetics – may require such migration from the Jurassic onwards.

# New Zealand

The subterranean fauna of New Zealand is not well documented, but there are several biogeographic issues that can be usefully addressed using troglobiont lineages. There has been vigorous debate concerning the nature of the *Gondwanan* component of the New Zealand fauna. Waters and Craw (2006) call for rigorous evidence, independent of plate tectonics, that the New Zealand biota survived through the Oligocene to the present. They contend that there is no conclusive evidence for emergent terrestrial landscapes during the Cretaceous–Oligocene submergence of New Zealand, but there is compelling evidence that many purported Gondwanan elements of the biota arrived after the Oligocene, and so they conclude that dispersal may account for the present composition of New Zealand's biota. Some subterranean lineages provide robust models to test such hypotheses (Humphreys 2008), especially some ancient lineages of obligate freshwater crustaceans such as the stygocarididian syncarids and phreatoicidean isopods, especially if the entire lineage has been troglobiont, like the order bathynellacean syncarids (Schminke 2011). The presence of all these lineages in New Zealand (Scarsbrook and Fenwick 2003), and several other Gondwanan terranes, indicates the presence of at least a freshwater lens within the New Zealand landmass, the lens itself indicative of emergent land allowing the rainfall recharge of the aquifer. The distribution of these lineages across the Gondwanan terranes may permit rigorous molecular phylogeographic interpretation independent of plate tectonic evidence.

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## Sampling Intensity and Biodiversity Measures

The measurement of biodiversity and the change in biodiversity with area is intricately related to the intensity and thoroughness of the sampling of the fauna (Iknayan *et al.* 2014). Troglobionts are difficult to sample and, where possible, they are difficult to sample thoroughly because most subterranean voids do not open to the surface (Curl 1966). On all other accounts as well, troglobiont fauna is problematic as access is sparse – cave openings or boreholes – and poorly distributed across the landscape. Furthermore, troglobiont species are typically rare, and so numerous sampling occasions are required to find a high proportion of the species at a site (Eberhard *et al.* 2009). In addition, most species are short-range endemics, which presents both taxonomic and sampling intensity issues owing to the high  $\gamma$  - and  $\beta$ -diversity; that is, the species composition of the fauna across the landscape differs over short distances, and the broader taxonomic composition of the troglobiont fauna changes between regions (Finston *et al.* 2007; Humphreys 2008, 2012).

The two best-reported regions are the Yilgarn and Pilbara regions, which are contiguous areas of the Western Shield, but, for several reasons, they are expected to yield considerably greater diversity when they have been adequately sampled. Firstly, the sampling density (no. sites  $\text{area}^{-1}$ ) is low even within these better-sampled regions (about one site per 400–500  $\text{km}^2$ , often with poor-quality access [Humphreys 2008]), while in large swathes of the deserts

access to groundwater is entirely lacking even where there is a highly prospective troglobiont habitat, such as groundwater calcrete. There are only a few published accounts of intensive sampling of small areas (Guzik *et al.* 2009; Abrams *et al.* 2012; Bradford *et al.* 2013), but there are numerous unpublished site-specific environmental review and management reports, although these typically lack formal taxonomic content, as in the published paper by Halse and Pearson (2014).

Nonetheless, in just over three decades the perception of Australia has changed from having a relative poverty of troglobionts to arguably among the most diverse troglobiont faunas in the world. This is attributed to the accumulation of taxa enabled by the exceptional tectonic stability of the continent, the range of climates and, especially, the range of subterranean habitats present. These include such novelties as groundwater calcretes and pisolites as well as typical Tertiary orogenic karst and anchialine systems (Humphreys 2012), and a range of fresh and saline groundwaters. Guzik *et al.* (2011a) considered that 960 species of noncrustacean terrestrial troglobionts await discovery, mainly in the Western Shield, but this is likely to be a considerable underestimate even for the Pilbara alone, as indicated by a detailed sample of just ~1% of the area of the Pilbara (Halse and Pearson 2014). Similarly, a single calcrete in the Yilgarn, intensively sampled for the proposed development of a uranium mine, yielded 22 morphospecies of copepods, 70% of the previously recorded copepod diversity of the region (Karanovic and Cooper 2012).

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## Bathynellacea

Bathynellacea are typically minute (< 1 mm) obligate freshwater interstitial syncarid crustaceans with a global distribution and considered to have established in the groundwater habitat across Pangaea (Schminke 2011). Some genera have global connections and are thought to have been dispersed by means of plate tectonics, although none of these intercontinental genera has yet been confirmed using molecular phylogenetic methods. The Australian bathynellid fauna is diverse but is still poorly sampled, as is the case everywhere save the Iberian Peninsula (Camacho *et al.* 2014). The order is best known in Australia from the family Parabathynellidae, some species of which have unusual characteristics for this family in that, rather than inhabiting the interstitial habitat, they swim freely in groundwater, are very large (at a body length of 6.3 mm, *Billibathynella humphreysi* Cho 2005 is globally the largest species) or occur near playas in groundwater calcrete aquifers in water with the composition and salinity of seawater (Cho and Humphreys 2010), such as the sympatric *Brevisomabathynella clayi* and *B. uramurdahensis* near Lake Way. Of particular interest is the morphologically well-characterised Gondwanan genus *Atopobathynella* that is widespread in Australasia (Western Australia, Northern Territory, Tasmania and New Zealand), and also found in India, Madagascar and South America. Other genera also have intercontinental distributions (e.g. *Notobathynella*, *Hexabathynella* and *Chilibathynella*), but some genera are endemic to Australia (e.g. *Kimberleybathynella*, *Billibathynella*, *Brevisomabathynella*, *Octobathynella* and other genera are recognised informally from molecular research; Abrams *et al.* 2012).

Globally, most parabathynellids are known only from their type locality, and as such they are typically endemic to very small areas (Schminke 2011), although in the Iberian Peninsula, the only region thoroughly sampled shows that many species do have broader ranges (Camacho *et al.* 2014). Parabathynellid species occur in specific bodies of groundwater calcrete in Western Australia (Guzik *et al.* 2008; Abrams *et al.* 2012), and they may have very limited gene flow over short distances, even within aquifers (Asmyhr *et al.* 2014), as reported in other Australian arid-zone lineages of both aquatic and terrestrial troglobionts (diving beetles, amphipods and isopods: Guzik *et al.* 2011b; isopods: Cooper *et al.* 2008; diving beetles: Guzik *et al.* 2009; amphipods: King *et al.* 2012; Bradford *et al.* 2013; millipedes: Humphreys and Adams 2001; Schizomida: Adams and Humphreys 1993; Harvey *et al.* 2008).

## Ostracoda

Globally, only about 10% of ostracod species have intercontinental distributions, and 94% of species and 60% of genera are known from only one zoogeographic region (Martens *et al.* 2007). In Australia 92% of ostracod species are endemic, but they remain poorly studied and have the lowest continental diversity (I. Karanovic 2012). In arid Western Australia ostracods are more diverse in subterranean waters than in surface waters and the diversity of Candoninae ostracods in groundwater of the arid Pilbara region is greater than that in Lake Baikal (I. Karanovic 2007), a recognised biodiversity hotspot in the largest freshwater lake. Many species of troglobiont ostracods are endemic to small karst regions and the endemism may occur at the generic level, indicative of an extended period of isolation of these lineages and great phylogenetic age. Suprageneric endemism is rare, however, being restricted to several tribes of Candoninae that occur widely across the Gondwanan terrane (Table 11.1). Remarkably, two of the three tribes of Candoninae (12 of 13 genera) are endemic to the Pilbara, with only one genus being in common with the contiguous Yilgarn region. The Candoniinae, as do the Timiriaseviinae (as *Gomphodella*), indicate the close Tethyan connections of the Australian subterranean fauna (I. Karanovic 2009). Although water chemistry is presumed to be a major factor in ostracod ecology (Radke *et al.* 2003), the distribution of species of candonine ostracods in the Pilbara shows scant relationship with water chemistry (Reeves *et al.* 2007).

TABLE 11.1

Number of Genera in Each of Three Tribes of Candoninae (Candonidae: Podocopida) from the Western Shield of Australia and Their Continental Distribution



Tribe <sup>a</sup>	Australia (Pilbara) (n)	South America (n)	Africa (n)	Pilbara Endemic Genera (%)	Species (n)
Candonopsini	2 (1)	2	0	50	42
Danielocandonini	3 (3)	1	1	100	24
Humphreyscandonini	8 (8)	0	0	100	58
Total	13 (12)	3	1	92.3	124

Source: Humphreys, W.F., *Invertebrate Systematics*, 22, 85–101, 2008; Karanovic, I., *Subterranean Biology*, 2, 91–108, 2004; Karanovic, I., *New Zealand Journal of Marine and Freshwater Research*, 39, 29–75, 2005; pers. comm.

Note: Most genera are endemic to the northern part of the Western Shield and these Pilbara endemics are denoted by brackets. The continental distribution of these troglobiont ostracods is indicative of the Gondwanan affinities of these ancient lineages.

<sup>a</sup> The Indian fauna known to date has Holarctic affinities (Karanovic, I., and Ranga Reddy, Y., *Crustaceana*, 81, 861–871, 2008.)

## Copepods and the Pulsating Desert Hypothesis

The Western Shield of Australia, which includes the Pilbara and Yilgarn cratons and intervening orogens, is among the oldest emergent landscapes on earth, having been above sea level since the Proterozoic (Figure 11.1) and where the regolith has been in situ since at least the Mesozoic (Bird and Chivas 1988). Consequently, it is surprising that 39% of the species considered by T. Karanovic (2006) belong to genera with clear marine origins, some genera being recent colonisers (*Halicyclops*, *Phyllopodopsyllus* and *Schizopera*), while others have distributions consistent with plate tectonic vicariance associated with the westward expansion of Tethys in the Jurassic (*Parapseudoleptomesochra*, *Archinitocrella*, *Abnitocrella*, *Stygonitocrella* and *Pseudectinosoma*), a hypothesis also suggested in relation to the anchialine fauna of Cape Range (see section Tethyan Connections in this chapter). In addition, the genera *Diacyclops*, *Metacyclops* and *Psammocyclops* represent a strong Eastern Gondwana signal in the Pilbara freshwater copepods.

T. Karanovic (2004, 2006) conducted sequential studies of the groundwater copepods of the Yilgarn and Pilbara regions of the Western Shield and noted the high proportion of species and genera endemic to each region (Table 11.2), with few occurring in both of these contiguous regions (4%,  $n = 70$ , and 21%,  $n = 31$ , respectively); those species found in both regions are also found more broadly in Australia or are cosmopolitan. He considered the exceptionally rich subterranean fauna to be the result of a long period of accumulation of species starting after the Permo-Carboniferous glaciation, the last continental glaciation of Australia. He hypothesised that some genera, such as *Parastenocaris* and *Allocyclops*, are likely to have invaded subterranean waters in the Jurassic because they lack both marine relatives and more recent connections with other continents, making it likely that they dispersed through plate tectonic movement. Conversely, some other species, having close surface relatives, are clearly of more recent origin.

T. Karanovic (2010) comments on the strange disjunction in the copepod assemblage between the contiguous Pilbara and Yilgarn regions (repeated in other taxa; see [Table 11.3](#)), especially as each of these regions has clear affinities with noncontiguous areas far away to the north (Kimberley), south (southwestern Australia) and east (Pioneer Valley, central Queensland). Like Giribet and Edgecombe (2006), he emphasised the importance of small (presumably subcontinental) scale patterns when inferring Gondwanan biogeography because different regions of Australia have different affinities with Gondwanan faunas, a situation he found unexceptional given the age of the Australian landscape. He is, however, silent on the probable importance of the temporarily distinct separation histories of India and Antarctica from Australia, information that may help to resolve the causes of these, to date, largely inexplicable distributions.

**TABLE 11.2**

Distribution of Australian Copepod Genera across Gondwanan Terranes

Genus	Family	Species ( <i>n</i> )( <i>N</i> = 171)	Africa	Madagascar	South America	Australian Region	India
<i>Kinnecaris</i>	Parastenocaridiidae	25	●	●		●	●
<i>Attheyella</i> (subgenus <i>Chappuisiella</i> )	Canthocamptidae	32			●	●	
<i>Attheyella</i> (subgenus <i>Delachauxiella</i> )	Canthocamptidae	42			●	●	
<i>Haplocyclops</i>	Cyclopidae	8	●	●	●	●	●
<i>Diacyclops</i> ( <i>alticola</i> group)	Cyclopidae	6				●	●
<i>Diacyclops</i> ( <i>michaelseni</i> group)	Cyclopidae	6	●			●	
<i>Boeckella</i>	Centropagidae	52	●			●	

Source: Data from Tomislav Karanovic, personal communication.

Note: Black-Harpacticoida; dark grey-Cyclopoida; light grey-Calanoida.

## Distributional Hypotheses

### Pulsating Desert Hypothesis

The hiatus in the distribution of lineages between the Pilbara and Yilgarn on the Western Shield, evident in the Karanovics’ studies and formally addressed by T. Karanovic in his *pulsating desert* hypothesis, is presented for a range of troglobiont lineages studied in [Table 11.3](#).

T. Karanovic (2006) proposed his pulsating desert hypothesis to explain the strange affinities and disjunctions recorded in the occurrence of troglobiont copepods between different regions of Australia (T. Karanovic and Cooper 2011). Namely, he advocated that the wide fluctuations in aridity (implied due to the circum-Antarctic ocean flow following the opening of the Tasmanian Gateway in the Late Eocene; Scher and Martin 2006) caused the area of deserts to expand and contract. This process resulted in the extinction of the fauna in the centre during peak aridity and reinvasion from the north and south during more humid times, and explains the diversity and disjunction in the distribution of the subterranean copepods (Box 11.1). This is the only hypothesis that has been proposed to account for the faunistic disjunction between the Pilbara and Yilgarn, but it is inconsistent with the evidence, especially given the almost complete separation of the adjacent faunas. First, Karanovic anchored the meeting place of this climatic convergence on the Tropic of Capricorn, the relative position of which would have moved southwards from about north Kimberley to its present position since the mid-Miocene (calculated from Dyksterhuis *et al.* 2005) as Australia drifted northwards towards the intertropical convergence zone. Thus, there has been no prospect for a consistent response to climate change to remain anchored on the Pilbara through prolonged periods, thus permitting the accumulation of the high species diversity. Second, it is inconsistent with his proposition that the high copepod diversity is due to the stable landscape allowing species to accumulate since the Permian glaciation, a period predominantly before the onset of aridity in the Tertiary. Third, troglobionts generally are not able to disperse widely to take advantage of changing climate as they are entrapped by their evolutionary adaptations, to the extent that their subterranean matrix is interconnected, and by their low capacity for dispersion in the subterranean environment (e.g. Humphreys and Adams 2001; Harvey *et al.* 2008; Guzik *et al.* 2011b; Asmyhr *et al.* 2012; T. Karanovic and Cooper 2012; Bradford *et al.* 2013; cf. Eme *et al.* 2013).

**TABLE 11.3**

Distribution of Some of the Better-Known Higher Taxa of Troglobiont Invertebrates between the Adjacent Pilbara and Yilgarn Regions on the Australian Western Shield

<b>Aquatic Troglobionts</b>	<b>Taxon</b>	<b>Yilgarn (n)</b>	<b>Pilbara (n)</b>	<b>Overlap (%)</b>
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: Tainisopidea	Species	1 <sup>a</sup>	5	17
Coleoptera: Dytiscidae	Species	89	1	1.1
Spelaeogriphacea	Species	0	2	0
<b>Terrestrial Troglobionts</b>				
Blattodea: Nocticolidae	Species	0	9	0
Arachnida: Schizomida	Species	0	26	0
<b>Total Species</b>		125	144	0.7
<b>Total Genera</b>		16	38	14.5

*Source:* Humphreys, W.F., *Encyclopedia of Caves*, Academic Press, San Diego, CA, 2012; Watts, C.H.S., and McRae, J., *Records of the Western Australian Museum*, 28, 141–143, 2013.

<sup>a</sup> Probably by drainage capture.

## BOX 11.1 PULSATING DESERT HYPOTHESIS

This hypothesis assumes that the Tropic of Capricorn was a long-term barrier between the two regions. It is almost a general knowledge now that there have been past episodes of very severe aridity in Australia. During these arid phases the real desert would have spread westwards from the central part of the continent, perhaps wiping out most of the stygofauna and forcing the rest to retreat, first towards the coast and then either northwards or southwards. During the periods of increased humidity the regions would be repopulated and two different faunas would meet around the Tropic of Capricorn. Then another cycle would begin and these faunas really did not have a chance to develop any stronger connections. (T. Karanovic 2006: 230)

Fourth, as seen previously, aridity and troglobiont diversity are not incompatible, and true desertification does not necessarily eliminate troglobionts as both aquatic and terrestrial troglobionts persist in areas covered by Pleistocene red dune systems in Cape Range (Humphreys 2000c). Fifth, there is now considerable evidence from molecular phylogenetic work for several lineages of disparate taxonomic and ecological groups that the development of aridity – biotic implication reviewed by Byrne *et al.* (2008) – has been a driver of the exploitation of subterranean voids and may have facilitated troglobiont adaptation by the elimination of surface ancestors (Leys *et al.* 2003; Leys and Watts 2008). Nonetheless, there is

no competing hypothesis to account for the extraordinary troglobiont faunal disjunction between the contiguous Pilbara and Yilgarn regions (Table 11.3) that would be consistent with the geological interpretation that the entire Western Shield has been a continuously emergent landmass since the Proterozoic (Hocking *et al.* 1987), albeit with substantial marine incursions along the coasts and up the palaeovalleys in the Cretaceous and Eocene.

## Headwater Isolation and Subterranean Island Models

Based on the environmental conditions found in the Pilbara (Eberhard *et al.* 2005), Humphreys (2001) hypothesised that isolated populations of aquatic troglobionts would occur in headwater tributaries; he reasoned that there would have been reduced flow and consequent upstream progression of salinity as aridity intensified through the Tertiary and confined the fauna in the headwaters, which I will here name the *headwater isolation* model. The model was developed for the Pilbara, where the rivers are still active, if episodic. It has been found that troglobiont amphipods do indeed occur as isolated populations in headwater tributaries, and molecular phylogenies (Finston *et al.* 2007) are consistent with the proposed headwater isolation model, although they are not informative of the processes by which such consistency arose.

The headwater isolation model was, however, first tested, and found wanting, in the northern Yilgarn, the region contiguous with and south of the Pilbara, with a mix of coastal and inland drainages with respectively episodic rivers and palaeodrainages largely lacking flow. In this region the troglobiont habitat comprises isolated groundwater calcretes near salt lakes (playas) spread along the palaeovalleys (Humphreys 2001). The model was appraised against data from the aquatic troglobiont communities that inhabit phreatic calcretes that are deposited from the groundwater flow near salt lakes (Humphreys 2001). Analysis of the molecular phylogeny of all the epigeal and diverse troglobiont diving beetle fauna (Dytiscidae) in Australia showed that the distribution of the troglobiont beetles does not map the drainage pattern but rather supports a model of multiple independent invasions of calcretes across a wide region (Leys *et al.* 2003). This model is also applicable to the parabathynellids, amphipods and isopods inhabiting the calcrete aquifers (Cooper *et al.* 2007, 2008; Abrams *et al.* 2012; Guzik *et al.* 2008, 2009; Watts and Humphreys 2009). Thus, although the Yilgarn troglobiont fauna is inconsistent with the headwater isolation model, this research established the *groundwater island* model, whereby each isolated calcrete contains a troglobiont fauna endemic to that calcrete. The model was originally established for aquatic troglobionts (Cooper *et al.* 2002) but is now being extended to terrestrial troglobionts (Javidkar *et al.* 2016.).

## Aridity as a Driver of Subterranean Colonisation

A consequence of the northern movement of the Indo-Australian Plate during the Tertiary was the loss of the widespread moist forests that covered Australia and the spreading desertification of the continent reaching peaks in intensity during glacial maxima and fluctuating widely in extent during the Pleistocene glacial–interglacial cycles. This process had

profound influence on the assembly of the entire arid-zone biota of Australia (Morton *et al.* 1995; Byrne *et al.* 2008) and the hypothesis that aridity has been a driver for the colonisation of subterranean spaces by surface lineages, and their subsequent isolation and speciation in caves has had a long history in Australia, being invoked early on for cave colonisation in the Nullarbor and even in humid Tasmania (Eberhard and Humphreys 2003). The development of aridity was proposed at a landscape scale to account for the formation in Cape Range of genetic 'provinces' within mostly humid forest lineages of terrestrial troglobionts – belonging to Diplopoda, Schizomida and Crustacea – for which no close relatives of the cave fauna have persisted on the surface. It is hypothesised that the fauna colonised caves as the humid vegetation was lost from the range but retained some continuity through karst conduits in the cavernous Tulki Limestone. As aridity deepened, the humid vegetation was lost from the deep gorges and cut both subterranean and forest dispersal routes because the gorges cut into a noncavernous underlying marly Mandu calcarenite (Humphreys 1993b; Humphreys and Adams 2001).

More recently, consistent evidence that the colonisation of subterranean habitats is associated with the development of aridity has come from studies on aquatic troglobionts in the groundwater calcretes of the Yilgarn region in various lineages of invertebrates (see the previous section; for a review, see Juan *et al.* 2010).

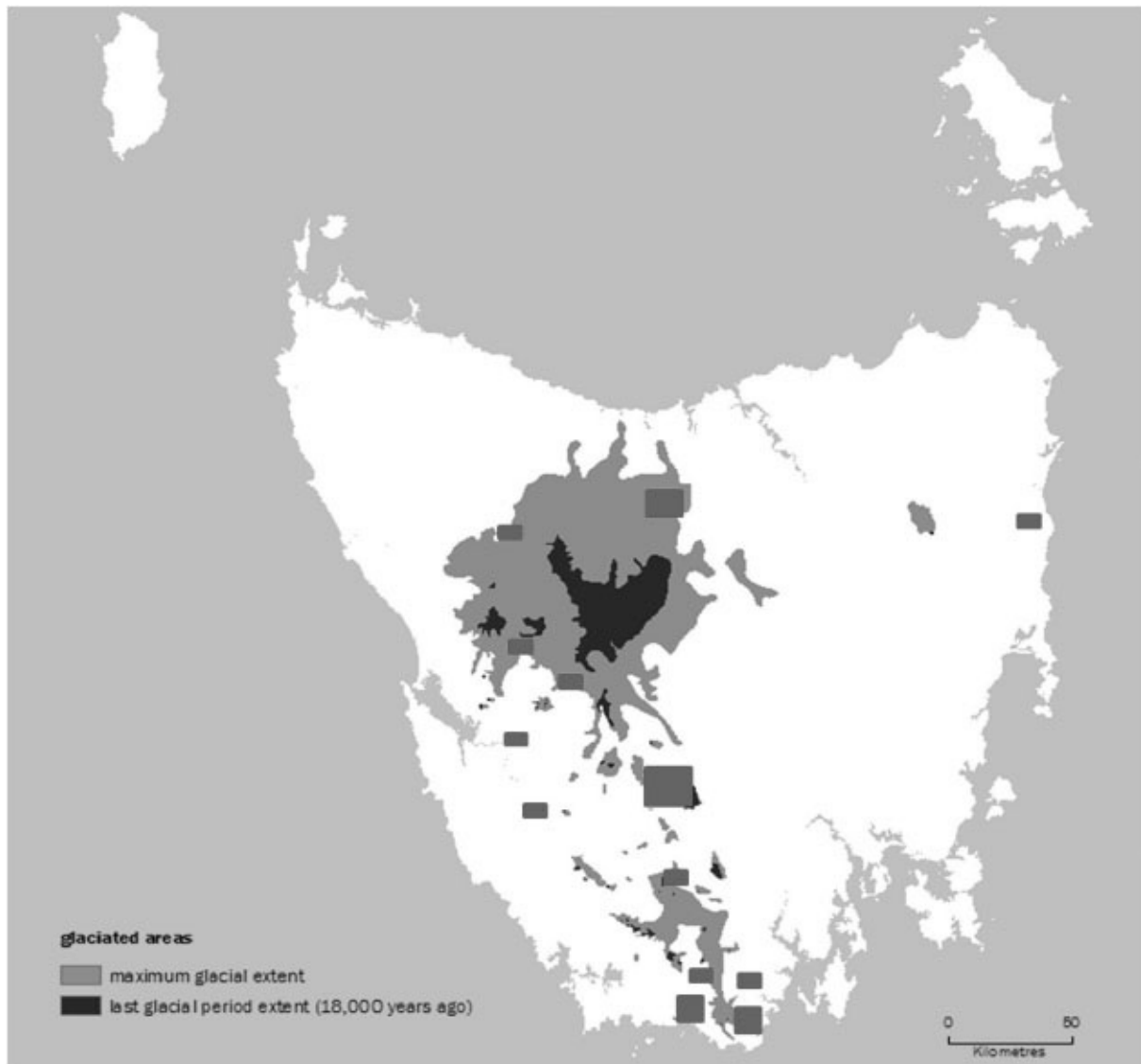
## **Pleistocene Effects in Periglacial Areas**

The Tasmanian cave fauna has distribution patterns in periglacial areas comparable to those found in Europe, North America and New Zealand. In Australia, unlike Northern Hemisphere continents, widespread coverage by ice sheets has not occurred since the Permian. During the Pleistocene in Australia the temperature effects of climate were most severe in Tasmania, where ice cover fluctuated around areas at higher altitude, with some glacier flow towards the lowlands. Several studies have linked the biogeography and diversity of cave faunas of Tasmania to the consequences of the climatic fluctuations during the Pleistocene – namely, the ebb and flow of ice fields in the Tasmanian high country and regional and altitudinal shifts in vegetation zones and humidity zones. Hunt (1990) showed that *Hickmanoxyomma*, a Tasmanian endemic genus of harvestmen (Opiliones), displayed clear morphological separation and regional endemism, and hypothesised that the speciation, distribution and expression of troglomorphisms were related to Pleistocene climatic fluctuations, particularly glaciation. While this hypothesis is consistent with the traditional Northern Hemisphere paradigm of Pleistocene-driven subterranean speciation, more recent work, both in Australia and Europe, has placed the roots of many subterranean lineages much earlier, to the late Miocene or before (see section Troglobionts and Biogeography in this chapter).

Although carabid beetles form a major component of subterranean faunas in the Northern Hemisphere (Eberhard and Giachino 2011), they are generally sparse in karst on the Australian mainland save for two highly troglomorphic species in the Nullarbor (Moore 1995), and species of Zuphini and Anilini have recently been found in BIFs in the Pilbara. In contrast, carabids are very diverse in Tasmania, where there are over 300 discrete karst areas, many impounded. There, the Trechinae are represented by 76 species in sixteen genera, of which 17



species in four genera are troglobionts, each endemic to specific karst areas (Eberhard and Giachino 2011). The presence of congeneric sympatric species exhibiting different stages of troglomorphy is proposed as evidence of the heterochronic colonisations of the karsts from adjacent forests by troglophilic lineages during the Pleistocene interglacials, followed by forest retreat isolating the subterranean populations and facilitating troglogenesis (Eberhard and Giachino 2011). Thus, considering the spatial changes in ice cover in Tasmania through the late Pleistocene, and as advocated earlier (Moore 1965), they follow the Northern Hemisphere paradigm, in which the Pleistocene climate changes resulted in the current species diversity and distribution of the cavernicolous Trechini (Figure 11.6).



**FIGURE 11.6** The extent of glaciation in Tasmania and the distribution of troglobitic Trechini and Zolini carabid beetles of the genera (no. species) *Goedetrechus* (6), *Tasmanotrechus* (4), *Tasmanorites* (1), *Idacarabus* (4) and *Pterocyrtus* (2). The size of squares denotes the number of species at a site (1–4). (Derived from Eberhard, S., and Giachino, P.M., *Subterranean Biology*, 9, 1–72, 2011. Base map of glacial extent from <http://soer.justice.tas.gov.au/2009/image/162/index.php>.)

The two studies of Tasmanian troglomorphic lineages, while of great interest, lack both phylogenies and any temporal context that would better able the testing of the proposed hypothesis. A molecular phylogeographic study of both these lineages would help unravel the apparent differences between the origins of the cavernicolous faunas of southeastern Australia and the apparent great age of origin of those elsewhere on the continent. The origin of troglogenesis starting in the Quaternary and driven by Pleistocene glacial cycles was a long-held interpretation in the Northern Hemisphere, especially for trechine beetles, which are such a prominent and well-studied component of the troglobiont fauna of the Europe. However, this interpretation is increasingly being shown to be invalid and the morphological interpretation of the relationships between trechines (and other troglobionts, both aquatic and terrestrial) is masked by the convergent morphologies exhibited by troglobionts. Faille *et al.* (2013 and earlier papers therein) have demonstrated, using molecular phylogenies, that most clades of carabid beetles belonging to the tribe Trechini, in the European Alps and the Pyrenean and Dinaric karsts, started their subterranean isolation at various phases since the Oligocene (possibly the Eocene) but that the trogloneogenesis continued into the Plio-Pleistocene. This time frame is in accord with studies in other systems in Australia (Leijs *et al.* 2003) and the resolution of the evolutionary timing of troglogenesis in the Tasmanian trechines must await molecular studies. It is notable that oscillating areas of refugia driven by Pleistocene climatic fluctuations are hypothesised to have resulted in the rapid radiation of a species flock in the epigeal genus *Sternopriscus* (Dytiscidae: Hydroporini) in the freshwaters of southeastern Australia (Hawllitschek *et al.* 2012); it would be very interesting if the trogloneogenesis of the Tasmanian carabids and harvestmen proves to be so recent because, given their much greater degree of morphological divergence than that found in *Sternopriscus*, it would suggest a very rapid rate of evolution. However, the divergence of evolutionary rates between surface and troglobiont lineages, or the high rates of evolution in subterranean habitats of both morphological and genetic characters, has been proposed previously on both theoretical and evidential grounds (Rétaux and Casane 2013; Rohner *et al.* 2013).

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## Concluding Remarks

Patchy sample coverage, incomplete sampling in the areas sampled and an undeveloped taxonomy all impede the development of a robust biogeographical understanding of the subterranean fauna, and some approaches to resolve these limitations follow. Most of the sampling for troglobionts has been conducted on the shield regions where ancient relictual faunas may be expected, but there has been minimal work in the areas inundated by the major flooding events in the Cenomanian (ca. 100 mya) and the Eocene (Figure 11.2). This is surprising as there is a rich body of literature and terminology on the origin of aquatic troglobionts from coastal invasion and, especially, due to stranding inland by eustatic changes (Boutin and Coineau 2000). The latter, particularly, can provide independent time markers to complement those derived from molecular phylogenetic methods, although the methodology requires the selection of the appropriate lineages to derive defensible analyses (Phillips *et al.*



2013). Information is needed on whether these 'lowland' areas contain suitable habitats to support troglobiont fauna and, if so, whether fauna is present and what the affinities of its members are. To delineate regions where troglobiont fauna really could be absent it is important that sampled sites and their characteristics be recorded even if no troglobionts are present.

In addition to eye and pigment loss – the overt troglomorphies commonly mentioned – troglobionts have highly convergent morphological characters which often obscure the relationship between species, even in the best-studied faunas (Faille *et al.* 2013). In practice it has often been found necessary to undertake molecular work on troglobionts as a prelude to identifying suitable taxonomic characters, as well as to establish the phylogenetic relationships (Cooper *et al.* 2008; Guzik *et al.* 2008; Abrams *et al.* 2012). Indeed, molecular methods are commonly used to indicate the presence of both described and undescribed species during the environmental management assessment of major mining projects in the absence of an adequate, even any, taxonomic base for many lineages. Molecular methods could also be used on a regional scale to ascertain the diversity and affinities of troglobionts in the broad areas yet to be sampled and for which a complete taxonomic base for troglobionts is unlikely to be feasible, owing both to convergence and a lack of taxonomic resources.

Finally, investment in the systematics of certain higher taxa that are especially well represented and/or informative, and relatively easy to collect, would facilitate progress on understanding biogeographic relationships, albeit on a narrower path that may mask important information. Among aquatic troglobionts, amphipods and copepods would be good targets on account of both their diversity and ubiquity in subterranean habitats, and the likely wide range of time since they transitioned to subterranean life. Troglobiont copepods have the disadvantage of very small size. Terrestrial troglobionts are more problematic to recommend as the distribution of higher taxa is more varied regionally. Oniscidean isopods are ubiquitous, diverse, narrow-range endemics (M. Javidkar pers. comm., University of Adelaide) and relatively simple to collect, whereas true spiders (Araneae) are ubiquitous but are less easily collected in nontraditional subterranean habitats.

Despite the immaturity of biogeographic studies on Australian troglobionts, where research has been conducted in ample depth and to a sufficient spatial extent, it is clear that troglobiont faunas have considerable untapped potential for the investigation of the timing and origin of broad elements of the fauna of Australia. This arises because of the mix of the attributes of subterranean animals, the geomorphological context in which they are found and the age and stability of the continent. The fauna itself is diverse – arguably the phylogenetically most diverse troglobiont fauna globally – on account of the age of the fauna and its varied intercontinental connections, and yet there are endemic higher taxa (to suborder) restricted to groundwater. Additionally, the continent covers a broad range of climates, ranging from the Wet Tropics, the humid, temperate eastern seaboard and, in places, the alpine south, together with the broad arid centre. Further, there is a wide range of aquatic habitats, with inland groundwater ranging from fresh- to seawater salinity and greater, as well as the salinity-stratified anchialine systems – groundwater estuaries – with actual seawater at depth. Troglobionts are known from all types of subterranean voids ranging from classical karst and coarse alluvial deposits to novel systems such as groundwater calcrete and goethite pisolite

formations. Yet the troglobiont fauna of Australia is sparsely known, with by far the greater proportion of the country having been unexplored for troglobionts. Over much of the continent, access to troglobiont communities will be obtained through artificial access (boreholes) to atypical, even novel, habitats, and these are proving to contain the most species-rich troglobiont communities in Australia, possibly globally.

## Acknowledgements

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## References

There are a number of collected works on the cave biology of Australia that include broad introductions (Wilkens *et al.* 2000; Wicks and Humphreys 2011) and edited volumes concerning subterranean fauna (Humphreys 1993, 2012; Humphreys and Harvey 2001; Austin *et al.* 2008). The fauna of epikarst – a perched aquifer lying between surface water and vadose water – an exciting area for ecological, evolutionary and biogeographic research (Pipan 2005; Pipan and Culver 2007), remains largely unpublished in Australia, save in the context of shallow subterranean habitats ([Chapter 5](#) in Culver and Pipan 2014).

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