

5

The crawling, creeping and swimming life of caves

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They are found ... in the dark recesses of caverns and of the waters under the earth, where no storm ruffles the everlasting stillness, no light illuminates the thick darkness, and no sound breaks the eternal silence. (Chilton, 1894:273).

Introduction

The first scientists to study subterranean life in Australia ascertained that caves in Australia, like those elsewhere, contained species of great interest and significance to biology. As early as 1883, Higgins and Petterd recognised the primitive affinities of the large Tasmanian Cave spider, *Hickmania troglodytes* (see plate 28). At about the same time, Charles Chilton pioneered the discovery of aquatic life forms from Australian and New Zealand underground waters. These early biospeleologists observed the specialisation of animals to underground life, and recognised that frequently they belonged to ancient and relict groups of great value to studies in adaptation and evolution.

Until very recently, the subterranean fauna of Australia was perceived as being poor compared with the well-studied caves of Europe and North America. However, during the past decade, in particular, that perception has been overturned by dramatic discoveries that have firmly propelled Australian biospeleology into the international scientific limelight. In this chapter we attempt to give the reader an understanding and appreciation of subterranean fauna in Australia, and the implications that this research has within a wider context.

The classification of subterranean animals

It has been found useful to classify animals according to their presumed degree of ecological/evolutionary dependence on subterranean environments. Some species are found only underground, while others move in and out of the underground environment at various times. A lexicon of terms has been developed to describe these relationships, based on morphological, behavioural and ecological adaptations of animals to underground life, and on their presence or absence in caves.

Troglobites are species that obligatorily spend their entire lives within caves and other subterranean habitats (note that troglodytes are people who inhabit caves). Troglobites are distinguished by the possession of clear morphological modifications that suit them to subterranean life. These modifications typically include the reduction, and often the complete loss, of eyes and body pigment. Troglobitic adaptations also

include the lengthening of appendages, and enhancement of non-optic sensory structures, such as antennae and sensory hairs. Collectively, these traits are referred to as troglomorphies (literally, cave forms). Troglobites can often be distinguished by their pale and fragile, almost ghost-like, appearance, for example, *Nocticola flabella* (see plate 23), the world's most troglomorphic cockroach from Cape Range, Western Australia.

Troglobites are highly specialised to life underground. They can endure prolonged periods of starvation in the generally food-poor regions of the deep cave zone, where other animals could not survive. At the same time, during the course of their evolution in the underground environment, troglobites have experienced reduced capacity to withstand environmental fluctuations, such as temperature and humidity for instance, so they are particularly sensitive to environmental perturbations. Because of the limited potential for dispersal or survival in surface habitats, troglobites generally have very limited distributions, often being confined to a single cave system or single karst area. Troglobites are of considerable interest to scientists because of their degree of specialisation, and because they are frequently found to be relicts that have survived in underground refugia long after their surface-dwelling ancestors have become extinct.

Troglophiles are facultative cave-dwelling species. They are found living permanently, and successfully completing their entire life cycles, in caves, but they also do this in suitable surface habitats. The Tasmanian Cave spider (see plate 28) is an example of a troglophile. Populations of this species occur both in caves and in similar cool, dark and moist surface habitats, such as hollow logs in forests. If they are prevented from interbreeding with their surface populations, some populations of troglophiles may eventually evolve into troglobites. This may occur, for example, if the surface populations become extinct or migrate elsewhere when conditions change on the surface.

Trogloxenes are species habitually found in caves but they do not complete their whole life cycle there and must return periodically to the surface or entrance zone for food. Cave-dwelling bats are trogloxenes, as are some cave crickets found in cave and bush habitats across southeastern Australia (see plate 30). During the day these moisture-loving insects tend to congregate in nooks and crannies inside the cave, away from the light and away from air currents that threaten them with desiccation. At dusk, or later, part of the cricket population moves outside the cave entrance to feed on vegetation, such as mosses or liverworts, or to scavenge dead or dying invertebrates, but they return underground before dawn.

Accidentals are species that wander, fall or are swept into caves. They survive for varying lengths of time, and larval forms may metamorphose to the adult, but further generations are not established within the cave.

Both accidentals and trogloxenes are influential in transporting food energy into caves, either through their excreta and carcasses, or as live prey for the permanent cave inhabitants, the troglophiles and troglobites. Bats and swiftlets are important because of the large quantities of guano (excreta) that they deposit in some Australian caves. Distinct communities of invertebrates are found associated with the bat guano and these animals are termed guanophiles.

There exist a number of sub-categories and variations to the classification scheme outlined above, but the other major categorisation is whether the fauna inhabits air- or water-filled subterranean habitats. While the term troglobite can apply to obligate inhabitants of both habitats, the term stygo- (hence, stygoxene, stygophile, stygobite) is used in preference for those species inhabiting underground waters of various kinds. Hence, stygofauna refers to subterranean aquatic fauna generally while the prefix troglo becomes restricted to terrestrial systems. One problem with the classification scheme, aside from the sometimes confusing terminology, is that it is not always possible

to assign an organism to the correct ecological category without a thorough knowledge of its distribution and life history. For most species of invertebrates this information is not available, nor can it be obtained without detailed study. Moreover, characteristics such as the reduction of pigment and eyes are not confined solely to troglobitic organisms. There are a great many animals living in similar habitats, such as soil and termite mounds, underneath stones, or within the layer of ground litter in forests, that are similarly depigmented and eyeless. As well, entire lineages may lack eyes, whether or not they inhabit caves; for example, the lineage to which the Cape Range troglobitic millipedes belong (see plate 26). However, these millipedes have other attributes that define them as troglomorphic, such as very elongate segments and legs, and a fragile exoskeleton.

Evolution of troglobites

Explaining the origins and geographic distributions of troglobites and stygobites has important general implications for evolutionary biology. Troglobites and stygobites have evolved from surface-dwelling ancestors that were already pre-adapted for life in a subterranean environment. They belong to animal groups that are well represented in the moist soil and ground litter of forest floors, or in streambeds, swamps, groundwater and marine crevice habitats. Animals living in these habitats frequently have reduced eyes and pigment. Under the right conditions it would be relatively easy for populations of these animals to colonise subterranean voids, while subsequent genetic isolation of the colonisers, followed by adaptive changes that further suit them to life underground, could lead to the evolution of distinct species.

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. Consequently, subterranean environments make ideal refugia for animals that, if they are unable to adapt to changing conditions on the surface, must migrate elsewhere or face extinction. So subterranean faunas often contain lineages of great antiquity that have been protected underground despite major surface perturbations in climate, geology, geomorphology, geographic position and altitude. As their powers of dispersal are very limited, their present affinities and distributions may contain a great deal of information about past geography and climates. In this respect aquatic subterranean faunas hold a special significance because, unlike terrestrial troglobites, the aquatic troglobite faunas (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 faunas occurred through rafting on tectonic plates moved by seafloor spreading. Recently, a number of notable discoveries of such relict faunas have been made in Australia; their geographical distribution and lifestyles suggest origins variously in Pangea, Gondwana, Eastern Gondwana and the Tethys Sea.

Continental drift and climate change

The composition of Australian cave fauna reflects the movement of the continental fragments over long periods of geological time as well as climatic changes over millions of years. Australia was originally part of the supercontinent Pangea which, simply stated, separated into a northern section and a more southerly part termed Gondwana. Between these sections the Tethys Sea formed. Australia is a fragment of Gondwana, along with Africa, India, Madagascar, South America and Antarctica. Gondwana itself fragmented and Eastern Gondwana (India, Antarctica and Australasia) became isolated

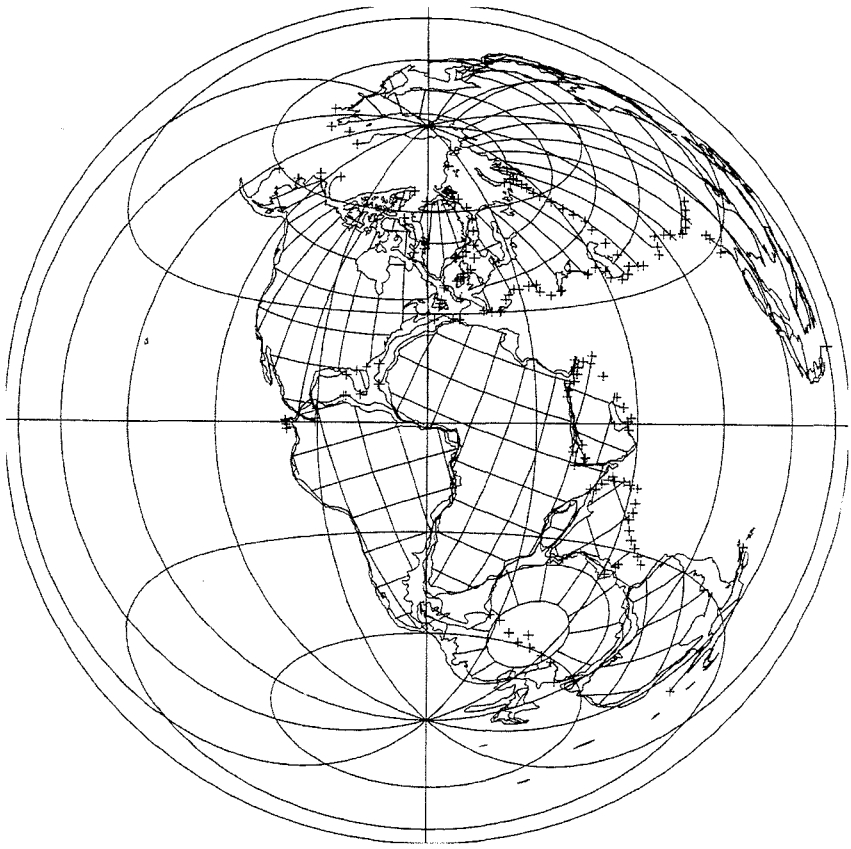


FIGURE 5.1

The relative location of the continental plates and the extent of the epicontinental seas in the Jurassic (151 mya) when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. *Hurley and Smith, 1981*

from South America and Africa about 133 mya. By the Upper Cretaceous (circa 80 mya), 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 mya), both lands were well watered and supported cool temperate and subtropical forests.

The quite rapid northward drift of Australia toward southeast Asia during the Tertiary led to the formation of the Southern Ocean seaway. The resulting circum-Antarctic ocean currents and winds markedly altered the climate of the Southern Hemisphere and Australia became much drier. The formation of the Antarctic ice cap 15 mya 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 cyclical fluctuations, superimposed upon a generally increasing and spreading aridity, provided conditions under which subterranean refugia played an important role.

Terrestrial troglobites

As the affinities of so many of the Australian terrestrial cave faunas lie with wet forest litter, increasing aridity during the Tertiary is likely to have been pivotal in the evolution and isolation of much of the Australian cave fauna, just as it resulted in the

massive contraction and latitudinal shift of the forest cover over much of mainland Australia. Aridity, combined with cold and windy conditions, has probably also been influential in the evolution of Tasmanian cave fauna, despite the island's more humid climatic history and episodes of Pleistocene glaciation.

A number of theories have been proposed to explain cave colonisation and troglobite evolution, the most compelling of which is the active colonisation of a vacant niche. However, in the history of Australian cave biology, the two theories of most relevance are the Pleistocene-effect theory and the adaptive-shift theory. Both theories have been applied in attempts to explain the evolution of Australia's cave fauna, with research conducted in Queensland contributing substantial evidence used to support the latter theory. However, a great deal more research is required before complete and adequate explanations can be given. In view of the variety in geological structure, geomorphic and climatic history, and the fauna that has colonised caves in different regions, it is unlikely that a single mechanism for the evolution of the fauna is applicable.

THE PLEISTOCENE-EFFECT THEORY

The pioneering studies of cave life were predominantly carried out in the karst areas of Europe and North America, areas directly or closely associated with regions repeatedly covered by ice during the Pleistocene. Hence, the effects of glaciation came to dominate the debate about both the distribution and the origin of troglobitic animals. The classic view of the evolution of terrestrial troglobites is, in essence, that climatic instability in the surface environment — especially changes to cold and arid conditions associated with the onset and retreat of Pleistocene glaciations — led to the extinction of surface populations of species that mostly lived in forest soil and litter. This process disrupted interbreeding between the various troglphilic populations and permitted adaptation to the cave conditions in the now-isolated cave populations.

The first troglobitic species discovered in Australia was a beetle, *Idacrabus troglodytes*, from Tasmania. Up until the 1960s, Tasmania had revealed a fauna of troglobitic beetles and other arthropods, while the rest of the Australian cave fauna appeared to be poor in troglobites. Only Tasmania and a small area of the Eastern Highlands were directly subject to glacial ice cover during the Pleistocene. The Pleistocene-effect was used to explain the evolution and distribution of the cave fauna as it was then known. So dominant was this theme — that glacial cycles were the driving force for the evolution of troglobites — that it was widely held that the tropics, where such effects would be minimal, would contain few troglobites. At that stage, only six troglobitic species were known. It was then argued that the lack of troglobites may have resulted from extinction of a supposed earlier fauna both through cave flooding and subsequent extreme aridity during the Quaternary. These views echoed the European paradigm that the climatic changes associated with the ice ages during the Pleistocene had been the driving force for cave colonisation and hence that the history of cave biology was essentially a Quaternary phenomenon, occurring during the past 1.8 million years. During the past decade or so, however, the discovery of rich troglobitic faunas in the tropics of Australia and elsewhere has altered some of these earlier notions. Australia is now known to hold some of the richest cave faunas and some of the most ancient subterranean species in the world.

Despite these advances in knowledge, climatic change and aridity have still clearly played a pivotal role in shaping the evolution of the Australian cave fauna, just as aridity has so profoundly shaped the surface fauna and flora. Despite the limited land areas directly subject to glaciation, Australia has experienced an enduring trend of recurrent and increasing aridity through the Cainozoic era, the past 65 million years. Aridity has

caused a gross retraction in range of moist forest and aquatic habitats, thus isolating cave populations from their founding surface populations. In Australia, the expansion and contraction of the area covered by forests would have been further enhanced because, during much of the critical time (the past 25 million years), the Australian continent was moving at relatively high speed toward southeast Asia, positioning Australia closer to the equator and causing increased aridity.

DISTRIBUTION PATTERNS IN TASMANIAN CAVE FAUNA

A number of Tasmanian cave species, particularly the beetles and arachnid harvestmen, display the disjunct and highly localised distribution patterns typical of cave faunas. The harvestmen and beetles are lineages in which isolation and extinction of the surface fauna during climate changes that occurred in the Quaternary Era (1.8 mya to the present) have been invoked to explain their evolutionary development. The speciation patterns observed in the cave beetles could have resulted from population fragmentation owing to the extinction of once-widespread surface-dwelling ancestor(s) brought about by the climatic and vegetation changes occurring during glacial episodes in the Pleistocene. Glacial conditions may have caused extinction of fauna in some alpine karsts as well as having contributed to the isolation and speciation of cave faunas in peripheral karsts. In these areas, where climatic conditions were less extreme, advance and retreat of the forest cover may have driven the evolution of troglodites, as in the classic model.

Tasmanian cave beetles belong to the Family Carabidae (ground beetles), a group with moisture-loving and ground-dwelling habits. One group of the cave beetles belongs to the genus *Idacarabus*, which is endemic to Tasmania. All species within this genus are exclusively trogloditic and are found only in the mountain karsts of southern and central Tasmania. The distribution of each species is limited to a single karst area. *Idacarabus troglodytes* is restricted to the Ida Bay karst, while *I. cordicollis* and *I. longicollis* occur at Hastings and Precipitous Bluff respectively. These three separate karst areas are situated within about 20 kilometres of each other, but the more southerly and westerly located karsts were subject to more intense glacial effects. That these three species form a series with decreasing troglomorphy, over a small arc from southwest to northeast, may reflect the length of time the separate populations have been confined to caves in the three localities. This distribution parallels the palaeoclimatic gradient suggested by a northeastward rise in cirque floor altitudes across southwestern Tasmania. Glaciers are likely to have formed earliest and persisted longest in the southernmost cirques.

The above hypothesis remains to be tested, but similar distribution patterns are seen in other groups of Tasmanian cave beetles and cave harvestmen. The fully trogloditic beetles, *Goedetrechus mendumae* and *G. parallelus*, occur in southern Tasmania, where Pleistocene glacial climates and vegetation changes were most extreme, while a third species, *G. talpinus*, dwells in forest soil and litter habitats in northeast Tasmania where glacial influences were more moderate. Similar patterns are seen within the harvestman group of arachnids. The speciation of *Hickmanoxyomma* could have resulted from population fragmentation owing to the extinction of once-widespread forest-dwelling ancestor(s) brought about by the climatic and vegetation changes occurring in the Pleistocene. Seven species of *Hickmanoxyomma* have been described, including surface-dwelling, troglodilic and fully trogloditic forms.

In the mountainous regions, where glacial and periglacial conditions were more extreme, *Hickmanoxyomma* species are exclusively cavernicolous (cave-dwelling). However, in the northern coastal lowlands, where climatic conditions were more moderate, the surface-dwelling *H. tasmanicum* occurs. The dispersal ability of *Hickmanoxyomma* species appears to be very limited as populations of *H. cavaticum*



Australia's first known terrestrial troglobite is the cave beetle, *Idacarabus troglodytes* (length about 10 millimetres). The eyes are reduced and the reddish-brown coloration indicates some loss of pigment. *Idacarabus troglodytes* is endemic to the Ida Bay karst in Tasmania. Photo: Stefan Eberhard

located only 3 kilometres apart seem from genetic studies to be completely isolated. In the Precipitous Bluff karst, the distributions of two troglobitic species, *Hickmanoxyomma cristatum* and *H. clarkei*, overlap, which may suggest two separate phases of cave invasion consistent with geomorphic evidence for multiple episodes of cold glacial climate.

THE ADAPTIVE-SHIFT THEORY

This theory offers an alternative explanation to the Pleistocene-effect theory for the evolution of troglobites. The presence of cave-adapted species in tropical latitudes, where climate and vegetation changes associated with glacial/interglacial cycles would have been strongly moderated, suggests that the extinction of surface populations may not be necessary for the evolution of troglobites. In both northeast Australia and Hawaii, closely related surface relatives of troglobites still exist in nearby surface habitats, hence, rather than being relicts isolated in caves by changing climate, such troglobites may have actively colonised caves through a process called adaptive-shift. The process invokes active colonisation of subterranean habitats by surface populations. The adaptive-shift theory was then proposed to account for specialised cave species that appeared to have evolved from species that are frequent accidentals in underground environments. If these accidentals find sufficient food resources, eventually some of them may make an adaptive shift and establish a population that, if successful, may genetically diverge from its parent population. Thus, some troglobites are closely related to species that can still be found living on the surface near the caves.

Research in the Undara lava tubes of far north Queensland provided additional evidence to support this theory. At Undara, a great diversity of planthoppers with closely related surface- and cave-dwelling species have been discovered. Further research is required to see if the adaptive-shift theory can be applied more widely to explain the evolution of tropical troglobites elsewhere. In view of the variety in geological structure, geomorphic and climatic history, and the fauna that has colonised caves in different regions of Australia, it is unlikely that a single mechanism for the evolution of the troglofauna will be found to apply.

Evolution of aquatic troglobites (stygobites)

Aquatic subterranean faunas have a special significance because, unlike terrestrial troglobites, the aquatic troglobite faunas (stygobites) contain many relict species that are only distantly related to surface forms. Stygofauna may have colonised subterranean waters directly from marine habitats or indirectly via surface freshwaters. Most stygofauna are crustaceans, including some major evolutionary lineages that survive today only in subterranean waters. There are also some stygobiont species with close relatives living nearby in surface waters.

MARINE RELICTS

Stygobites of marine origin are thought to have become isolated inland following the retreat of the sea, for example, during ice ages. A species of amphipod crustacean, *Nurina poultera*, (see plate 29) is an example of a marine relict stranded inland by changes of sea level. It occurs in the groundwater of caves on Western Australia's Roe Plains, which are low-elevation plains less than 20 metres above current sea level. The plain was eroded into the limestone cliffs of the Great Australian Bight and Nullarbor Plain, which forms a more extensive and higher plateau surface about 100 metres above sea level.

Nurina poultera belongs to a family of predominantly marine stock, the Melitidae. It seems likely that the ancestors of *N. poultera* colonised groundwaters from the sea, when the Roe Plains were inundated after a 30-metre-high sea level rise during the late Pliocene and early Pleistocene, about 2 mya. The higher plateau surface of the Nullarbor Plain was not inundated by the sea at this time, but has remained emergent since Miocene times about 15 mya. Thus, the distribution of the amphipod does not extend into the groundwaters of caves beneath the elevated plateau, and intensive searching has failed to identify any aquatic fauna apart from micro-organisms.

Other melitid amphipods, however, are found at higher altitudes. The endemic genus *Norcapensis* is known only from several caves at altitudes of about 200 metres in Cape Range. Its ancestors were probably elevated to this altitude by the mountain-building processes that formed the Cape Range anticline from marine limestones of Miocene age. Similarly, the inland extent of the groundwater-inhabiting crustacean order Thermosbaenacea in northwestern Australia reaches an altitude of about 300 metres above sea level, possibly as a consequence of stranding after a marine incursion during the Eocene.

Marine stranding or colonisation events may be much more ancient than the case of *Nurina poultera*, however, while the presence of presumed ancient troglobitic lineages in geologically much younger rocks requires that some movement through underground dispersal routes must have occurred through geological eras, as proposed for the Cape Range Tethyan fauna. The Tethyan fauna from Cape Range is closely allied with similar species elsewhere found only in caves on either side of the North Atlantic; their distribution is consistent with the hypothesis that tectonic plate movement was the isolating mechanism (Figure 5.1). As they contain solely troglobitic lineages, they were presumably present in subterranean habitats before Australia broke free of Gondwana and prior to the opening of the Atlantic Ocean in the Jurassic. The ancestors of at least one lineage, the ostracod crustacean genus *Danielopolina*, were already inhabiting sub-marine caves in the northern Tethys Sea in the Upper Jurassic, about 150 mya.

ANCHIALINE ECOSYSTEMS: ANCIENT TETHYAN RELICTS

Anchialine ecosystems have been described only in the past two decades. These inland groundwater systems have limited surface connections and are affected by marine tides. They usually show strong stratification in the water column, with sharp gradients in

physical parameters (for example, temperature and pH) and chemical parameters (for example, salinity, hydrogen sulfide) between the different water layers. They are best observed in cavernous rocks, either limestone or lava, which can be entered by cave divers. In the past decade at least ten new families of crustaceans have been described from anchialine systems, including a new class of organism, the Remipedia.

Living remipeds were described in 1981 from the Bahamas, where they were collected from anchialine caves by divers — to this day they have only ever been collected by cave divers. They caused great scientific interest because, unlike other crustaceans such as crabs and shrimps, the head region was followed by a series of undifferentiated appendages or paddles (remiped means ‘oar foot’) running along the length of the body. Thus, they seem to be similar to a hypothetical ancestor to all crustaceans — a so-called ‘missing-link’. About ten species of remipeds belonging to several genera are now known from the Caribbean region, both from islands and Quintana Roo, Mexico, but mostly from the Bahamas Bank, which once was part of the mid-Atlantic ridge.

The finding of a new species in a lava tube on Lanzarote, Canary Islands, led to the hypothesis that remipeds were already living in caves before the development of the North Atlantic during the Jurassic, more than 150 mya. They are thought to have dispersed subsequently by rafting on the tectonic plates (Figure 5.1).

In 1996 a new species of remiped, belonging to a genus previously known from Turks and Caicos on the Bahamas Bank, was described from the Cape Range peninsula in northwestern Australia (see plate 27). If the distribution of remipeds occurred by rafting on the tectonic plates, as suggested for those on either side of the North Atlantic, then, owing to the sequence in which the continental plates separated, the Australian remipeds are likely to be ancestral to those in the North Atlantic. Indeed this seems to be the case in two other better-studied species with similar distributions, an ostracod and a thermosbaenacean. The ancestors of at least one of the lineages present on Cape Range, the ostracod *Danielopolina*, already inhabited marine caves during the Jurassic in a northern branch of Tethys (now the Czech Republic). The remiped site at Cape Range and the associated ecosystems have yielded at least seven lineages of crustaceans with similar associations with the North Atlantic, including copepods, amphipods, ostracods, thermosbaenaceans and isopods. To date remipeds are known from a single Australian locality, one that is both highly complex in its physico-chemical structure and vulnerable — it is fully protected under both state and commonwealth legislation.

FRESHWATER RELICTS

Subterranean waters may be colonised by animals living in surface freshwater habitats, or from neighbouring near-surface aquatic habitats, such as the loose gravels beneath and alongside river beds (hyporheic habitats), and other porous unconsolidated sediments (interstitial habitats). Surface fauna may enter deep groundwater habitats where these habitats are in continuity with shallow groundwaters and surface waters, or at points where streams are captured underground, or where springs emerge. These subterranean founder populations may become isolated in underground waters by subsequent down-cutting and lowering of groundwater tables, or by regional uplift and alteration to stream-flow patterns. Cave colonisation and subsequent differentiation of the populations can also occur, actively and repeatedly from adjacent surface populations, even in the absence of physical barriers to dispersal. Directional selection leads to convergent evolution of troglomorphic characters, but the process is not necessarily unidirectional, and troglomorphies may be lost if the populations again become surface-dwellers.

The Syncarida are a group of Crustacea that are well represented in Australian groundwaters and caves. Most syncarid species are entirely subterranean, and their biogeography is explicable if they entered Pangean freshwater before the Triassic and were subsequently dispersed on the continental fragments. The Syncarida are one of the most interesting invertebrate groups in Australian inland waters because they formed a separate branch of crustacean evolution at a very early period, perhaps as far back as the late Devonian (circa 360 mya).

Syncarids are of great interest to zoologists because they are regarded as structurally similar to the ancestral higher crustaceans, such as crabs and crayfish. Syncarids have a relatively simple body form and appendages, suggestive of a primitive condition. They have remained basically unchanged for millions of years — modern syncarids closely resemble fossil forms found in Triassic (248–206 mya) rocks. Living specimens of the two major groups of syncarids, previously known from fossils, were first discovered in the late 19th century, the Bathynellacea in a Prague aquifer in 1882 and the Anaspidacea in Tasmania in 1893. Only in the wetter environments of Tasmania have syncarids managed to survive in surface waters. The Tasmanian mountain shrimp, *Anaspides tasmaniae*, inhabits upland streams and pools, as well as cave waters. The cave populations are slightly depigmented from living in darkness, but they still retain their eyes (see plate 25). Outside of Tasmania, most other species of syncarid have been restricted to subterranean environments for a very long time, so they are completely depigmented and have lost all trace of eyes (see plate 24).

The variety of subterranean habitats

Australia holds a great variety of subterranean habitats, which are discussed in more detail below with emphasis upon relevant Australian studies. The study of troglobites and the fauna restricted to caves were, for centuries, synonymous, because such caves were where people accessed the underground to study the fauna. However, it is now appreciated that:

- 1 most caves do not have surface openings;
- 2 the vast bulk of subterranean voids comprise air- and water-filled spaces much too small for people to enter — the so-called mesocaverns and microcaverns;
- 3 the major habitat of most subterranean species is probably the mesocaverns and microcaverns rather than the macrocaverns, or caves per se;
- 4 many species found in these alternative habitats are not found in caves at all;
- 5 there is a continuum of underground spaces, both air- and water-filled, that merge, often imperceptibly, with surface habitats;
- 6 processes and changes occurring in surface habitats may affect subterranean habitats, and vice versa; and
- 7 far from being totally dependent on surface inputs, some terrestrial and aquatic ecosystems are fuelled by chemical processes originating underground (chemoautotrophic systems) independent of surface inputs.

These realisations were investigated initially by European biospeleologists. However, a number of Australian studies have supported them and contributed additional information, which has both extended the field of subterranean biology and the range of plausible hypotheses pertaining to the dispersal and evolution of subterranean fauna.

Subterranean habitats may be classified according to the size of the air- or water-filled voids. The voids inhabited by animals range in size from minute cavities less than a millimetre in size (microcaverns), through cavities 1–200 millimetres in diameter (mesocaverns), up to larger caverns tens of metres in extent (macrocaverns). There is a continuum of void sizes, but the preferred habitat of many terrestrial troglobites appears to be the smaller, so-called mesocavernous voids where the microclimatic conditions tend to be most stable.

The discovery of mesocavernous habitats had wide implications for our general understanding of the nature of underground habitats, and had a strong influence on theories concerning the distribution and migration of subterranean animals among different cave systems. It means that macrocaverns represent a tiny fraction of the total subterranean habitat space, and caves that are large enough for humans to enter can no longer be considered to discrete 'island-like' refugia. Research in Queensland has added to our understanding of the nature of mesocavernous habitats.

Terrestrial habitats

The terrestrial cave environment is strongly zonal, with four major zones being recognised — entrance, twilight, transition and deep zone. Some caves contain a fifth zone — the stagnant-air zone, characterised by elevated concentrations of carbon dioxide and lowered oxygen levels. The entrance zone is where the surface and underground environments meet each other. Beyond the entrance is the twilight zone, where light progressively diminishes to zero. The transition zone is totally dark but environmental effects from the surface are still felt. In the deep zone, environmental conditions are relatively stable, with a fairly constant temperature (usually approximating the mean annual surface temperature) and with relative humidity near saturation, resulting in an extremely low rate of evaporation.

The extent of the different zones depends on the size, shape and location of the entrance(s), on the configuration of the cave passages, and on the subterranean moisture supply. The boundary between the transition, deep and stagnant-air zones is dynamic, changing on a seasonal or even daily basis, as air is pushed into and pulled out of caves in response to changes in air density related to temperature and barometric pressure fluctuations on the surface (see plate 3). In temperate regions caves are generally cooler than the outside air in summer and warmer in winter. The resulting vapour pressure gradients tend to humidify caves in summer and dry them in winter. In the tropics, where average seasonal temperature differences are more muted, 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 vapour leaves the cave along the vapour pressure gradient — the so-called 'tropical winter effect'.

The distribution of terrestrial cave fauna is strongly influenced by the cave zonation. Troglobites are usually restricted to the deep zone, and the most critical environmental factor governing their distribution appears to be the stable saturated atmosphere. However, many troglobites migrate closer to the entrance, even into full sunlight under suitably humid conditions, and further into the cave as the passages dry out. Many troglaphiles and troglonexes are also prone to desiccation outside of the moist and sheltered cave environment. The stagnant-air zone may be quite significant for the distribution of some troglobites, as suggested by research conducted at the Undara lava tubes.

THE STAGNANT-AIR ZONE

Research in the lava tubes of Hawaii and at Undara clearly showed the relationship between the different cave zones, entrance, twilight, transition and deep zones, and this work is significant in suggesting a fifth cave zone — the stagnant-air zone. At Undara, this zone contains a distinct and specialised fauna which, it is hypothesised, is tolerant not only of perpetual darkness, but also of the low food supply, elevated carbon dioxide and depressed oxygen levels, in which other species would not survive.

The discovery helped the development of ideas on the distribution and migration of fauna within the so-called mesocavernous voids (see above) of fractured rocks, such as basalt. Too small for humans to enter, these voids represent an enormous volume available for colonisation by subterranean species and also represent a potential underground migration route between different 'cave' systems. It was observed that extremely troglomorphic species were rarely seen in large cave passages — and then only when there were high carbon dioxide levels, low oxygen levels and saturated humidity — and so it was postulated that the preferred habitat of the most troglomorphic 'cavernicoles' was the mesocavernous voids rather than caves in the strict sense.

Aquatic habitats

Aquatic subterranean habitats encompass the underground streams, pools and seepages of the vadose zone (occurring above the level of the watertable) within caves. These may merge with interstitial, phreatic, groundwater, and anchialine habitats. Subterranean aquatic habitats connect with surface habitats at places where water sinks underground, and where it reappears at the surface. These include the sinking points of streams and diffuse seepage, as well as at springs (including mound springs and tufa dams), cenotes (flooded sinkholes) and anchialine pools. Surface waters merge imperceptibly with groundwaters in porous sediments beneath and alongside surface watercourses (interstitial/hyporheic habitats). The microcavernous voids (see above) that exist within riverine gravels, for example, frequently support a specialised but abundant interstitial stygofauna.

Anchialine describes inland groundwaters with minimal surface connection that are affected by marine tides and which have both freshwater and marine influences.

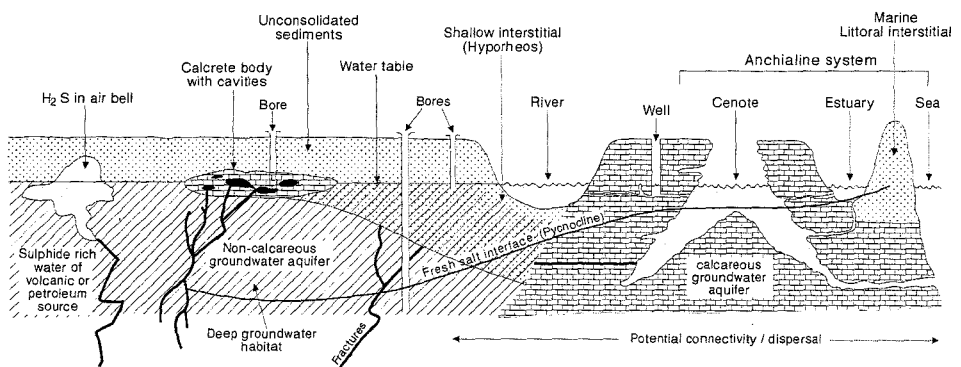


FIGURE 5.2

Schematic cross-sectional representation of the variety of groundwater ecosystems. The size of water-filled subterranean spaces inhabited by stygofauna range in size from intergranular pore spaces between particles of unconsolidated sediment (interstitial habitats), through fissures and fractures, to large open conduits explored by cave-diving.

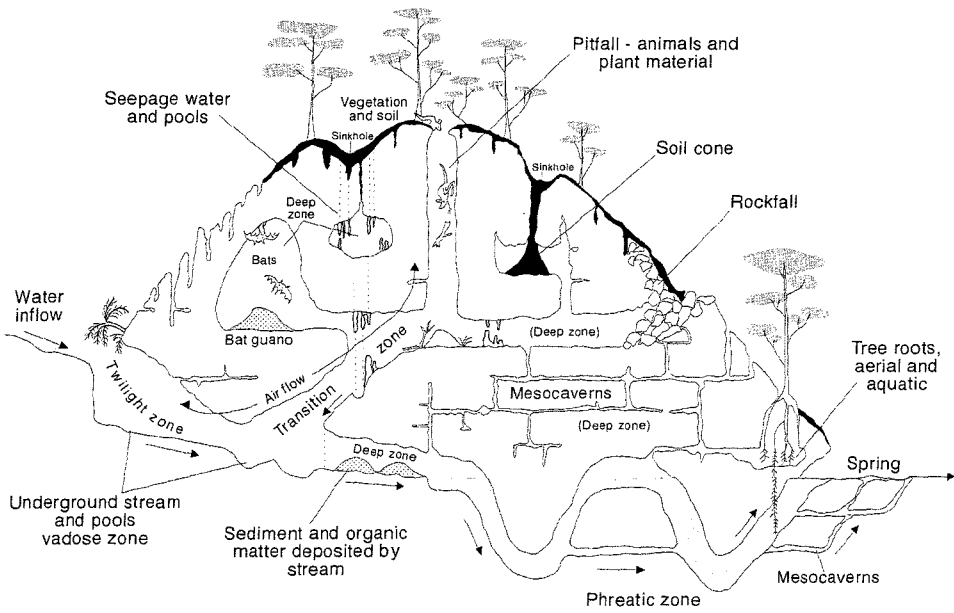


FIGURE 5.3
Schematic cross-sectional representation of a fluvial karst system showing cave environment zones (entrance, twilight, transition and deep); types and structure of different fauna habitats; inputs, through-flow and outputs of water, air, sediment and organic materials.

Typically they consist of a freshwater lens overlying a deeper layer of seawater. They exhibit strong vertical stratification with respect to temperature, salinity and other physico-chemical parameters. These recently recognised groundwater ecosystems form subterranean estuaries at the interface between continental and marine systems and have been found to contain relict faunas of great scientific and conservation significance. The only continental anchialine ecosystem known in the southern hemisphere occurs in the Cape Range karst. This site is inhabited by a widely disjunct, but recognisable and predictable community, known elsewhere only from caves on either side of the North Atlantic. This specialised, evolutionary and distributional relictual fauna comprises mainly obligate stygobiont taxa containing several species that are very closely related but now widely dispersed geographically.

These many and varied groundwater habitats that feature so prominently in karst biology investigations in the Northern Hemisphere have been little investigated in Australia, but recent research has revealed a rich and interesting stygofauna. Of particular relevance in this regard is the recent discovery of an exceptionally rich stygofauna associated with calcrete aquifers in Australia's arid regions. The variety of submerged underground habitats in karst and non-karst environments is depicted schematically in Figure 5.2, while the variety of subterranean habitats (and food inputs) in a generalised fluvial karst ecosystem is depicted in Figure 5.3.

CALCRETE AQUIFERS

Calcrete is a sedimentary carbonate rock that forms at or near the watertable in arid regions. Groundwater calcretes form in Australian arid regions where the low rainfall (about 200 millimetres per year) is less than 10 per cent of the potential evaporation, the movement of the groundwater is slow and the rainfall is episodic so that the watertable fluctuates. Karst development that occurs near the watertable provides an ideal habitat for stygofauna.

The archaean rocks of the Western Shield of Australia (comprising both the Pilbara and Yilgarn Cratons and associated basins) are furrowed by palaeo-drainage systems that predate the separation of Australia from Antarctica. Most of the palaeodrainage systems are inactive (those draining to the interior of the continent) or are over-large for the rivers they now contain (for example, the Fortescue and Murchison rivers, both of which drain to the Indian Ocean).

Calcrete deposits occur intermittently along these palaeodrainage systems and are associated with the salt lakes or playas. Rainfall recharges the groundwater at, for example, alluvial fans, and moves imperceptibly downgradient toward a salt lake, gradually approaching the surface through which evaporation occurs. This results in the deposition of carbonates. This process is associated with major changes in the groundwater chemistry and the water progressively changes from fresh to hypersaline. This process is repeated at intervals down the length of the palaeochannel and consequently a series of isolated calcrete deposits forms.

These isolated calcrete aquifers, islands in the desert, promote speciation in the fauna, with each major calcrete body examined so far containing a separate and unique complement of species. In the past few years a hitherto largely unknown, but remarkably diverse and significant groundwater calcrete stygofauna has been revealed within Australia. The fauna as known so far includes some highly relictual and ancient groups of Crustacea, in addition to a diversity of stygal water beetles that is the richest known in the world. The calcrete aquifer at Millstream, Western Australia, for example, contains a diverse aquatic fauna first discovered in late 1996. This comprises Gondwanan

relicts, including Spelaeogriphacea, an order of crustaceans previously known only from caves in South Africa and Brazil. The extent of groundwater calcrete aquifers in Australia has as yet been barely examined biologically, and many more discoveries are expected.

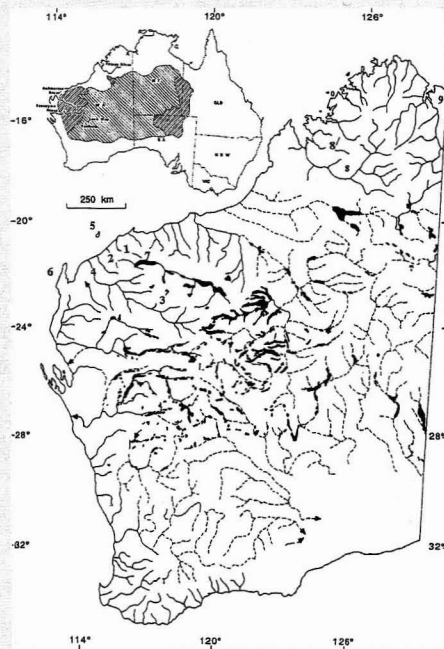


FIGURE 5.4

The distribution of groundwater calcrete (limestone) aquifers in Western Australia. Groundwater calcrete is deposited from the groundwater flow as it nears the surface immediately upstream of salt lakes (playas). Inset: The general distribution of groundwater calcrete in mainland Australia. *Humphreys 1999*

Food and water

The energy (food) sources for subterranean ecosystems are largely derived from the surface and carried underground by water, gravity, air currents and animals. The food resources in Australian caves include bat and swiftlet guano; tree roots that penetrate into cave passages; surface 'accidentals'; and, especially, plant matter such as wood and leaves. Plant material falls into cave entrances or is carried deep underground by water, while seepage water transports underground fine particulate organic matter and dissolved nutrients. Energy is transported underground through the daily movements of trogloneic animals, such as cave crickets and bats. Excreta, nest material and carcasses of vertebrates utilising caves for shelter (for example, swallows, owls, wombats, possums, platypus and rodents) also constitute a food resource. Different types of food resources are colonised by different animals and, while many species are generalists, others are restricted to a particular food type. Food resources in the deep cave zone are often scarce and usually patchily distributed, an exception being caves with large bat or swiftlet colonies, where guano deposits support abundant populations of guanophiles. Some of the variety of food inputs into a generalised fluvial karst ecosystems are shown in Figure 5.3.

Groundwater ecosystems are fed by downward movement of surface water, which carries with it dissolved and particulate organic matter. Groundwater ecosystems may also be driven, to varying degrees, by bacterial–chemical processes, for example, the oxidation/reduction of sulfides derived from the surrounding rocks and sediments, or other sources. These chemoautotrophic energy inputs have only recently been described and have been little investigated in Australia to date, but they do occur and may prove to be significant in some cases, such as in the anchialine systems at Cape Range/Barrow Island. The structure and interrelationships of groundwater ecosystems are depicted in Figure 5.2.

Moisture and a source of food are two of the key ingredients required to sustain subterranean animals. The importance of these two factors has been clearly demonstrated for troglobites in the semi-arid tropical karst at Cape Range. These low-energy caves receive water and energy (plant matter) in unpredictable pulses, sometimes separated by many years, due to flooding from cyclonic storms. An experiment was established, involving the addition of water and plant matter, in a cave that had become largely devoid of fauna as a result of drying and energy depletion. The addition of water alone or plant matter alone had little effect, but the combination of water and organic matter together was sufficient to encourage the troglobite populations to expand rapidly and reproduce.

The availability of food to the guanophile communities in bat caves may also occur in pulses, but it is generally more predictable than irregular storm events. The regular roosting by large numbers of bats affects cave climate and markedly affects the cave ecology due to the deposits of guano, urine, food remains, such as moth wings, and dead bats that accumulate beneath the roosting sites. These remains constitute a highly nutritious food source that supports a characteristic community of guanophilic invertebrates. Fresh guano is initially colonised by a microflora, consisting of fungi, bacteria and protozoans, and an assemblage of larger invertebrates that feed either directly on the guano or on the microflora growing on it. These members of the guano community include nematode worms, millipedes, mites, springtails, booklice, moths and flies belonging to several different families. The life cycle of some guanophiles revolves completely around dung, for example, the small tineid moth, *Monopis crocicapitella*, which can often be observed in bat guano in Australian caves. The obligate guano

dwellers, in turn, attract a suite of parasites or other cave predators, including, for example, wasps, pseudoscorpions (see plate 31), harvestmen, spiders and beetles. These may exploit the guano community on an opportunistic basis, for example, the Carrai Cave spider, *Progradungula carraiensis*, which constructs a specialised web to ensnare its prey, which includes the guano moths (see plate 33).

Life in the guano heap goes through an annual cycle, which is coupled with the cycle of cave usage by the bats that provide the input of guano, urine and bat corpses. Every year when the bats arrive and fresh guano begins to be deposited, invertebrate activity is stimulated within the guano heap. The bonanza food supply is consumed in a frenzy of invertebrate feeding and breeding, which results in huge abundances of some species, such as coprophilic mites. A study undertaken in Carrai Bat Cave in northern New South Wales for example, measured a mean density of the guano mite, *Uroobovella coprophila*, as 12.6 million individuals per square metre of guano. Invertebrate activity and abundance rapidly tapers off as the supply of fresh nutrients becomes exhausted after the bats depart. At this stage the guano community enters a period of relative quiescence, many individuals lay eggs and then die, or undergo metamorphosis into adult forms, or enter resting stages of their life cycle. The 'boom-to-bust' cycle of the guano communities takes place each year depending on the annual cycle of cave usage by the bats. However, if bat colonies abandon a cave roosting site, the guanophile communities die out.

Work in Carrai Bat Cave showed that the metabolism of the bats and the guano community together increased the temperature, humidity and ammonia concentration in the cave air. These results challenged the widely held beliefs that cave environments have a low energy (food) input, and also that caves are very stable, almost constant environments. Bat caves — of which there are many in Australia — have significantly different biological and physical dynamics compared to caves without bats, a finding that has important implications for our general understanding of cave ecology.

Some subterranean ecosystems, however, do have a relatively stable and constant food supply. Two examples include caves with permanent streams and caves that contain tree roots. In Tasmania there are streams that flow into caves all year round. The streams carry underground food supplies in the form of plant material and surface stream-dwelling invertebrates, both of which constitute a food base for the permanent cave inhabitants. One spectacular cave species is the glow-worm, *Arachnocampa tasmaniensis*, the luminous larval stage of a fungus gnat. Glow-worms construct a 'hammock' of silk and mucus from which they suspend long sticky threads, or 'fishing lines'. The accidental stream fauna swept into the cave includes the larvae of insects with aquatic immature stages in their life cycle, such as stoneflies, mayflies and caddis flies. When these metamorphose into the adult forms they fly upward, attracted by the glow-worms' light, and become entangled in their snares. The glow-worms then haul up the appropriate fishing lines and consume their prey (see plate 35). Glow-worms can be seen in caves all year round because of the permanent and predictable food supply. However, if changes such as forest clearing occur within the surface stream catchment area, the continued survival of the glow-worm colonies may be threatened.

Tree roots also represent a reasonably reliable food supply for some subterranean communities, provided, of course, that an adequate moisture supply is maintained and the trees continue to grow on the surface. In Australia, there are some diverse subterranean communities, both aquatic and terrestrial, that appear to be primarily sustained by tree roots. The roots form an abundant food base for grazing species, which, in turn, are preyed upon by a suite of predators. In southwest Western Australia, tree roots in

groundwaters of caves contain rich communities of aquatic invertebrates; consistent and high-energy input may be the factor that permits the survival of so many non-troglobitic species underground in these rootmat systems. The Nullarbor Plain also contains aquatic and terrestrial troglobite communities that are most abundant where there is a food supply of tree roots. The blind Nullarbor cave cockroach, *Trogloblatella nullarborensis*, is known to graze on tree roots (see plate 36), and is, in turn, preyed upon by the blind Nullarbor Cave spider, *Tartarus nurinensis* (see plate 32).

The character of Australian subterranean fauna

The character of Australian subterranean fauna, which is of great diversity and significance, is still only beginning to be appreciated and understood. A great diversity of habitats is present which, in turn, supports a richness of fauna that ranks significantly on the world scale. The fauna includes some extremely ancient and relictual groups of animals, with many that are unique to Australia. However, there are many broad similarities among the groups of animals that have colonised subterranean environments in Australia compared with elsewhere. The species occurring in Australia are generally restricted to this continent, although they may be closely or distantly related to species occurring in subterranean environments elsewhere in the world. There are some major faunal differences between fragments of the northern and southern supercontinents, and this has affected the pool of potential cave-dwelling lineages in Australia. Subsequent to the fragmentation of the continents there has been a long period of isolation that has allowed the development of a distinctively Australian fauna and this isolation is reflected in the cave fauna of today.

The Australian cavernicolous fauna reflects, to varying degrees, the ancient fauna provinces related to the various combinations and fragmentations of the tectonic plates that have occurred through the Eras. The origins of some cavernicolous animals may be traced back to lineages present in Australia, Gondwana or Pangea, and to the Tethys Sea. The fauna of some karst areas probably incorporates elements of each affinity class. The Cape Range karst, for example, is located on the edge of the Pilbara Craton, which formed the eastern shore of Greater Tethys during the Mesozoic, thus accounting for the probable origin of the anchialine species found there. Cape Range has apparently been covered with rainforests, and this is reflected in the characteristics of the terrestrial troglobite fauna, some also having clear Gondwanan affinities.

Subterranean habitats, especially caves, are best developed in carbonate rocks, such as limestones and dolomites, but substantial cave systems occur in other types of rock. Although carbonate rocks occur less frequently in Australia and other fragments of Gondwana compared with the world average, more than 500 discrete localities are documented. Additional cave and groundwater communities are established in calcrete aquifers (Figure 5.4), voids within non-carbonate rocks, and these include lava tunnels, sea caves, boulder and talus caves, wind-eroded caves and interstitial environments.

Karst, pseudokarst and groundwater localities are widely distributed across Australia and so encompass climate types ranging from tropical to temperate and mesic to arid. Regional climates, which are reflected in surface vegetation and animal communities, have been used as a basis for delineating five major cave fauna provinces within Australia (Figure 5.5). These provinces are: a tropical type climate, a subtropical dry type climate, a transitional zone with winter rain, a warm temperate type, and warm temperate/tropical transitional type climate. The biophysical characteristics of the karst areas and subterranean fauna within each of these provinces are briefly described below.

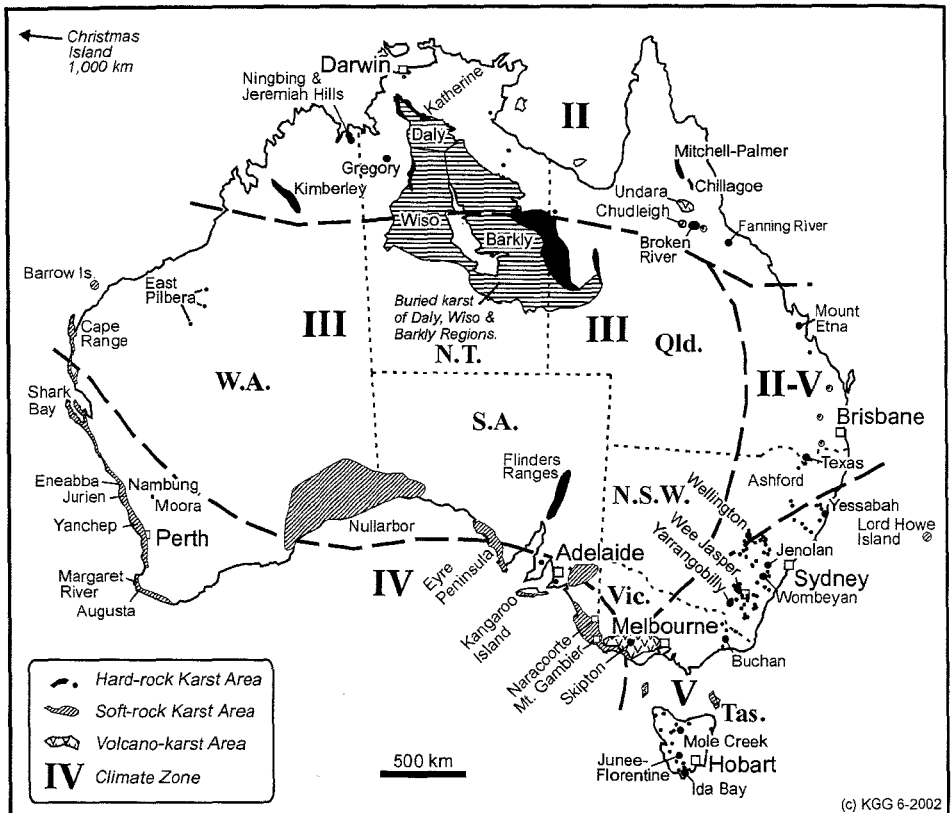


FIGURE 5.5

Climatic zones and karst areas in Australia. Karst areas are distributed across the Australian continent, encompassing climate types ranging from tropical through to temperate. KG Grimes, after Bridgewater, 1987

The tropical type climate (zone II) is characterised by mild seasonality in mean daily temperatures and monsoonal summer rainfall. This province includes about a dozen major karst areas distributed throughout the ‘top end’ and, in addition, pseudokarst features are developed in sandstones and quartzites, and there are extensive lava tunnels at Undara.

Many of the tropical cave systems consist of spacious interconnected passages with multiple entrances, so they are poorly insulated from daily and seasonal climate changes occurring on the surface. This influences the distribution of cave fauna and the extended transition zone faunal communities are relatively depauperate, and largely comprise non-troglobitic species. Terrestrial troglobites are found in the deeper, poorly ventilated recesses where the atmosphere is saturated with water vapour.

In far north Queensland (Chillagoe and Undara) the deep zone contains communities of troglomorphic taxa — among the most diverse known globally — while less diverse faunas are known from Katherine, Camooweal and the Kimberley. Studies undertaken at Chillagoe and Undara on speciation and reductive evolutionary trends in plant-hoppers and cockroaches and of the fauna in the stagnant-air zone have contributed important evidence toward the development of theories concerning cave colonisation, underground dispersal of cavernicoles, and the evolution of non-relictual troglobites.

The affinities of many of the terrestrial cave-dwelling taxa in the tropical climate zone lie with a tropical rainforest soil and litter fauna, while the stygobiotic taxa are mainly relictual Crustacea that have colonised from surface freshwater, rather than having marine origins.

The subtropical dry type climate (zone III) is characterised by very low rainfall, high daytime temperatures in summer with low winter minima. Although carbonate rocks are poorly represented and karst development is retarded by the arid climate, the zone contains highly significant subterranean faunas. Both the mainstream karsts and the groundwater calcretes of the subtropical dry climate contain significant subterranean faunas representing marine, freshwater and terrestrial lineages.

This region is rich in often extensive groundwater calcretes, which form in arid climates (annual rainfall less than 200 millimetres) with high potential evaporation (more than 3000 millimetres per year). They are associated with present and former drainage channels and may develop typical karst features with voids and cavities forming a conduit system typical of karst aquifers, as, for example, the Millstream aquifer in the Pilbara.

Each isolated calcrete body examined so far has a separate fauna but there are regional differences between the stygofauna of the Pilbara and Yilgarn calcrete aquifers. Spelaeogriphacea, a new order for Australia, occur in the Western Fortescue Plain aquifer (Millstream) but an undescribed family of isopods that is also in the Kimberley, and diverse amphipods and ostracods characterise most of the remaining Pilbara sites with lower taxonomic level difference between the aquifers.

Those aquifers in the Yilgarn are characterised by dytiscid water beetles (54 species to date compared with 17 species previously known world-wide) and a diversity of bathynellid syncarids. Syncarids are seemingly replaced by an aquatic 'terrestrial' isopod (Oniscoidea) in saline waters, the only saline continental stygofauna known globally. Both areas contain a wealth of undescribed crustaceans (ostracods, copepods, isopods, syncarids, amphipods), turbellaria, oligochaetes, mites and gastropods.

Cape Range and related Barrow Island comprise one of the more significant cave fauna provinces on earth. The terrestrial fauna is primarily a relict wet-forest litter fauna — attesting to a much wetter past — and includes both tropical and temperate elements comprising at least 41 species (31 genera) exhibiting highly developed troglomorphies. However, the aridity of the climate has resulted in the extinction of related surface-dwelling species. The remarkable stygobiotic fauna, comprising at least 22 species in 12 genera, includes Australia's only two troglobitic fish (see plate 34), together with anchialine habitats holding an assemblage of ancient crustaceans with Tethyan affinities. It includes the only known Southern Hemisphere representatives of an entire class (Remipedia) and order (Thermosbaenacea) of crustaceans.

By contrast, the terrestrial cave fauna on the Nullarbor Plain is sparse but highly troglomorphic. The species also appear to be distributional relicts dating from times of more humid climate and some have congeneric cave-dwelling relatives located on the eastern and western margins of the continent. Despite the existence of a large aquifer beneath the Nullarbor, and in places a potential energy source based on chemoautotrophic bacteria, only two aquatic crustacean species are known and only from a small area (Roe Plains) subject to late Pliocene-early Pleistocene marine transgression.

The transitional zone (zone IV) with winter rain climate — characterised by summer drought and cyclonic rains during winter — is experienced in two disjunct regions, the southwest corner of Western Australia and parts of South Australia and Victoria. There are a number of important karst areas within both these regions, including extensive 'soft rock' karsts developed in Quaternary coastal dune limestones.

Few terrestrial troglobites are known, but the aquatic fauna within this province is quite diverse, for instance, in southwest Western Australia, where unusual tree root mats support rich communities. In the Otway Basin, the Mount Gambier cenotes and springs harbour few stygobiotic species. A great diversity of stromatolitic communities that are

restricted to carbonate areas occur in freshwater at Mount Gambier, brackish and fresh waters in southwestern Australia and hypersaline waters at Shark Bay.

The warm temperate climate (zone V) coincides with the Eastern Highlands, including Tasmania. The province includes areas with poorly defined winters and with year-round rainfall, and it grades northward into a warmer transitional zone (zone II–V) under some monsoonal influence.

These provinces contain more than 300 discrete karst localities, mostly developed in ‘hard rock’ Palaeozoic limestones, as well as extensive basalt plains containing lava tunnels in western Victoria. Owing to the relative accessibility of these karsts to early European settlements most of the early collections of cave animals were made in these climatic provinces, and this influenced initial perceptions of the significance of the Australian cave fauna and probably impeded the development of biospeleology in Australia. It appeared, initially, that there were few highly specialised troglobites, except in Tasmania, and the cave fauna appeared to be dominated by guanophiles and troglaphiles. Only recent collections have demonstrated the existence of a significant cryptic stygofauna on the mainland. Many of the cave taxa in the warm temperate province have Gondwanan affinities and some have Pangean affinities. Tasmanian cave communities are the richest within Australia’s temperate zone and some individual cave systems contain more than 70 resident species, of which 15 or more are troglobites.

Exciting research opportunities

Subterranean faunas are of special interest for reasons other than the contribution they may make to the functioning of ecosystems and biodiversity. First, many cave or groundwater restricted species, protected from surface cataclysms, represent relict groups of great antiquity long disappeared from surface ecosystems (for example, Remipedia, Spelaeogriphacea, Syncarida, Thermosbaenacea), truly ‘living fossils’ perhaps even surviving Mesozoic communities. Second, subterranean systems characteristically contain locally endemic species, many of which belong to speciating lineages whose evolution reflects, and is affected by past and continuing changes, inter alia, in climate, geomorphology, landscape development and eustatic events.

Discoveries made over the past two decades, especially, have secured Australia’s position as a major province of subterranean biodiversity. It includes some of the richest and most ancient subterranean faunas known in the world. The subterranean fauna has added greatly to the known biodiversity of Australia, including a number of major lineages previously thought confined to the Northern Hemisphere. This fauna has great potential to aid our understanding of the evolution of lineages both within Australia and Gondwana, as well as the evolution of Tethyan stygofaunas and the colonisation of Tethys as its development spread westward, eventually to separate the ‘New World’ from the ‘Old World’.

Large areas, even of traditional karst terrain, remain to be explored both for caves and their biology. However, especially in Australia, great opportunities exist for research and discovery in less-traditional subterranean realms. While cave divers have explored the larger drowned cave passages, the continuity of cave waters with the great variety of other groundwaters means that these waters often contain faunas with elements in common. The subterranean fauna in these varied waters lie within the domain of biospeleology, not least because they provide opportunities for fauna migration between adjacent karst regions. The discovery of relictual freshwater faunas in the calcretes of the Pilbara and Yilgarn (the ‘Western Shield’), and the Northern Territory suggests that most of the inland palaeodrainage systems of central Australia may yield

similar faunas. These could provide information pivotal to understanding the evolution both of their lineages and of this ancient landscape.

The most exciting research areas are not necessarily those where ancient relict faunas are to be found, but where closely related surface-dwelling and subterranean species occur together. Such karst regions permit the exploration of many questions not available in areas where the faunas are entirely relictual. Three areas stand out as being particularly worthy of closer examination. The numerous Tasmanian karsts proffer opportunities with good replication to conduct work analogous to the classic European studies. The Undara lava tube and the Chillagoe karst both seem to contain a range of lineages with varying degrees of troglomorphy and with well-replicated populations. Both areas are well-suited to comparative and experimental research.