

Is the Australian subterranean fauna uniquely diverse?

Michelle T. Guzik^{A,G}, Andrew D. Austin^A, Steven J. B. Cooper^{A,B}, Mark S. Harvey^C,
William F. Humphreys^C, Tessa Bradford^A, Stefan M. Eberhard^D, Rachael A. King^{A,B},
Remko Leys^{B,E}, Kate A. Muirhead^A and Moya Tomlinson^F

^AAustralian Centre for Evolutionary Biology and Biodiversity, The University of Adelaide, SA 5005, Australia.

^BSouth Australian Museum, North Terrace, Adelaide, SA 5000, Australia.

^CWestern Australian Museum, Collections and Research Centre, Locked Bag 49, Welshpool DC, WA 6986, Australia.

^DSubterranean Ecology Pty Ltd, 8/37 Cedric St, Stirling, WA 6021, Australia.

^ESchool of Biological Sciences, Flinders University, SA 5042, Australia.

^FDepartment of Environment and Resource Management, GPO Box 2454, Brisbane, Qld 4001, Australia.

^GCorresponding author. Email: michelle.guzik@adelaide.edu.au

Abstract. Australia was historically considered a poor prospect for subterranean fauna but, in reality, the continent holds a great variety of subterranean habitats, with associated faunas, found both in karst and non-karst environments. This paper critically examines the diversity of subterranean fauna in several key regions for the mostly arid western half of Australia. We aimed to document levels of species richness for major taxon groups and examine the degree of uniqueness of the fauna. We also wanted to compare the composition of these ecosystems, and their origins, with other regions of subterranean diversity world-wide. Using information on the number of ‘described’ and ‘known’ invertebrate species (recognised based on morphological and/or molecular data), we predict that the total subterranean fauna for the western half of the continent is 4140 species, of which ~10% is described and 9% is ‘known’ but not yet described. The stygofauna, water beetles, ostracods and copepods have the largest number of described species, while arachnids dominate the described troglifauna. Conversely, copepods, water beetles and isopods are the poorest known groups with less than 20% described species, while hexapods (comprising mostly Collembola, Coleoptera, Blattodea and Hemiptera) are the least known of the troglifauna. Compared with other regions of the world, we consider the Australian subterranean fauna to be unique in its diversity compared with the northern hemisphere for three key reasons: the range and diversity of subterranean habitats is both extensive and novel; direct faunal links to ancient Pangaea and Gondwana are evident, emphasising their early biogeographic history; and Miocene aridification, rather than Pleistocene post-ice age driven diversification events (as is predicted in the northern hemisphere), are likely to have dominated Australia’s subterranean speciation explosion. Finally, we predict that the geologically younger, although more poorly studied, eastern half of the Australian continent is unlikely to be as diverse as the western half, except for stygofauna in porous media. Furthermore, based on similar geology, palaeogeography and tectonic history to that seen in the western parts of Australia, southern Africa, parts of South America and India may also yield similar subterranean biodiversity to that described here.

Introduction

The subterranean fauna of Australia has recently revealed numerous higher taxa (classes, orders and families) not previously recorded from the southern hemisphere, as well as living representatives of lineages previously known only as fossils (see Humphreys 2008 for summary). Obligate subterranean lineages remain trapped *in situ* and are consequently potent subjects to test biogeographical and evolutionary hypotheses. This is especially the case for the numerous higher taxa of Crustacea that are found solely represented as obligate subterranean fauna. Here we present current estimates of newly described or identified subterranean taxa from several key regions in the western half of Australia, particularly in the arid

zone (see Fig. 1). We also make projections on possible total subterranean biodiversity in this area, in particular to assess whether the diversity of the Australian subterranean fauna is notably high compared to that found elsewhere. Our aim is to document the scale of this biodiversity to encourage further exploration of these and other regions of the continent. We also make predictions about other locations in the world that reflect similar geomorphology to that seen in Australia’s arid region, and represent potential new sites for subterranean fauna.

Globally, the northern hemisphere dominates as a region of subterranean biodiversity hotspots, in particular temperate mid-latitude locations (Culver *et al.* 2006; Stoch and Galassi 2010) such as the Balkan Peninsula, the USA (Culver and Sket 2000),

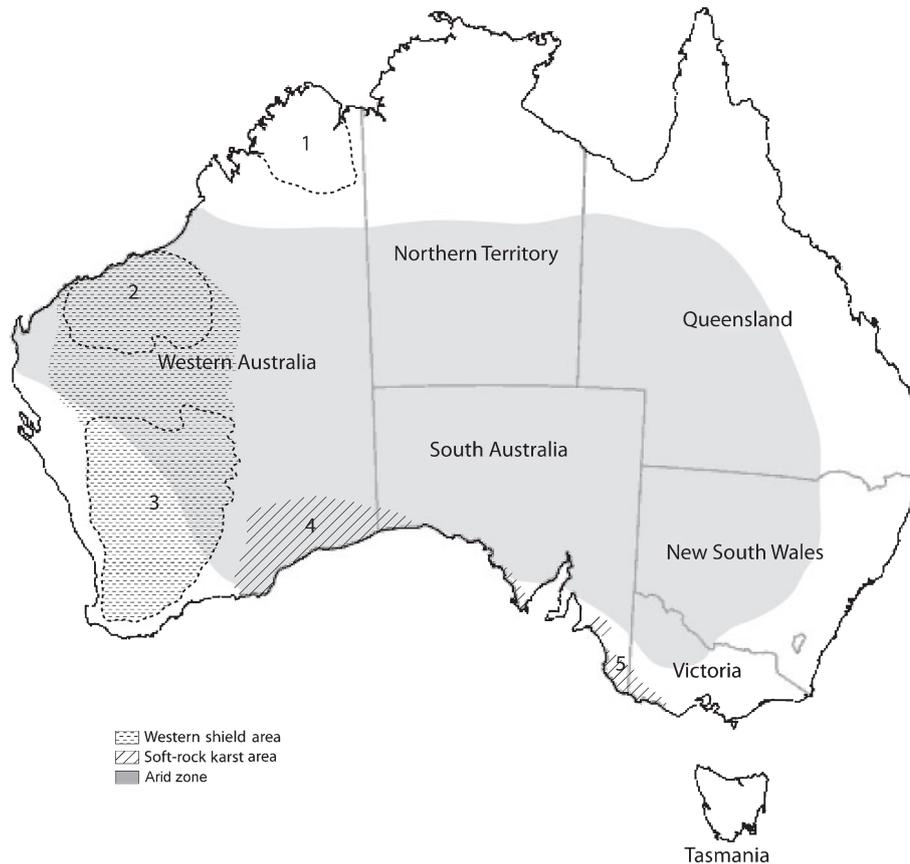


Fig. 1. Geological and climatic regions of Australia from which we describe a subterranean faunal biodiversity hotspot. Five regions are named including the Western Shield, an area that has been continually emergent since the Proterozoic. Dashed lines delineate the (1) Kimberley, (2) Pilbara and (3) Yilgarn. Additionally, the Gondwanan refuges that comprise soft-rock karst are the (4) Nullarbor and (5) south-east of South Australia.

Mexico (Reddell 1981) and, most recently, caves of south-east Asia (Deharveng 2005). Subterranean faunal diversity is generally concentrated in karst and pseudokarst areas (Juberthie and Decu 1994; Culver *et al.* 2001; Christman *et al.* 2005; Deharveng 2005). Even within this geomorphological constraint (i.e. it is patchily distributed, Fong and Culver 1994; Culver *et al.* 2004) the density of caves and the sampling intensity by generations of researchers in these regions have provided biologists with the opportunity to efficiently document caves and their fauna (Christman and Culver 2001; Culver *et al.* 2004; Zagamajster *et al.* 2008). Consequently, knowledge of these regions and their biodiversity, phylogeography and functional ecology are well progressed (Gibert *et al.* 1994; Wilkens *et al.* 2000; Culver and White 2004).

As recently as 16 years ago, Humphreys (1994) advocated a knowledge gap of subterranean fauna in Australia, especially in areas other than the lava tubes of tropical north Queensland, which are a noted troglifauna hotspot (Culver and Sket 2000). Considered depauperate of karstic habitat and having widespread aridity, historically, Australia was considered a poor prospect for subterranean fauna. Australia's arid Pleistocene climatic history was deemed to lack key climate history events, such as

Pleistocene glaciations (Moore 1964; Hamilton-Smith 1967; Barr 1973), which were considered drivers of subterranean biodiversity in the northern hemisphere (Peck 1980; Boutin 1994). This excludes Tasmania (Derbyshire 1972), which is richly endowed with karst and caves and was subject to Pleistocene glaciations. These hypotheses, coupled with a paucity of research on the southern hemisphere subterranean biota over the last two centuries, have led to a prolonged lag in discovery of Australia's obligate subterranean species. Historically, the most sampled cave regions in Australia were south-eastern South Australia (SA), New South Wales (NSW), Tasmania, and the Nullarbor Plain (spanning parts of SA and Western Australia (WA)). It is now appreciated that Australia holds a great variety of subterranean habitats, with associated invertebrate faunas, found both in karst and non-karst environments (Eberhard and Humphreys 2003). Notable differences between Australia and other regions of the world are the absence of urodele amphibians and stenassellid isopods, and a scarcity of carabid beetles and cave fishes.

Focussed research on subterranean fauna from karst regions in WA comprising troglobionts (Humphreys *et al.* 1989) and stygobionts soon after (Humphreys and Adams 1991),

substantially advanced our knowledge of subterranean fauna in Australia. Further, the discovery of rich subterranean faunas in non-karstic substrates 20 years ago, also led to a rapid expansion in the discovery and documentation of subterranean faunal diversity. Increasingly, regulations requiring the inclusion of subterranean fauna during the environmental review process for major resource projects in WA by the Environmental Protection Agency (EPA) (EPA 2003) have accelerated the discovery of new species, based on either morphology or genetic differences, or both. Coupled with these environmental impact assessments (EIA) is an increased interest in groundwater biology research (Humphreys 2006, 2009; Boulton 2009). Government and privately funded research in the past five years has primarily focussed on the fauna of the Yilgarn and Pilbara regions of WA and aquifers in SA, in particular utilising boreholes and drill holes installed for exploration and exploitation of water, minerals and monitoring of groundwater levels and salinity, rather than fauna. This work has revealed a diverse subterranean fauna inhabiting both aquatic and terrestrial habitats found in a wide range of substrates, including alluvium, calcretes, fractured rock, karst in soft and hard rock, pisolites and pseudokarst in lava and sandstone (Poore and Humphreys 1998, 2003; Finston and Johnson 2004; Eberhard *et al.* 2005; Harvey *et al.* 2008; Humphreys 2008; Eberhard *et al.* 2009). Many of the resultant data are unavailable publicly during the EIA process but many become public after formal environmental approvals occur.

In an era when human induced extinction rates are high (Pimm *et al.* 1995), biodiversity estimates are a vital tool for identifying knowledge gaps for the purpose of prioritising research effort and funding resources, and also developing conservation policies (Brooks *et al.* 2006). Estimates of invertebrate species richness in Australia are typically centred around terrestrial arthropods (e.g. Yeates *et al.* 2003). Published studies suggest Australia's subterranean fauna is diverse, especially the Pilbara region with 78 described species of stygofauna (Eberhard *et al.* 2005) and an estimated 500–550 undescribed species (Eberhard *et al.* 2009). However, a firm estimate of total species diversity is constrained by the generally sparse geographical coverage and the inevitable lag in taxonomic descriptions. Our position here is that, historically, Australia's subterranean fauna have been vastly underestimated. Given the short duration of research targeting this field in Australia, it is not possible to realistically attempt an estimate of subterranean faunal diversity for the whole continent. Rather, we concentrate on several areas in the western half of the Australian continent that are better studied; we summarise the number of described and recognised species from morphological and molecular studies, and then project, based on the collective experience of the specialists currently working on these faunas, the likely species richness of broad taxonomic groups. The areas that were included and assessed in this study from north-west to east include: (1) the Kimberley and (2) Pilbara regions of north-western WA; (3) the Yilgarn region of WA; (4) the Nullarbor region; and (5) SA, including the Eyre Peninsula, Flinders Ranges, and the south-east (Fig. 1). We also note that a diverse stygofauna has recently been identified from alluvial aquifers in eastern Australia (Hancock and Boulton 2008; Tomlinson 2009; Camacho and Hancock 2010), but this

region requires considerably more intensive surveying and taxonomic work to obtain reliable estimates of faunal diversity.

Methodology for estimating subterranean faunal diversity

The criteria employed to identify species richness in subterranean habitats of Australia's west (see Table 1 for data) were 5-fold.

(1) We surveyed the relevant literature for formally 'described' species, mostly from the last 10–20 years, which has been the most productive time for exploration and description of subterranean taxa (see references in Table 2 for a representative summary of this literature).

(2) Extensive surveys of key regions were carried out primarily by teams represented by three of the authors of this study (SA: Leys; Pilbara and Nullarbor: Eberhard; Yilgarn and Kimberley: Humphreys). The areas most comprehensively sampled were the Western Shield, a single long-emergent (since the Paleozoic) landmass comprising the Yilgarn and Pilbara cratons and associated orogens, southern SA, and the northern Carnarvon Basin. These surveys were conducted using a variety of access points, mostly boreholes drilled for water extraction, groundwater monitoring and mineral exploration, but also pastoral wells and caves, where present. In general, even in the better surveyed regions, sampling density was low. For example, in the only regional survey of the Pilbara region (Eberhard *et al.* 2009), sample density was 0.0022 km² (one site every 460 km²) in an area of ~220 000 km². In the Yilgarn, sampling has largely been restricted to groundwater calcretes, which are highly prospective for subterranean fauna, whereas other habitats have been found to be largely devoid of subterranean fauna.

(3) Identification of morphologically distinct species (morphospecies) beyond family or genus using current descriptions and keys was not always possible. Therefore we canvassed numbers of species from taxonomic experts (listed in

Table 1. Species richness of major subterranean invertebrate groups from the western half of the Australian continent, showing the number of 'described' species, the number of 'known' but undescribed species from collections and molecular studies, and an estimate of the likely diversity for each group (see text for further details)

| Taxonomic group | No. species described | No. known species | Estimated size of fauna | % described or known |
|--------------------|-----------------------|-------------------|-------------------------|----------------------|
| Stygofauna | | | | |
| Coleoptera | 98 | 3 | 510 | 19.8 |
| Amphipoda | 28 | 91 | 560 | 21.3 |
| Isopoda | 19 | 30 | 300 | 16.3 |
| Bathynellacea | 17 | 66 | 270 | 30.7 |
| Ostracoda | 70 | 4 | 180 | 41.1 |
| Copepoda | 79 | 4 | 580 | 14.3 |
| Gastropoda | 3 | 1 | 20 | 20.0 |
| Other stygofauna | 10 | 20 | 260 | 11.5 |
| Troglofauna | | | | |
| Hexapoda | 11 | 52 | 500 | 12.6 |
| Arachnida | 57 | 44 | 380 | 26.6 |
| Myriapoda | 7 | 12 | 80 | 23.8 |
| Crustacea | 2 | 43 | 500 | 9.0 |
| Total | 403 | 367 | 4140 | 18.6 |

Table 2. Subterranean groups, the experts we consulted on the estimated number of species and the references we used for estimating the number of 'described' species

| Taxonomic group | Experts | References |
|--------------------|------------------------|---|
| Stygofauna | | |
| Coleoptera | Watts, C. | Summary and checklist, Watts and Humphreys (2009), Leys and Watts (2010) |
| Amphipoda | Bradbury, J., King, R. | Bradbury and Williams (1997a, 1997b), Bradbury (1999), Bradbury and Eberhard (2000) |
| Isopoda | Taiti, S. | Wilson and Ponder (1992), Bruce and Humphreys (1993), Wilson and Johnson (1999), Wilson and Keable (1999), Taiti and Humphreys (2001), Wilson (2001, 2003, 2008), Bruce (2008) |
| Bathynellacea | Cho, J.-L. | Cho (2005), Cho <i>et al.</i> (2005, 2006a, 2006b), Cho and Humphreys (2010) |
| Ostracoda | Karanovic, I. | Karanovic and Marmonier (2002, 2003), Karanovic (2003a, 2003b, 2004, 2005a, 2005b, 2007) |
| Copepoda | Karanovic, T. | Pesce and De Laurentiis (1996), Pesce <i>et al.</i> (1996a, 1996b), Karanovic <i>et al.</i> (2001), Karanovic and Pesce (2002), Karanovic (2003, 2004a, 2004b, 2005, 2006) |
| Gastropoda | | Ponder <i>et al.</i> (1989) |
| Other stygofauna | | Acari: Harvey (1998), Anchialine faunas: Humphreys (2001), Jaume and Humphreys (2001), Jaume <i>et al.</i> (2001) |
| Troglofauna | | |
| Hexapoda | Stevens, M. | Koch (2009) |
| Arachnida | Harvey, M. | Harvey and Humphreys (1995), Harvey (2001), Harvey and Edward (2007), Harvey and Volschenk (2007), Barranco and Harvey (2008), Edward and Harvey (2008), Harvey and Leng (2008a, 2008b), Harvey <i>et al.</i> (2008), Platnick (2008), Volschenk and Prendini (2008), Burger <i>et al.</i> (2010) |
| Myriapoda | | Edgecombe (2005) |
| Crustacea | | Poore and Humphreys (1998) |

Table 2) to identify probable new morphospecies. These experts used their prior knowledge to assign likely species.

(4) Molecular data have proven a major innovation in delineation of new species, both cryptic and otherwise (Juan *et al.* 2010). Hence, in situations in which it was uncertain whether there were distinct species present, genetic methods were used to estimate 'known' but undescribed species from recent collections and molecular studies. Such situations arose when geographically isolated populations were observed, but morphological differences were not immediately recognisable, or in situations in which expertise was unavailable or sample volumes were too large. In these cases, the mtDNA cytochrome *c* oxidase subunit I gene (*cox1*) was primarily used for assessing the presence of new genetic lineages.

Criteria for discriminating whether genetic lineages for *cox1* were likely to be species here are as follows. (1) Reciprocally monophyletic lineages with >90% posterior probability support, and the position of these lineages within the broader phylogeny, were considered. (2) On the basis of total evidence, geographically discrete lineages that complied with all other criteria listed here and were also known to be spatially isolated were included. Isolation could be geographical distance and/or barriers or geological barriers. This criterion was crucial in situations in which percentage genetic divergence might have been low and provided insights into the possible mechanisms for species divergences. In particular, it was shown in several studies that major geographic barriers inhibit gene flow between regions, i.e. tributaries (Pilbara amphipods Finston and Johnson 2004; Finston *et al.* 2007, 2009) or geology of calcrete aquifers (Cooper *et al.* 2007, 2008; Guzik *et al.* 2008). (3) Genetically divergent lineages were conservatively $\geq 16\%$ for pairwise distances based on a Kimura 2-parameter (Kimura 1980) model (i.e. between 'species' lineages, Lefebvre *et al.* 2006). In some cases, where genetic lineages satisfied all of the other criteria (i.e. genetically monophyletic and geographically

isolated), then lower divergences were considered. The justification for allowing lower divergences is that, in cases of recent speciation events, divergences as low as 11% have been observed in morphologically distinct but sympatric species (Bradford *et al.* 2010; R. A. King, unpubl. data). These findings have been observed in other crustaceans, particularly amphipods and parabathynellids (Cooper *et al.* 2007, 2008; Guzik *et al.* 2008; K. M. Abrams, unpubl. data). Where possible, evidence from a second marker was also taken into account to strengthen the hypothesis of distinct species. Genes such as 16S rRNA (mtDNA) and 28S rRNA (nuclear DNA) were used to supplement the *cox1* data for parabathynellids and amphipods (R. Leys, unpubl. data).

An example of how these criteria were implemented is as follows. Using DNA alone ~90 new crustacean 'lineages' were identified from published studies (e.g. up to 21 Pilbara amphipods (Finston and Johnson 2004; Finston *et al.* 2007, 2009), 22 Yilgarn amphipods (Cooper *et al.* 2007), 1 anchialine shrimp (Page *et al.* 2008), 24 aquatic isopods (Cooper *et al.* 2008) and 17 parabathynellids (Guzik *et al.* 2008)). Each of these studies also demonstrated geographic isolation for each of the lineages (as above) confirming our species concept using a combined approach as exemplified by Harvey *et al.* (2008) where both morphological and molecular data reinforced conclusions. Finally, some unpublished molecular work by Eberhard, Leys and Abrams, generated largely for EIA datasets, were also assessed using the same criteria as that for published work.

(5) In order to provide an estimate of the potential size of the fauna for different taxonomic groups and the percentage that was currently 'described' or 'known' we extrapolated from the existing surveys. This extrapolation was carried out in different ways for different regions, for which we give two examples. First, in the Pilbara region it is likely that most of the landscape provides potential habitat for troglofauna and stygofauna and, hence, it is difficult to assign sampled/unsampled area estimates based on

points (bores or caves). In this case, extrapolation of richness estimates was based on accumulation curves as outlined by Eberhard *et al.* (2009). Second, in the Yilgarn region, since subterranean taxa are restricted to calcretes, and each sampled calcrete was found to have a unique fauna, extrapolation of the data from sampled to unsampled calcretes was warranted. Of 200 major calcretes in the Yilgarn region ~50 (25%) have been surveyed allowing extrapolation based on the average number of described plus known species in different calcretes.

Australia's subterranean fauna: a biodiversity hotspot

Here, we estimate 4140 species for subterranean systems in Australia's western half (Table 1), many of which are restricted to arid and semiarid regions. Based on this figure, over 80% of the likely fauna remain undiscovered, a figure that is not surprising given that large tracts of potentially suitable habitat remain unexplored. 'Described' species represent slightly more taxa (403) than those 'known', but not described (367). In particular, beetles, ostracods and copepods have the largest number of described species for the stygofauna, while arachnids dominate the described troglifauna. This situation largely reflects the current taxonomic effort by specialists. While other potentially diverse groups have not been investigated in detail, either because of a lack of attention by existing specialists or a general lack of expertise for specific groups, they are still likely to represent significant diversity. For the 367 undescribed taxa, the majority represent geographically isolated monophyletic lineages, based on molecular studies, reflecting long-term isolated populations that are likely to be equivalent to distinct species, especially for crustaceans, such as parabathynellids (Guzik *et al.* 2008), amphipods (Finston and Johnson 2004; Cooper *et al.* 2007; Finston *et al.* 2007) and isopods (Cooper *et al.* 2008). Based on the data presented in Table 1, we predict for the stygofauna that copepods, isopods and beetles are the most poorly known groups, with less than 20% described species, followed by gastropods and amphipods, and for the troglifauna, hexapods (comprising mostly Collembola, Coleoptera, Blattodea and Hemiptera) are the least known relative to the number predicted. The beetles are interesting here because, despite rigorous taxonomic work on this group, the majority of newly discovered taxa remain undescribed or undiscovered.

Much of the subterranean faunal diversity has been identified from the Yilgarn and Pilbara regions (Fig. 2), largely due to the sustained research efforts of several groups over the last decade, in addition to the numerous EIAs fuelled by Australia's mineral exploration boom (Eberhard *et al.* 2009). Geologically, the Pilbara and Yilgarn cratons of WA comprise the Western Shield, an area that has been continually emergent since the Proterozoic (Humphreys 1999, 2001) (Fig. 1). Suggestive of an ancient and remnant fauna, the aquifers of the Pilbara and Yilgarn contain an extraordinarily diverse stygofauna (Humphreys 2006) that largely appear unrelated to each other. Alternatively, troglifauna are better known in the Pilbara, with extensive sampling of fractured rock and pisolites associated with mining surveys revealing high faunal diversity. In the Yilgarn, troglifauna are comparatively poorly sampled but diversity is expected to be high especially in karstic calcretes.

It is likely that our species richness values are considerably underestimated in both the Yilgarn and Pilbara but we consider it useful to provide an estimate based on the current state of knowledge and the overall conclusion that the western half of Australia represents a hotspot for subterranean faunal diversity. A survey of SA aquifers (2007–10) by Leys revealed stygobitic species in more than 200 localities across the Flinders Ranges (fractured rocks, springs and alluvia), Eyre Peninsula (limestone), Lofty Ranges (fractured rocks, springs and alluvia) and the south-east (limestone). The subterranean faunal diversity in SA appears to be lower than that of WA, however numerous taxa are yet to be worked through (e.g. Ostracoda, Gastropoda (Hydrobiidae), Turbellaria and Oligochaeta).

Australia-wide projections

Our estimate of 4140 species in the western half of Australia is a substantially higher figure than that postulated by Humphreys (2008). In that study, 560 stygofauna species were estimated from the Western Shield and this area comprises ~50% of the area examined in this study, thus clearly representing an underestimate of species richness based on the data presented here. Just for the Pilbara region, which represents an even smaller area of the Western Shield, Eberhard *et al.* (2009) estimated 500–550 undescribed species using species accumulation curves. Our results show that much of the subterranean taxa in the western half of Australia remain undiscovered and the potential for new species discovery is extremely high. In the event of broader investigations of Australia's subterranean regions, besides caves and karst, several specific areas of Australia would benefit from a targeted approach. In particular, research on four alluvial systems in eastern Australia has uncovered a substantial fauna (Hancock and Boulton 2008; Tomlinson 2009; Camacho and Hancock 2010) indicating that a rich stygofauna occurs in eastern alluvial habitats. In particular, different river catchments have revealed distinct faunas offering a tantalising insight into potential diversity in this region. Arid regions of the Northern Territory and central Queensland, particularly in limestone areas, are also likely to harbour rich stygofaunas similar to those of the Yilgarn in WA. Additional taxa are likely to be found in SA, particular in springs and alluvia of less studied areas such as the Yorke Peninsula, southern Flinders Ranges and the Lofty Ranges. Temperate south-eastern Australia has already revealed significant diversity of subterranean fauna, predominantly collected from limestone caves (Hunt 1990; Eberhard *et al.* 1991; Eberhard 1996; Thurgate *et al.* 2001a, 2001b; Ponder *et al.* 2005; Rix *et al.* 2008) suggesting that Tasmania, Victoria and southern NSW would benefit from additional sampling effort in non-limestone terrains. In particular the Great Dividing Range and surrounds would be of interest.

The predicted origins of this diversity

Australia represents an ancient landscape and some of the subterranean habitats that we focus on here have survived throughout the formation and dissolution of Pangaea and the subsequent fragmentation of Gondwana. Indeed, some of the oldest known cave soils are found at Jenolan Caves, NSW, and

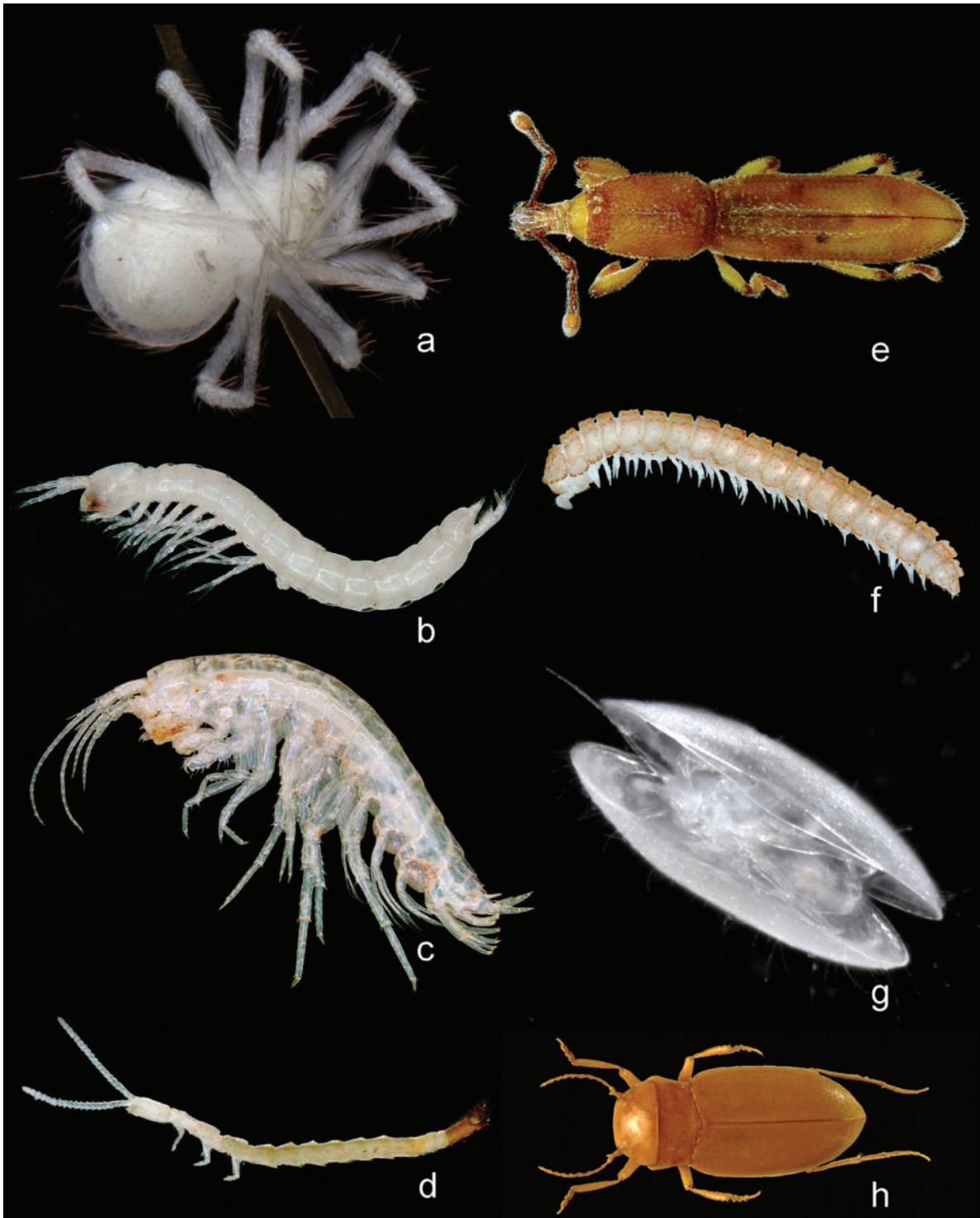


Fig. 2. Examples of subterranean invertebrates from Western Australia. (a) Troglobitic spider, unknown genus and species (Araneae: Theridiidae) from the Pilbara; (b) stygobitic parabathynellid, *Atopobathynella* sp. (Syncarida: Parabathynellidae) from the Pilbara; (c) stygobitic amphipod, unknown genus and species (Amphipoda: Paramelitidae) from the Pilbara; (d) troglobitic dipluran, unknown genus and species (Hexapoda: Diplura: Parajapygidae) from the Pilbara; (e) troglobitic beetle, unknown genus and species (Hexapoda: Coleoptera: Curculionidae) from the Pilbara; (f) troglobitic millipede, unknown genus and species (Diplopoda: Doratodesmidae) from the Pilbara; (g) stygobitic ostracod, *Meridiescandona lucerna* Karanovic (Ostracoda: Candonidae) from the Pilbara; (h) stygobitic beetle, *Paroster plutonicensis* (Watts and Humphreys 2003) (Hexapoda: Coleoptera: Dytiscidae) from the Yilgarn. (Photos by Giulia Perina (a–g) and Kate Muirhead (b–f), Subterranean Ecology Pty Ltd (www.subterraneanecology.com.au) (Copyright); photo h by Chris Watts.)

have been dated to the Devonian 375 million years ago (Mya; Osborne *et al.* 2006), and in the Kimberley, caves were formed from ancient Devonian reefs beneath the Permian ice sheet (Playford 2009). The full breadth of subterranean ecosystems exists in Australia, in contrast to other parts of the world where only one or two ecosystem types are typically found. Australia has a variety of water types including anchialine, saline and freshwater, as well as better known subterranean types such as karst and pseudokarst, alluvial, and fractured rock. These ecosystems provide links to other global regions and reflect a vicariant relictual fauna, especially the apparent ‘Tethyan connections’ of anchialine fauna of epicontinental regions (e.g. the highly charismatic remipede species *Lasionectes exleyi* Yager and Humphreys 1996). Also providing links are isolated seamounts (Namiotko *et al.* 2004; Humphreys 2008) and Gondwanan lineages (Poore and Humphreys 1998) although the Tethyan origin of some anchialine faunal elements may be uncertain (Karanovic and Eberhard 2009). As discussed elsewhere (Humphreys 2008), subterranean ecosystems may be very persistent through geological time and many lineages probably have ancient origins (Cho *et al.* 2006b; Wilson 2008).

In the Yilgarn and Pilbara regions a myriad of short-range endemic species, including both stygobitic (Taiti and Humphreys 2001; Leys *et al.* 2003; Leys and Watts 2008; Page *et al.* 2008; Guzik *et al.* 2009; Bradford *et al.* 2010) and troglotic (Humphreys and Adams 2001; Harvey *et al.* 2008) taxa have been identified. Much of this diversity is likely to have resulted from vicariance associated with the aridification of the Australian continent after the late Miocene (Byrne *et al.* 2008), which led to biotic isolation of calcretes and other subterranean habitats (e.g. pisolithic iron ore mesas in the Pilbara). Colonisation of these habitats by multiple unrelated surface species has also contributed to the high levels of diversity (Leys *et al.* 2003; Cooper *et al.* 2008; Guzik *et al.* 2008). Further, *in situ* speciation within aquifers is also considered a plausible source of species diversity, particularly in the Yilgarn (Guzik *et al.* 2009; Juan *et al.* 2010) and Pilbara (Finston *et al.* 2009). Abiotic heterogeneity within habitats (i.e. salinity clines, temperature variation and water level fluctuations) has been noted as possible sources of ecological variation and niche partitioning.

What is found in the rest of the world?

Regional assessments of the diversity of subterranean faunas have predominantly been conducted in the best studied locations, particularly North America and Europe. In the USA, 973 obligate subterranean species and subspecies were recorded by Culver *et al.* (2000), comprising 673 terrestrial species and 269 aquatic species. More than 650 stygobitic species have been recorded from the longest and most intensively researched region, the Balkan Peninsula, where the first stygal animal was described in 1768, and from where 975 species of troglifauna have been recorded (Sket *et al.* 2004). Slovenia, a key cave region in Europe, has 114 known stygobitic species (Culver and White 2004), while six other European countries (Belgium, France, Italy, Portugal, Slovenia, Spain (Malard *et al.* 2009; Michel *et al.* 2009)) have recorded 1059 stygobitic taxa with no more than 80 species from any one karst region. Most of these taxa are considered remnants of the Pleistocene, during which

time cave populations were colonised during interglacial cycles, and isolated during glacial periods (Peck 1984; Peck and Christiansen 1990; Culver *et al.* 2006). However, this is likely not the sole source of species origins with pre-Pleistocene processes being well recognised (Hedin 1997; Buhay and Crandall 2005; Buhay *et al.* 2007). Culver *et al.* (2006) predicted that other regions of interest for cave fauna in the northern hemisphere are likely to include the Eurasian continent including Georgia and Kyrgyzstan. Alternatively, the southern hemisphere subterranean fauna are well documented for New Zealand, where 102 described species are known from groundwater habitats, particular Hydracarina (70 species) and crustacean groups such as Amphipoda (four species), Isopoda (four species), and Syncarida (seven species) (Scarsbrook *et al.* 2003). South and Central America have also been recognised to maintain novel cave fauna but which are under threat from deforestation. In particular, Brazil (Trajano 2000), Ecuador (Peck 1990), Mexico (Desutter-Grandcolas 1993), and several Caribbean islands (Peck 1974, 1999) have also yielded new cave fauna.

Possible subterranean biodiversity hotspots elsewhere in the world

Based on geology we expect that Africa and India may yield similar subterranean biodiversity hotspots to those described here for Australia. There are established links with Australia for some stygal lineages from India (Phreatoicoidea (Wilson 2008); *Atopobathynella* (Cho *et al.* 2006b)), Africa (Phreatoicoidea (Wilson and Keable 1999)), and more widely with Gondwana (Candoninae (Karanovic 2004, 2005a, 2005b); Spelaeogriphacea (Poore and Humphreys 1998, 2003)). Further these Gondwanan links between the major continents (e.g. the ‘cosmopolitan’ Bathynellacea (Lopretto and Morrone 1998)) are likely to be an indicator of new regions of subterranean faunal significance. To date, Africa remains largely unexplored, apart from the Mediterranean north coast and Atlas Mountains. While Botswana (Modisi 1983) and Namibia (Irish 1991; Christelis and Struckmeier 2001) are considered possible locations that may harbour an undocumented diversity of stygofauna, southern Africa as a whole is a likely subterranean hotspot, as similar geology, karst and calcrete aquifers to those observed in WA exist there (Pickford *et al.* 1999). South Africa has the endemic subterranean amphipod family Sternophysingidae (Tasaki 2006), within the globally distributed superfamily Crangonyctoidea (Holsinger 1992) and the order Spelaeogriphacea (Sharratt *et al.* 2000). The Spelaeogriphacea are only known from two other locations in the world (Brazil and Australia), indicating a shared Gondwanan distribution (Jaume 2008). In South America, the best characterised caves are in central Brazil and include the Serra do Ramalho karst area in Bahia state, well known for its populations of the troglomorphic catfish *Rhamdia enfiurnada* Bichuette & Trajano, 2005 (e.g. Mattox *et al.* 2008), and Minas Gerais state, which is well known for its troglotic invertebrate fauna (Ferreira and Horta 2001; Souza and Ferreira 2010). Future work would benefit from assessment of the geology and current literature of these continents as indicators of possible new areas of rich biodiversity.

Conclusion

Here we identify the western part of the Australian continent as a region of extremely rich biodiversity for subterranean fauna with a projected 4140 stygobitic and troglobitic species; a significant subterranean fauna is also likely to occur across the eastern part of the continent, but considerable survey work is required to estimate the diversity of this fauna. Compared with other regions of the world, we consider the Australian subterranean fauna to be unique in its diversity for three key reasons: (1) the range and diversity of subterranean habitats where fauna have been discovered are both extensive and novel compared with the northern hemisphere; (2) direct faunal links to Gondwana are found in Australia's west, emphasising its early biogeographic history; and (3) tertiary events, particularly developing aridity in the late Miocene/Pliocene (14–2 Mya), appear to have dominated the diversification of Australia's subterranean fauna, unlike much of the northern hemisphere (Stoch and Galassi 2010), where the fauna was not greatly modified during Pleistocene glaciations.

Order of authorship

MTG, ADA, SJBC, MSH and WFH all contributed to writing the manuscript and collating the taxonomic, geographical and species richness data. The remaining authors, listed in alphabetical order, contributed data and ideas during a workshop in Darwin in 2009 (see 'Acknowledgements') and during the writing of the manuscript. Images were kindly contributed by SME.

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