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# **SUBTERRANEAN ECOSYSTEMS**

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## THE HYPOGEAN FAUNA OF THE CAPE RANGE PENINSULA AND BARROW ISLAND, NORTHWESTERN AUSTRALIA

W.F. HUMPHREYS

### INTRODUCTION

Rich troglobite communities have recently been found to inhabit caves in tropical limestones and lavas of both oceanic islands and continental areas (Howarth, 1973, 1980, 1982, 1988; Hoch and Howarth, 1989a,b, 1993; Howarth and Stone, 1990; Humphreys, 1993a-d). In addition, plate tectonics is increasingly invoked to explain the distribution of both island (Manning et al., 1986) and continental (Stock, 1994) troglobites, especially those associated with Tethys. These changes in perception have re-invigorated debates in biospeleology (see Humphreys, Chapter 22, this volume).

*A priori*, the arid northwest of Australia might be thought to be peripheral to these debates – not only is it far removed from the classical Tethyan regions centered on the Mediterranean and on either side of the Atlantic, but arid zones were considered to be sparsely populated with troglobites owing to lack of water (Howarth, 1980) and low food input from xeric plant communities (Peck, 1978). Hence, the discovery of the troglobite communities, amongst the world's richest, in the arid Cape Range region adds another level to the re-invigorated debates concerning the origin of troglobites.

This chapter addresses the nature of the karst area on the Cape Range peninsula of Western Australia and includes references to the geologically related Barrow Island lying 170 km to the northeast on the North West Shelf.

### REGIONAL SETTING

#### Location

The Cape Range peninsula lies just within the tropics

of north-western Australia (Figs. 30.1, 30.2) in the arid zone that occupies much of Central and Western Australia. It lies more than 1200 km from the nearest wet temperate forest in southwestern Australia, and more than 3000 km from the lowland rainforests of eastern Australia.

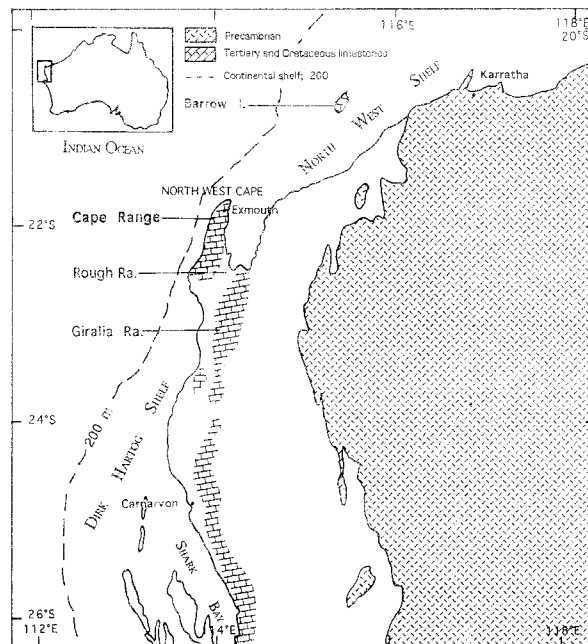


Fig. 30.1. The regional setting of the Cape Range peninsula and Barrow Island. The Precambrian Pilbara Craton has not undergone major regional deformation since 2400 Ma ago (Trendall, 1990) and has been continuously emergent for more than 600 Ma. This is fringed to the west by middle Mesozoic deposits (~100 Ma old). A series of anticlines of Cretaceous and Tertiary limestones occur further to the west. The cavernous Tulki Limestone is known only from Cape Range, and the Cape Range (*sensu stricto*) troglobite fauna is restricted to it. Compiled from Hocking et al. (1987) and Wyrwoll et al. (1993).

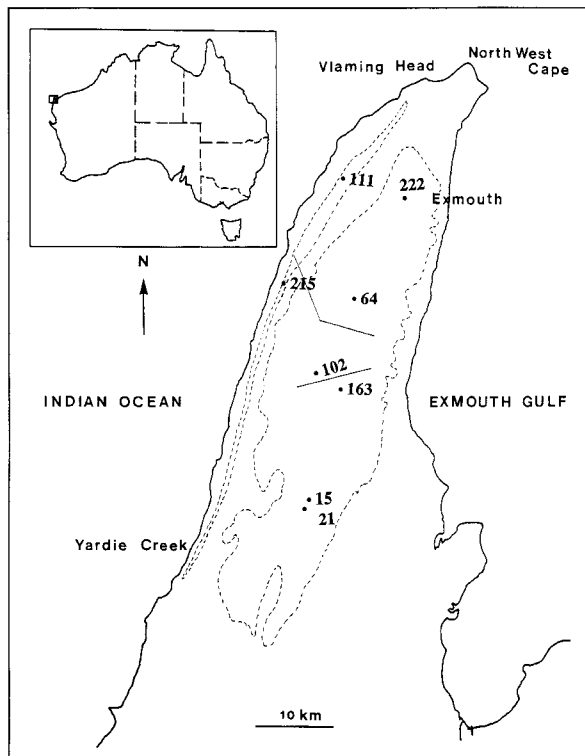


Fig. 30.2. The Cape Range peninsula. The dotted lines show the extent of the surface exposure of the cavernous Tulki Limestone, and the numbered points denote the location of caves mentioned in the text. The straight lines indicate the approximate boundaries between the genetic provinces determined from allozyme electrophoresis of the millipede *Stygiochiropus communis* (see Fig. 30.5).

### Geomorphology

Cape Range lies in the Carnarvon Basin, which is bounded in the east by a Precambrian craton – the Pilbara Craton, which has been continuously emergent for more than 600 Ma (million years). It is a faulted, gently folded Phanerozoic basin containing up to 7 km of Palaeozoic sediments covered by a Mesozoic veneer which thickens to the north and west. The break-up of Gondwana occurred here in the mid-Jurassic when rapid subsidence formed a transgression–regressive couplet 3 km thick. In the Late Cretaceous carbonate deposition occurred on the marine shelf and continental slope (Hocking et al., 1987).

Tectonic activity during the Cenozoic has resulted in the domination of the Cape Range–Exmouth Gulf region by a series of anticlines in marine limestones exposed at the surface at the Cape, Rough and Giralia Ranges (Fig. 30.1). Geologically the Cape Range

Group comprises a sequence of marine, mainly carbonate, sediments comprising the Mandu (Late Oligocene), Tulki and Trealla (Middle [?Late] Miocene) Limestones (Wyrwoll et al., 1993). The Tulki-like Poivre Formation of Middle Miocene age occurs on Barrow Island (McNamara and Kendrick, 1994).

A series of emerged and warped marine erosion terraces cut into Tulki Limestone on the western side of Cape Range up to an altitude of ~60 m (van de Graaff et al., 1976), the lowest forming a continuous coralline bench up to 1.7 km wide. Warping of the upper terraces has been considered to result from tectonic uplift during the Quaternary (van de Graaff et al., 1976), whereas the lowest terrace (Tantabiddi Member) belongs to the last interglacial of the Late Pleistocene (132 000–127 000 years BP: Kendrick et al., 1991). However, recent fossil evidence suggests that the next highest terrace (Jurabi Member) is not younger than late Pliocene (>1.8 Ma BP: Wyrwoll et al., 1993).

Cape Range attains an altitude of about 314 m and is deeply dissected on the dip slopes. Erosion has removed much of the Trealla Limestone and several of the deeper gorges have cut through to the Mandu Limestone. Nearly all caves in the range occur in Tulki Limestone (Humphreys, 1993d: frontispiece).

The west coast of Cape Range is the closest point on the Australian continent to the outer edge of the continental shelf (Kendrick et al., 1991), but to the northeast extends the broad, shallow North West Shelf (Fig. 30.1), which is contiguous with a series of shelves stretching around northern Australia to New Guinea; the shelf also broadens southwards towards Shark Bay.

### Caves

Currently, 416 caves and 13 man-made wells are known from the Cape Range. (R.D. Brooks, personal communication, 1998). Within the Cape Range *sensu stricto*, most of the caves are vertical, reaching depths of up to 80 m (C-102), and only one cave has significant lateral extent (~5 km, C-163). Permanent water can be reached in only four of the caves within Cape Range proper, at an altitude of ~180 m above sea level, and only one outflow cave is known (C-64).

On the coastal plain several caves and sinkholes, a number of wells and numerous bores permit access to the groundwater. Marine tides are apparent in water

bores up to 3.5 km inland (Forth, 1973) indicating open-conduit flow of the groundwater within the coastal plain. Such conduits form at the water table, especially by mixture-corrosion<sup>1</sup>, and are thought to have developed in karstified Tulki Limestone as it dips beneath sea level. Owing to Pleistocene sea-level fluctuations, the limestone is likely to be cavernous to depths of more than 100 m below sea level – divers have penetrated caves to 32 m below sea level, deeper than the sea over much of the North West Shelf.

Barrow Island has only three caves of biospeleological interest, permanent water being reached in only one, but bores permit access to the groundwater and the mesocaverns above.

**Groundwater**

The general hydrogeological model for oceanic islands has been applied to the ground water of Cape Range peninsula (Allen, 1993), namely, following the Ghyben–Herzberg principle, a freshwater lens overlies salt water, so that locally a wedge of salt water intrudes under the fresh water contained in the limestone – a zone of mixing occurs between them, broadening towards the coast. In the Exmouth area the freshwater-salt-water transition is at ~5 km (Martin, 1990), exceptionally far inland (cf., 0.5 km on the coral island of Niue; Jacobson and Hill, 1980), but this is to be expected as the greater the transmissivity of the limestone and the more arid the area, the further inland the wedge should penetrate. In the Exmouth area the inland limit to the salt-water interface appears to be controlled by the presence below the water table of solution cavities and channels (Martin, 1990).

**Climate**

Annual evaporation (3219 mm) exceeds the sparse precipitation (median = 280 mm; 10th percentile = 100 mm; 90th percentile = 500 mm) by more than an order of magnitude. The mean daily temperature is 27°C but the mean monthly maximum temperature exceeds 35°C for four months of the year, and the mean relative humidity is persistently low (53% at 09.00; 33% at 15.00; Vine et al., 1988; Humphreys, 1991a).

Rainfall in the region results from at least four processes – tropical cyclones, monsoons, northwesterly tropical flows, and frontal events (Gentilli, 1972) –

and this results in very low predictability, even for the driest inhabited continent (Humphreys et al., 1989: table 1), in both the seasonal distribution and the between-year variation in rainfall (Fig. 30.3). The very high temperature, low humidity, and high evapotranspiration excess make it a difficult place for cryptozoic animals.

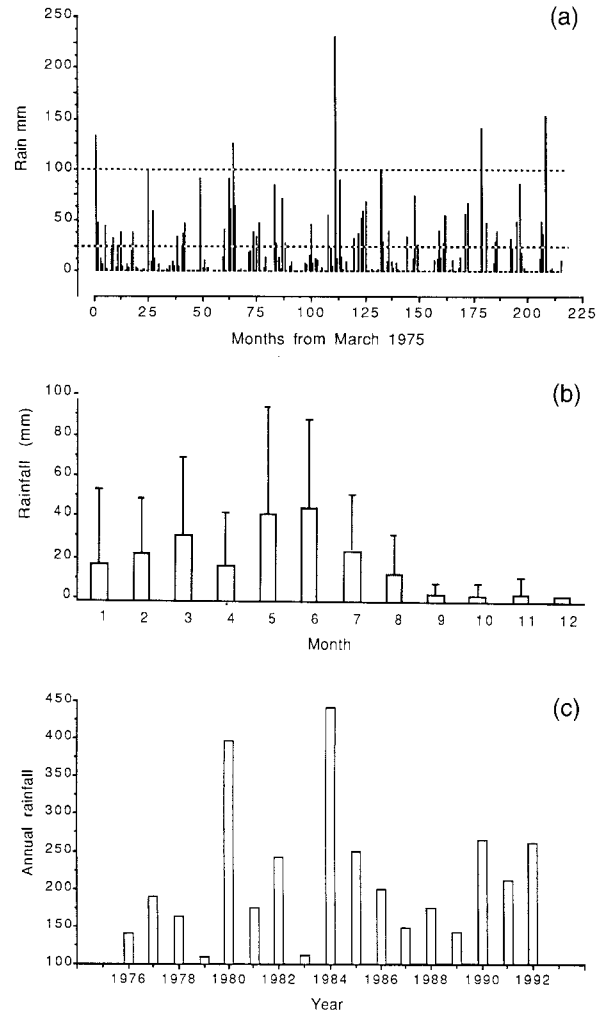


Fig. 30.3. (a) Monthly rainfall (mm) at Learmonth from March 1975. Broken lines at 25 mm and 100 mm are, respectively, the amount of rainfall required for surface flow for minor recharge of some caves, and the amount of rainfall required to flood the major caves deeply. (b) Mean monthly rainfall (mm) (± standard deviation) at Learmonth (January = 1). (c) Annual rainfall at Learmonth, 1976–1992.

**Rainfall necessary to flood caves**

As the caves are recharged with organic matter

<sup>1</sup> See necessary, p. 6.

primarily carried by the influx of water, the intensity, frequency and periodicity of rainfall will also determine that of the energy recharge.

The karst terrain precludes surface run-off except after exceptional rainfall (Figs. 30.3, 30.4). No recharge is likely to occur following a single rainfall of less than about 25 mm – such rainfall, and hence minor recharge of some caves, occurs on average once every 5.4 months, but with very low predictability (Humphreys et al., 1989). Major flows of water sufficient to flood caves deeply are likely to occur once in 4.7 years (single falls of rain >150 mm: Humphreys et al., 1989) – rainfalls of more than 100 mm occur about once every three years (Fig. 30.3).

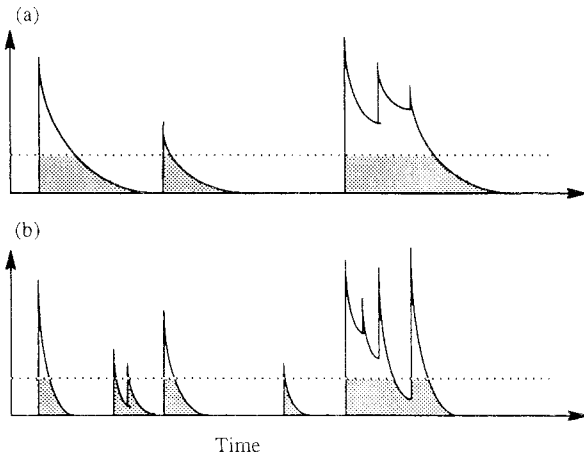


Fig. 30.4. Hypothetical availability and depletion of resources in Cape Range caves: (a) Slow-drying (small entrance) cave with a small catchment; (b) fast-drying cave with large catchment. The fine horizontal line denotes the resource level (energy or water) below which the populations are eliminated from the cave (shaded areas). Population responses would lag following the influx of new resources. Caves with large catchments (b) flood and are recharged more frequently. Slow-drying caves (a) maintain populations for longer after flooding. After Humphreys (1991c, 1993c).

### Vegetation

Essentially a widespread arid-zone flora covers the limestone hills, and the adjacent sand and coastal plains. The limestone ranges are dominated by *Eucalyptus* over *Triodia* and the lower slopes by *Acacia* over *Triodia*. The coastal plains are vegetated by grasslands, low shrublands, or by sandplain heath over *Triodia* (Keighery and Gibson, 1993).

### BIOSPELEOLOGICAL HISTORY

The biological diversity of the subterranean fauna

of the Cape Range area has been recognized only recently.

### Aquatic fauna

The first anchialine fauna, considered to be a fresh-water fauna (Knott, 1993) until recently (Humphreys, 1993b, 1994), was reported from the west side of the peninsula (Whitley, 1945; Mees, 1962), and later from the east side (Cawthorn, 1963) of the peninsula. Two species of blind fishes *Milyeringa veritas* (Whitley, 1945) and *Ophisternon candidum* (Mees, 1962) and two of atyid shrimps, *Stygiocaris lancifera* and *S. stylifera* (Holthuis, 1960) remained the only aquatic fauna reported until the 1990s, when many more taxa were described and other biospeleological studies commenced: these covered distribution, environment and genetic relations of the fauna (Humphreys and Adams, 1991; Humphreys, 1993b,d); Thermosbaenacea (Poore and Humphreys, 1992); Cirolanidae (Bruce and Humphreys, 1993); Mollusca (Slack-Smith, 1993); recognition of a Tethyan connection (Humphreys, 1993b; Knott, 1993); broad-scale distributions and recognition of anchialine habitat (Humphreys, 1994); trophic relations (Humphreys and Feinberg, 1995); *Danielopolina* (Ostracoda: Thaumato-cyprididae: Baltanas and Danielopol, 1995; Danielopol et al., 2000); amphipods (Barnard and Williams, 1995); cyclopoid copepods (Pesce et al., 1996a,b); and Remipedia (Yager and Humphreys, 1996). Representatives of the fauna were later found on Barrow Island on the North West Shelf, 170 km to the northeast (Bruce and Humphreys, 1993), together with the recognition of the great diversity of the amphipod stygofauna on Barrow Island (Bradbury and Williams, 1996a,b, 1997).

### Terrestrial fauna

Arachnids (Schizomida and a troglobitic spider) were collected (Main, 1980) from an unidentified cave (Humphreys, 1990a) in Cape Range in 1962. However, the diversity of the terrestrial troglobitic fauna in Cape Range and its status as a relict wet-forest fauna was not appreciated until the late 1980s (Humphreys, 1989), when sustained work commenced on the terrestrial fauna; this was followed by an ever-increasing amount of work in the range, including studies of the Schizomida (Harvey, 1988, 1992; Vine et al., 1988; Humphreys et al., 1989; Humphreys, 1990b), pseudoscorpions (Harvey, 1991, 1993), spiders

(Deeleman-Reinhold, 1993; Millidge, 1993), arachnids and myriapods (Harvey et al., 1993), millipedes (Shear, 1992; Humphreys and Shear, 1993; Shear and Humphreys, 1996), terrestrial isopods (Dalens, 1992, 1993), insects (Roth, 1991, 1995; Sturm and Smith, 1993; Hoch, 1993), Mollusca (Slack-Smith, 1993), ecophysiology of cave arthropods (Humphreys and Collis, 1990; Humphreys, 1991c), biological and other surveys (Humphreys, 1991b,d, 1993a,c,d), experimental ecology of troglobite populations (Humphreys, 1991c), and isozyme variation (Humphreys, 1991d; Humphreys and Adams, 1991; Adams and Humphreys, 1993).

Distinct faunas were later found on the Cape Range coastal plain (Humphreys, 1994; Harvey and Humphreys, 1995; Shear and Humphreys, 1996), and on Barrow Island (Humphreys, 1991e; Hoffman, 1994), and subsequently taxa common to these two areas were recognized (Adams and Humphreys, 1993; Harvey and Humphreys, 1995; Humphreys, 1999).

## FOOD SUPPLY

### Primary production

No data are available for the primary productivity of hummock grasslands comprising *Triodia* spp. in Australia (G. Griffin, pers. comm., 1995). Nonetheless, plant biomass and productivity is low in deserts and highly correlated with rainfall (Noy-Meir, 1985), which is itself unpredictable (see above, p. 583). The effects of variability in rainfall are exacerbated because the ratio of production to rainfall (P/R) decreases below an annual rainfall of 100 mm (cf., Fig. 30.3c), and there is a threshold rainfall below which production is zero (Noy-Meir, 1985). Hence, the resource base for hypogean communities is very limited, variable and unpredictable.

### Food sources

Large troglonexen populations (e.g., bats and crickets) and the abundance of roots (e.g., in lava tubes), which characterize many cave systems (Harris, 1973; Norton et al., 1975; Kane et al., 1975; Studier and Lavoie, 1990), are lacking in Cape Range caves. In consequence, both the fauna and the energy inputs that are characteristically associated with them are absent from Cape Range.

These caves vary widely in food supply. Many have no obvious source of food other than organic carbon within the cave soil (Humphreys et al., 1989; Humphreys, 1990b; Humphreys and Adams, 1991); others receive irregular aseasonal influx of vegetable matter with flood waters (Vine et al., 1988; Humphreys et al., 1989), while others on the coastal plain contain dense mats of tree roots proliferating in the ground-water. Quantities of vegetable material, sometimes large, are washed into the caves after exceptional and unpredictable rainfall and, if they enter humid areas, serve as a major food supply for long periods; otherwise, they dry out and become unsuitable as food resources (Humphreys, 1991c).

Caves in the Cape Range rarely contain drip-water, and then it is mostly very localized following heavy rain. Hence, the percolation of fine particulate and dissolved organic matter into caves must be extremely restricted or even non-existent.

### Seasonality

Owing to the unpredictable climate there is no consistent seasonality associated with rainfall, energy influx, or plant root activity, etc., nor are seasonal cues to be had from inputs by bats, cave crickets or other troglonexes, as is found elsewhere.

### Transport to caves

Owing to the aridity of the surface, primary productivity is low and the mechanisms to transport it to the hypogean system unreliable. However, these factors are offset to some extent because old tropical karst areas in arid climates are largely devoid of soil cover (Poulson and Culver, 1969), so that percolation to deep karst areas will be unimpeded – in consequence a superficial underground compartment [the MSS of Juberthie and Delay (1981); see also Chapter 1, this volume] is likely to be absent from the region.

Owing to these factors the hypogean realm in the Cape Range is largely dependent on the influx into caves of water-borne organic material. The energy entering a given cave is strongly determined by physical factors unrelated to amount and seasonality of the rainfall – it depends *inter alia* on catchment size and porosity, and on how fine-scale surface morphology directs drainage (Humphreys, 1991c).

The caves dry at rates that are a function, *inter alia*, of their size, water storage capacity (mainly

in the cave soils), the opening size relative to cave volume, and characteristic ventilation. In addition, the drying rate is strongly seasonal owing to tropical winter effects (cf., Howarth, 1980). Dry caves do not support troglobites in Cape Range, and those occasionally drying become temporarily unsuitable for troglobites, probably by affecting food availability (Humphreys, 1991c). In consequence the occupation of caves, as opposed to mesocavernous spaces (*sensu* Howarth, 1983), is cyclical, determined by the influx pattern (Fig. 30.4).

In essence, some caves may receive inflow after relatively low rainfall (every few months) but then dry rapidly (over months). In contrast, other caves take inflow only after heavy rainfall (every few years) but thereafter dry very slowly, over several years [Fig. 30.4; see also Humphreys et al. (1989) and Humphreys (1991d)]. In consequence there is no level of energy input into caves on Cape Range that can be regarded as characteristic, either over the area or through time. Individual caves may, on average, have a higher energy input than others, but all experience periods of relative abundance and scarcity depending on their characteristics.

#### Transport within the matrix

As it is a tropical karstland largely devoid of soil, rainfall would be expected to infiltrate rapidly to the groundwater. In consequence, fine particulate and dissolved organic carbon entering the system, other than by flooding, is likely to bypass the caves, either entering the groundwater or becoming lodged within the rock matrix; hence this is where the bulk of the fauna is likely to occur.

Owing to the large evaporation excess, there is a tendency for water within the more superficial parts of the karst to move upwards, with a net downward movement only after exceptional rainfall. The resulting bidirectional movement of water in the phreatic zone is likely to strand organic carbon somewhere within the limestone where it serves as a food resource. The depth at which this equilibrium occurs is variable both in time (depending on the momentary vectors of inputs and outputs) and in space (depending on the local characteristics of the karst). In consequence, the troglobitic fauna is likely to need to move widely to harvest this temporally and spatially variable resource.

#### Tree roots

Tree roots penetrate some caves on the coastal plain (C-215) in quantity, and to depths of over 27 m in the range (e.g., C-21); they are roots of *Ficus* and probably *Brachychiton*, as found in Queensland (Howarth, 1988). Within a humid cave tree roots frequently do not reach the floor, but the fine rootlets serve as foci for condensation from which the tree probably absorbs water. Roots are not a major resource in most Cape Range caves – the caves may be too deep, unlike those in North Queensland (Howarth, 1988). Tree roots are used by planthoppers of the families Meenoplidae (*Phaconeura* spp.) and Cixiidae (gen. indet.), the former being attended by an undescribed species of ant (*Paratrechina* sp.) with much reduced eyes – it is one of few ants known that are especially adapted for cave life (S. Shattuck, pers. comm.).

On the coastal plain, root mats form in the underground water (cf., Jasinska and Knott, Chapter 15, this volume), although no characteristic fauna is known (W.F. Humphreys, unpublished; E. Jasinska, pers. comm.). Such root mats probably occur at the water table throughout the coastal plain – on which *Ficus* are common even though no cavities may be apparent – and provide a widespread habitat. The thermosbaenacean *Halosbaena tulki* was first found in such a habitat (Poore and Humphreys, 1992).

#### Accidentals

Probably owing to the aridity of the surface, accidentals appear to be relatively sparse in the Cape Range caves. However, they make a substantial contribution to the aquatic food chain on the coastal plain (Humphreys and Feinberg, 1995).

#### Trophic interactions: aquatic

The presence of characteristic red mud in the digestive tracts, and the deep layers of faecal pellets, suggests that thermosbaenaceans, atyid shrimps and harpacticoid copepods forage in the flocculent cave mud, presumably for microbiota.

The Cape Range atyids occur in a wide variety of habitat and salinity, being found in groundwater, caves and anchialine pools (Humphreys, 1994). Anchialine atyids occupy a more complex habitat (Bailey-Brock and Brock, 1993) than their more typical freshwater relatives (Fryer, 1977) for *Halocaridina rubra* does not

rely only on filter-feeding, but also scrapes the benthic algal/cyanobacterial crust, ingesting Cyanobacteria, diatoms and other algae (Bailey-Brock and Brock, 1993).

Examination of the food of the two blind fishes showed them to be opportunistic feeders, taking specialized stygofauna (*Halosbaena*, *Stygiocaris*), freshwater fauna inhabiting the open pools (larval Odonata, Diptera and Trichoptera), and invertebrates accidentally entering the water (oniscoid isopods, cockroaches, ants). For *Milyeringa veritas* the number of prey items were as follows: cockroaches 26%, isopods 42%, *Stygiocaris* 5% (?10%), ants 11%.

### Trophic interactions: terrestrial

The presence of characteristic red mud in the digestive tracts of *Stygiochiropus* spp. and the accumulation of faecal pellets, suggests that the millipedes process the cave soil for microbiota; they also forage directly on wet vegetable matter (Humphreys, 1991c). Oniscoid isopods (several species) are primarily associated with moist vegetable matter.

The prey are poorly known; the following associations have been observed. *Draculooides vinei* eats individuals of the same species, *Stygiochiropus*, and armadillid and philosciid isopods. *Draculooides vinei* is eaten by the undescribed genus of miturgid spider, which also itself eats *Stygiochiropus*. *Trichocyclus septentrionalis* (Pholcidae) eats weevils (*Myllocerus* sp.). An undescribed species of *Forsterina* sp. (Desidae) eats other individuals of the same species.

### Baits

Trophic clues can be found from the acceptance of baits. In the terrestrial system a variety of baits (cheese, fish, sweet potatoes) were largely unsuccessful in attracting troglobites. In contrast, the provision of moist dead vegetable matter slowly attracts a succession of species (Humphreys, 1991c; W.F. Humphreys and R.D. Brooks, unpublished). In contrast, baits (cheese, fish, etc.) were successful in attracting many species of the aquatic cave fauna.

### SPECIES RICHNESS OF CAVE FAUNA

The karst region contains at least 55 species of highly troglomorphic animals, of which 33 belong to

terrestrial taxa (Table 30.1) and 22 to aquatic taxa (Table 30.2). In the terrestrial realm there are a large number of other species whose survival in arid Cape Range is probably dependent on caves (Harvey et al., 1993), although overt troglomorphies may be weakly developed; a number of taxa in the anchialine system are similarly of uncertain status (Table 30.3).

Of the terrestrial troglobites, all the species and many genera (>7) are endemic to the Cape Range Formation (Table 30.1), while amongst the aquatic troglobites the genera *Milyeringa* and *Stygiocaris*, and three genera of amphipods, are apparently endemic to the region (Table 30.2), most of the remaining being congeneric with species inhabiting anchialine caves on both sides of the North Atlantic (Humphreys, 1993b, 1994; Knott, 1993).

Stygobiont amphipods are diverse (Table 30.2), and on Barrow Island just 11 specimens yielded a diversity comparable to that of the Edwards Aquifer in the United States (total diversity = 2.197; generic diversity = 0.687; within-genus diversity = 1.513; Holsinger and Longley, 1980). Available data (Holsinger, 1994) indicate that Barrow Island alone contains ~1% of all known stygobiont amphipods.

Considerable genetic diversity occurs in those recognized species that have been examined, on the coastal plain and, especially, within the Cape Range (Adams and Humphreys, 1993). The borders of the major genetic provinces are associated with the deeper gorges that cut through the cavernous Tulki Limestone into the underlying non-cavernous Mandu Limestone (Humphreys and Shear, 1993) – as, for example, in the millipede *Stygiochiropus* (Fig. 30.5).

As the region is remote and has been examined only recently, many more species surely await discovery. The Cape Range karst is much smaller than many others that have been examined in Australia, and yet the richness of this fauna is notable (Tables 30.4 and 30.5), in part because of the juxtaposition of terrestrial, freshwater and anchialine faunas.

In a world context, for comparison, 43 species of troglobite have been reported from the Hawaiian archipelago, with no more than 24 species on any one island (Howarth, 1987), and 40 species were found in the Galapagos archipelago (Peck, 1990), whereas the well-worked Appalachians area of the United States, which is ~20 times the area of the Cape Range, contains 140 species of troglobites, of which 42 are aquatic and 98 terrestrial (Holsinger and Culver, 1988). Mexico, Guatemala and Belize combined contained



Table 30.1  
Some terrestrial troglotic fauna known from caves in northwestern Australia

Major taxa	Genera and species <sup>1</sup>	Locations
<i>CHELICERATA</i>		
Schizomida <sup>2</sup>	* <i>Draculoides vinei</i> * <i>Draculoides bramstockeri</i> Harvey and Humphreys  * <i>Draculoides</i> sp. nov. * <i>Bamazomus</i> sp. nov.	Cape Range coastal plain of Cape Range peninsula; Barrow Island coastal plain of Cape Range peninsula coastal plain of Cape Range peninsula
Pseudoscorpionida		
Hyidae	* <i>Hyella humphreysi</i> * <i>Hyella</i> sp. nov.	Cape Range coastal plain of Cape Range peninsula
Chthoniidae	* <i>Tyrannochthonius butleri</i>	Cape Range
Opilionida		
Assamiidae	* <i>Anjulus</i> sp. (undescribed)	Cape Range
Phalangodidae	*Gen. indet. <sup>3</sup>	coastal plain of Cape Range peninsula
Araneae		
Hahniidae	*Gen.	coastal plain of Cape Range peninsula; Cape Range
Desidae	*Gen. & sp. indet. (Harvey et al., 1993)	?coastal plain of Cape Range peninsula; Cape Range
Ctenidae	*Gen. & sp. nov. 1 (Harvey et al., 1993)	Cape Range
Pholcidae	<i>Trichocyclus septentrionalis</i>	
Symphytognathidae	* <i>Anapistula troglobia</i>	Cape Range
Theridiidae	* <i>Steatoda</i> sp. 1. (Harvey et al., 1993) * <i>Pholcomma</i> sp. (Harvey et al., 1993)	Cape Range Cape Range
Linyphiidae	* <i>Dunedinia occidentalis</i> * <i>Chthiononetes tenuis</i>	Cape Range Cape Range
<i>MYRIAPODA</i>		
Polyzoniida		
Siphonotidae	*Gen. & sp. indet.	Cape Range
Polydesmida <sup>4</sup>		
Paradoxosomatidae	* <i>Stygiochiropus communis</i> * <i>Stygiochiropus isolatus</i> * <i>Stygiochiropus sympatricus</i> * <i>Stygiochiropus peculiaris</i>	Cape Range Cape Range Cape Range coastal plain of Cape Range peninsula
Spirobolida		
Pachybolidae	* <i>Speleostrophus nesiotis</i>	Barrow Island
<i>INSECTA</i>		
Diplura		
Japygidae <sup>5</sup>	<i>Indjapyx</i> n. sp. 1 <i>Indjapyx</i> n. sp. 2 <b>Gen. nov.</b> & sp. nov. 1 Gen. nov. & sp. nov. 2	Cape Range Cape Range Cape Range Cape Range
New family or sub-family		?coastal plain of Cape Range peninsula; Cape Range

continued on next page

Table 30.1, *continued*

Major taxa	Genera and species <sup>1</sup>	Locations
Thysanura		
Nicoletiidae: Atelurinae	* <i>Trinemura trogliphila</i>	Cape Range
Blattodea	* <i>Nocticola flabella</i>	Cape Range
	* <i>Nocticola</i> sp. nov.	Barrow Island
Orthoptera		
Nemobiinae	* <b><i>Ngamarlanguia luisae</i></b>	Cape Range
Coleoptera		
Curculionidae: Polydrosinae	<i>Mylocerus</i> sp. 1 <sup>6</sup>	Cape Range
Hemiptera		
Meenoplidae	* <i>Phaconeura proserpina</i>	coastal plain of Cape Range peninsula
	* <i>Phaconeura</i> sp. nov. 1 (H. Hoch, pers. com.)	coastal plain of Cape Range peninsula
	* <i>Phaconeura</i> sp. nov. 2	Cape Range
Cixiidae	*?gen.	Cape Range
<b>CRUSTACEA</b>		
Isopoda		
Philosciidae	*Gen. & spp. indet. >2	coastal plain of Cape Range peninsula; Cape Range

<sup>1</sup> Those marked \* exhibit extreme troglomorphies; the remainder are possibly restricted to cave environments; genera in **bold** are endemic to the area, as are all determined species.

<sup>2</sup> Only genus of Schizomida endemic to Australia.

<sup>3</sup> First blind Phalangodidae in Australia, though usual in European caves (G. Hunt, pers. comm., 1994).

<sup>4</sup> *Antichiropus humphreysi* and *Boreothesperus capensis* are also found in caves but are well adapted to outside conditions.

<sup>5</sup> J. Pagés, pers. comm., 1994–95.

<sup>6</sup> *Mylocerus* sp. 2 is found outside caves.

317 species of troglobites, most being found in the Mexican states of Tamaulipas and San Luis Potosí with 51 and 48 species of troglobites, respectively (Reddell, 1981).

Hypogean communities are noted for the low frequency of sympatry of congeners (Notenboom, 1991), and in the eastern United States no two congeneric millipedes are known to be sympatric, and the few cavernicolous pseudoscorpions that coexist do so only in pairs (Barr Jr and Holsinger, 1985).

The Cape Range is unusual in the number of coexisting taxa and congeners – four species of pseudoscorpions coexist in C-15, two species of schizomids coexist in C-215, and congeneric species occur sympatrically in C-111 (the millipede *Stygiochiropus*: Humphreys and Shear, 1993), and in the western seaboard of the Cape Range (the shrimp *Stygiocaris*: Humphreys and Adams, 1991).

This troglobite fauna is almost devoid of beetles, as has been noted for other tropical areas (Vandel, 1965;

Reddell, 1981: p. 217; see also Deharveng, Chapter 31, this volume); this is in sharp contrast to the diverse beetle fauna associated with temperate caves in both northern and southern hemispheres (Peck, 1978; Barr Jr and Holsinger, 1985; Juberthie, 1988; Eberhard et al., 1991).

#### DEGREE OF REGRESSIVE EVOLUTION

Taxonomists commonly comment on the high degree of troglomorphy seen in species from the Cape Range, and this general high level of regressive evolution is in accord with the apparent great age of this fauna (see next section). “*Nocticola flabella* Roth is probably the most troglitic cockroach ever known for its remarkable depigmentation and very slender appendages” (Izquierdo and Oromi, 1994).

The millipede genus *Stygiochiropus*, endemic to the Cape Range, contains four species that are strongly modified for cave life, with greatly elongated legs and

Table 30.2  
The composition of the stygofauna of northwestern Australia<sup>1</sup>

Major taxon	Genus and species <sup>2</sup>	Locality
Pisces: Eleotridae	<i>Milyeringa veritas</i>	coastal plain bordering Cape Range; Barrow Island
Pisces: Synbranchiformes	<i>Ophisternon candidum</i>	coastal plain bordering Cape Range
Decapoda: Atyidae	<b><i>Stygiocaris lancifera</i></b>	coastal plain bordering Cape Range
	<i>Stygiocaris stylifera</i>	coastal plain bordering Cape Range; Barrow Island
Isopoda: Cirolanidae	<i>Haptolana pholeta</i>	coastal plain bordering Cape Range; Barrow Island
Thermosbaenacea	<i>Halosbaena tulki</i>	coastal plain bordering Cape Range; Barrow Island
Amphipoda: Melitidae	<b><i>Nedsia douglasi</i></b>	coastal plain bordering Cape Range
	<i>N. fragilis, N. humphreysi, N. hurlberti, N. macrosculptilis, N. sculptilis, N. straskraba, N. urifimbriata</i>	Barrow Island
	<b><i>Norcapensis mandibulis</i></b>	Cape Range
Amphipoda: Bogidiellidae	<b><i>Bogidomma australis</i></b>	Barrow Island
Amphipoda: Hadziidae	<i>Liagoceradocus subthalassicus</i>	Barrow Island
	<i>Liagoceradocus branchialis</i>	coastal plain bordering Cape Range
Ostracoda: Halocyprida	<i>Danielopolina kornickeri</i>	coastal plain bordering Cape Range
Syncharida: Bathynellacea	<i>Atopobathynella</i> sp. nov. (H.K. Schminke, pers. comm.)	Barrow Island
Copepoda: Harpacticoida	?	coastal plain bordering Cape Range; Cape Range; Barrow Island
Copepoda: Cyclopoida	<i>Metacyclops mortoni</i>	coastal plain bordering Cape Range
	<i>Microcyclops varicans</i>	coastal plain bordering Cape Range; Cape Range
	<i>Apocyclops dengizicus</i>	coastal plain bordering Cape Range
	<i>Halicyclops longifurcatus</i>	coastal plain bordering Cape Range
	<i>Halicyclops spinifer</i>	coastal plain bordering Cape Range; Cape Range
Remipedia: Nectiopoda	<i>Lasionectes exleyi</i>	coastal plain bordering Cape Range
Turbellaria	?	coastal plain bordering Cape Range; Barrow Island

<sup>1</sup> About half of this fauna has been found since 1991.

<sup>2</sup> Genera in **bold** are endemic to the area, as are all the species save some copepods.

antennae, total lack of pigment, brittle cuticle, and narrow, elongated segments with short angular, spine-like paranota (Humphreys and Shear, 1993).

Amongst the pseudoscorpions, *Hyella humphreysi* has elongate appendages and is of very large size (Harvey, 1993); *Austrochthonius easti* has lost the posterior eyes and has reduced anterior eyes; *Tyrannochthonius butleri* has no eyes and is pale in colour. Many of the troglobitic spiders and the cave cricket are entirely eyeless. Comparative work on congeners is usually

impossible as no closely related surface species, even congeners, are known.

All the aquatic species are depigmented and lack eyes, with a remarkable exception – the bogidiellid amphipod is the only member of the family known which has eyes (Bradbury and Williams, 1996a), despite it having been collected down a borehole 50 m deep towards the centre of Barrow Island.

Table 30.3  
High-level taxonomic groupings of taxa collected in open water bodies<sup>1</sup>

Taxon	Notes	Authority <sup>2</sup>
Protista (sundry)	<i>Euplotes</i> sp.; <i>Paramecium</i> sp.	Knott (1993)
Rotatoria		
Turbellaria		
Nematoda		
Polychaeta	Syllidae (two species)	G. Hartmann-Schröder, pers. comm.
Oligochaeta		
Mollusca	<i>Iravadia</i> ( <i>Iravadia</i> ) sp.? <i>I. ornata</i> <sup>3</sup>	Slack-Smith (1993)
Ostracoda		
Amphipoda: Aoridae	<i>Grandidierella</i> n. sp.	Myers and Lowry, pers. comm.
Acarina: Hydracarina	<i>Coaustraliobates</i> sp.	Harvey, pers. comm.
Ephemeroptera		
Odonata		
Hemiptera		
Diptera: Chironomidae	<i>Kiefferulus intertinctus</i>	Knott (1993)
Coleoptera		
Pisces: Poeciliidae	<i>Poecilia reticulata</i> [feral guppies!]	

<sup>1</sup> These taxa may not constitute part of the stygofauna proper. However, a number of stygofaunal species are also known from the same habitats.

<sup>2</sup> The references denote the source of determinations.

<sup>3</sup> Status ambiguous (cf. Slack-Smith, 1993).

Table 30.4  
The number of troglobites and stygobionts in four Tasmanian karst regions and New South Wales, compared with the Cape Range

	Precipitous Bluff <sup>1</sup>	Exit Cave <sup>1</sup>	Vanishing Falls <sup>1</sup>	Kubla Khan <sup>1</sup>	New South Wales <sup>2,3</sup>	Cape Range
Troglobites	15	15	14	11	9	41
?Troglo/stygobites	4	1	3	2	8 taxa	>10
Stygobionts	3	7	5	0	8	22

<sup>1</sup> Locations in Tasmania. Data from Knott (1993), after Eberhard (1992).

<sup>2</sup> Data from A.P. Spate and S.M. Eberhard (pers. commun., 1995).

<sup>3</sup> Forty-eight karst areas combined; numbers given are of genera.

#### AGE OF CAVE SYSTEMS AND CAVE FAUNA

Detailed geological and palaeoclimatic data, which are widely available for much of Europe (Juberthie, 1988) and North America (Peck, 1981, 1984) are unavailable for northwestern Australia, primarily because of the great age of the landscape. The age of the cave systems in Cape Range is unknown, but there are a number of clues which are pursued in the following paragraphs. It should be stressed, however, that the age of a cave system may not provide any clue as to the age of the fauna – either phylogenetically or geographically – because both aquatic and terrestrial troglobites may

move widely through the interstices on a scale which may be local (Juberthie, 1983; Uéno, 1987; Howarth, 1981; Oromi et al., 1991; Humphreys, 1993c) or regional (Humphreys, 1993b,c, 1994); the system may possibly be in geologico-temporal continuity on a large, even global scale through plate tectonics and sea-floor spreading (Hart et al., 1985; Boxshall, 1989).

The cave systems must have formed after the Miocene limestones (>25 Ma ago) were thrust above sea level. Recent evidence suggests that the uplift of the Cape Range anticline had been completed by no later than the late Pliocene (>1.8 Ma BP) and possibly by the late Miocene (>5 Ma BP; Wyrwoll et al., 1993). Clearly

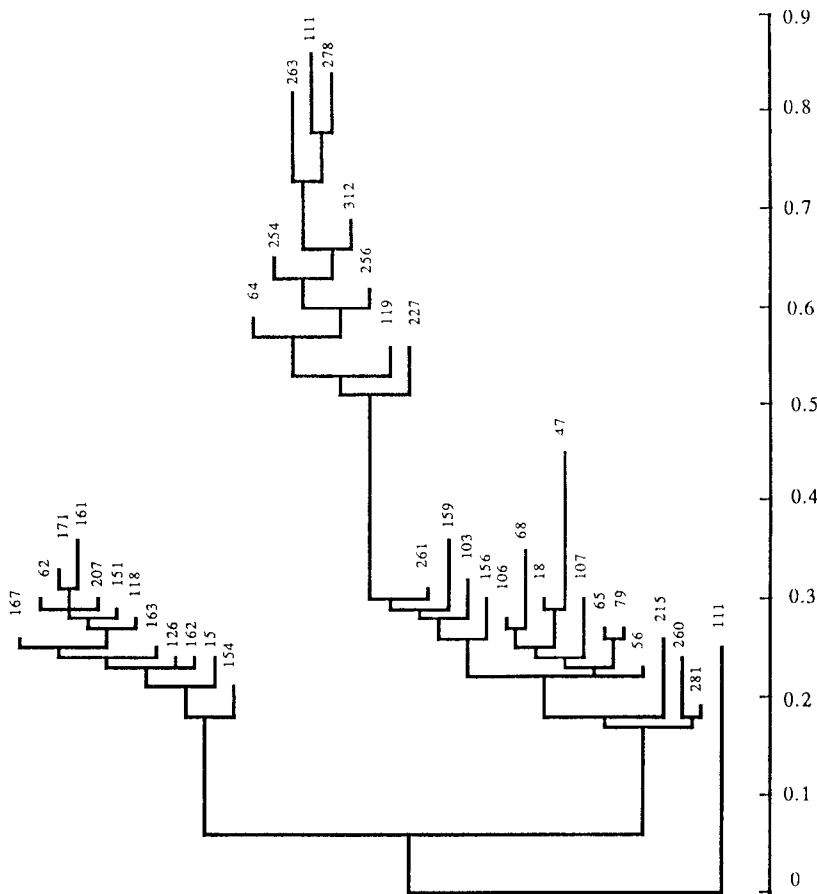


Fig. 30.5. Tree of the troglitic millipede populations *Stygiochiropus communis* from the 38 caves numbered, produced by a Distance Wagner Analysis on the matrix of Rogers' Genetic Distance (Humphreys, 1991d) rooted on sympatric *S. sympatricus* from C-111.

Table 30.5  
Number of troglitic species of arachnids and myriapods in five regions of Australia<sup>1</sup>

Region	Number of species
Nullarbor	8
Chillagoe	14
Tasmania <sup>2</sup>	34
New South Wales <sup>3</sup>	8+
Cape Range	23 <sup>4</sup>

<sup>1</sup> Data from Harvey et al. (1993).

<sup>2</sup> Thirty karst regions combined.

<sup>3</sup> Forty-eight karst regions combined; the figure given is of genera.

<sup>4</sup> Updated from Harvey et al. (1993).

the limestones would have been emergent much earlier than this, as they currently reach an altitude of 311 m despite erosion having stripped the Trealla Limestone

off more than 95% of the area of the range (Humphreys 1993d: frontispiece). The deeply dissected landscape, the caves and the cave morphology indicate that the caves formed at a time when the area was much wetter than at present.

Limited examination of speleothems has dated material up to 184 000 BP (D. Ford, pers. comm.); but the caves are much older – the location of some samples (e.g., hanging floors) shows that the caves were well developed at the time the speleothems were produced. Dates covering the period 170 000–80 000 years ago (D. Smith, pers. comm.) show growth rates of  $0.72 \mu\text{m yr}^{-1}$  (Humphreys, 1991d), an order of magnitude slower than any recorded by Shaw (1993: appendices 14 and 15) or Ford and Williams, 1989: table 8.5), suggesting that there was no major wet episode in that time interval.

The surface biota of the Cape Range region is largely

that found in the broad arid zone on the western border of which the Cape Range lies (see papers in Humphreys, 1993d); but the flora gives some evidence of a wetter past (Keighery and Gibson, 1993), with some tropical relicts. In contrast, the subterranean terrestrial fauna has clear affinities with the leaf-litter fauna found on the floor of wet forests, both temperate and tropical (Harvey et al., 1993; Humphreys, 1993a,c). Hence, study of the palaeoclimate and palaeovegetation may provide indicators as to the age of the fauna.

Palaeoclimatic data are sparse for northwestern Australia, hence one needs to rely unduly on data from further afield, in eastern and southern Australia – the affinities of the cave fauna provide the main evidence that there were extensive wet forests in the region from the Eocene onwards. While plants can establish rainforest patches by propagule dispersal (Kenneally et al., 1991), there is no evidence that this is the case with physico-chemically sensitive cryptozoic invertebrates – these are often found in rainforest as separate species with small ranges (e.g., the Schizomida: Harvey, 1992). Hence, it is argued, the caves were colonized at a time when Australia was widely blanketed with complex rainforest.

Complex rainforest occurred on the western shoulder of Australia during the Eocene (Truswell, 1990), but global drying in the late Miocene led to massive contraction of the rainforest (Kemp, 1981). While subsequent palaeovegetation data are lacking for Western Australia, the continental trends (Truswell, 1990) suggest that by the Pliocene there had been a progressive retreat of both complex rainforest and closed forest communities to the eastern and southwestern seabords of the continent, as is the case today (Fig. 30.6). The regional rainforest would have progressively fragmented (Webb and Tracey, 1981) through the Miocene and Pliocene owing to the easterly wind pattern (Bowler, 1982). Along river valleys forest persisted (Truswell, 1990), providing corridors of suitable habitat between the Neogene Cape Range Formation and older landmasses (see also Wyrwoll et al., 1993). Hence, by the late Miocene extensive rainforest must have been eliminated from the Cape Range area, but possibly would have persisted until later in the deep gorges of the range, permitting genetic exchange between cave areas (Humphreys, 1993c).

Ages of vicariance in troglobites estimated from figures for genetic distance are often in broad agreement with the palaeogeographic evidence (Delay et al., 1980; Sbordoni, 1982; Juberthie, 1988). Data for genetic

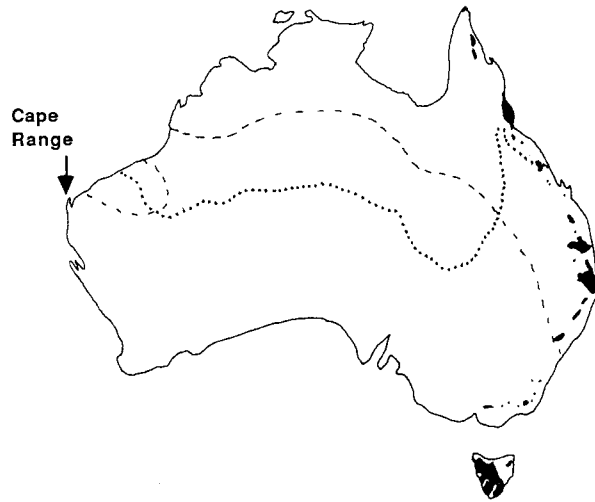


Fig. 30.6. The current distribution of extensive coastal rainforest (black) and the southerly limit (dashed lines) of remnant coastal rainforest elements in contemporary Australia (after Webb and Tracey, 1981). The former occurs in an arc through eastern Australia, with a distribution similar to the Pliocene limits of forest with *Nothofagus*. The dotted line shows the known northerly extent of forest with *Nothofagus* in the Eocene; data from further north are mostly lacking. By the middle Eocene (45 Ma ago), complex rainforest was restricted to riverine and lacustrine areas across the southern half of Australia and was absent by the early Miocene (20 Ma ago). Through the Pliocene, forest with *Nothofagus* retreated to the eastern seaboard (Truswell, 1990: fig. 7). After Humphreys (1993c).

distance are available for a number of taxa within the Cape Range (Table 30.6). Data for melitid amphipods on the coast and those inhabiting fresh cave waters at ~200 m altitude within the Cape Range suggests that the elevation of the range could have occurred ~7 Ma ago (Table 30.6). There is evidence from both the strongly troglomorphic congeneric species within the genera *Stygiocaris* (shrimps) and *Stygiochiropus* (millipedes), that by 4.3–4.0 Ma ago they were already inhabiting the subterranean realm, and that this realm was fragmenting, permitting speciation (Table 30.6). Hence both the aquatic and terrestrial components of the fauna were present and speciating in the Late Miocene/Upper Pliocene.

The genetic provincialization of the cave fauna occurred during the Pleistocene – within the Cape Range from 2.6 to 0.8 Ma ago (Humphreys and Shear, 1993), as indicated by the data for *Stygiochiropus communis* (Table 30.6). From 1.3 to 0.6 Ma ago the perched water bodies became separated, isolating populations of melitid amphipods within the Range (Table 30.6), and possibly indicating continued drying. Differentiation

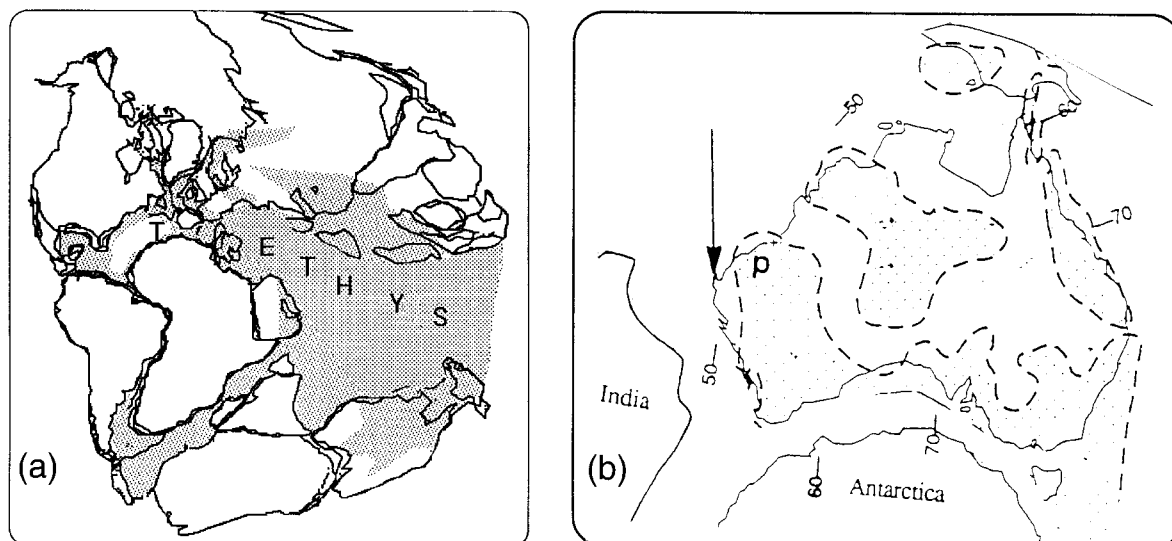


Fig. 30.7. (a) The relative location of the continental plates in the Jurassic (151 Ma ago) when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. Even with this reconstruction the genera *Halosbaena* (Thermosbaenacea), *Haptolana* (Isopoda: Cirrolanidae) and *Lasionectes* (Remipedia), known from the Cape Range area, have widely disjunct distributions variously including Somalia, the Canary Islands and Caribbean islands. The plate map was produced by the technique of Scotese and Denham (1988). (b) The current outline of Australia superimposed on the emergent parts of the Australian plate (dashed lines) in the early Cretaceous (118 Ma ago), when shallow seas surround the Pilbara Craton (p); the arrow shows the location of the present Cape Range. The numbers on the map show the latitude. Continental margins after Veevers et al. (1991).

of populations of the amphipods, *Draculoides vinei* and *S. communis* between various caves within the broadly defined genetic provinces continued through the Pleistocene (550 000–100 000 BP; Table 30.6).

There is general accord between the geological, fossil and biological evidence as to the age of emergence of the Cape Range. However, for the anchialine fauna the evidence is quite different. While our "ignorance about the time of colonization of cave waters is complete" (Culver, 1982: p. 141), the presence of species in the anchialine fauna congeneric with obligatory troglobites in the North Atlantic (e.g., *Halosbaena*, *Haptolana*, and *Lasionectes*) suggests that the fauna had colonized caves prior to the disruption of Pangea in the Mesozoic (Fig. 30.7). In this case a spatial and temporal continuity of crevicular habitat must be sought to explain their occurrence in Cape Range, which is of Miocene age. This must be sought between the Mesozoic formations that fringe the Precambrian Pilbara Craton (Fig. 30.1) and their current location in Miocene strata; this continuity needs to be sought in the following geological context.

The Permian Callytharra Formation, which is karstic in places and up to 244 m deep, occurs widely at depth, extending from Onslow in the north to Wooromel

at the foot of the Cape Range peninsula, and from the coast to well inland (Hocking et al., 1987). In the lower Mesozoic there were successive waves of sedimentation, giving marine silt and clay stones, alluvial fans and fluvial sandstones, followed by shallow marine and coastal sandstone (Jurassic). During the Cretaceous there was a progradation of a deltaic complex over marine clays followed by calcareous pelagic deposition formed on the extensive low-energy shelf deepening towards the northwest. The advent of calcareous deposition was part of a worldwide event caused by changed oceanic-circulation patterns following continental break-up, which continued through the remainder of the Cretaceous. Such carbonate deposition continued in the northern Carnarvon Basin throughout the Tertiary. The subsequent uplift of the area by reverse thrust may be the result of compensation for the break-up, adjustment and foundering of the continental margin.

#### CONCLUDING REMARKS

The hypothesis that regions lacking forest throughout the Pleistocene, such as parts of the American southwest and Australia, have a very depauperate terrestrial

Table 30.6  
The evidence supporting a proposed sequence of events in the Cape Range area<sup>1</sup>

Event	Period	Date	Evidence
<b>1000 years ago</b>			
N.W. Shelf inundated <sup>2</sup>	Holocene	8–0	calculated from Chappell and Thom (1977)
Wetter period	Pleistocene	14–11	U/Th speleothem date, C-125 <sup>4</sup>
E and W coast populations isolated	Pleistocene	25	<i>D</i> between <i>Stygiocaris stylifera</i> populations <sup>3,5</sup>
Differentiation of populations	Pleistocene	30	<i>S. stylifera</i> <sup>5</sup>
N. W. Shelf inundated <sup>2</sup>	Pleistocene	85–80	calculated from Chappell and Thom (1977)
Differentiation <sup>6</sup> ; southern province	Pleistocene	100	<i>D</i> between millipede populations <sup>5,7,14</sup>
N.W. Shelf inundated <sup>2</sup>	Pleistocene	111–99	calculated from Chappell and Thom (1977)
Wetter period	Pleistocene	128	<i>Anadara trapezia</i> distribution <sup>9</sup>
N.W. Shelf inundated <sup>2</sup>	Pleistocene	135–116	calculated from Chappell and Thom (1977)
Differentiation in central province	Pleistocene	165	<i>D</i> between amphipods in range <sup>5,7,10,15</sup>
Differentiation of populations	Pleistocene	200	<i>D</i> between <i>Draculoides</i> populations <sup>7</sup>
Atyid populations isolated	Pleistocene	205	<i>D</i> between <i>S. lancifera</i> populations <sup>7,10</sup>
Wetter period	Pleistocene	219–68	U/Th speleothem date, C-126 and C-163 <sup>4</sup>
N.W. Shelf inundated <sup>2</sup>	Pleistocene	222–216	calculated from Chappell and Thom (1977)
Wetter period	Pleistocene	225	<i>Anadara trapezia</i> distribution <sup>9</sup>
Differentiation <sup>6</sup> ; central populations	Pleistocene	400	<i>D</i> between millipede populations <sup>5,7</sup>
E and W coast populations isolated	Pleistocene	315	<i>D</i> between cave fish <sup>11</sup> populations <sup>5,7,10,12</sup>
Differentiation <sup>6</sup> ; northern populations	Pleistocene	350	<i>D</i> between millipede populations <sup>5,7</sup>
Barrow Island isolated from Cape Range	Pleistocene	380	<i>D</i> between <i>S. stylifera</i> populations <sup>5,7,13</sup>
Schizomid populations diverge	Pleistocene	450	<i>D</i> within <i>Draculoides vinei</i> populations <sup>5,7</sup>
Within-province differentiation	Pleistocene	550	<i>D</i> within millipede genetic provinces <sup>5,7,14</sup>
Northern cave waters isolated	Pleistocene	650	<i>D</i> between amphipods in range <sup>5,7,10,15</sup>
Southern caves isolated from rest	Pleistocene	800	<i>D</i> between millipede populations <sup>5,7,14</sup>
<b>1 000 000 years ago</b>			
Wet forest lost from gorges	Pleistocene	4.3–1.6	Deduced from genetic distances above
Southern cave waters isolated	Pleistocene	1.3	<i>D</i> between amphipods in range <sup>5,7,10,15</sup>
Northern cave areas isolated	Pleistocene	1.6	<i>D</i> between millipede genetic provinces <sup>5,7</sup>
Cape Range fully emergent	Pliocene	>2	Marine terraces; Wyrwoll et al. (1993)
Southern cave areas isolated	Pliocene	2.2	<i>D</i> between millipede genetic provinces <sup>5,7,14</sup>
Shrimps speciate	Pliocene	4.0	<i>D</i> between congeneric atyid shrimps <sup>5,7</sup>
Millipedes speciate	Pliocene	4.3	<i>D</i> between congeneric millipedes <sup>5,7,14</sup>
Anticline uplift	Miocene/Pliocene	7	<i>D</i> between amphipod genera <sup>5,7,10,15</sup>
Indian and Pacific Oceans isolated <sup>16</sup>	Late Miocene	7	Kennett et al. (1985)
Anticline uplift	Late Miocene	>7	Malcolm et al. (1991)
Closed forest with <i>Nothofagus</i>	Miocene	>7	Truswell (1990)
Cooling sea and land	Miocene	8–6	MacFadden and Cerling (1994)
Indian and Atlantic Oceans separate <sup>17</sup>	Middle Miocene	14–12	Kennett (1982)
Pilgrammuna Formation formed	Middle Miocene	~17	Hocking et al. (1987)
Trealla Limestone formed	Middle Miocene	~17	Hocking et al. (1987)

continued on next page



Table 30.6, *continued*

Event	Period	Date	Evidence
Increased aridity <sup>18</sup>	Early Miocene	~22	Circum-Antarctic circulation
Tulki Limestone formed	Early Miocene	~22	Hocking et al. (1987)
Mandu Limestone formed	Late Oligocene	~28 onwards	Hocking et al. (1987)
Complex rainforest in vicinity	Eocene	>38	Truswell (1990)
Tethys Seaway ends	Late Eocene	40	Smith and Briden (1977)
Carbonate deposition continues	Cainozoic	65 onwards	Hocking et al. (1987)
Epicontinental sea connection cut	Middle Cretaceous	~100	Cande and Mutter (1982)
Tethys encircles Pilbara craton	Cretaceous	118	Veevers et al. (1991)
NW Australia is E. shore of Tethys	Early Cretaceous	~120	M.K. Howarth (1981)
E. and W. Gondwana well separated	Cretaceous	125	M.K. Howarth (1981)
Eastern Gondwana fragments	Cretaceous	133–96	Veevers et al. (1991)
Advent of calcareous deposition <sup>19</sup>	Cretaceous-		Hocking et al. (1987)
Extensive low energy shelf	Cretaceous		Hocking et al. (1987)
E. and W. Gondwana separated	Upper Jurassic	145	M.K. Howarth (1981)
Onset of seafloor spreading	Jurassic	155	Hocking et al. (1987)
Tethys Seaway starts	Triassic	200	Smith and Briden (1977)
Shallow marine environments start	Triassic	~200	Hocking et al. (1987)
Deltaic progradation	Mid Triassic	210	Hocking et al. (1987)
Marine transgression; local seaways	Early Triassic	220	Hocking et al. (1987)
Broad marine shelf	Permian	250	Hocking et al. (1987)
Clear water carbonate deposition <sup>8</sup>	Early Carboniferous	340	Hocking et al. (1987)
Pilbara Craton emergent	Precambrian	>600	Hocking et al. (1987)

<sup>1</sup> The purpose of this Table is to provide a heuristic focus for the timing of biogeographically pertinent events in the area. Expanded from Humphreys (1993c).

<sup>2</sup> Defined as Barrow Island being separated from the mainland when the sea level rises above a level more than 20 m below the present level.

<sup>3</sup> “*D*” is Nei’s (1987) genetic distance.

<sup>4</sup> The ages include the 95% confidence intervals for the date. The dating was conducted by Dr D. Smith, Department of Inorganic Chemistry, University of Melbourne. Owing to low uranium content the error bounds are large.

<sup>5</sup> Adams and Humphreys (1993), unpublished.

<sup>6</sup> By inference, caves isolated.

<sup>7</sup> Calculated from the average Nei’s genetic distance (*D*) assuming *D* = 1 corresponds to five million years of divergence (Nei, 1987).

<sup>8</sup> Moogooree Limestone.

<sup>9</sup> Kendrick et al. (1991).

<sup>10</sup> Humphreys and Adams (1991).

<sup>11</sup> *Milyeringa veritas*.

<sup>12</sup> Between populations on the east and west coast of the Cape Range peninsula.

<sup>13</sup> Between populations on Barrow Island and the Cape Range peninsula.

<sup>14</sup> Humphreys and Shear (1993).

<sup>15</sup> The populations within the Cape Range *sensu stricto* are not congeneric with those on the coastal plain or Barrow Island (J. Bradbury, pers. comm., 1995).

<sup>16</sup> Diversion of North Equatorial Current from the Indian Ocean to the North Pacific.

<sup>17</sup> Tropical connection only.

<sup>18</sup> The opening of a seaway between South America and Antarctica in the Early Miocene permitted the West Wind Drift and hence the establishment of the circum-Antarctic circulation pattern; Antarctica became refrigerated and the temperature gradient between the equator and the poles intensified, creating the arid regions where they are currently found (see Main, 1993).

<sup>19</sup> Part of a worldwide event caused by changed oceanic-circulation patterns following continental break-up (Hocking et al., 1987).

cave fauna (Peck, 1980) is not supported by the Cape Range data.

Howarth (1988) suggested that tropical cave faunas were associated with parts of cave systems free from draughts, where the air was rich in carbon dioxide; there is no evidence for such requirements by the diverse and highly troglomorphic fauna of the Cape Range area. Indeed, some species, such as *Stygiochiropus communis* and *S. isolatus*, will move into sunlight at the cave threshold if the humidity is high (e.g., C-222) and moisture in the air flowing out of the cave condenses there (e.g., C-15).

The history of the Cape Range area is complex, and as yet poorly documented. However, a plurality of factors appear to have been involved in the evolution of the fauna of the Cape Range peninsula (see Table 30.7), as has been suggested for some other regions (Peck, 1990; Botosaneanu and Holsinger, 1991: p. 34).

Table 30.7  
Vicariance and the presence of relictual and relic taxa in the subterranean fauna of the Cape Range peninsula

Item <sup>1</sup>	Terrestrial	Groundwater	
Vicariant event	aridity	plate tectonics	
	eustatic	eustatic	
	orogenic	orogenic	
Relictual taxa			
	global	Hyidae	many stygofauna spp.
	regional	Schizomida	amphipods
local	<i>Stygiochiropus</i>	amphipods in Cape Range	
Relic taxa	e.g., Remipedia, Thermosbaenacea, Atyidae		
	Refugium	caves	freshwater
	crevicular habitats	anchialine	

<sup>1</sup> See definitions in Glossary, p. 6.

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#### REFERENCES

- Adams, M. and Humphreys, W.F., 1993. Patterns of genetic diversity within selected subterranean fauna of the North West Cape peninsula, Western Australia: systematic and biogeographic implications. *Rec. West. Aust. Mus. Suppl.*, 45: 145–164.
- Allen, A.D., 1993. Outline of the geology and hydrogeology of Cape Range, Carnarvon Basin, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 25–38.
- Bailey-Brock, J.H. and Brock, R.E., 1993. Feeding, reproduction, and sense organs of the Hawaiian anchialine shrimps *Halocaridina rubra* (Atyidae). *Pac. Sci.*, 47: 338–355.
- Baltanas, A. and Danielopol, D.L., 1995. Cladistic analysis of *Danielopolina* species (Ostracoda: Thaumatozoididae) and the origin of anchialine fauna. *Mitt. Hamb. Zool. Mus. Inst.*, 92: 315–324.
- Barnard, J.L. and Williams, W.D., 1995. The taxonomy of freshwater Amphipoda (Crustacea) from Australian freshwaters: Part 2. *Rec. Aust. Mus.*, 47: 161–201.
- Barr Jr., T.C. and Holsinger, J.R., 1985. Speciation in cave faunas. *Annu. Rev. Ecol. Syst.*, 16: 313–337.
- Botosaneanu, L. and Holsinger, J.R., 1991. Some aspects concerning colonisation of the subterranean realm – especially of subterranean waters: a response to Rouch & Danielopol. *Stygologia*, 6: 11–39.
- Bowler, J.M., 1982. Aridity in the late Tertiary and Quaternary of Australia. In: W.R. Barker and P.J.M. Greenslade (Editors), *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Frewville, South Australia, pp. 35–45.
- Boxshall, G.A., 1989. Colonisation of inland marine caves by misophrioid copepods. *J. Zool. (London)*, 219: 521–526.
- Bradbury, J.H. and Williams, W.D., 1996a. Freshwater amphipods from Barrow Island, Western Australia. *Rec. Aust. Mus.*, 48: 33–74.
- Bradbury, J.H. and Williams, W.D., 1996b. Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia. *Rec. West. Aust. Mus.*, 17: 395–409.
- Bradbury, J.H. and Williams, W.D., 1997. The amphipod (Crustacea) stygofauna of Australia: description of new taxa (Melitidae, Neophargidae, Paramelitidae), and a synopsis of known species. *Rec. Aust. Mus.*, 49: 249–341.
- Bruce, N.L. and Humphreys, W.F., 1993. *Haptolana pholeta* sp. nov., the first subterranean flabelliferan isopod crustacean (Cirrolanidae) from Australia. *Invertebr. Taxon.*, 7: 875–884.
- Cande, S.C. and Mutter, J.C., 1982. A revised identification of the oldest sea-floor spreading anomalies between Australia and Antarctica. *Earth Planet. Sci. Lett.*, 58: 151–160.
- Cawthorn, P., 1963. Discovery of subterranean freshwater fauna on the eastern side of North West Cape. *West. Aust. Nat.*, 8: 129–132.
- Chappell, J. and Thom, B.G., 1977. Sea levels and coasts. In: J. Allen, J. Golson and R. Jones (Editors), *Sunda and Sakul: Prehistoric*

- Studies in Southeast Asia, Melanesia & Australia*. Academic Press, London, pp. 275–291.
- Culver, D.C., 1982. *Cave Life: Evolution and Ecology*. Harvard University Press, Cambridge, MA, 189 pp.
- Dalens, H., 1992. Oniscidea (Crustacea, Isopoda) from caves of Cape Range in Western Australia. I. The genus *Buddelundia*. *Rec. West. Aust. Mus.*, 16: 87–102.
- Dalens, H., 1993. Two new genera of terrestrial isopods (Crustacea: Isopoda: Oniscidea) from north-western Western Australia. *Rec. West. Aust. Mus.*, 16: 257–267.
- Danielopol, D.L., Baltanas, A. and Humphreys, W.F., 2000. *Danielopolina kornickeri* sp. n. (Ostracoda: Thaumatocepridoidea) from a western Australian anchialine cave – morphology and evolution. *Zool. Scr.*, 29: 1–16.
- Deeleman-Reinhold, C.L., 1993. *Trichocyclus septentrionalis* n. sp. a new species of cave dwelling pholcid spider from northwestern Australia (Araneae: Pholcidae). *Rec. West. Aust. Mus.*, 16: 323–329.
- Delay, B., Sbordoni, V., Cobolli Sbordoni, M. and De Matthaeis, E., 1980. Divergences génétique entre les populations de *Speonomus delarouzei* du Massif du Canigou (Colcoptera, Bathysciinae). *Mém. Biospéol.*, 7: 235–247.
- Eberhard, S.M., 1992. *The invertebrate cave fauna of Tasmania: ecology and conservation biology*. M.Sc. Thesis. Department of Zoology, University of Tasmania, Hobart, 184 pp.
- Eberhard, S.M., Richardson, A.M.M. and Swain, R., 1991. *The Invertebrate Cave Fauna of Tasmania*. Zoology Department, University of Tasmania, 174 pp.
- Ford, D.C. and Williams, P.W., 1989. *Karst Geomorphology and Hydrology*. Unwin Hyman, London, 601 pp.
- Forth, J.R., 1973. Exmouth water supply. *Geol. Surv. West. Aust. Annu. Rep.*, 1972: 11–15.
- Fryer, G., 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica. *Philos. Trans. R. Soc. London B*, 277: 57–128.
- Gentilli, J., 1972. *Australian Climatic Patterns*. Nelson, Melbourne, 285 pp.
- Harris, J.A., 1973. Structure and dynamics of a cave population of the guano mite, *Uroobovella coprophila* (Wolmersley). *Aust. J. Zool.*, 21: 239–275.
- Hart, C.W., Manning, R.B. and Iliff, T.M., 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proc. Biol. Soc. Washington*, 98: 288–292.
- Harvey, M.S., 1988. A new troglitic schizomid from Cape Range, Western Australia (Chelicerata: Schizomida). *Rec. West. Aust. Mus.*, 14: 15–20.
- Harvey, M.S., 1991. The cavernicolous pseudoscorpions (Chelicerata: Pseudoscorpionida) of Cape Range, Western Australia. *Rec. West. Aust. Mus.*, 15: 487–502.
- Harvey, M.S., 1992. The Schizomida (Chelicerata) of Australia. *Invertebr. Taxon.*, 6: 77–129.
- Harvey, M.S., 1993. The systematics of the Hyidae (Pseudoscorpionida). *Invertebr. Taxon.*, 7: 1–32.
- Harvey, M.S. and Humphreys, W.F., 1995. Notes on the genus *Draculoides* Harvey (Schizomida: Hubbardiidae), with the description of a new troglitic species. *Rec. West. Aust. Mus. Suppl.*, 52: 183–189.
- Harvey, M.S., Gray, M.R., Hunt, G.S. and Lee, D.C., 1993. The cavernicolous Arachnida and Myriapoda of Cape Range, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 129–144.
- Hoch, H., 1993. A new troglitic planthopper species (Homoptera: Fulgoroidea: Meenoplidae) from Western Australia. *Rec. West. Aust. Mus.*, 16: 393–398.
- Hoch, H. and Howarth, F.G., 1989a. Six new cavernicolous cixiid planthoppers in the genus *Solonaima* from Australia (Homoptera: Fulgoroidea). *Syst. Entomol.*, 14: 377–402.
- Hoch, H. and Howarth, F.G., 1989b. The evolution of cave-adapted cixiid planthoppers in volcanic and limestone caves in North Queensland, Australia (Homoptera: Fulgoroidea). *Mém. Biospéol.*, 16: 17–24.
- Hoch, H. and Howarth, F.G., 1993. Evolutionary dynamics of behavioral divergence among populations of the Hawaiian cave-dwelling planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae). *Pac. Sci.*, 47: 303–318.
- Hocking, R.M., Moors, H.T. and van de Graaff, W.J.E., 1987. Geology of the Carnarvon Basin, Western Australia. *Geol. Surv. West. Aust. Bull.*, 133: 1–289.
- Hoffman, R.L., 1994. Studies on spiroboloid millipeds. XVIII. *Speleostrophus nesiotis*, the first known troglitic spiroboloid milliped, from Barrow Island, Western Australia (Diplopoda: Pachybolidae: Trigonulinae). *Myriapodologia*, 3: 19–24.
- Holsinger, J.R., 1994. Pattern and process in the biogeography of subterranean amphipods. *Hydrobiologia*, 287: 131–145.
- Holsinger, J.R. and Culver, D.C., 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: zoogeography and ecology. *Brimleyana*, 14: 1–164.
- Holsinger, J.R. and Longley, G., 1980. The subterranean amphipod crustacean fauna of an artesian well in Texas. *Smithson. Contrib. Zool.*, 308: 1–62.
- Holthuis, L.B., 1960. Two new species of Atyid shrimps from subterranean waters in N.W. Australia (Decapoda: Natantia). *Crustaceana*, 1: 47–57.
- Howarth, F.G., 1973. The cavernicolous fauna of Hawaiian lava tubes, 1. Introduction. *Pac. Insects*, 15: 139–151.
- Howarth, F.G., 1980. The zoogeography of specialized cave animals: a bioclimatic model. *Evolution*, 34: 394–406.
- Howarth, F.G., 1981. Non-relictual terrestrial troglitics in the tropics: Hawaiian caves. In: *Proceedings of the 8th International Congress of Speleology, Bowling Green, Kentucky*, Vol. 2, pp. 539–541.
- Howarth, F.G., 1982. Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian cave insects. *Entomol. Gen.*, 8: 17–26.
- Howarth, F.G., 1983. Ecology of cave arthropods. *Annu. Rev. Entomol.*, 28: 365–389.
- Howarth, F.G., 1987. The evolution of non-relictual tropical troglitics. *Int. J. Speleol.*, 16: 1–16.
- Howarth, F.G., 1988. Environmental ecology of north Queensland caves: or why are there so many troglitics in Australia. In: L. Pearson (Editor), *17th Biennial Conference, Australian Speleological Federation Tropic Conference, Lake Tinaroo, Far North Queensland, 27–31 December 1988*. Australian Speleological Federation, Cairns, pp. 76–84.
- Howarth, F.G. and Stone, F.D., 1990. Elevated carbon dioxide levels in Bayliss Cave, Australia: implications for the evolution of obligate cave species. *Pac. Sci.*, 44: 207–218.
- Howarth, M.K., 1981. Palaeogeography of the Mesozoic. In:

- L.M.R. Cooks (Editor), *The Evolving Earth*. Oxford University Press, Oxford, pp. 197–220.
- Humphreys, W.F., 1989. *The status of relict cave fauna of Cape Range, Western Australia, especially the Schizomida*. Report to the Australian National Parks and Wildlife Service, Canberra, 104 pp.
- Humphreys, W.F., 1990a. The location of Spiral Cave, Cape Range. *West. Caver*, 30: 36–37.
- Humphreys, W.F., 1990b. The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. *Acta Zool. Fenn.*, 190: 181–186.
- Humphreys, W.F., 1991a. Biological research into the Cape Range karst area, North West Cape peninsula, Western Australia. In: S. Brooks (Editor), *Cave Leeuwin – Proceedings of the 18th Biennial Conference of the Australian Speleological Federation Inc., Margaret River, Western Australia, 30 December 1990–5 January 1991*. Australian Speleological Federation Inc., Nedlands, Western Australia, pp. 6–14.
- Humphreys, W.F., 1991b. *Survey of caves in Cape Range, North West Cape Peninsula, Western Australia*, Report to the Australian Heritage Commission and the Western Australian Heritage Committee, 178 pp.
- Humphreys, W.F., 1991c. Experimental reactivation of pulse driven populations in a terrestrial troglobite community. *J. An. Ecol.*, 60: 609–623.
- Humphreys, W.F., 1991d. *The cave fauna of Cape Range: specific analyses*, Report to the Australian National Parks and Wildlife Service, Canberra, 132 pp.
- Humphreys, W.F., 1991e. Troglobites on Barrow Island, Western Australia. *West. Caver*, 31: 11–14.
- Humphreys, W.F., 1993a. Cave fauna in semi-arid tropical Western Australia: a diverse relict wet-forest litter fauna. *Mém. Biospéol.*, 20: 105–110.
- Humphreys, W.F., 1993b. Stygofauna in semi-arid tropical Western Australia: a Tethyan connection? *Mém. Biospéol.*, 20: 111–116.
- Humphreys, W.F., 1993c. The significance of the subterranean fauna in biogeographical reconstruction: examples from Cape Range peninsula, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 165–192.
- Humphreys, W.F. (Editor), 1993d. The Biogeography of Cape Range, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 1–228.
- Humphreys, W.F., 1994. *The subterranean fauna of the Cape Range coastal plain, Northwestern Australia*, Report to the Australian Heritage Commission and the Western Australian Heritage Committee, 202 pp.
- Humphreys, W.F., 1999. The distribution of the Australian cave fishes. *Rec. West. Aust. Mus.*, 19: 469–472.
- Humphreys, W.F. and Adams, M., 1991. The subterranean aquatic fauna of the North West Cape peninsula, Western Australia. *Rec. West. Aust. Mus.*, 15: 383–411.
- Humphreys, W.F. and Collis, G., 1990. Water loss and respiration of cave arthropods from Cape Range, Western Australia. *Comp. Biochem. Physiol.*, 95A: 101–107.
- Humphreys, W.F. and Feinberg, M.N., 1995. Food of the blind cave fishes of northwestern Australia. *Rec. West. Aust. Mus.*, 17: 29–33.
- Humphreys, W.F. and Shear, W.A., 1993. Troglobitic millipedes (Diplopoda: Paradoxosomatidae) from semi-arid Cape Range, Western Australia – systematics and biology. *Invertebr. Taxon.*, 7: 173–195.
- Humphreys, W.F., Adams, M. and Vine, B., 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. *J. Zool. (London)*, 217: 177–201.
- Izquierdo, I. and Oromi, P., 1994. Dictyoptera – Blattaria. In: C. Juberthie and V. Decu (Editors), *Encyclopaedia Biospeologica*. Société de Biospéologie, Moulis (France) and Bucarest, pp. 295–300.
- Jacobson, G. and Hill, P.J., 1980. Hydrogeology of a raised coral atoll, Niue Island, South Pacific. *J. Aust. Geol. Geophys.*, 5: 271–278.
- Juberthie, C., 1983. Le milieu souterrain: tendue et composition. *Mém. Biospéol.*, 10: 17–65.
- Juberthie, C., 1988. Palaeoenvironment and speciation in the cave beetle complex *Speonomus delarouzei* (Coleoptera, Bathysciinae). *Int. J. Speleol.*, 17: 31–50.
- Juberthie, C. and Delay, B., 1981. Ecological and biological implications of the existence of a Superficial Underground Compartment. *Proc. 8th Int. Congr. Speleol., Bowling Green, Kentucky*, 6: 203–206.
- Kane, T.C., Norton, R.M. and Poulson, T.L., 1975. The ecology of predacious troglobitic beetles, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae). I. Seasonality of food input and early life history stages. *Int. J. Speleol.*, 7: 45–54.
- Keighery, G. and Gibson, N., 1993. Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 51–85.
- Kemp, E.M., 1981. Tertiary palaeogeography and the evolution of Australian climate. In: A. Keast (Editor), *Ecological Biogeography of Australia*. Dr W. Junk, The Hague, pp. 31–49.
- Kendrick, G.W., Wyrwoll, K.H. and Szabo, B.J., 1991. Pliocene – Pleistocene coastal events and history along the western margin of Australia. *Quat. Sci. Rev.*, 10: 419–439.
- Kennally, K.F., Keighery, G.J. and Hyland, B.P.M., 1991. An ecological survey of tropical rainforests in Western Australia: background and methods. In: N.L. McKenzie, R.B. Johnston and P.G. Kendrick (Editors), *Kimberley Rainforests*. Surrey Beatty and Sons Pty Limited, Chipping Norton, New South Wales, pp. 93–131.
- Kennett, J.P., 1982. *Marine Geology*. Prentice-Hall, New York, 813 pp.
- Kennett, J.P., Keller, G. and Srinivasan, M.S., 1985. Miocene planktonic foraminiferal biogeography and paleoceanographic development of the Indo-Pacific region. *Geol. Soc. Am. Mem.*, 63: 197–236.
- Knott, B., 1993. Stygofauna from Cape Range peninsula, Western Australia: Tethyan relicts. *Rec. West. Aust. Mus. Suppl.*, 45: 109–127.
- MacFadden, B.J. and Cerling, T.E., 1994. Fossil horses, carbon isotopes and global change. *Trends Ecol. Evol.*, 9: 481–486.
- Main, A.R., 1993. Synthesis and prospects. *Rec. West. Aust. Mus. Suppl.*, 45: 243–248.
- Main, B.Y., 1980. Record of the arachnid order Schizomida in Western Australia. *West. Aust. Nat.*, 14: 236–237.
- Malcolm, R.J., Pott, M.C. and Delfos, E., 1991. A new tectono-stratigraphic synthesis of the North West Cape area. *APEA J.*, 1991: 154–176.
- Manning, R.B., Hart, C.W. and Illiffe, T.M., 1986. Mesozoic relicts in marine caves of Bermuda. *Stygologia*, 2: 156–166.

- Martin, M.W., 1990. *Exmouth town water supply investigation report and recommendations for future work, hydrogeology report No. 1990/36*. Western Australian Geological Survey, 12 pp.
- McNamara, K.J. and Kendrick, G.W., 1994. Cenozoic molluscs and echinoids of Barrow Island, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 51: 1–50.
- Mees, G.F., 1962. The subterranean fauna of Yardie Creek station, North West Cape, Western Australia. *J.R. Soc. West. Aust.*, 45: 24–32.
- Millidge, A.F., 1993. Three new species of the spider family Linyphiidae from Australia (Araneae). *Rec. West. Aust. Mus.*, 16: 211–219.
- Nei, M., 1987. *Molecular Evolutionary Genetics*. Columbia University Press, New York, 512 pp.
- Norton, R.M., Kane, T.C. and Poulson, T.L., 1975. The ecology of predacious troglitic beetles, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae). II. Adult seasonality, feeding and recruitment. *Int. J. Speleol.*, 7: 55–64.
- Notenboom, J., 1991. Marine regressions and the evolution of ground dwelling amphipods (Crustacea). *J. Biogeogr.*, 18: 437–454.
- Noy-Meir, I., 1985. Desert ecosystem structure and function. In: M. Evenari, I. Noy-Meir and D.W. Goodall (Editors), *Hot Deserts and Arid Shrublands*, Vol. 12A of *Ecosystems of the World*. Elsevier, Amsterdam, pp. 93–103.
- Oromi, P., Martin, J.L., Medina, A.L. and Izquierdo, I., 1991. The evolution of the hypogean fauna of the Canary Islands. In: E.C. Dudley (Editor), *The Unity of Evolutionary Biology*, Vol. 1. Dioscorides Press, Portland, OR, pp. 380–395.
- Peck, S.B., 1978. New montane *Ptomaphagus* beetles from New Mexico and zoogeography of southwestern caves (Coleoptera: Leiodidae; Catopinae). *Southwest. Nat.*, 23: 227–238.
- Peck, S.B., 1980. Climatic change and the evolution of cave invertebrates in the Grand Canyon, Arizona. *Natl. Speleol. Soc. Bull.*, 42: 53–60.
- Peck, S.B., 1981. The geological, geographical, and environmental setting of cave faunal evolution. *Proc. 8th Int. Congr. Speleol., Bowling Green, Kentucky*, 2: 501–502.
- Peck, S.B., 1984. The distribution and evolution of cavernicolous *Ptomaphagus* beetles in the southeastern United States (Coleoptera: Leiodidae; Cholevinae) with new species and records. *Can. J. Zool.*, 62: 730–740.
- Peck, S.B., 1990. Eyeless arthropods of the Galapagos Islands, Ecuador: composition and origin of the cryptozoic fauna of a young, tropical, oceanic archipelago. *Biotropica*, 22: 366–381.
- Pesce, G.L., De Laurentiis, P. and Humphreys, W.F., 1996a. Copepods from ground waters of Western Australia. I. The genera *Metacyclops*, *Mesocyclops*, *Microcyclops* and *Apocyclops* (Crustacea: Copepoda: Cyclopidae). *Rec. West. Aust. Mus.*, 18: 67–76.
- Pesce, G.L., De Laurentiis, P. and Humphreys, W.F., 1996b. Copepods from ground waters of Western Australia. II. The genus *Halicyclops* (Crustacea: Copepoda: Cyclopidae). *Rec. West. Aust. Mus.*, 18: 77–85.
- Poore, G.C.B. and Humphreys, W.F., 1992. First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. *Invertebr. Taxon.*, 6: 719–725.
- Poulson, T.L. and Culver, D.C., 1969. Diversity in terrestrial cave communities. *Ecology*, 50: 153–158.
- Reddell, J.R., 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize. *Tex. Mem. Mus. Univ. Tex. Austin Bull.*, 27: 1–327.
- Roth, L.M., 1991. A new cave-dwelling cockroach from Western Australia (Blattaria: Nocticolidae). *Rec. West. Aust. Mus.*, 15: 17–21.
- Roth, L.M., 1995. New species and records of cockroaches from Western Australia (Blattaria). *Rec. West. Aust. Mus.*, 17: 153–161.
- Sbordoni, V., 1982. Advances in speciation of cave animals. In: C. Barrigozzi (Editor), *Mechanisms of Speciation*. A.R. Liss, New York, pp. 219–240.
- Scotese, C.R. and Denham, C.R., 1988. *Terra Mobilis: Plate Tectonics for the Macintosh*. Earth in Motion Technologies, Houston, TX.
- Shaw, T.R., 1993. *History of Cave Science: the Exploration and Study of Limestone Caves to 1900*, 2nd edn. Sydney Speleological Society, Sydney, 338 pp.
- Shear, W.A., 1992. A new genus and two new species of millipedes from Cape Range, Western Australia (Diplopoda, Polydesmida, Paradoxosomatidae). *Rec. West. Aust. Mus.*, 15: 777–784.
- Shear, W.A. and Humphreys, W.F., 1996. A new *Stygiochiropus* from a North West Cape (Western Australia) coastal plain cave (Diplopoda, Polydesmida, Paradoxosomatidae). *Rec. West. Aust. Mus.*, 17: 447–449.
- Slack-Smith, S.M., 1993. The non-marine molluscs of the Cape Range peninsula, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 87–107.
- Smith, A.G. and Briden, J.C., 1977. *Mesozoic and Cenozoic Paleontological Maps*. Cambridge University Press, Cambridge, 63 pp.
- Stock, J.H., 1994. Biogeographic synthesis of the insular groundwater fauna of the (sub)tropical Atlantic. *Hydrobiologia*, 287: 105–117.
- Studier, E.H. and Lavoie, K.H., 1990. Biology of cave crickets, *Hadenoeus subterraneus*, and camel crickets, *Ceuthophilus stygius* (Insecta: Orthoptera): metabolism and water economies related to size and temperature. *Comp. Biochem. Physiol.*, 95A: 157–161.
- Sturm, H. and Smith, G.B., 1993. New bristle tails (Meinertellidae, Machiloidea, Archaeognatha, Insecta) from Australia. *J. Aust. Entomol. Soc.*, 32: 233–240.
- Trendall, A.F., 1990. Pilbara Craton, introduction. Geology and mineral resources of Western Australia. *Geol. Surv. West. Aust. Mem.*, 3: 128–194.
- Truswell, E.M., 1990. Australian Rainforest: the 100 million year record. In: L.J. Webb and J. Kikkawa (Editors), *Australian Tropical Rainforest, Science – Values – Meaning*. CSIRO, Melbourne, pp. 7–22.
- Uéno, S.-I., 1987. The derivation of terrestrial cave animals. *Zool. Sci.*, 4: 593–606.
- van de Graaff, W.J.E., Denman, P.D. and Hocking, R.M., 1976. Emerged Pleistocene marine terraces on Cape Range, Western Australia. *Geol. Surv. West. Aust. Annu. Rep.*, 1975, 63–70.
- Vandel, A., 1965. *Biospeleology: The Biology of Cavernicolous Animals*, translated by B.E. Freeman. Pergamon Press, Oxford, 524 pp.
- Veevers, J.J., Powell, C.McA. and Roots, S.R., 1991. Review of seafloor spreading around Australia. I. Synthesis of the patterns of spreading. *Aust. J. Earth Sci.*, 38: 373–390.
- Vine, B., Knott, B. and Humphreys, W.F., 1988. Observations on

- L.M.R. Cooks (Editor), *The Evolving Earth*. Oxford University Press, Oxford, pp. 197–220.
- Humphreys, W.F., 1989. *The status of relict cave fauna of Cape Range, Western Australia, especially the Schizomida*. Report to the Australian National Parks and Wildlife Service, Canberra, 104 pp.
- Humphreys, W.F., 1990a. The location of Spiral Cave, Cape Range. *West. Caver*, 30: 36–37.
- Humphreys, W.F., 1990b. The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. *Acta Zool. Fenn.*, 190: 181–186.
- Humphreys, W.F., 1991a. Biological research into the Cape Range karst area, North West Cape peninsula, Western Australia. In: S. Brooks (Editor), *Cave Leeuwin – Proceedings of the 18th Biennial Conference of the Australian Speleological Federation Inc., Margaret River, Western Australia, 30 December 1990–5 January 1991*. Australian Speleological Federation Inc., Nedlands, Western Australia, pp. 6–14.
- Humphreys, W.F., 1991b. *Survey of caves in Cape Range, North West Cape Peninsula, Western Australia*, Report to the Australian Heritage Commission and the Western Australian Heritage Committee, 178 pp.
- Humphreys, W.F., 1991c. Experimental reactivation of pulse driven populations in a terrestrial troglobite community. *J. An. Ecol.*, 60: 609–623.
- Humphreys, W.F., 1991d. *The cave fauna of Cape Range: specific analyses*, Report to the Australian National Parks and Wildlife Service, Canberra, 132 pp.
- Humphreys, W.F., 1991e. Troglobites on Barrow Island, Western Australia. *West. Caver*, 31: 11–14.
- Humphreys, W.F., 1993a. Cave fauna in semi-arid tropical Western Australia: a diverse relict wet-forest litter fauna. *Mém. Biospéol.*, 20: 105–110.
- Humphreys, W.F., 1993b. Stygofauna in semi-arid tropical Western Australia: a Tethyan connection? *Mém. Biospéol.*, 20: 111–116.
- Humphreys, W.F., 1993c. The significance of the subterranean fauna in biogeographical reconstruction: examples from Cape Range peninsula, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 165–192.
- Humphreys, W.F. (Editor), 1993d. *The Biogeography of Cape Range, Western Australia*. *Rec. West. Aust. Mus. Suppl.*, 45: 1–228.
- Humphreys, W.F., 1994. *The subterranean fauna of the Cape Range coastal plain, Northwestern Australia*, Report to the Australian Heritage Commission and the Western Australian Heritage Committee, 202 pp.
- Humphreys, W.F., 1999. The distribution of the Australian cave fishes. *Rec. West. Aust. Mus.*, 19: 469–472.
- Humphreys, W.F. and Adams, M., 1991. The subterranean aquatic fauna of the North West Cape peninsula, Western Australia. *Rec. West. Aust. Mus.*, 15: 383–411.
- Humphreys, W.F. and Collis, G., 1990. Water loss and respiration of cave arthropods from Cape Range, Western Australia. *Comp. Biochem. Physiol.*, 95A: 101–107.
- Humphreys, W.F. and Feinberg, M.N., 1995. Food of the blind cave fishes of northwestern Australia. *Rec. West. Aust. Mus.*, 17: 29–33.
- Humphreys, W.F. and Shear, W.A., 1993. Troglobitic millipedes (Diplopoda: Paradoxosomatidae) from semi-arid Cape Range, Western Australia – systematics and biology. *Invertebr. Taxon.*, 7: 173–195.
- Humphreys, W.F., Adams, M. and Vine, B., 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. *J. Zool. (London)*, 217: 177–201.
- Izquierdo, I. and Oromi, P., 1994. Dictyoptera – Blattaria. In: C. Juberthie and V. Decu (Editors), *Encyclopaedia Biospéologica*. Société de Biospéologie, Moulis (France) and Bucarest, pp. 295–300.
- Jacobson, G. and Hill, P.J., 1980. Hydrogeology of a raised coral atoll, Niue Island, South Pacific. *J. Aust. Geol. Geophys.*, 5: 271–278.
- Juberthie, C., 1983. Le milieu souterrain: tendue et composition. *Mém. Biospéol.*, 10: 17–65.
- Juberthie, C., 1988. Paleoenvironment and speciation in the cave beetle complex *Speonomus delarouzei* (Coleoptera, Bathysciinae). *Int. J. Speleol.*, 17: 31–50.
- Juberthie, C. and Delay, B., 1981. Ecological and biological implications of the existence of a Superficial Underground Compartment. *Proc. 8th Int. Congr. Speleol., Bowling Green, Kentucky*, 6: 203–206.
- Kane, T.C., Norton, R.M. and Poulson, T.L., 1975. The ecology of predacious troglobitic beetles, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae). I. Seasonality of food input and early life history stages. *Int. J. Speleol.*, 7: 45–54.
- Keighery, G. and Gibson, N., 1993. Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. *Rec. West. Aust. Mus. Suppl.*, 45: 51–85.
- Kemp, E.M., 1981. Tertiary palaeogeography and the evolution of Australian climate. In: A. Keast (Editor), *Ecological Biogeography of Australia*. Dr W. Junk, The Hague, pp. 31–49.
- Kendrick, G.W., Wyrwoll, K.H. and Szabo, B.J., 1991. Pliocene – Pleistocene coastal events and history along the western margin of Australia. *Quat. Sci. Rev.*, 10: 419–439.
- Kenneally, K.F., Keighery, G.J. and Hyland, B.P.M., 1991. An ecological survey of tropical rainforests in Western Australia: background and methods. In: N.L. McKenzie, R.B. Johnston and P.G. Kendrick (Editors), *Kimberley Rainforests*. Surrey Beatty and Sons Pty Limited, Chipping Norton, New South Wales, pp. 93–131.
- Kennett, J.P., 1982. *Marine Geology*. Prentice-Hall, New York, 813 pp.
- Kennett, J.P., Keller, G. and Srinivasan, M.S., 1985. Miocene planktonic foraminiferal biogeography and paleoceanographic development of the Indo-Pacific region. *Geol. Soc. Am. Mem.*, 63: 197–236.
- Knott, B., 1993. Stygofauna from Cape Range peninsula, Western Australia: Tethyan relicts. *Rec. West. Aust. Mus. Suppl.*, 45: 109–127.
- MacFadden, B.J. and Cerling, T.E., 1994. Fossil horses, carbon isotopes and global change. *Trends Ecol. Evol.*, 9: 481–486.
- Main, A.R., 1993. Synthesis and prospects. *Rec. West. Aust. Mus. Suppl.*, 45: 243–248.
- Main, B.Y., 1980. Record of the arachnid order Schizomida in Western Australia. *West. Aust. Nat.*, 14: 236–237.
- Malcolm, R.J., Pott, M.C. and Delfos, E., 1991. A new tectono-stratigraphic synthesis of the North West Cape area. *APEA J.*, 1991: 154–176.
- Manning, R.B., Hart, C.W. and Illiffe, T.M., 1986. Mesozoic relicts in marine caves of Bermuda. *Stygologia*, 2: 156–166.

- the environment and biology of *Schizomus vinei* (Chelicerata: Schizomida) from Cape Range, Western Australia. *Rec. West. Aust. Mus.*, 14: 21–34.
- Webb, L.J. and Tracey, J.G., 1981. The rainforests of northern Australia. In: R.H. Groves (Editor), *Australian Vegetation*. Cambridge University Press, Cambridge, pp. 67–101.
- Whitley, G.P., 1945. New sharks and fishes from Western Australia. *Aust. Zool.*, 11: 34–37.
- Wyrwoll, K.H., Kendrick, G.W. and Long, J.A., 1993. The geomorphology and Late Cenozoic geological evolution of the Cape Range – Exmouth Gulf region. *Rec. West. Aust. Mus. Suppl.*, 45: 1–23.
- Yäger, J. and Humphreys, W.F., 1996. *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. *Invertebr. Taxon.*, 10: 171–187.