at 22 000 BP, and bone beads at 13 000 BP. The remains of wallabies and other animals in Devils Lair were hunted by both humans and *Sarcophilus*, and lower layers contain extinct marsupial megafauna. Nombe, a karst rock shelter in the New Guinea highlands, has a similar antiquity and contents: wallabies and possums hunted by the occupants, as well as the occasional bones of extinct megafauna (Mountain, 1993). *Sarcophilus* apparently never reached New Guinea, so the highly distinctive chewed fragments of its prey are missing from this site. A pattern emerges: extinct Pleistocene species occur in lower units, overlaid by rich, and often mixed, archaeological and predator accumulations of bone, but no firm evidence of human predation of the megafauna.

Finally, New Guinea also has the highest and most unusual karst archaeological site, Mapala Rockshelter, at 4000 m, set beneath a limestone block perched by retreating ice across lateral moraines near the Carstenz Glacier in the Indonesian west of the island. Again, this is a hunting camp, containing wallaby and possum bones, dating back more than 4000 BP, but used in living memory by the Damal people (Hope & Hope, 1976).

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See also **Art: Cave Art in Australasia**

Works Cited

Archer, M., Hand, S.J. & Godthelp, H. 1991. *Riversleigh: The Story of Animals in Ancient Rainforest of Inland Australia*, Sydney: Reed Books

Flood, J. 1999. *The Riches of Ancient Australia: A Journey into Prehistory*, 3rd edition, St Lucia: University of Queensland Press

Hope, G.S. & Hope, J.H. 1976. Man on Mt Jaya. In *The Equatorial Glaciers of New Guinea*, edited by G.S. Hope, J.A. Peterson, U. Radok & I. Allison, Rotterdam: Balkema

Loy, T.H., Jones, R., Nelson, D.E., Meehan, B., Vogel, J., Southon, J. & Cosgrove, R. 1990. Accelerator radiocarbon dating of human blood proteins in pigments from Late Pleistocene art sites in Australia. *Antiquity*, 64: 110–16

Mountain, M.J. 1993. Bones, hunting and predation in the Pleistocene of northern Sahul. In *Sahul in Review: Pleistocene Archaeology in Australia, New Guinea and Island Melanesia*, edited by A. Smith, M. Spriggs & B. Fankhauser, Canberra: Australian National University, Department of Prehistory

Porch, N. & Allen, J. 1995. Tasmania: Archaeological and palaeoecological perspectives. In special issue: Transitions Pleistocene to Holocene in Australia and New Guinea. *Antiquity*, 69: 714–32

Rich, P.V., van Tets, G.F. & Knight, F. (editors) 1985. *Kadimakara Extinct Vertebrates of Australia*, Melbourne: Pioneer Design Studio; 2nd edition, Princeton, New Jersey: Princeton University Press, 1990

Spate, A. 1997. Karsting around for bones: Aborigines and karst caves in southeastern Australia. *Australian Archaeology*, 45: 35–44

Wells, R., Moriarty, K. & Williams, D.L.G. 1984. The fossil vertebrate deposits of Victoria Fossil Cave Naracoorte: An introduction to the geology and fauna. *Australian Zoologist*, 21(4): 305–33

AUSTRALIA: BIOSPELEOLOGY

In the late 19th century scientists recognized that Australian caves contained terrestrial and aquatic species that belonged to ancient and relict groups of value to studies in evolution. Widespread studies of Australian cave life did not commence until the 1970s and there have still been few systematic surveys of cave or groundwater (aquifer) faunas. While a few detailed studies have been conducted of hypogean ecology, environment, and evolution, much of the known fauna remains undescribed. The composition of Australian cave fauna is influenced by past connections with the supercontinents Pangaea and Gondwana, and by it having formed part of the eastern seaboard of the Tethys Ocean during the Cretaceous. Above all, it is shaped by the onset of aridity, following the separation of Australia from Antarctica about 45 million years ago, which displaced well-watered, cool temperate, and subtropical forests, as Australia drifted northwards. Aridity appears to have played a prominent role in isolating cave species now far from the humid ecosystems of their ancestors.

Australia, which covers 7.7 million km^2 and is of generally low relief, contains extensive shield regions that have remained above sea level since the Paleozoic and so support numerous relictual lineages of freshwater stygobites. Over 500 discrete areas of carbonate rocks occur in Australia (see map in Australia entry). The caves and karst support terrestrial, fresh and saltwater, and anchialine ecosystems.

Hamilton-Smith and Eberhard (2000) presented a regional classification of the subterranean fauna based on recognized bioclimatic zones. These include tropical climates in the north, a large subtropical dry province occupying the centre and the western seaboard, a transitional zone with winter rain along southwestern coasts, and a warm temperate/tropical transition zone largely covering the Eastern Highlands.

Until recently, the subterranean fauna of Australia—with the exception of that in Tasmania which has had a more humid climatic history than the mainland with periods of Cainozoic glaciation—was perceived as being much less diverse than those from the well-studied caves of Europe and North America. This coincidence in Tasmania of glaciation with speciose troglobite communities was consistent with the Northern Hemisphere model in which glaciation was perceived as the driving factor in troglobite evolution. However, recently this perception has been overturned, especially by discoveries within the tropics and the arid parts of the continent. Notably diverse cave faunas occur in Tasmania, Jenolan Caves (New South Wales), Far North Queensland (Chillagoe karst and Undara lava tube), and Cape Range and Barrow Island (see Cape Range, Australia: Biospeleology). Areas where strongly cave-adapted species are sparse include the aeolian limestones of the southwestern coasts and the extensive Nullarbor karst (especially stygofauna).

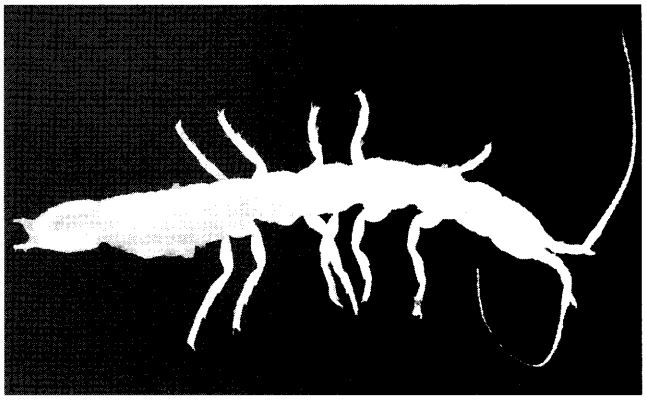
The island state of Tasmania, with 300 discrete karst areas, exhibits a higher proportion of troglobites than found on the mainland in New South Wales, with 200 discrete karst areas, having 34 and 17 troglobitic genera respectively, distributed among a comparable number of families. However, by comparison, some tropical caves are species rich (Malipatil & Howarth, 1990) and the arid tropical Cape Range and Barrow Island karst

in Western Australia supports 51 obligate subterranean genera in 42 families (32 troglobite and 19 stygobite genera). In the tropics, numerous cave-adapted planthoppers (Homoptera: Fulgoroidea) occur in which the adults retain the underground root-feeding behaviour common amongst the nymphs. These co-occur with epigean species and provide a graded series of morphological change associated with adaptation to cave life. Different species display all grades of cave adaptation from almost no modification from surface relatives to the loss of eyes and pigment and strongly reduced wings (Hoch & Howarth, 1989).

Amphipods, a major component of world cave faunas, were long considered sparse in Australian inland waters, and thought especially to abhor the tropics. Recent work has uncovered a diversity of amphipods in the arid zone and in the tropics, represented by a number of families considered to belong to both marine and freshwater lineages. The distribution of the latter, along with other ancient freshwater crustacea, coincides closely with areas not covered by marine incursions during the Cretaceous (Bradbury, 1999).

In southwestern Australia, root mats forming in shallow streams of caves in aeolian limestone support a diverse aquatic community, largely lacking overt modification to cave life (Jasinska *et al.*, 1996). Whether these mats also support a terrestrial component, such as seen in the tropical planthoppers, is unrecorded.

Many species are restricted to single karst areas, especially in the impounded karsts of eastern Australia (Thurgate *et al.*, 2001), but even within a given karst area there is often no interbreeding between populations of troglobites in adjacent caves (Humphreys & Adams, 2001). Unexpected small-scale endemicity also occurs in the stygofauna inhabiting groundwater calcretes of arid Australia. These are limestone masses deposited from groundwater flow into the alluvium filling ancient paleochannels. They form where the baselevel of the groundwater approaches the surface and are found upstream of the saltlakes (playas) that occur at intervals along the length of the paleochannels. For example, most of the 49 known species of stygal diving beetles (Dytiscidae) are restricted to a single calcrete body (Watts & Humphreys, 2000). Molecular data suggest that separate dytiscid lineages invaded groundwater in the middle Miocene with the onset of general aridity (Cooper *et al.* 2002), but other calcretes appear to support much more ancient faunas with Gondwanan affinities (Poore & Humphreys, 1998), or contain rich assemblages of amphipods.



Australia: Biospeleology: *Phreatoicoides gracilis*, a groundwater phreatoicidean isopod from Australia, showing lack of eyes and pigment characteristic of subterranean animals. (Photo by G.D.F. Wilson)

Owing to sparse research in Australia, meaningful comparison with the diversity of subterranean faunas of other continents is premature. Certain areas, such as Chillagoe, Undara, Jenolan, and Cape Range, contain rich troglobite faunas by world standards. But there are extensive karst areas, such as the Barkley Tableland, the Nullarbor and the syngenetic karst in aeolian dunes of the southwestern coasts, that apparently contain low to very low diversity of strongly cave-adapted species. These factors, combined with the generally low proportion of carbonate landscape in the fragments of Gondwana, suggest that the overall diversity in Australia may not be high by world standards, but the case remains open.

Biospeleology has resulted in the discovery in Australia of a number of higher taxonomic groups (e.g. Class Remipedia; Orders Thermosbaenacea, Misophrioida and Spelaeogriphacea), and of important evolutionary linkages between phreatoicidean isopods (see figure) from Africa, Australia, and New Zealand (Wilson & Keable, 1999). A number of troglobitic and stygobitic species and several cave communities are specifically protected under fauna legislation, part of an Australian ethos of cave and cave fauna protection that is projected strongly internationally (Watson *et al.*, 1997).

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See also **Cape Range, Australia: Biospeleology**

Works Cited

Bradbury, J.H. 1999. The systematics and distribution of Australian freshwater amphipods: A review. In *Crustaceans and the Biodiversity Crisis: Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998*, edited by F.R. Schram & J.C. von Vaupel Klein, Leiden: Brill

Cooper, S.J.B., Hinze, S., Leys, R., Watts, C.H.S. & Humphreys, W.F. 2002. Islands under the desert: Molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics*, 16(4): 589–90

Hamilton-Smith, E. & Eberhard, S.M. 2000. Conservation of cave communities in Australia. In *Subterranean Ecosystems*, edited by H. Wilkens, D.C. Culver & W.F. Humphreys, Amsterdam and New York: Elsevier

Hoch, H. & Howarth, F.G. 1989. The evolution of cave-adapted cixiid planthoppers in volcanic and limestone caves in North Queensland, Australia (Homoptera: Fulgoroidea). *Mémoires de Biospéologie*, 16: 17–24

Humphreys, W.F. & Adams, M. 2001. Allozyme variation in the troglobitic millipede *Stygiochiropus communis* (Diplopoda: Paradoxosomatidae) from arid tropical Cape Range, northwestern Australia: population structure and implications for the management of the region. *Records of the Western Australian Museum*, Supplement 64: 15–36

Jasinska, E.J., Knott, B. & McComb, A.J. 1996. Root mats in ground water: A fauna-rich cave habitat. *Journal of the North American Benthological Society*, 15: 508–19

Malipatil, M.B. & Howarth, F.G. 1990. Two new species of *Micropolytoxus* Elkins from Northern Australia (Hemiptera:

Reduviidae: Saicinae). *Journal of the Australian Entomological Society*, 29: 37–40
Poore, G.C.B. & Humphreys, W.F. 1998. First record of Spelaeogriphacea from Australasia: A new genus and species from an aquifer in the arid Pilbara of Western Australia. *Crustaceana*, 71: 721–42
Thurgate, M.E, Gough, J.S., Clarke, A.K., Serov, P. & Spate, A. 2001. Stygofauna diversity and distribution in Eastern Australian cave and karst areas. *Records of the Western Australian Museum*, Supplement 64: 49–62
Watson, J., Hamilton-Smith, E., Gillieson, D. & Kiernan, K. (editors) 1997. *Guidelines for Cave and Karst Protection*, Gland, Switzerland and Cambridge: International Union for Conservation of Nature and Natural Resources
Watts, C.H.S. & Humphreys, W.F. 2000. Six new species of *Nirridessus* and *Tjirtudessus* (Dytiscidae; Coleoptera) from underground waters in Australia. *Records of the South Australian Museum*, 33: 127–44
Wilson, G.D.F. & Keable, S.J. 1999. A new genus of phreatoicidean isopod (Crustacea) from the North Kimberley Region, Western Australia. *Zoological Journal of the Linnean Society, London*, 126: 51–79

Further Reading

Eberhard, S.M. & Humphreys, W.F. 2003. The crawling, creeping and swimming life of caves. In *Australia Underground: A Tribute to Joe Jennings*, edited by B. Finlayson & E. Hamilton-Smith, Sydney: University of New South Wales Press
Humphreys, W.F. & Harvey, M.S. (editors) 2001. Subterranean biology in Australia 2000. *Records of the Western Australian Museum*, Supplement 64: 1–242

AUSTRALIA: HISTORY

The first verified report of limestone in Australia was of abundant quantities of stratified limestone in the vicinity of the Tamar Estuary in northern Tasmania, in a report to Governor King by Colonel William Patterson in October 1804 (Lane, 1975). The first such report on mainland Australia was made in Governor Macquarie's dispatch to Earl Bathurst of 30 June 1815, which recorded the discovery of limestone by G.W. Evans at Limestone Creek, a tributary of the Belubula River, west of what was to become the town of Bathurst in New South Wales (Carne & Jones, 1919: pp.6–8). The Bathurst district also provided the first record of a European entering an Australian cave, when, on 8 November 1821, William Lawson, one of the trio credited with the crossing of the Blue Mountains, explored Limekilns Cave. Lawson recorded in his journal (Lawson, 1821):

> Camped at the Limestone Hills, here government has a kiln built for burning of lime for the use of the settlement which proves to be the very best quality. Here is a curious cave through a solid rock of limestone. Its entrance is very narrow. At nine o'clock at night I took four men with three candles and proceeded into it about one hundred yards. At the end is a fine pool of clear water. In many places for several yards together I was obliged to creep on my hands and knees. The inside of the cave is very curious and well worth seeing. I got some fine specimens. Came out at one o'clock in the morning.

While it is likely that caves were discovered at Bungonia in New South Wales by early settlers around 1820, the earliest written report was by botanist and explorer Alan Cunningham, who noted in his diary on 27 April 1824 that, passing through limestone country, "we found the land exceedingly cavernous. Orifices four feet in diameter connected with capacious subterraneous Excavations, appeared in every part of the Forestland, of whom some presented yawning fissures of apparently great depth . . ." (Cunningham, 1824). The report went on to describe a visit to what is now known as Drum Cave (B13), though they were stopped by a pit of "unfathomed depth"—later surveyed at 43 m.

The earliest-known illustrations of Australian caves were three watercolours executed in 1826 by a professional painter, Augustus Earle, of "Mosman's Cave, Wellington Valley, NS Wales". These pre-dated by two years the publication of the first written report on the Wellington Caves by Hamilton Hume, a member of Sturt's 1828 expedition (Hamilton-Smith, 1997). The paleontological value of the caves at Wellington was realized about 1830 and became well known following the publication of Major Mitchell's journals in 1838 (Mitchell, 1838). These include a plan of the caves, which was the first accurate cave plan to be published in Australia (Figure 1).

Australia's earliest-known cave map was prepared by surveyor Henry Hellyer in August 1827, but this was not to scale and was not published until 1990 (Figure 2) The cave, at Rocky Cape on the north coast of Tasmania, is in quartzite and was noted by Hellyer as being 10 feet (3 m) wide at the entrance and 80 feet (24 m) deep. The cave became known as Rocky Cape North Cave and yielded important information on the Aboriginal inhabitants of the area over the previous 8000 years (Middleton, 1990).

The first published plans of Australian caves accompanied Capt. John Henderson's record of his observations in New South Wales (Figure 3) (Henderson 1832). Although relatively crude and not to scale, the two sketches are identifiably of Tunnel Cave (BN25–28) at Borenore and Breccia Cave (or Bone Cave No. 3) at Wellington.

Caves were easier to find in Western Australia. In March 1827, two years prior to European settlement, Capt. James Stirling noted that the "heads" at the mouth of the Swan River were composed of limestone which, "subject to the action of the surge, is worn into Caverns". Exploring inland in the vicinity of Cape Naturaliste, Stirling noted "compact limestone, sections of which were seen 200 feet in depth" and "under the limestone cliffs, many magnificent Caverns; some of these are remarkable for their extent and some for the beautiful stalactites and incrustations which they contain" (Stirling, 1827).

While the Jenolan Caves (formerly Binda or Fish River Caves) in the Blue Mountains of eastern New South Wales would have been known to the Gundungura people for millennia, their discovery by Europeans is shrouded in mystery. A widely accepted story is that they were found by James Whalan in 1838 while searching for a cattle thief named McKeown. Unfortunately there is no contemporary record of this event, or any reliable