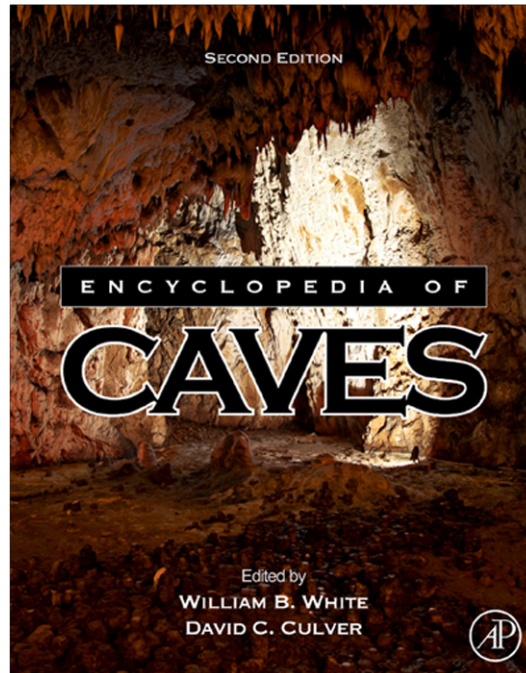


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DIVERSITY PATTERNS IN AUSTRALIA

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INTRODUCTION

The diversity of subterranean fauna in Australia, and tropical areas worldwide, has not long been recognized. Until recent decades, Australia was thought to be deficient in overtly cave-adapted (troglomorphic) animals. This circumstance was considered to have resulted from a number of causes: (1) the relative sparseness of carbonate rocks in Australia, as found in other Gondwanan fragments, compared with the world average (Fig. 1); (2) the general aridity of the

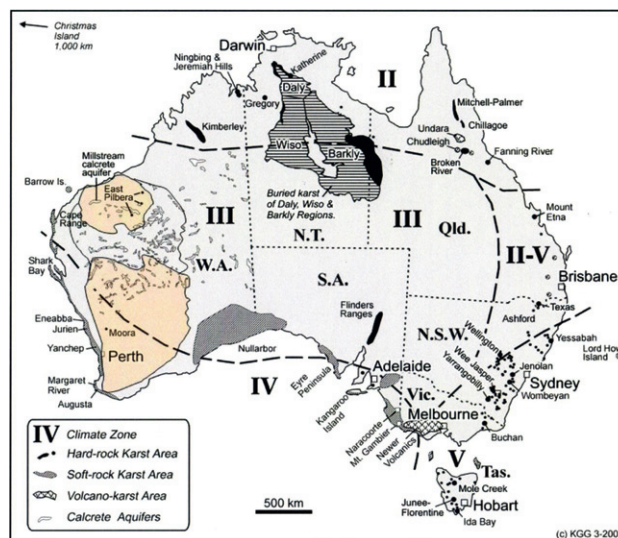


FIGURE 1 Karst areas of Australia and the bioclimatic zones: II, tropical; III, subtropical dry; IV, transitional zone with winter rain; V, warm temperate; II–IV warm temperate/tropical transition zone. The two pink areas within the common outline represent the Pilbara (north) and Yilgarn (south) cratons and their associated orogens that together comprise the western shield. After Hamilton-Smith and Eberhard, 2000. Graphic by K. G. Grimes, modified.

continent—it is the most arid inhabited continent, two-thirds of which receives less than 500 mm of rain annually—generally resulting in both dry caves and low input of food energy into the underground voids; (3) the global lack of cave-adapted animals in tropical areas; and (4) the lack of widespread and repeated glaciations, which was perceived to be the main factor driving the evolution of trogllobites in the Northern Hemisphere, then the focus of research on subterranean animals. Concomitantly, in Australia there was perceived to be a high proportion of animals found only in caves but not specialized for cave life, that is, lacking overt troglomorphisms. Although not articulated, these arguments would have applied also to stygofauna, the inhabitants of underground waters in both karstic and alluvial aquifers.

Understanding the biogeography of an area is reliant on having a broad spatial and taxonomic sample of the biota, a comprehensive taxonomy, a well-developed systematic and paleoclimate framework, and a fully developed geographical understanding (especially of paleodrainage and plate tectonics). There are serious deficiencies in information on most of these fields of endeavor in Australia. The taxonomic and systematic framework is very patchy and many groups of interest to hypogean questions remain largely unstudied (e.g., Thysanura, Collembola, Diplura, Oligochaeta), or are just beginning to be studied, so it is still too early for them to contribute in detail to biogeographical understanding (e.g., many higher taxa in Oligochaeta,

Copepoda, Ostracoda, Amphipoda, Diplura, Gastropoda). Hence, the focus here will be on some higher taxa for which there is more adequate information, and on some systems, such as the groundwater inhabitants of the smaller voids (mesovoids), for which there is a useful body of data.

During the last two decades of the twentieth century, more focused, as well as more widespread, exploration of caves (Humphreys 2000; Eberhard and Humphreys 2003) and later, in the third millennium, groundwater and nonkarst substrates, has shown that the Australian tropics and arid zones contain especially rich subterranean faunas (Humphreys and Harvey 2001; Austin *et al.*, 2008). However, no area of Australia has been well studied for its hypogean life, the distribution of effort has been very uneven across the country, and many areas remain effectively unexplored for subterranean fauna. Detailed examination of subterranean biology in Australia is sparse and studies have been largely restricted to faunal surveys. Prominent karst areas, such as the Barkley and Wiso regions, have barely been examined because of their remoteness from population centers. Other remote areas, such as the Nullarbor, in which there has been a long history of cave research, have proved to have sparse hypogean assemblages, especially among the stygofauna, but interesting occurrences of the misophrioid copepod *Speleophria*, and heavily sclerotized troglobitic species such as the cockroach *Trogloblatella* and the mygalomorph spider *Troglo diplura* which has South American affinities, and very diverse chemoautotrophic microbial communities form mantles in the saline groundwater (Holmes *et al.*, 2001). Even within those relatively well-surveyed areas, the taxonomic effort is seriously underdeveloped. For example, in one compilation, 63% of the stygofauna from New South Wales was undescribed. Where species have been described, there are many oddities, not yet well placed within their lineage and thus contributing poorly to understanding the biogeography of the Australian hypogean biota. The main knowledge base and most active research are from the western shield and South Australia.

GEOGRAPHIC FACTORS

In contrast to the widespread glaciation that directly influenced many of the classical karst areas in the Northern Hemisphere, Australia has not been subjected to extensive glaciation since the Permian. The biogeography of the hypogean fauna of Australia has been influenced by the continent's past connections with Pangaea and Gondwana, as well as having formed the eastern seaboard of the Tethys Ocean during the Mesozoic. Australia is a fragment of

Gondwana together with Africa, India, Madagascar, South America, and Antarctica. Gondwana itself fragmented and Eastern Gondwana (India, Antarctica, and Australasia) became isolated from South America and Africa by 133 million years ago. By the Upper Cretaceous (*ca.* 80 million years ago), Australia was joined only to Antarctica and it formed the eastern seaboard of Tethys. These lands shared a Gondwanan flora and fauna, and when the final separation between them occurred (45 million years ago), both lands were well watered and supported cool temperate and subtropical forests.

The separation of Australia from Antarctica, and its subsequent rapid northward drift toward Southeast Asia, has been the most significant factor that has shaped the Australian subterranean fauna in the Tertiary. It resulted in the formation of the Southern Ocean seaway that led to the development of the circum-Antarctic Ocean winds and currents that markedly altered the climate of the Southern Hemisphere, causing Australia to become much drier. The formation of the Antarctic ice cap 15 million years ago saw the beginning of a series of marked climatic fluctuations that have greatly stressed the Australian (and other Gondwanan) flora and fauna. Warm and wet interglacial periods alternated with very dry, cool, and windy glacial stages, but only a small area of the Eastern Highlands and Tasmania were subject to extensive ice cover. These cyclic fluctuations, superimposed on a generally increasing and spreading aridity, provided conditions under which subterranean refugia played an important role. Most of the detailed molecular phylogenetic studies of Australian subterranean fauna indicate an origin of subterranean species associated with this developing aridity.

Shield Regions and the Cretaceous Marine Transgressions

Australia has several major shield regions—parts of the Earth's crust little deformed for a prolonged period—that have been emergent since the Paleozoic. The largest is the *western shield*, which includes the Pilbara and Yilgarn cratons and associated orogens (Fig. 1). These stable, truly continental areas of Australia have a nonmarine, presumably freshwater history extending through several geological eras. The Cretaceous marine inundation, at *circa* 120 Ma BP, would have eliminated nonmarine life in the submerged areas (Fig. 2) and only 56% of the current land area of the continent remained above sea level. This has important implications for lineages with poor dispersal ability, as is typical of subterranean fauna. The distribution of ancient lineages, both epigeal and subterranean, may be expected to reflect this marine incursion in two

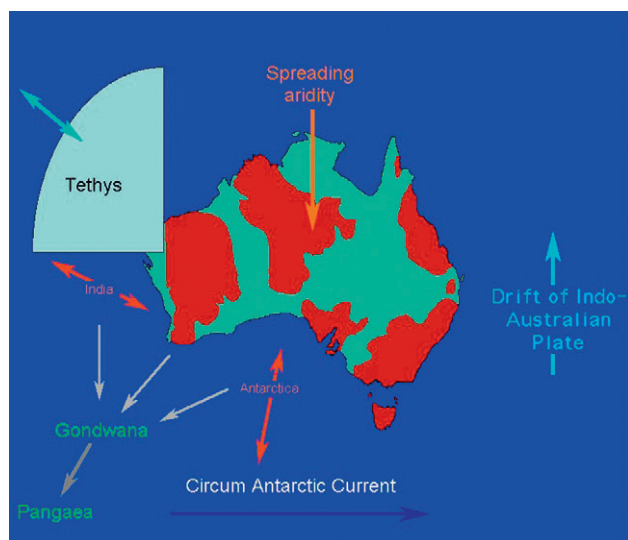


FIGURE 2 Deep history events that have influenced the biogeography of Australian subterranean faunas (see text). The shaded continental areas have not been covered by the oceans since the Paleozoic.

ways. First, ancient terrestrial and freshwater lineages may have survived on these continually emergent landmasses. Second, marine ancestors may have become stranded along the shores as the Cretaceous seas retreated and today may be represented as relictual marine lineages now far inland.

Caves and other subterranean habitats can remain as relatively stable environments over long periods of time because they are well insulated from the climatic perturbations that profoundly affect surface environments and surface animals. There, a number of ancient geographical and phylogenetic relictual groups have survived (Spelaeogriphacea, Remipedia, Thermosbaenacea, etc.) (Fig. 3). Owing to their limited potential for dispersal, their present distributions may contain a great deal of information about past geography and climates. The ghost of Cretaceous and earlier marine transgressions is probably reflected in the distribution of Phreatoicidea, an ancient group of isopods, in both their epigeal and subterranean forms, the latter being restricted to the tropics, and it has been well documented in the crangonyctoid amphipods (see Box 1).

In this respect aquatic subterranean faunas hold a special significance because, unlike terrestrial troglobionts (troglobites), the aquatic troglobiont (stygo-bites) fauna contain many relict species that are only distantly related to surface forms. These lineages provide the most compelling evidence that the distribution of some relict fauna occurred through rafting on tectonic plates moved by seafloor spreading. Recently a number of notable discoveries of such relict fauna have been made in Australia whose geographical

distribution and lifestyles suggest origins variously in Pangaea, Gondwana, Eastern Gondwana, and Tethys.

Cave Atmosphere

The latitudinal position and general aridity of Australia make cave atmosphere a significant biogeographic determinant in Australia. Cave environments have traditionally been separated into different zones—the entrance, twilight, transition, and deep zones—with characteristics related to the remoteness from the surface environment, such as more stable temperature and humidity and reduced light and food energy input. On the basis of research in the Undara lava tube, Howarth and Stone (1990) developed the concept of a fifth zone, the *stagnant-air zone*, which is characterized by elevated carbon dioxide and depressed oxygen levels. Only in such areas were highly troglomorphic species found in cave passages. However, in other tropical areas, such as arid Cape Range, highly troglomorphic species occur in caves that have unremarkable concentrations of oxygen and carbon dioxide, some even occurring in sunlight near cave entrances, but only where the air is saturated, or nearly saturated, with water vapor.

Howarth (1987) also addressed the importance of water content in the cave atmosphere, largely from his Australian studies. Both tropical and temperate cave systems lose water when the outside air temperature (strictly, the outside water vapor pressure) drops below that in the cave. In the tropics, where average seasonal temperature differences are less than in temperate regions, caves tend to be warmer than the surface air at night and cooler during the day. Even if both air masses are saturated with water, the cave will tend to dry out as water vapor leaves the cave along the vapor pressure gradient—the so-called *tropical winter effect*.

Owing to widespread aridity, this concept has particular relevance to Australia and also in tropical areas where the general form of many caves (giant grikes, small and shallow caves) and/or low subterranean water supply make them vulnerable to drying. Within this context the extent of the deeper cave zones (transition and deep) will fluctuate as the boundary of threshold humidity levels migrates with the changing atmospheric conditions farther into or out of the cave. Such changes occur in ecological time, associated with daily and seasonal fluctuations in air density and humidity, and through evolutionary time, in response to climatic cycles and long-term climatic trends. Such changes should have little effect on groundwater or on troglobites in deep caves, which are extensive enough

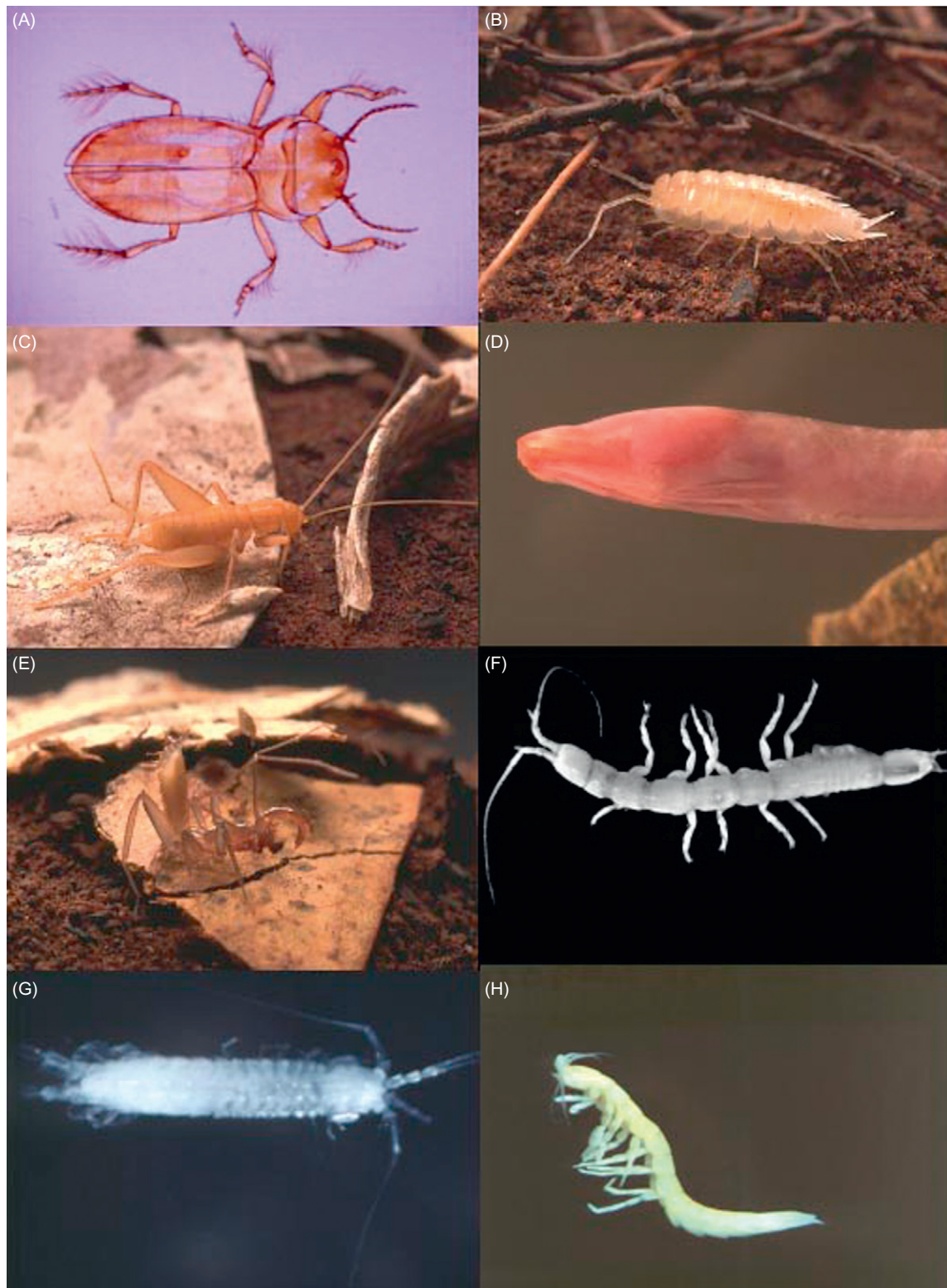


FIGURE 3 Subterranean animals: (A) *Limbodessus eberhardi* (Dytiscidae), one of 100 species of blind diving beetles from calcrete aquifers in the Australian arid zone; (B) unnamed blind philosciid isopod; (C) *Ngamarlanguia luisae* (Gryllidae: Nemobiinae) from Cape Range, the only troglitic cricket in Australia; (D) head of *Ophisternon candidum* (Synbranchiformes), one of two Australian cavefish; (E) *Draculoides vinei* (Schizomida), one of seven species of microwhip scorpions known from Cape Range; (F) the phreatoicid isopod *Phreatoicoides gracilis*; (G) *Mangkurto mityula* (Spelaeogriphacea), a subterranean family that is known from only four species, two in Australia, and Africa and Brazil; (H) *Pygolabis humphreysi*, from Ethel Gorge calcrete, belongs to a family of flabelliferan isopods, the Tainisopidae, known only from groundwater in the Kimberley and Pilbara regions of Western Australia. Photographs (B–E) Douglas Elford, Western Australian Museum; (A and G) William Humphreys, former from a painting by Elyse O’Grady; and (F and H) GDF Wilson, Australian Museum.

BOX 1

AMPHIPODS

Australia is a major center of amphipod diversity and much of this diversity is represented by stygobitic species. In a checklist of the Australian inland aquatic amphipods, Bradbury and Williams (1999) reported 74 species belonging to nine different families, of which 29 species in five families were reported from subterranean waters. Ten years later the number of stygobitic amphipod species has significantly increased, particularly because of systematic surveys in the Pilbara and Yilgarn region of Western Australia and various regions in South Australia. The data provided here are based on taxonomic descriptions and on (partly unpublished) molecular assessments. At present, there is evidence for more than 144 stygobitic amphipod species: more than 37 species (8 genera) in the Paramelitidae; more than 24 species (9 genera of which 3 are undescribed) in the Neoniphargidae; more than 51 species (several undescribed genera) in the Chiltoniidae; more than 30 species (4 genera) in the Melitidae; and 4 species (2 genera) in the Bogidiellidae. An interesting pattern of amphipod distribution and diversity is emerging. The majority of the species have distributions that are restricted to individual aquifers or tributaries, as is expected for taxa that are confined to groundwater and that have low dispersal

abilities. Much of the diversity is occurring in groundwaters of the arid region. Whereas some families appear to be restricted to the temperate southeast and southwest of the continent (Neoniphargidae), others are much more widespread and encompass parts of the arid zone (Chiltoniidae, Melitidae, Paramelitidae) and tropical areas (Melitidae, Paramelitidae). Some families are more restricted, such as the Bogidiellidae, which are known only from coastal (anchihaline) habitats in the Cape Range and Barrow Island of Western Australia and Eyre Peninsula of South Australia. Notably, while taxa in southern areas comprise both stygobitic and epigeal species, northern taxa, in the arid tropics and subtropics, comprise only stygobitic taxa.

Speciation and adaptation to subterranean habitats probably involved marine transgressions in the context of the Melitidae and Bogidiellidae because species in these families are all found near present or historical shorelines. The evolution of the stygobitic species in the Paramelitidae, Neoniphargidae, and Chiltoniidae, which occur predominantly in the areas that were not inundated by the high sea level stand in the Cretaceous, probably was driven by aridification, forcing epigeal freshwater species to seek refuge in subterranean habitats.

to contain the entire change. But, in the shallow caves common in the Australian tropics, such changes are likely to cause large areas of cave systems to dry out. Such processes may lead to the extinction of certain cave fauna, or impede movement through the epikarst and thus could promote speciation between different karst areas. The high diversity of Schizomida in the Pilbara and Cape Range, and of the paradoxosomatid millipede *Stygiochiropus* in arid Cape Range, are candidates for such analysis.

Humid caves within the arid zone have permitted the survival of a diverse troglobitic fauna in arid Cape Range, the affinities of which lie with the inhabitants on the floor of the rainforest, both temperate and tropical, habitats now thousands of kilometers distant. While the fauna is now geographically relict, the driving force resulting in the initial invasion of the caves is unknown—species may have established in caves coincident with the onset of aridity to escape the surface drying, or they may have established in caves seeking resources unrelated to the onset of aridity. This question cannot be resolved for Cape Range because the aridity has been sufficiently intense to extirpate

entirely close relatives at the surface. Other tropical areas, such as North Queensland, offer greater prospect of resolving such issues because contemporary lineages occur with surface and cavernicolous species exhibiting various degrees of troglomorphy. However, the recent finding of diverse troglobiont communities also throughout the arid western shield supports the hypothesis that aridity has driven the fauna to seek more humid habitat underground and where it has evolved troglomorphic traits, because the lineages to which they belong are not commonly subterranean in more humid regions with suitable subterranean voids.

Another area where a resolution of the causes of colonization of the hypogean environment may be resolved is in the groundwater calcrete deposits (see Box 2) in the arid zone. There, many different lineages of diving beetles (Dytiscidae) have invaded the groundwater and become eyeless and flightless (Fig. 3). Each calcrete body has a unique dytiscid assemblage, there is no overlap in species between different calcretes, and speciation appeared to have taken place *in situ* because multiple species (1 to 4 of different sizes in many cases being sister species) are common among the 100 stygal

BOX 2

GROUNDWATER CALCRETES

The long period of emergence and the ensuing erosion down to the Archaean basement has resulted in classical karst terrain being absent from the western shield. However, thin carbonate deposits are widespread throughout the arid zone and are well developed as groundwater (valley) calcretes (hereafter termed *calcrete*) which occur widely in Australia but in isolated, though sometimes extensive, pockets usually associated with paleodrainage lines (Fig. 5). Calcretes are carbonate deposits forming from groundwater near the water table in arid lands as a result of concentration processes by near-surface evaporation. They form immediately upstream of salt lakes (playas), chains of which form a prominent part of the landscape in the more arid parts of Australia. The playas, which reflect the groundwater base level, are the surface manifestation of paleodrainage channels incised into Precambrian basement rocks by rivers that largely stopped flowing when the climate changed from humid to arid in the Paleocene. Hence, the paleovalleys predate the fragmentation of Gondwana.

Calcretes are especially important in the Australian context as they form in arid climates (annual rainfall <200 mm) with high potential evaporation (>3000 mm per year). Although quite thin (10–20 m thick) the groundwater calcretes often develop typical karst features and within them easy movement of groundwater reflecting open conduits. Groundwater salinity may vary

markedly owing to the episodic recharge characteristic of the arid zone (Humphreys 1999, 2001) and the calcrete aquifers have been described as subterranean estuaries (Humphreys *et al.*, 2009).

Because they are deposited at intervals from the groundwater flow, the calcrete masses are separated by habitat that is unsuitable for stygofauna, namely, Tertiary valley-fills, largely clays, and salt lakes. Consequently, they form isolated karst areas along the numerous major paleovalleys, some of which may date from the Permian. The sediments filling the paleochannels are mostly Eocene or later but the age of the calcretes is poorly defined. The extensive alluvial fan calcretes and some of the river valley calcretes formed in the Oligocene (37–30 Ma BP) may have followed the onset of the continental aridity. Many of the calcrete areas, especially those north of 31°S, are being actively deposited and the others have probably been remobilized and redeposited, attributes that make the dating of calcrete deposits using standard radiometric methods problematic. However, molecular phylogenies of the diverse diving beetle, oniscidean isopod, parabathynellid, and amphipod faunas, the numerous species of which are each restricted to a single major calcrete area or paleodrainage tributary (*e.g.*, Leys *et al.*, 2003; Finston *et al.*, 2007; Guzik *et al.*, 2009), indicate that the calcretes have been present for at least 5–8 million years.

species in the arid zone. Molecular studies suggest that numerous lineages invaded the calcrete aquifers during the constrained time period (8–4 Ma BP), which suggests that it occurred in response to a widespread factor, such as might be expected from spreading aridity.

Within the third millennium there has been a recognition that nonkarst and nonalluvial substrates, such as pisolites and fractured rocks, support extremely diverse subterranean faunas in both aquatic and terrestrial habitats, particularly in the western shield region of Western Australia. This recognition has resulted from the requirement in Western Australia to include subterranean fauna as a component of environmental assessment for major mining projects in this mineraliferous region. At a local scale this troglobiont diversity is comparable to that found in the richest karst areas, such as Bayliss Cave in Queensland. Regionally, consultancy companies report between 150 and 300 troglobiont species from their projects within the 220,000 km² Pilbara region, about the same size as the massive Nullarbor

karst of southern Australia where 27 troglobiont species are known. The proportion of species in common to the consultancy companies is currently unknown but is likely to be low, as many troglobiont species occupy small geographic areas.

Energy Supply

Energy enters subterranean systems largely mediated by water, but also by animals and plant roots. Because these elements themselves are not uniformly distributed across Australia they have the potential to influence Australian cave biogeography. The carriage of organic matter in surface water is strongly affected by seasonal rainfall and plant growth. The episodic rainfall, characteristic of the arid zone, means that some areas potentially have unpredictable energy supplies. Evaporation greatly exceeds rainfall in arid zones and groundwater recharge—which carries

dissolved organic matter, the predominant energy supply in subterranean waters—occurs only following episodic large rainfalls, sometimes years apart.

Plants provide the raw material that is transported by water into the subterranean realm, but they also directly transport energy into hypogean habitats by means of sap transport within the roots and by root growth to depths of up to 76 m. Roots, especially tree roots, are an important and reliable source of energy for troglobitic cixiid and meenoplid fulgoroid Homoptera. These occur in the lava tubes of tropical North Queensland and similar fauna are found in karst across the tropics, into the Kimberley and down the arid west coast, to the south of Cape Range. They are also found on roots in calcrete, pisolite, and fractured rock substrates on the western shield. Tree roots are also utilized by cockroaches throughout the country (*e.g.*, in the Nullarbor, *Troglobatella nullarborensis*).

Tree root mats also represent a reliable food supply for elements of the rich communities of aquatic invertebrates, including some exhibiting troglomorphisms, occurring in some shallow stream caves of Western Australia. They provide habitat, and probably food, for stygofauna in the Nullarbor, in calcrete aquifers of the western shield, and in anchihaline caves in Cape Range and Christmas Island where they are associated with a diverse fauna largely comprising crustaceans.

Roots, like guano, often provide copious quantities of energy to cave communities, which may be quite diverse. Roots in the Undara lava tube, Queensland, and the Tamala Limestone of Western Australia, support diverse cave communities. However, whereas the former contain numerous highly troglomorphic species, the latter has few stygomorphic species, many being indistinguishable for surface species. Superficial subterranean systems are often supported by roots but to what extent is unknown, as, for example, the cave and groundwater faunas of groundwater calcretes in the arid zone.

Animals may transport energy into cave systems and deposit it there as excreta, exuvia, carcasses, and eggs. In Australia such troloxenic agents exhibit marked latitudinal differences. In the south, raphidophorid crickets are the most conspicuous troglloxenic agents, whereas bats, while not diverse, are locally abundant where they form breeding colonies. In the tropics bats are widespread, diverse, and important producers of guano, as, to a lesser degree, are swiftlets in more humid areas.

Guano is usually intermittently distributed in both space and time because it is dependent on the seasonal biology of the birds and bats. In consequence, the cave communities associated with guano are highly specialized and differ markedly from the cave

fauna not dependent on guano. Markedly troglomorphic species are not commonly found in the energy-rich, but temporally unstable, guano communities. However, immense populations of mites ($>100 \text{ cm}^{-2}$) are seasonally present and numerous, mostly rare, species (50+) may occur, occupying distinct parts of the cave system.

STYGOFAUNA AND CRUSTACEA

Stygofauna are discussed in the context of Crustacea, which comprise the overwhelming majority of stygofauna, but the Dytiscidae example above introduced the insect component.

The magnitude of the biodiversity present in subterranean waters globally has only recently been given prominence. Australia, especially the northwestern and southeastern parts, has unexpectedly come to the attention of stygobiologists and systematists on account of its diverse regional groundwater fauna (stygofauna). Recently, these have been determined to include a number of higher order taxa variously new to science (*i.e.*, the flabelliferan isopod family Tainisopidae from Kimberley and Pilbara), new to the Southern Hemisphere (Thermosbaenacea, Remipedia, Epacteriscidae), or new to Australia (Spelaeogriphacea, Pseudocyclopiidae). Many of these taxa occur near coastal and anchihaline waters and are widely interpreted as comprising a relictual tethyan fauna, although molecular phylogeographic support has yet to be demonstrated. Several of these lineages have congeneric species, which are known elsewhere only from subterranean waters on either side of the North Atlantic—the northern Caribbean region and the Balearic and Canary archipelagos (see [Box 3](#)).

Syncarida

The Syncarida are crustaceans now entirely of inland waters. The Anaspidacea are confined to Australia, New Zealand, and southern South America. In southeastern Australia they are often large and mostly surface living, although several stygomorphic species occur in cave streams and groundwater, and an undescribed family has been reported that is restricted to caves. In contrast, both families of Bathynellacea have a global distribution, often even at the generic level, and are widespread in Australia. *Bathynella* (Bathynellidae) is found from Victoria to the Kimberley and elsewhere the genus occurs globally. Genera within the Parabathynellidae known from Australia exhibit different regional affinities. *Chilibathynella* and *Atopobathynella* are known from

BOX 3

ANCHIHALINE HABITATS—TETHYAN RELICTS?

Anchihaline (or *anchialine*) habitats comprise near-coastal mixohaline waters, usually with little or no exposure to open air and always with more or less extensive subterranean connections to the sea. They typically show salinity stratification and may usefully be considered groundwater estuaries. They typically occur in volcanic or limestone bedrock and show noticeable marine as well as terrestrial influences. The water column is permanently stratified with a sharp thermohalocline separating a surface layer of fresh or brackish water from a warmer marine, oligoxic water mass occupying the deeper reaches. They have a significant amount of autochthonous primary production, via a sulfide-based chemoautotrophic bacterial flora, as well as receiving advected organic matter from adjacent marine or terrestrial epigeal ecosystems. Anchihaline habitats are mostly found in arid coastal areas and are circumglobally distributed in tropical/subtropical latitudes.

Anchihaline habitats support specialized subterranean fauna (Fig. 6), predominantly crustaceans representing biogeographic and/or phylogenetic relicts. These specialized anchihaline endemics are largely restricted to the oligoxic reaches of the water column below the thermohalocline. The structure of these assemblages is predictable, and, remarkably, however remote an anchihaline habitat, this predictability frequently extends to the generic composition.

In continental Australia, anchihaline systems occur adjacent to the North West Shelf (Cape Range and Barrow Island) and on Christmas Island (Indian Ocean), an isolated seamount 360 km south of Java but separated from it by the Java Trench.

Cape Range supports a fauna comprising atyids, thermosbaenaceans, hadziid amphipods, cirrolanid isopods, remipeds, thaumatocypridid ostracods (*Danielopolina*), and an array of copepods such as epacteriscid and pseudocyclopiid calanoids, and speleophriid misophrioids.

Some are the only known representatives of higher taxa in the Southern Hemisphere (Class Remipedia; Orders Thermosbaenacea, Misophrioida), and several genera are known elsewhere from anchihaline systems on either side of the North Atlantic (*Lasioneectes*, *Halosbaena*, *Speleophria*, *Danielopolina* (Fig. 6)) and the atyid *Stygiocaris* (Fig. 6) is closely related to the ampho-Atlantic genus *Typhlatya*. These obligate stygal lineages are thought to have poor capability or opportunities for dispersal, and this attribute, combined with their distributions which closely match areas covered by the sea in the late Mesozoic, suggest that their present distributions could have resulted by vicariance as a result of the movement of tectonic plates (Fig. 2).

Anchihaline systems on oceanic islands support a different group of fauna, but the structure of these assemblages is similarly predictable, even between oceans. Christmas Island is a seamount and supports an anchihaline fauna characterized by the stygobitic shrimp *Procaris* (Decapoda), which belongs to the primitive, highly aberrant family, Procarididae which appears globally to be restricted to anchihaline caves. This family has been reported elsewhere only from other isolated seamounts, namely, Bermuda and Ascension Island in the Atlantic Ocean, and Hawaii in the Pacific. In each case, as with Christmas Island, the procaridids are associated with alpheid, hippolytid, and atyid shrimp. These co-occurrences of two primitive and presumably ancient caridean families support the contention that crevicular habitats have served as faunal refuges for long periods of time. Recently, an endemic species of *Danielopolina* has been described from Christmas Island, the first juxtaposition of a member of the anchihaline faunas characteristic of epicontinental and seamount island anchihaline faunas. There is no coherent theory as to their distribution to remote seamounts such as Christmas Island.

Chile and southeastern Australia, while the latter is also found in India and throughout northwestern Australia, including Barrow Island and Cape Range, and the paleodrainage channels of the arid center. *Notobathynella* is found across Australia and New Zealand, while *Hexabathynella*, from the eastern Australian seaboard, has a more global distribution, being found in New Zealand, southern Europe, Madagascar, and South America. Endemic genera include *Kimberleybathynella* from the Kimberley,

Brevisomabathynella and *Billibathynella* from the western shield, and *Octobathynella* from New South Wales. As 30 described species are endemic to single calcrete masses the overall diversity is expected to be very high. Bathynellacea are small stygobites, mostly inhabitants of interstitial freshwater environments, although an undescribed genus of large, free-swimming parabathynellid occurs in water close to marine salinity (>30 000 mg L⁻¹ TDS) in the Carey paleodrainage systems of the arid zone, where it is associated with a

number of maritime copepod lineages such as Ameiridae (Harpacticoida) and *Halicyclops* (Cyclopoida).

Copepoda

Remarkably little work had been conducted on non-marine copepods in Australia until this millennium. Recent work on groundwater copepods, largely from groundwater calcretes of the western shield, and the near coastal, especially anchihaline systems of the northwest, has revealed higher taxa not previously described from Australia, in some cases even from the Southern Hemisphere.

Numerous species of copepods are being described from Australian groundwaters, largely from the western shield, including ten new genera of Cyclopoida and Harpacticoida, and several genera are reported for the first time from Australia [*Nitocrella* Ameiridae (Eurasia), *Parapseudoleptomesochra* Ameiridae (global), *Nitocrellopsis* Ameiridae (Mediterranean) *Haifameira* Ameiridae (depth of Mediterranean Sea), *Pseudectinosoma* Ectinosomatidae (Europe) and the family Parastenocarididae (Pangaea, freshwater)]. The broader distribution of these lineages within Australia awaits investigation but some of them have been found in tropical Queensland.

The occurrence of about 17 near-marine lineages (e.g., *Halicyclops*) in the center of the western shield alongside lineages considered to be ancient freshwater lineages (*Parastenocaris*: Parastenocarididae) is notable. It may reflect both the salinity stratified, often hypersaline groundwater in the more southerly paleodrainage systems, as well as the ancient origins of the fauna. Interestingly, *Halicyclops* is almost completely absent from marine interstitial in Australia, although it is the world's most speciose element in this habitat. It was probably replaced here by the genus *Neocyclops*, which is very diverse, testifying to an ancient invasion of inland waters by *Halicyclops*. *Mesocyclops* has a mostly tropical distribution; *Metacyclops* (*trispinosus* group) and *Goniocyclops* have an Eastern Gondwanan distribution; and the limits of the distributions of newly described genera of Ameiridae, Canthocamptidae, and Cyclopinae await confirmation.

Ostracoda

Ostracods recorded from Australian inland waters are mainly from the families Limnocytheridae, Ilyocypridae, and Cyprididae. In the Murchison, ostracods from the families Candonidae, Cyprididae, and Limnocytheridae have been recorded in open groundwater but stygophilic species occur only in the Limnocytheridae and Candonidae, the latter including the globally widespread genus *Candonopsis* (subfamily

Candoninae), which occurs widely and in a wide variety and age of substrates. Species are known from Pleistocene syngenetic dune karst (Tamala Limestone), several species from Tertiary (probably Miocene) groundwater calcretes on the western shield, and from the Kimberley (Devonian Reef Limestone). In Europe there are only a few, mostly hypogean species that are considered to be Tertiary relicts with surface relatives today occurring in tropical and subtropical surface waters; they are especially diverse in Africa. The subfamily Candoninae (family) Candonidae are common elements of stygofauna globally but recent finds from the Pilbara describe about 25% of the world's genera but these are more closely related to the South American and African Candoninae than to those of Europe.

The thaumatocypridid genus *Danielopolina*, previously unreported in the Southern Hemisphere, occurs as a tethyan element in the anchihaline system at Cape Range and on Christmas Island, Indian Ocean, an isolated seamount island where it occurs with the first living representative of *Microceratina* (Cytheruridae). Fossils in marine cave facies in the Czech Republic suggest that the former lineage already inhabited marine caves in the Jurassic.

In the five years to 2010 there was major progress in the describing and understanding of the subterranean ostracods from Australia. One of the hotspots of their diversity is the Pilbara region from where 86 species have been described belonging to 12 genera in the subfamily Candoninae. Only one of the species and one genus is not endemic to this region, while all the other species have a very limited distribution, comprising short-range endemics. The tribe Humphreyscandonini was described to accommodate eight Candoninae genera endemic to the Pilbara. This tribe shows some close similarities with the fossil, Tertiary fauna of the Northern Hemisphere. Other genera from this region have a clear Gondwanan connection, and even the genus *Candonopsis*, of the tribe Candonopsini, is here represented by a distinct lineage, and a separate subgenus. This subgenus is the only taxon connecting the Pilbara's candonins with those from the Kimberley and Murchison regions. Candoninae fauna from the Murchison is less rich, but also comprises only endemic species. Even though it has been quite thoroughly explored, the Murchison Candoninae comprises only five described species. East Australia also has a unique Candoninae fauna, but only one monotypic genus have been described from Queensland, while many more await description. The east Australian Candoninae belongs to the tribe Candonopsini and they are more closely connected with the South and Central American Candoninae than to the rest of Australia. Few taxa other than

Candoninae have been described from Australian subterranean waters, and most belong to the genus *Gomphodella* (family Limnocytheridae) and are endemic to the Pilbara and Murchison regions, and represent a very old lineage of freshwater ostracods. Most of the species are known from fossils, and some close relatives today live in the subterranean waters of the Balkan Peninsula, and ancient African Lakes. One species of the family Cyprididae has been described from the Kimberley region, but, as all the other Cyprididae species found in the wells and occasionally bores around Australia, probably represents only a stygophile, rather than a true stygobiont.

The western shield is considered to have been a single landmass continuously emergent from the sea since at least the Paleozoic. If this is the case then there is no clear hypothesis to account for the extraordinary disparity (Table 1) in the gross composition of the subterranean fauna between contiguous parts of the western shield, loosely termed the Pilbara (to the north) and the Yilgarn (to the south) and the associated orogens.

Isopoda

Phreatoicidan isopods (Fig. 3) have a Gondwanan distribution and occur widely across southern Australia (and in tropical Arnhem Land and the Kimberley) in surface habitats that have permanent water—surface expressions of groundwater—usually as cryptic epigean species. Their distribution is strongly associated with the areas of the continent not submerged by Cretaceous seas (see also Fig. 4). About 76 species in 30 genera are described from Australia, of which 10 species in 8 genera are hypogean (cavernicolous or spring emergents). They are under active

revision and numerous taxa are being described. Five hypogean species occur on the Precambrian western shield. 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). These occurrences suggest that Hypsimetopidae were hypogean prior to the separation of Greater Northern India from the western shore of Australia (ca. 130 My BP). *Crenisopus*, a stygobitic genus occurring in a sandstone aquifer in the Kimberley and another new species on Koolan Island off Western Australia, is a link between African and Australasian lineages of phreatoicidians. The genus is 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.

The family Cirolanidae with three species and two genera occurs on Cape Range, Barrow Island, and in the Pilbara of Western Australia. The family Tainisopidae, endemic to northwestern Australia, occurs in the exposed and greatly fragmented Devonian Reef system throughout the western Kimberley as well as in remote outcrops of this fossil reef in northeastern Kimberley. A second clade of this family (Fig. 3) with five described species inhabits groundwater calcretes in the Pilbara, from which the Kimberley was separated by the Cretaceous marine incursions. The location and distribution of this family is indicative of ancient marine origins. Recent cladistic analysis suggests that this family is related to the cosmopolitan marine Limnoriidae but at a basal level, suggesting

TABLE 1 The Distribution of the better known higher taxa of subterranean invertebrates between the adjacent Pilbara and Yilgarn regions on the Australian Western Shield that has been continuously emergent since the Paleozoic

Taxon	Pilbara	Yilgarn	% in Common
Candonine ostracod genera	13	1	8
Candonine ostracod species	58	5	0
Copepoda genera	43	30	4
Copepoda species	25	15	21
Spelaeogriphacea species	2	0	0
Tainisopidae species	5	0	0
Schizomida species	26	0	0
Dytiscidae species	0	89	0
Nocticolidae species	9	0	0

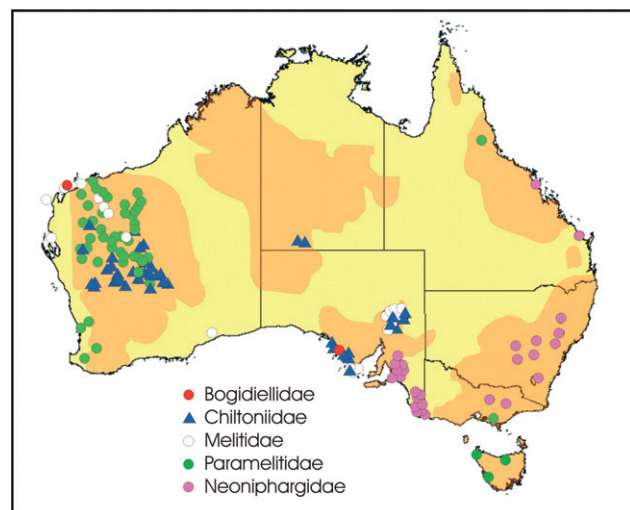


FIGURE 4 The distribution of subterranean amphipod families in relation to long emergent land areas (deeper shading) in Australia. Map by Remko Leijts.

the family is older than the more derived families like the Cirolanidae, which have an extensive Cretaceous fossil record. Among Asellota, the Janiridae occur widely across southern Australia and Tasmania and the genus *Heterias*, which also occurs in New Zealand, is likely to be highly speciose. Protojaniridae occur in the Northern Territory and this family has a Gondwanan distribution similar to the Phreatoicoidea.

Terrestrial isopods (Oniscidea) are a prominent component of cave fauna throughout Australia, as elsewhere in the world, yet there are few described highly troglomorphic Oniscidea (Fig. 3) and these are placed in the genera *Abebaioscia*, *Andricophiloscia*, and *Haloniscus* (Philosciidae), and *Troglarmadillo* (Armadillidae) that occur widely on the western shield. Numerous other troglobitic species are recognized belonging to the genera *Styloniscus* (Styloniscidae), an undescribed genus (Stenoniscidae), *Laevophiloscia* and *Haloniscus* (Philosciidae), *Hanoniscus* (Oniscidae), and *Buddelundia* and *Troglarmadillo* (Armadillidae). Their distribution

seems to reflect the general aridity that developed following the separation of Australia from Antarctica, rather than to suggest more ancient relictual distributions. So, in the more humid southern regions Styloniscidae are a prominent component of cave fauna, as they are in the wet forest of the surface, but they are troglophilic. Armadillidae, Ligiidae, and Scyphacidae are also common in Tasmanian caves but none is troglomorphic. On the mainland, Olibrinidae, Philosciidae, and Armadillidae are prominent among subterranean fauna. In the drier areas of Australia, where armadillids are such a prominent part of the surface fauna, they appear in caves more frequently, and many have overt troglomorphies. These troglobites are known from the Nullarbor, North Queensland (Chillagoe), Cape Range, and Kimberley and the western shield. The troglobitic Philosciidae, Platyarthridae, and Oniscidae from Western Australia are undescribed.

A single epigeal species of *Haloniscus* *searlei*, an aquatic oniscidean isopod, is known from salt lakes (playas) across southern Australia. Numerous stygobitic species of *Haloniscus* occur in groundwater calcrete deposits of the Yilgarn region of the western shield sometimes in saline waters, and from Ngalia Basin northwest of Alice Springs in Central Australia.

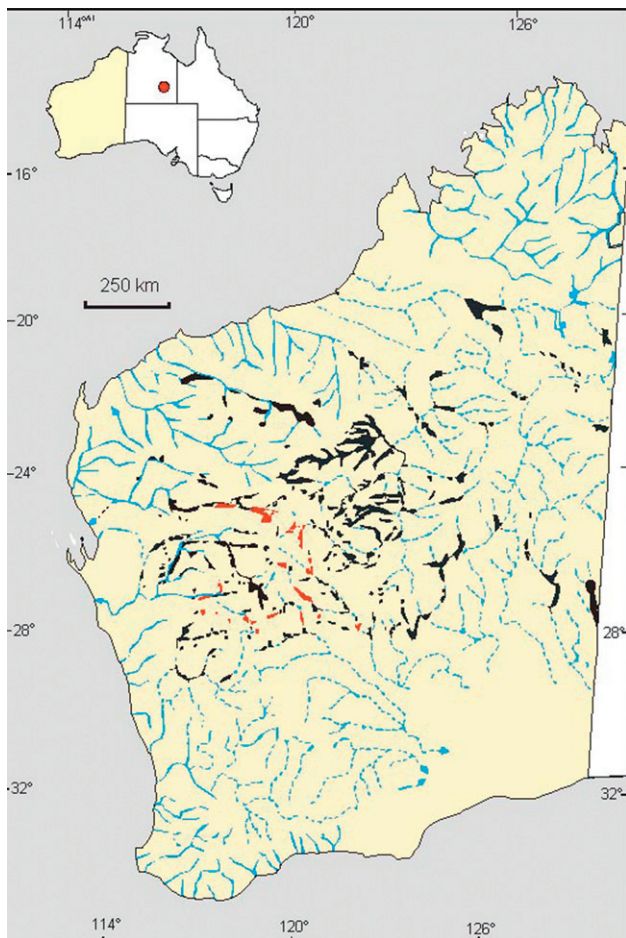


FIGURE 5 The distribution of groundwater calcretes in Western Australia, which occur throughout the arid land north of 29°S. Most occur immediately upstream of salt lakes (playas) within paleo-drainage channels (dotted lines).

Spelaeogriphacea

In Australia, this order of stygal crustaceans is known from two species, each in a separate lacustrine calcrete deposit in the Fortescue Valley, a major ancient paleovalley of the northern Pilbara region. The four extant species of spelaeogriphaceans occur with very circumscribed distributions in subterranean freshwater habitats of Africa (Table Mountain, South Africa), South America (western Mato Grosso, Brazil), and Australia, all fragments of Gondwana. The supposition of a Gondwanan origin is possibly refuted by a marine fossil, *Acadiocaris novascotia*, from shallow marine sediment of Carboniferous age in Canada, which has been attributed to this order. All living spelaeogriphaceans occur in or above geological contexts that are earliest Cretaceous or older. The colonization of Gondwanan freshwater is likely to have occurred after the retreat of the Gondwanan ice sheet (after 320 Ma BP) and prior to the dissolution of Gondwana (142–127 Ma BP).

Decapoda

Atyid shrimps (Decapoda) are widespread in surface waters throughout the tropics. They may have colonized Australia from Asia via the Indonesian archipelago, but their presence as stygobitic species in caves and groundwaters of the Canning Basin suggest a more

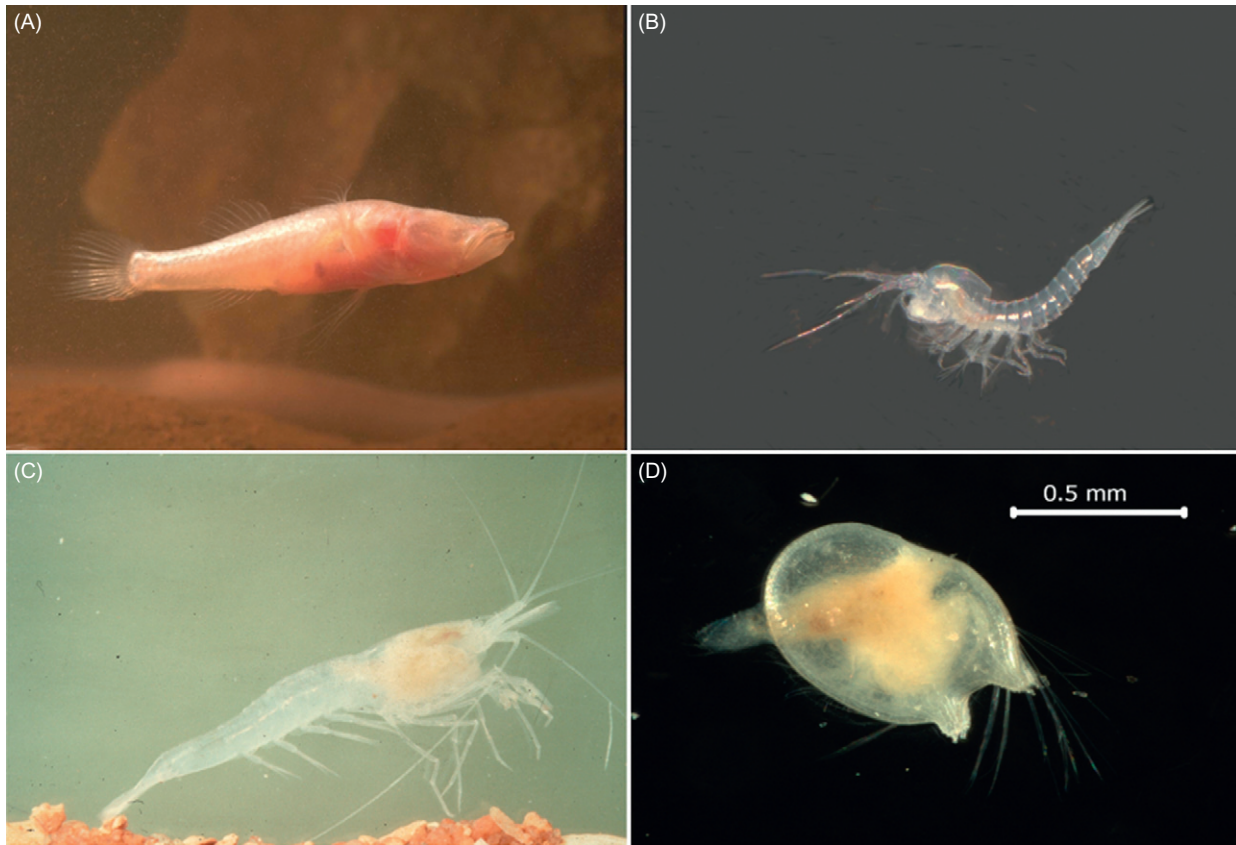


FIGURE 6 Stygal animals from Australian anchihaline waters. (A) *Milyeringa veritas* (Eleotridae); (B) *Halosbaena tulki* (order Thermosbaenacea); (C) *Stygiocaris stylifera* (Decapoda: Atyidae); (D) *Danielopolina kornickeri* (Ostracoda: Thaumatoctyprididae). Photographs (A) and (B) by Douglas Elford; (C) and (D) by William Humphreys; both of the Western Australian Museum.

ancient origin. The genera *Parisia*, *Pycnisia*, *Pycneus*, and *Caridina*, the first three being endemics, form a paraphyletic clade and occur as species with small ranges in northern and central Australia. A second clade includes *Antecaridina* and the endemic genus *Stygiocaris* (Fig. 6) from anchihaline systems of an isolated seamount (Christmas Island, Indian Ocean) and the epicontinental system of the northwest, respectively. *Stygiocaris* is most closely related to *Typhlatya* found in subterranean waters on either side of the North Atlantic.

CHELICERATA

The chelicerates globally comprise a biodiverse component of cave communities and the class is represented in the Australian cave fauna by the orders Acarina, Palpigradi, Amblypygi, Opiliones, Pseudoscorpiones, Schizomida, Scorpiones, and Araneae.

Acarina

The mite family Pediculochelidae (Acariformes) was first recorded in Australia from a dry cave in Cape Range where a specimen was attributed to

Paralycus lavoipierrei that is described from California. *Tiramideopsis* (Mideopsidae) occurs in the Millstream aquifer, a genus previously known from similar habitats of India and suggesting ancient links (cf. Phreatoicidea). Generally, the poorly known mesostigmatid mite fauna of Australian caves does not appear to constitute a distinctive cave fauna or exhibit any of the morphological characteristics of deep-cave arthropods.

Palpigradi

The first native species, *Eukoenenia guzikae*, was described in 2008, collected from a borehole in calcrete substrate in the southern western shield. Since then other species have been recovered from the Pilbara, Barrow Island, and Kimberley of Western Australia, all from boreholes in karst and fractured rock substrates, or caves.

Amblypygi

Troglophilic species of *Charon* are found on Christmas Island and in the Northern Territory.

Opiliones

Cavernicolous species of Triaenonychidae in Tasmania and New South Wales often show depigmentation, attenuation of pedipalps and legs, a reduction in size (but not loss of) eyes, reduced sclerotization, and other troglomorphic features. The cave fauna of Tasmania, unlike continental Australia, have distribution patterns more like those of other periglacial areas of the world in which profound environmental changes were associated with Cainozoic glacial cycles. The distribution of the opilionid genus *Hickmanoxyomma*, which is exclusively cavernicolous, appears to have resulted from the ablation of surface forms in the south and east of Tasmania, where the effect of glaciation was most intense, and the occurrence of some sympatric species suggests that there may have been multiple phases of cave invasion. In contrast, in the coastal lowlands to the north and northeast, where periglacial conditions were less extreme, surface-dwelling species of *Hickmanoxyomma* are present. A cavernicolous assamiid with reduced eyes, but not strongly troglomorphic, and the strongly troglomorphic *Glennhuntia glennhunti* ("Phalangodidae") from arid Cape Range, are both probably rainforest relicts although the wider affinities of both families are unknown. Several species of unknown affinity have recently been collected from boreholes in the arid Pilbara region.

Pseudoscorpiones

The worldwide family Chthoniidae is most commonly represented among troglomorphic species in Australia. The genera *Tyrannochthonius*, *Pseudotyrannochthonius*, and *Austrochthonius* are widespread with cave populations in eastern and western parts of the continent. Syarinidae, which occur in the rainforests of Africa, Asia, and the Americas, occur widely in Australia and as a troglophile in Cape Range and the Pilbara. The Hyidae, known from India, Madagascar, and southeast Australia, are represented in Australia in the Kimberley and by markedly troglomorphic species of *Indohya* from arid ecosystems.

Schizomida

Schizomids are essentially a tropical forest element that occurs across the top of the continent, as far south as the humid caves in the arid Cape Range and subterranean systems throughout the Pilbara. Troglobitic species are known from various genera, of which the most troglomorphic belong to the genera *Draculoidea* (Fig. 3) and *Paradraculoidea*.

Scorpiones

A troglobitic scorpion (*Liocheles*: Liochelidae) occurs on rainforest-covered Christmas Island, Indian Ocean. *Aops oncodactylus*, a genus endemic to arid Western Australia, is the first troglobitic urodacid and the first troglobitic scorpion recorded from continental Australia. Only one other troglobitic scorpion is known outside the Americas, from Sarawak (Malaysia).

Araneae

Troglodiplura, which has South American affinities, is the only troglobitic mygalomorph spider in Australia, and occurs in caves in the arid Nullarbor region. Like the sympatric cockroach *Troglolatella*, it is heavily sclerotized, suggesting a more drying atmosphere than is generally associated with troglomorphic animals found elsewhere, such as in the arid zone caves of Cape Range, which have affinities with rainforest floor communities. The primitive araneomorph (true) spider *Hickmania troglodytes* from Tasmania is a troglophilic member of Austrochilidae, a family that also occurs in Chile and Argentina.

Large lycosoid spiders occur widely in the arid areas, one of which, *Bengalla bertmaini* (Tengellidae), from Cape Range, is highly troglomorphic, lacking eyes and pigment.

Symphytognathidae occur as troglobitic elements in the tropical caves of arid Cape Range and monsoonal Northern Territory (Katherine) as *Anapistula*, found as epigeal elements in the wet tropics of Australia, Malaysia, and Indonesia.

Cavernicolous Filistatidae occur throughout Australia (*Wandella*) but the monotypic *Yardiella* from Cape Range has relatives in northeast India and the family has a generally Gondwanan distribution.

A blind troglobitic *Tetrablemma* (Tetrablemmidae) occurs in the Pilbara, presumably a relict from past humid environments. Likewise *Desognanops* (Trochanteriidae), from the Pilbara, is a blind rainforest relict.

Among the Pholcidae, *Wugigarra* occurs along the eastern seaboard and to the southeast of the continent while the western three-quarters of the continent contains old elements of the pholcid fauna. If the distribution of the genus were restricted by current ecological conditions, then the genus would be expected to be found in the west and other refugia, but this apparently is not the case. This distribution may be due to the marine subdivision of the continent by the Cretaceous marine transgression. The genus *Trichocyclus* occurs as a cavernicolous element throughout much of the rest of the continent from the Nullarbor to the tropics. Both genera are considered to be Gondwanan relicts.

MYRIAPODA

Diplopoda

Troglobitic millipedes have rarely been reported in Australia. The Cape Range karst hosts a number of paradoxosomatid millipedes of the genus *Stygiochiroopus*, three of which are declared rare fauna being known from single small caves, while *S. communis* comprises a species swarm occurring through the range in three regions each with a major genetic cluster. Caves between regions differ by a mean of 25.6% fixed allelic differences (allozymes), while caves within regions show 0.92–3.06% fixed differences. The first recorded troglobitic spirobolid millipede is *Speleostropus nesiotus*, a genus endemic to Barrow Island.

Chilopoda

The scolopendrid centipede *Cryptops (Trigonocryptops) roeplainsensis* occurs along the coastal boundary of the Nullarbor karst. Large scutigerid centipedes of the genus *Allothureura* are seen in the more superficial parts of both humid and dry caves in the arid areas but are not troglobitic.

INSECTS

Diplura

Numerous undescribed species belonging to Campoideidae, Japygidae, Projapygidae, and Parajapygidae have been collected from limestone caves and boreholes in karst and fractured rock aquifers.

Zygentoma

Among the Nicoletiidae, *Trinemura* is represented in caves in the west, while *Metrinura* is found in the caves of the northeast. Numerous species of Nicoletiidae and Ateluridae have recently been collected from boreholes in the western shield, especially the Pilbara region.

Collembola

The composition of collembolan fauna changes between the south and north of Australia. Caves in the south of the continent contain up to five genera of troglobitic Collembola, while those in tropical areas have only two genera. The genera *Adelphoderia* and *Arrhopalites* are not recorded as troglobites in tropical caves, but because the former is known from both temperate and tropical rainforest litter it seems likely to occur in tropical caves. This apparent trend in

diversity may well reflect the greater sampling effort in southeast Australia. *Oncopodura* occurs in southeast Australia and in the Northern Hemisphere.

Planthoppers: Relicts or Invaders?

There is continuing debate as to whether cave fauna result from active colonization or occur as relicts as a result of the extirpation of surface populations by adverse conditions (e.g., glaciation, aridity). The cave fauna on arid Cape Range are clearly relictual in that they are now remote from the humid forest from which the fauna were sourced. However, the aridity is sufficiently intense to have obliterated all close surface relatives and so the process by which it became relictual cannot be resolved. By contrast, in a grossly similar fauna in Far North Queensland, the troglobitic cixiid and meenoplid planthoppers have some members with surface relatives and many intermediate forms. These lineages show many reductive, but no progressive trends, and this has been interpreted as support for the active colonization of the subterranean realm, rather than as a process of relictualization (Hoch and Howarth, 1989).

In North Queensland seven evolutionary lines of planthoppers (Fulgoroidea) of the families Cixiidae (genera *Solonaima*, *Undarana*, *Oliarus*) and Meenoplidae (*Phaconeura*, a continent-wide genus) are found. *Solonaima* (Cixiidae) exhibits four independent invasions of the caves and shows a full range of adaptations to cave life, from epigeal to troglobitic, together with intermediate stages. This lineage provides an excellent model for the stepwise evolution of cave forms and the reconstruction of the historic process of cave adaptation—the loss of eyes and pigmentation, reduction of wings and tegmina, and increased phenotypic variation, such as wing venation, even within same species, suggesting a relaxation of selection pressure. To Hoch and Howarth (1989) this suggested that there had been fragmentation of the rainforest owing to the drying climate during the Miocene. This model, argued on other evidence, has also been suggested for the arid Cape Range region on the west coast of the continent.

Blattodea

Cockroaches represent a widespread and common element of many Australian caves, particularly those where the predominant energy source is guano from bats or swiftlets where. *Paratemnopteryx* and related genera (*Gislenia*, *Shawella*) are prominent. *Paratemnopteryx stonei* exhibits significant morphological variation in seven tropical caves spread over a 150-km distance in

North Queensland, such variation being consistent with molecular variation (Slaney and Weinstein, 1996). The genus *Neotemnopteryx* is widespread on the east coast and is represented by 14 species, of which five species are cavernicolous, but troglotic species occur in the Nullarbor and the southwest coast: *N. wynnei* and *N. douglasi*, respectively. In the Nullarbor, where caves are relatively dry, the large, eyeless but highly sclerotized *Trogloblatella nullarborensis* is found. In contrast, the Nocticolidae occur widely in the Old World tropics and a number of cave species occur throughout the Australian tropics, down to arid Cape Range where *Nocticola flabella* is found, the world's most troglomorphic cockroach, which is distinguished by its pale, fragile, translucent appearance. In contrast, a more robust monotypic troglobite, *Metanocticola*, is found on Christmas Island. Numerous species of troglotic *Nocticola* (and Blattidae) are being collected from baited traps inserted down holes bored in pisolites and fractured rocks of the arid Pilbara region. The genus *Nocticola* also occurs in the Philippines, Vietnam, Ethiopia, South Africa, and Madagascar.

Orthoptera

Many cave crickets (Rhopidophoridae), which occur in cave and bush habitats across southern Australia, are troglloxenes, like some bats. During the day these moisture-loving insects tend to congregate in relatively cool, moist, and still air to avoid desiccation. In the evening, part of the cricket population moves outside the cave entrance to feed but they return underground before dawn and so transport organic matter into the cave. Rhopidophoridae have a disjunct global distribution in the temperate zones of both hemispheres. The Macropathinae are considered to be the basal group and these have a circum-Antarctic distribution, suggesting a Gondwanan origin. Generic diversity is much greater in Australia and New Zealand than elsewhere. Four genera are restricted to Australian temperate zones and a further three genera to Tasmania itself. The remaining three subfamilies inhabit the Boreal zone, suggesting vicariance owing to the Mesozoic dissolution of Pangaea.

In contrast, the only truly troglotic cricket in Australia is the pigmy cricket *Ngamalanguia* (Nemobiinae: Grylliidae) (Fig. 3), a monotypic genus endemic to Cape Range that lacks eyes, ocelli, tegmina, wings, and auditory tympana; is pale; and has exceptionally long antennae.

Coleoptera Dytiscidae

Globally, beetles are by far the most intensively studied cave animals. Chief among them are the

trechine carabid beetles, of which more than 2000 species have been described. Of these, more than 1000 species are troglomorphic, inhabiting caves from periglacial areas of Australia and New Zealand (25 species), eastern Palearctic (*ca.* 250 species), western Palearctic (*ca.* 600 species), and Nearctic and Neotropical (*ca.* 200 species).

Unlike mainland Australia, Tasmanian caves support a distinctive cave fauna of carabid beetles from the tribes Trechini (a strongly hydrophilous group forming a dominant element of cave fauna of the periglacial areas of Europe, North America, New Zealand, and Japan) and Zolini (confined to Australasia) each containing two genera with troglotic species. In the periglacial areas of Tasmania, vicariant patterns similar to those for opilionids may be deduced for the trechine and zoline carabid beetles, which form such a prominent part of the Tasmanian cave fauna. Harpalinae, a globally widespread and predominantly phytophagous group, typical of dry country, are considered unsuitable for cave colonization, and yet many genera are represented in caves in Australia. Two genera of the Calleidini occur in guano caves in Australia, which suggests, because these beetles are typically arboreal, the possibility of a reversal from the arboreal habit typical of this tribe, to an edaphic or subterranean life.

Although the Cholevidae is well represented in the more humid parts of Australia, the tribe Leptodirinae (Bathysciinae), which comprises the predominant component of the rich cholevid beetle fauna of the Northern Hemisphere, is entirely missing from Australia and the rest of the Southern Hemisphere. In the Snowy Mountains area of the mainland, where periglacial conditions also persisted, is found the only troglomorphic psydrid beetle known globally. Numerous other families of beetles occur in caves throughout Australia, in both the humid and arid areas, but most seem to be accidentals. The Australian troglotic fauna, especially those that associate with periglacial areas, differ from those in the Northern Hemisphere, owing to the composition of the surface fauna, rather than due to different evolutionary trends. Recent collections from baited traps lowered into bores drilled in karst, pisolites, calcretes, and fractured rock have yielded a sparse but diverse troglomorphic beetle fauna awaiting study including members of the families Carabidae, Curculionidae, Staphylinidae (Pselaphinae), and Tenebrionidae. In addition, Trogidae are commonly associated with guano deposits derived from cave roosting bats and swiftlets.

Australia hosts more species of stygobitic diving beetles (Dytiscidae) than the rest of the world combined. More than 100 species of Hydroporinae (and the only two stygobitic species of Copelatinae) are

found mainly in shallow calcrete aquifers in the Yilgarn, western shield, and in Ngalia Basin, Northern Territory. Several species occur in alluvia of New South Wales and South Australia.

VERTEBRATES

Caves in the wet-dry (monsoonal) tropics commonly provide refuge to vertebrates during the dry season and clearly this temporary habitation has an impact on the trophic relations of these caves. Among them are tree frogs (e.g., *Litoria caerulea*), which are also abundant in uncapped boreholes, and fish, such as the common eel-tail catfish, *Neosilurus hyrtlui*, and the spangled perch or grunter, *Leiopotherapon unicolor*. In the dry season, the fish may survive in caves and underground water systems and from there they would contribute to the repopulation of the seasonally inundated floodplains.

Australia has two described highly troglomorphic fishes which are sympatric where they occur at Cape Range. The blind gudgeon, *Milyeringa veritas* (Eleotridae) (Fig. 6), is of unknown affinity but inhabits water ranging from seawater to freshwater in a largely anchihaline system in Cape Range (a second, undescribed species is known from Barrow Island). Swamp eels (Synbranchidae) are represented in Australia by two species of *Ophisternon*, of which *O. candidum* is a highly troglomorphic species (Fig. 3). Stygobitic specimens of unknown affinity were recorded from Barrow Island and the Pilbara during 2010. The genus occurs widely in the coastal wetlands of the Indo-Malayan region, with one other troglomorphic species inhabiting caves in Quintana Roo, Mexico.

Snakes are commonly seen in caves, especially in the tropical regions where they predate bats (e.g., the banded cat-snake *Boiga fusca ornata*). The blind snake, *Ramphotyphlops longissimus*, from the Barrow Island karst has apparent troglomorphies and may represent the first troglotic reptile.

Birds are rarely represented in Australian caves other than as superficial components inhabiting cave openings. The exceptions are swiftlets (*Collocalia* species) that build their nests in the dark zone, on smooth concave walls high above the cave floor in some tropical caves in Far North Queensland and Christmas Island (Indian Ocean). The nests of some species are intensively harvested for the gourmet delicacy "birds' nest soup" in Southeast Asia and India. The Christmas Island glossy swiftlet (*Collocalia esculenta natalis*) is endemic to Christmas Island where, in the absence of cave bats, they are the prime source of guano in caves. A number of other species of *Collocalia* occur in the

Indian Ocean, Southeast Asia, and Queensland, mostly nesting in caves. The nests detach from the cave walls in dry air, a factor that may account for their absence from the drier tropical areas, such as the Kimberley. The various subspecies inhabit few of the caves available, being known from only five caves on Christmas Island, whereas the white-rumped swiftlet (*Collocalia spodiopygus chillagoensis*) occurs in less than 10% of approximately 400 caves at Chillagoe in Queensland.

Bats comprise nearly a third of the Australian mammalian fauna. Seven families of bats, comprising about 30% of the Australian bat fauna, are found in caves. The 17 species of cave-dwelling bats in Australia are largely restricted to the tropics and comprise insectivorous and frugivorous bats and vertebrate predators (ghost bats, *Macroderma gigas*). Six species are restricted to the Cape York peninsula and 11 species occur across the northern part of the continent, two of them extending along the west coast to the arid Pilbara region. Only four species are restricted largely to the center of the continent, two being restricted to the western plains of Queensland and New South Wales.

CONCLUSIONS

In a global context, the most striking features of the subterranean fauna of Australia are (1) the apparent age of the lineages present in subterranean environments, and (2) the high proportion of geographic relicts present in the subterranean systems that are widely separated from their near relatives. Although much remains to be done to establish consistent patterns, numerous independent examples suggest similar processes but at a range of spatial and temporal scales.

In the southeast, there is evidence that Pleistocene glaciation influenced the cave fauna. But, over most of mainland Australia, the overwhelming influence seems to have been relict distributions resulting from increasing aridity during the Tertiary, particularly in the Miocene. Numerous terrestrial and aquatic lineages have affinities with Gondwana, or with Western Gondwana, often at the generic level. In terrestrial lineages, these are commonly associated with rainforests. Numerous crustaceans, often lineages entirely comprising stygal species, and even a fish lineage, have distributions throughout the area of the former Tethys Ocean. Many lineages from northwestern Australian anchihaline waters comprise species congeneric with those inhabiting caves on either side of the North Atlantic.

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See Also the Following Articles

Diversity Patterns in the Dinaric Karst
Diversity Patterns in Europe
Diversity Patterns in the Tropics
Diversity Patterns in the United States

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DIVERSITY PATTERNS IN EUROPE

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INTRODUCTION

To an extent that is unusual in most branches of zoology systematics, Europe is both a hotspot of subterranean biodiversity and a hotspot of research into subterranean biology, both historically and at present.

The scientific study of cave life can be traced back to Johann von Valvasor's comments in 1689 on the European cave salamander *Proteus anguinus*. This species, the only stygobiotic salamander in Europe, reaches a length of more than 25 cm, making perhaps the largest stygobiont known anywhere. It occurs throughout the Dinaric mountains in northeast Italy, Slovenia, Croatia, and Bosnia and Herzegovina. During the late eighteenth century and much of the nineteenth century, living *Proteus* were collected and delivered to many scientists throughout Europe. It was this animal more than any other cave animal that played a formative role in the emerging theories of evolution of Lamarck and Darwin. The first invertebrate was described in 1832, also from Slovenia, as *Leptodirus hochenwartii*, a bizarre appearing beetle with an enlarged abdomen and long spindly appendages.

Besides the caves of the Dinaric region, the cave fauna of the French and Spanish Pyrenees began to attract attention, and the Pyrenean fauna began to be described by the mid-nineteenth century. In 1907, the Romanian zoologist E.G. Racovitza published the enormously influential "Essai sur les problèmes biospéologiques," which set the agenda for biospeleological research in the coming decades. Together with the French entomologist René