Alabama is one of these centers of biodiversity for troglobites and stygobites. Of particular note, Jackson County has 1526 caves and 66 obligate cavernicoles, which translates into more than three times the number of caves and nearly twice as many species as any other Alabama county. This shows the strong relationship between the number of caves observed and the number of species reported ($r^2 = 0.81$).

Troglobites and stygobites make up slightly more than 50% of the imperiled U.S. fauna that is tracked in the central databases of the Natural Heritage Program. There are far too many potential (and realized) disturbances to discuss herein that threaten these out-of-sight organisms and the reader is referred to Elliott (2000) for an excellent review of them. Suffice it to say that the ultimate long-term survival of subterranean karst communities depends on appropriate management and protection of the cave, the groundwater, and the entire catchment area.

It becomes clear that these subterranean species are geographically concentrated in a small percentage of the landscape, with more than 50% of cave-inhabiting species occurring in less than 1% of the land. Hence, it is much easier to preserve a large percentage of at-risk species by focusing habitat conservation efforts in those areas of high concentrations of obligate cave fauna, or "hot spots." Protecting and conserving karst habitats and their biodiversity is a challenging but most important task for modern and future speleologists. The subterranean biodiversity of the United States is globally significant but highly vulnerable.

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Diversity Patterns in Australia

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INTRODUCTION

That Australia, and tropical areas worldwide, have diverse subterranean fauna has not been long 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 sparsity of carbonate rocks in Australia, as found in other Gondwanan fragments, compared with the world average (Fig. 1); (2) the general aridity of the 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 the low input of food energy into the underground voids; (3) the global lack of cave-adapted

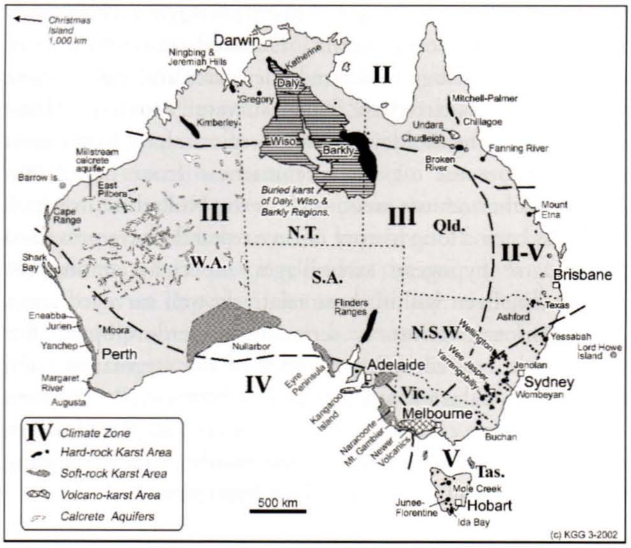

FIGURE 1 Karst areas of Australia and the bioclimatic zones: II, tropical; III, subtropical dry; IV, transitional zone with winter rain; V, warm temperate; II–IV warm temperate/tropical transition zone. (After Hamilton-Smith and Eberhard, 2000. Graphic by K. G. Grimes.)

animals in tropical areas; and (4) the lack of widespread glaciation, which was perceived to be the main driving force driving the evolution of troglobites in the Northern Hemisphere, then the focus of biospeleological research. Concomitantly, 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 20th century, more focused, as well as more widespread, exploration of caves and later groundwater has shown that the Australian tropics and arid zones contain especially rich subterranean fauna. However, no area of Australia has been well studied for its hypogean life, the distribution of the effort has been very uneven across the country, and many areas remain effectively unexplored for cave 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. 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.

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 continent-wide 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 resulting 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 and the development of the circum-Antarctic ocean currents and winds 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.

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 Yigarn cratons. These stable, truly continental areas of Australia have a nonmarine, presumably freshwater history extending through several geological eras. The Cretaceous marine inundation, at ca. 120 Ma, 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 epigean and subterranean, may be expected to reflect this marine incursion in two 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

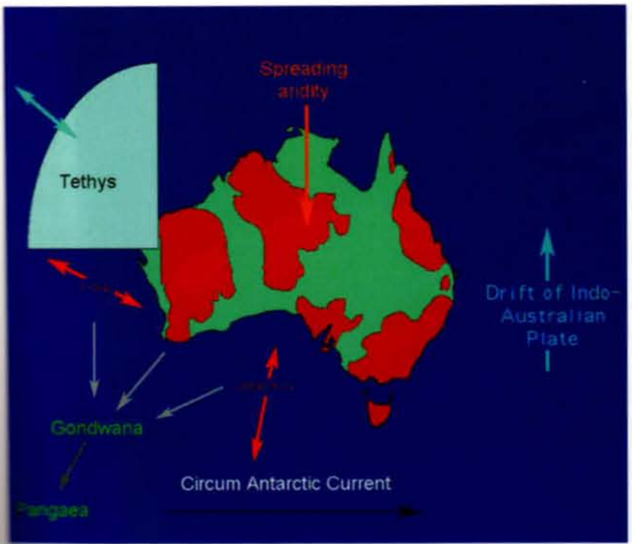

FIGURE 2 Deep history events that have influenced the biogeography of Australian subterranean faunas (see text). The shaded continental areas have not been covered by the oceans since the Paleozoic.

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 phreatoicideans, an ancient group of isopods, in both their epigean 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 fauna hold a special significance because, unlike terrestrial troglobites, the aquatic troglobite fauna (stygobites) 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 [illegible] 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 colleagues 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 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 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 further 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 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 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 estab-

FIGURE 3 Subterranean animals, clockwise from upper left: 1, *Tjirtudessus eberhardi* (Dytiscidae), one of 50 species of blind diving beetles from calcretes aquifers in the Australian arid zone; 2, unnamed blind philosciid isopod; 3, head of *Ophisternon candidum* (Symbranchiformes), one of two Australian cave fish; 4, the phreatoicidean isopod *Phreatoicoides gracilis*; 5, *Pygolabis humphreysi*, from Ethel Gorge calcrete belongs to a family of flabelliferan isopods, the Tainisopidae, known only from groundwater in Kimberley and Pilbara regions of Western Australia; 6, *Mangkurtu mityula* (Spelaeogriphacea), a subterranean family that is known from only two locations in each of Australia, Africa, and Brazil; 7, *Draculoides vinei* (Schizomida), one of seven species of micro-whipscorpions known from Cape Range; 8, *Ngamarlanguia luisae* (Gryllidae: Nemobiinae) from Cape Range, the only troglobitic cricket in Australia. (Photographs by Douglas Elford, Western Australian Museum, except 1, W. F. Humphreys from a painting by Elyse O'Grady; and 4, from GDF Wilson Australian Museum.)

Amphipods

Australia is a major center of amphipod diversity and much of this diversity is represented by stygal species. Unexpectedly, they are diverse in the tropic areas and in the arid center of Australia, in typical karst and in groundwater calcrete aquifers. They belong to a number of higher taxa including the crangonyctoids (Paramelitidae, Perthiidae, Neoniphargidae), hadziods (Fig. 6) (Melitidae, Hadziidae), Ceinidae, Bogidiellidae, and Eusiridae, but there is scant knowledge of their distribution and diversity. About 65 described species occur in these eight families, with much of the diversity occurring in groundwaters of the arid region (Bradbury and Williams, 1997). Whereas some families appear to be restricted to the moist temperate southeast and southwest of the continent (Eusiridae and Neoniphargidae), others are much more widespread and encompass parts of the arid zone and tropical areas (Melitidae, Paramelitidae). Other families are more restricted and Bogidiellidae are known only from the northwest, whereas Perthidae and Ceinidae occur in the southwest and south, respectively. Bogidiellid, melitids, and hadziids are known from the anchialine waters of the northwest, especially Cape Range and Barrow Island. Notably, while taxa in southern areas comprise both stygal and epigean species, northern taxa, in the arid tropic and subtropics, comprise only stygal taxa.

A clear relationship can be seen between the Cretaceous marine transgressions and the distribution of amphipods. Melitoid taxa occur near the shorelines of areas that have been transgressed, while in those areas that have not been transgressed, crangonyctoid taxa and niphargiids are found. Paramelitids are diverse and abundant in Tasmania but seemingly sparse in New South Wales, where neoniphargids are diverse. More comprehensive collecting in Western Australia suggests that family distributions may be circumscribed (Fig. 4).

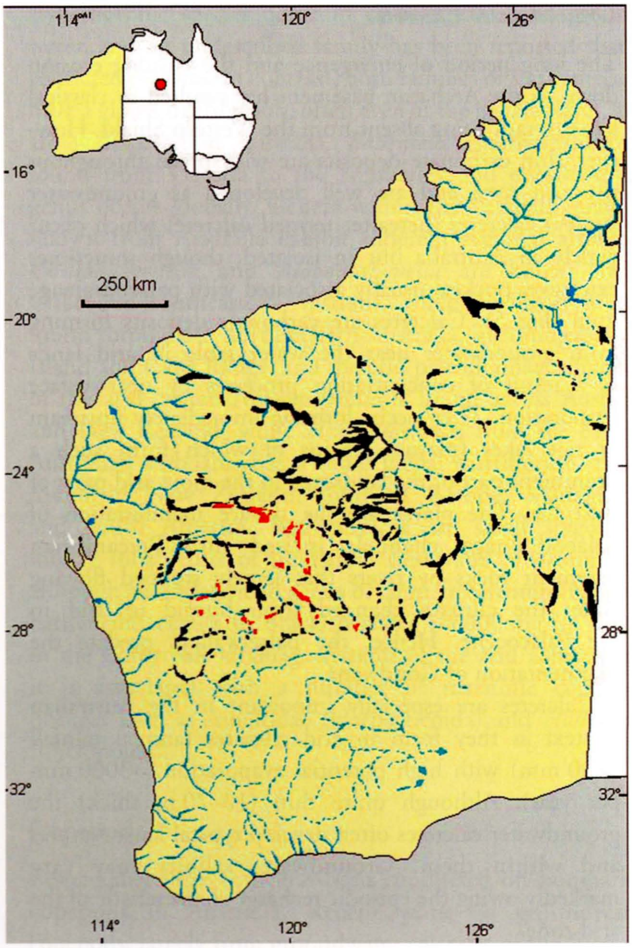

FIGURE 4 The distribution of groundwater calcretes in Western Australia, which occur throughout the arid land north of 29°S. Most occur immediately upstream of salt lakes (playas) within paleodrainage channels (dotted lines).

lished 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.

Another area where a resolution of the causes of colonisation 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 almost no overlap in species between different calcretes, and speciation appeared to have taken place *in situ* because species pairs (one large and one small) are common among the 50 stygal species in the arid zone. Molecular studies suggest that numerous lineages invaded the calcrete aquifers during the constrained time period, which suggests that it occurred in response to a widespread factor, such as might be expected from spreading aridity.

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 palaeodrainage 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 occur forming immediately upstream of salt lakes (playas), chains of which form such a prominent part of the landscape in the more arid parts of Australia. The playas are the surface manifestation of palaeodrainage channels incised into Precambrian basement rocks by rivers that largely stopped flowing when the climate changed from humid to arid in the Palaeocene. Hence, the palaeovalleys 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. Groundwater salinity may vary markedly owing the episodic recharge characteristic of the arid zone.

Because they are deposited at intervals from the groundwater flow, the scalcrete masses are separated by habitat—Tertiary valley-fills, largely clays, and saltlakes—that is unsuitable for stygofauna. Consequently, they form isolated karst areas along the numerous major palaeovalleys, some of which date from the Permian. The sediments filling the palaeochannels are mostly Eocene or later but the age of the calcretes is unknown. The extensive alluvial fan calcretes and some of the river valley calcretes formed in the Oligocene ((37–30 Ma) may have following 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, a molecular phylogeny of the diverse diving beetle fauna, the numerous species of which are each restricted to a single major calcrete area (Leys *et al.*, in press), indicate that the calcretes have been present for at least 5–8 million years.

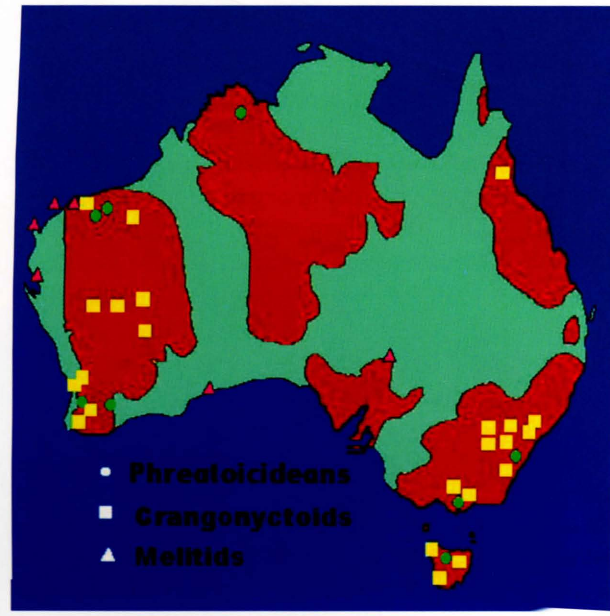

FIGURE 5 The distribution of subterranean amphipod and isopod taxa in relation to long emergent land areas in Australia. The phreatoicidean isopods and crangonyctoid amphipods are ancient continental lineages, whereas the melitid amphipods have a more recent marine ancestry.

Energy Supply

Energy enters subterranean systems largely mediated by water, animals, and plants. 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.

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. Roots, especially tree roots, were identified as an important and reliable source of energy for troglobitic cixiid and meenoplic fulgoroid Homoptera. These occur in the lava tubes o tropical North Queensland and similar fauna are found i karst across the tropics, into the Kimberley and down th arid west coast, to the south of Cape Range. Tree roots a also utilized by cockroaches throughout the country (e.g., i the Nullarbor, *Trogloblatella nullarborensis*).

Tree rootmats also represent a reliable food supply f elements of the rich communities of aquatic invertebrat including some exhibiting troglomorphisms, occurring some shallow stream caves of western Australia. They provi habitat, and probably food, for stygofauna in the Nullarb in calcrete aquifers of the Western Shield, and in anchial caves in Cape Range and Christmas Island where t 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 both 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.

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 rhaphidophorid crickets are the most conspicuous trogloxenic 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 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.

STYGOFAUNA AND CRUSTACEA

Stygofauna are discussed in the context of Crustacea, which comprise the overwhelmingly 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 (for instance, an undescribed family of flabelliferan isopod), new to the Southern Hemisphere (Thermosbaenacea, Remipedia, Epacteriscidae), or new to Australia (Spelaeogriphacea, Pseudocyclopiidae). Many of these taxa occur near coastal and anchialine waters and are interpreted as comprising a relictual tethyan fauna. 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 caves 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. *Chiliobathynella* and *Atopobathynella* are known from Chile and southeastern Australia, while the latter is also found throughout northwestern Australia, including Barrow Island and Cape Range, and the arid 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. Bathynellacea are small stygobites, mostly inhabitants of interstitial freshwater environments, although an undescribed genus of large, free-swimming parabathynellid occurs in brackish water (<6000 mg L^{-1} TDS) in the Carey paleodrainage systems of the arid zone, where it is associated with a number of maritime copepods lineages such as Ameiridae (Harpacticoida) and *Halicyclops* (Cyclopoida).

Copepoda

Remarkably little work has been conducted on nonmarine copepods in Australia. Recent work on groundwater copepods, largely from groundwater calcretes of the Western Shield, and the near coastal, especially anchialine systems of the northwest, has revealed higher taxa not previously described from Australia, in some cases even from the Southern Hemisphere.

Numerous new species of copepods are being described from Australian groundwaters, largely from the Yilgarn area of the Western Shield including five new genera of Cyclopoida and Harpacticoida, and several genera are reported for the first time from Australia [*Nitocrella* Ameiridae (Eurasia), *Parapseudoleptomesochra* (global), *Haifameira* Ameiridae (depth of Mediterranean Sea), and the family Parastenocarididae (Pangaea, freshwater)]. The broader distribution of these lineages within Australia awaits investigation.

The occurrence of 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 these paleodrainage systems, as well as the ancient origins of the fauna. *Mesocyclops* has a mostly tropical distribution; *Metacylcops* (*trispinosus* group) and *Goniocyclops* have an Eastern Gondwanan distribution; and the limits to the distributions of newly described genera of Ameiridae, Canthocamptidae, and Cyclopinae await confirmation.

Anchialine Habitats—Tethyan Relicts

Anchialine (or *anchihaline*) 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 to be 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 epigean ecosystems. Anchialine habitats are mostly found in arid coastal areas and are circum-globally distributed in tropical/subtropical latitudes.

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

In continental Australia anchialine 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 such a fauna comprising atyids, thermosbaenaceans, hadziid amphipods, cirolanid isopods, remipeds, thaumatocypridid ostracods, and an array of copepods such as epacteriscid and pseudocyclopiid calanoids, and speleophriid misophrioids. Some are the

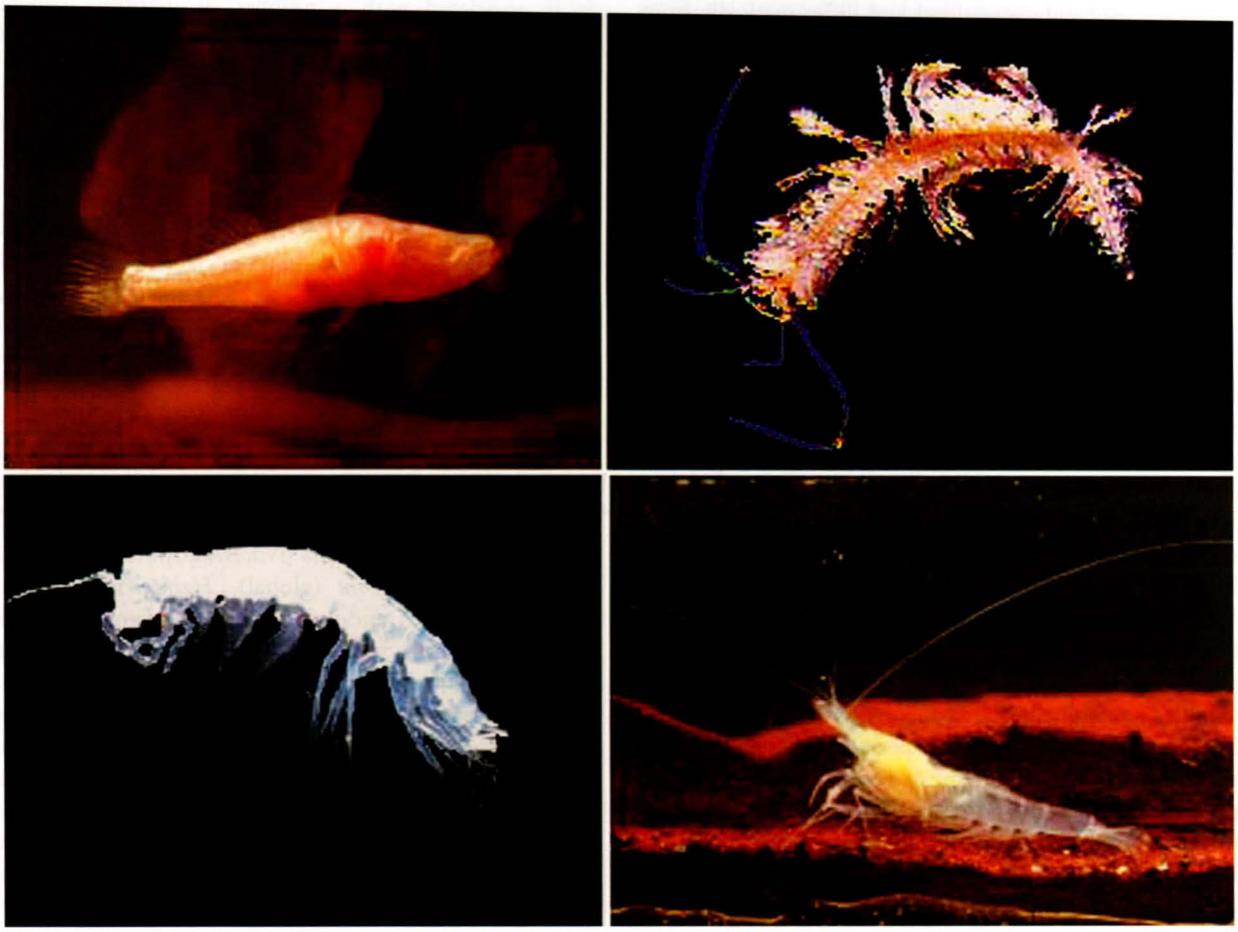

FIGURE 6 Stygal animals from Australian anchialine waters. Clockwise from upper left: *Milyeringa veritas* (Eleotridae); *Lasionectes exleyi* (class Remipedia); *Stygiocaris stylifera* (Decapoda: Atyidae); *Liagoceradocus branchialis* (Hadziidae).

Anchialine Habitats—Tethyan Relicts—cont'd

only known representatives of higher taxa in the Southern Hemisphere (Class Remipedia; Orders Thermosbaenacea, Misophrioida), and several genera are known elsewhere from anchialine systems on either side of the North Atlantic (*Lasionectes, Halosbaena, Speleophria*). The poor dispersal abilities of these stygal lineages and their close fit with the areas covered by the sea in the late Mesozoic suggests that their present distributions could have resulted from vicariance by plate tectonics (Fig. 2).

Anchialine 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 anchialine fauna characterized by the stygobitic shrimp *Procaris* (Decapoda), which belongs to the primitive, highly aberrant, family Procarididae that appears globally to be restricted to anchialine caves. This family has been reported elsewhere only from other isolated seamounts, 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 cooccurrences of two primitive and presumably ancient caridean families support the contention that crevicular habitats have served as faunal refuges for long periods of time. There is no coherent theory as to their distribution to remote seamounts such as Christmas Island.

Ostracoda

Ostracods recorded from Australian inland waters are mainly from the families Limnocytheridae, Ilyocyprididae, 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 relics 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 European ones.

The thaumatocypridid genus *Danielopolina*, previously unreported in the Southern Hemisphere, occurs as a tethyan element in the anchialine system at Cape Range. Fossils in marine cave facies in the Czech Republic suggest that this lineage was already inhabiting marine caves in the Jurassic.

Isopoda

*Phreatoicidean isopods (Fig. 3) have a Gondwanan distri*bution and occur widely across southern Australia (and in tropical Arnhemland) in surface habitats that have permanent water—generally 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. About 59 species in 23 genera are described from Australia, of which 10 species in eight 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" and the family Hypsimetopodidae is represented with a genus each on the Pilbara (*Pilbarophreatoicus*) and the Yilgarn (*Hyperoedesipus*) regions (separate cratons of the western shield). These are closely related to the hypogean genus *Nichollsia* found in the Ganges Valley of India, suggesting they were hypogean prior to the separation of Greater Northern India from the western shore of Australia. *Crenisopus*, a stygobitic genus occurring in sandstone aquifer in the Kimberley, is the link between African and Australasian lineages of phreatoicideans. The genus is basal to the Phreatoicidae, suggesting divergence after they entered freshwater but prior to the fragmentation of East Gondwana during the Mesozoic era.

The flabelliferan isopod 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) 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 origins but its sister relationship has yet to be established. Cladistic analysis suggests that this family is related to the cosmopolitan marine Limnoriidae and Sphaeromatidae, but at a basal level, suggesting it is much older than the more derived families like the Cirolanidae. 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 great; Protojaniridae are known from the Northern Territory.

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). 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 humid Tasmania the Styloniscidae are a prominent component of cave fauna, as they are in the wet forest of the surface, but only one species is troglomorphic. Armadillidae, Ligiidae, and Scyphacidae are also common in Tasmanian caves but none is troglomorphic. On the mainland Olibrinidae, Philosciidae, and Armadillidae are prominent among cave fauna. In the drier areas of Australia, where armadillidians are such a prominent part of the surface fauna, they appear in caves more frequently, and a few have overt troglomorphies. These troglobites are known from the Nullarbor, North Queensland (Chillagoe), Cape Range, and Kimberley. The troglobitic Philosciidae and Oniscidae from Cape Range and the trogloxene Platyarthridae remain undescribed.

A single species of *Haloniscus*, an aquatic oniscidean isopod, is known from salt lakes (playas) across southern Australia. Numerous stygobitic species occur in groundwater calcrete deposits of the Yilgarn region of the Western Shield, a long emergent landmass in arid Australia, sometimes in saline waters. The occurrence of a congeneric species in anchialine waters in New Caledonia suggests a considerable age for the genus and remarkable morphological conservation—New Caledonia separated from the Australian plate in the Late Cretaceous, about 74 Ma. Other stygobitic oniscideans, belonging to the Philosciidae and probably other families, are widespread in Australia but are largely unknown.

Spelaeogriphacea

This order of stygal crustaceans has populations known only from two species in separate lacustrine calcrete deposits in the Fortescue Valley, a major ancient paleovalley of the northern Pilbara region of Australia. All extant spelaeogriphaceans occur with very circumscribed distributions in subterranean freshwater habitats on Gondwanan fragments known from two locations in each of Africa (Table Mountain, South Africa), South America (western Mato Grosso, Brazil), and Australia. The supposition of a Gondwanan origin is refuted by the fossil record. A marine fossil from a shallow marine sediment of a laurentian plate was of Carboniferous age in Canada, while modern-looking fossil spelaeogriphaceans occur in lacustrine deposits of the Jurassic of China and from lower Cretaceous freshwater deposits in Spain. All living spelaeogriphaceans occur in or above geological contexts that are earliest Cretaceous or older. Their broad occurrence suggests a Pangaean origin. The colonization of Gondwanan freshwater is likely to have occurred after the retreat of the Gondwanan ice sheet (after 320 Ma) and prior to the dissolution of Gondwana (142–127 Ma).

Decapoda

Atyid shrimps (Decapoda) are widespread in surface waters throughout the tropics and they appear as stygobitic species in caves and groundwaters where they are represented by four short-range endemic genera. Stygal species occur widely across northern Australia, into the arid zone (Canning Basin), and in anchialine and freshwater systems of northwestern Australia (*Stygiocaris*; Fig. 6) and Christmas Island. They may have colonized Australia from Asia via the Indonesian archipelago, but their presence in caves of the Canning Basin and the apparent Madagascan affinities of some genera suggest a more ancient origin.

CHELICERATA

The chelicerates globally comprise a biodiverse component of cave communities and they are represented in the Australian cave fauna by the orders Acarina, Amblypygida, Opilionida, Pseudoscorpionida, Schizomida, Scorpionida, 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.

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 species often show depigmentation, attenuation of pedipalps and legs, a reduction in (but not loss of) eye size, reduced sclerotization, and other troglomorphic features. The cave fauna of Tasmania, unlike continental Australia, have distribution patterns more like those of the 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 assamid 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.

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. The Hyidae, known from India, Madagascar, and southeast Australia, are represented in Australia in the Kimberley and by the markedly troglomorphic *Hyella* from arid Cape Range.

Schizomida

Schizomids are essentially a tropical forest element that occur across the top of the continent, as far south as the humid caves in the arid Cape Range. The latter contains six troglobitic species in the genera *Draculoides* (Fig. 3) and *Bamazomus*. (Only five other troglobitic species, in the genera *Bamazomus* and *Apozomus*, are known from the rest of Australia.) *Draculoides* is endemic to Cape Range and Barrow Island.

Scorpiones

A troglobitic scorpion (*Liocheles*: Liochelidae) occurs on rainforest-covered Christmas Island, Indian Ocean. An unknown species in a new genus of troglobitic scorpion occurs on the arid Barrow Island and shares morphological features of the families Urodacidae (species in the genus *Urodacus* and endemic to Australia) and Heteroscorpionidae (species in the genus *Heteroscorpion*, endemic to Madagascar). 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 cockroach *Trogloblattella*, it is heavily sclerotized, suggesting a more drying atmosphere than 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 Austrochilidae, a family that also occurs in Chile and Argentina.

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

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

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.

Among the Pholcidae *Wugigarra* occurs along the eastern seaboard and 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.

INSECTS

Zygentoma

Among the Nicoletiidae, *Trinemura* is represented in caves in the west, while *Metrinura* is found in the caves of the northeast.

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 (Greenslade, personal communication), 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 relative 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 epigean 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, 1997). The genus *Neotemnopteryx* is widespread on the east coast and is represented by 14 species, of which five species are cavernicolous, but troglobitic species occur in the Nullarbor and the southwest coast represented by the troglobitic, respectively *N. wynnei* and *N. douglasi*. 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. The genus *Nocticola* also occurs in the Philippines, Vietnam, Ethiopia, South Africa, and Madagascar.

Orthoptera

Many cave crickets (Rhapdidophoridae), which occur in cave and bush habitats across southern Australia, are trogloxenes, 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. Rhaphidophoridae 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 troglobitic cricket in Australia is the pigmy cricket *Ngamalanguia* (Nemobiinae: Gryliiidae) (Fig. 3), a genus endemic to Cape Range that lacks eyes, ocelli, tegmina, wings and auditory tympana, is pale, and has exceptionally long antennae.

Coleoptera

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 troglobitic 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 past 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 reversa from the arboreal habit typical of this tribe, to an edaphic o subterranean life.

Although the Cholevidae is well represented in th more humid parts of Australia, the tribe Leptodirina

(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 psydrinid 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 troglobitic 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.

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 hyrtlii* 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 only two 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 anchialine system in Cape Range. Swamp eels (Synbranchidae) are represented in Australia by two species of *Ophisternon*, of which *O. candidum* is a highly troglomorphic species (Fig. 3). The genus occurs widely in the coastal wetlands of the Indo-Malayan region, with one other troglomorphic species inhabiting caves in Quintana Roo, Mexico, a distribution suggesting a tethyan origin.

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 blindsnake, *Ramphotyphlops longissimus*, from the Barrow Island karst has apparent troglomorphies and may represent the first troglobitic 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 encompass insectivorous and vertebrate predators (ghost bats, *Macroderma gigas*) and frugivorous bats. Six species are restricted to the Cape York peninsula and 11 species occur across the northern part of the continent, 2 of them extending in the west coast to the arid Pilbara region. Only 4 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 anchialine waters comprise species congeneric with those inhabiting caves on either side of the North Atlantic.

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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 a both a hot spot of subterranean biodiversity and a hot spot 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*. The only stygobitic salamander in European, *Proteus* 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, Bosnia, and Herzegovina. During the late 18th century and much of the 19th 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-19th 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 Jeannel, as well as Pierre-Alfred Chappuis and Louis Fage, he established in 1907, an association named *Biospeologica*. This association had three objectives: (1) to explore caves and look for subterranean species, (2) to obtain identifications and descriptions from specialists for all material sampled, and (3) to publish results in the *Mémoires de Biospeologica*. Ultimately, Biospeologica was responsible for the inventory of the fauna of more than 1500 caves, mostly in Europe. More than 50 monographic treatments of the taxonomy and distribution of European cave fauna were published between 1907 and 1962.

Even with more than a century and a half of description and cataloging of the European subterranean fauna, both species descriptions and inventories are far from complete. At present, several large-scale inventory projects of European fauna are ongoing. The most important of these is PASCALIS (Protocol for the Assessment and Conservation of Aquatic Life in the Subsurface), which has developed common protocols for the comparison of subterranean aquatic species diversity at six sites in five countries (France, Spain, Belgium, Italy, and Slovenia). Individual country assessments of subterranean biodiversity are active as well, and at the beginning of the project the most advanced of these was in Italy, where there were more than 6000 records for 899 subterranean species.

DIVERSITY COMPARISONS TO OTHER CONTINENTS

As of 2000, approximately 5000 obligate subterranean aquatic (stygobitic) and terrestrial (troglobitic) species from Europe had been described. By contrast, 1200 have been described from Asia, 500 from Africa, and 1000 from North America. The dominance of Europe in known subterranean species is the result of several factors. First, Europe has been better studied than the other continents. This is particularly evident in the status of biodiversity assessment in noncave subterranean habitats. About half of the stygobitic species known from Europe are not primarily cave-dwellers, but rather live in other subterranean habitats such as the underflow of streams. In North America, these habitats are little studied and account for less than a fifth of the known stygobionts. The terrestrial equivalent, the M.S.S. (*milieu superficiel souterrain*), accounts for half of the subterranean species richness in Italy and this habitat is unsampled in