Chapter 30

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

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## 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 that 1200 km from the nearest wet temperate forest in southwestern Australia, and more than 3000 km from the lowland rainforests of eastern Australia.

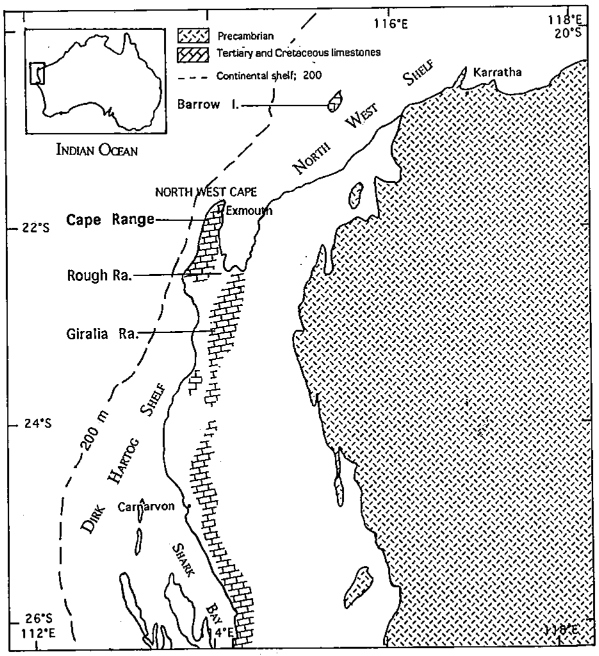

Fig. 30.1. The regional setting of the Cape Range peninsula and Barrow Island. The Precambrian Pilbara Craton has not undergone major regional deformation since 2400 Ma ago (Trendall, 1990) and has been continuously emergent for more than 600 Ma. This is fringed to the west by middle Mesozoic deposits (~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).

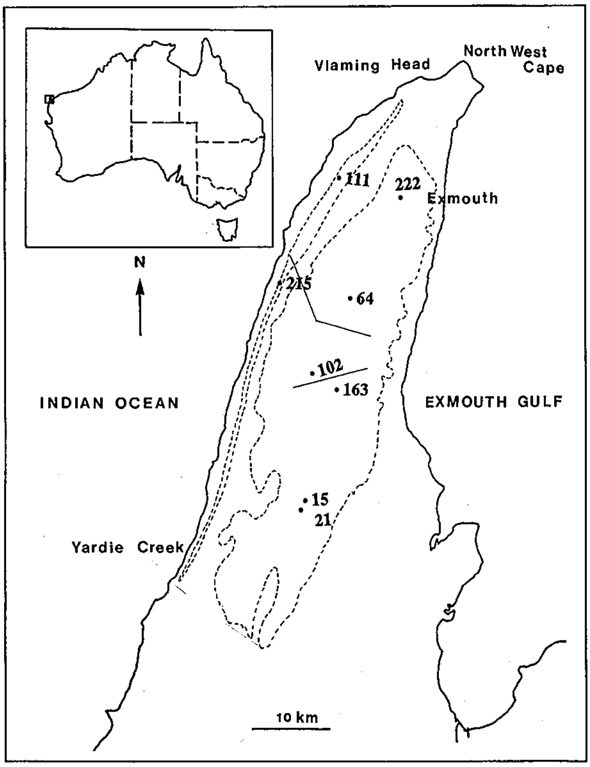

Fig. 30.2. The Cape Range peninsula. The dotted lines show the extent of the surface exposure of the cavernous Tulki Limestone, and the numbered points denote the location of caves mentioned in the text. The straight lines indicate the approximate boundaries between of the genetic provinces determined 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[1], 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 epitropical 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.

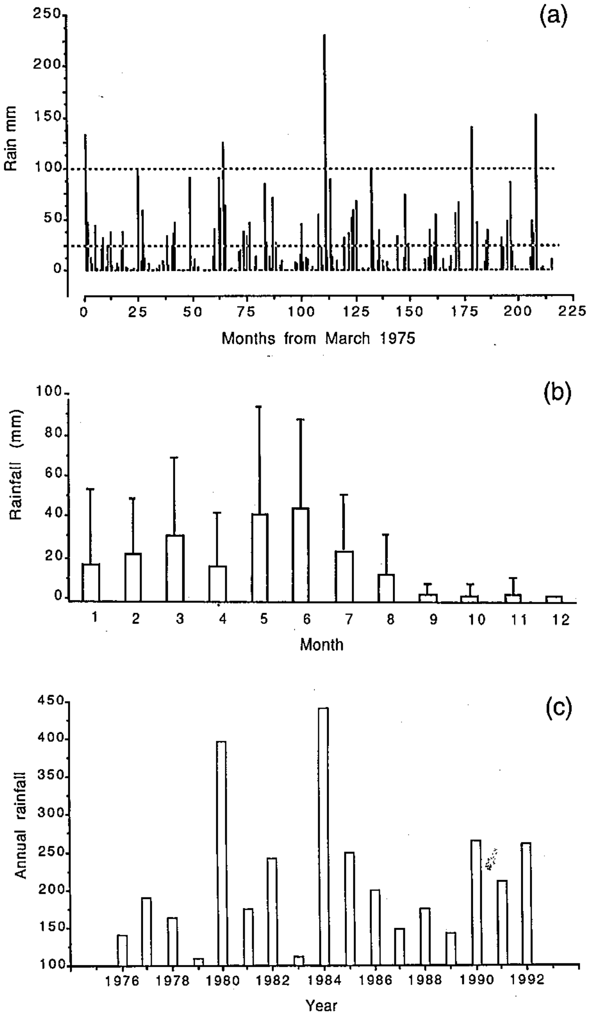

Fig. 30.3. (a) Monthly rainfall (mm) at Learmonth from March 1975. Broken lines at 25 mm and 100 mm are, respectively, the amount of rainfall required for surface flow for minor recharge of some caves, and the amount of rainfall required to flood the major caves deeply. (b) Mean monthly rainfall (mm) ( 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

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[1] See Glossary, 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).

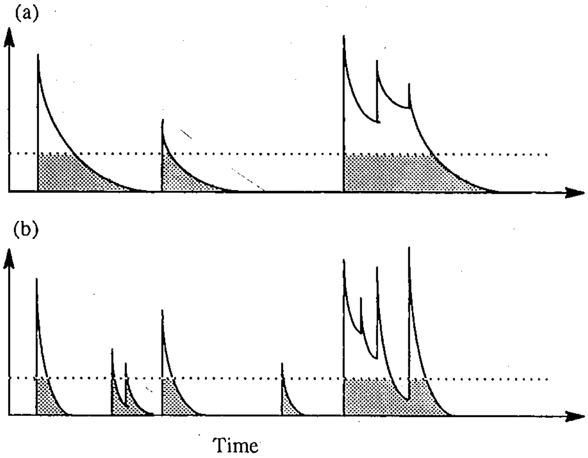

Fig. 30.4. Hypothetical availability and depletion of resources in Cape Range caves: (a) Slow-drying (small entrance) cave with a small catchment; (b) fast-drying cave with large catchment. The fine horizontal line denotes the resource level (energy or water) below which the populations are eliminated 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 freshwater 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: Thaumatocyprididae: 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 trogloxene 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 groundwater. 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 trogloxenes, 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. *Draculoides vinei* eats individuals of the same species, *Stygiochiropus,* and armadillid and philosciid isopods. *Draculoides 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, Guatamala and Belize combined contained

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

| Major taxa | Genera and species[1] | Locations |
|---|---|---|
| *CHELICERATA* | | |
| Schizomida[2] | ∗***Draculoides*** *vinei* | Cape Range |
| | ∗*Draculoides bramstockeri* Harvey and Humphreys | coastal plain of Cape Range peninsula; Barrow Island |
| | ∗*Draculoides* sp. nov. | coastal plain of Cape Range peninsula |
| | ∗*Bamazomus* sp. nov. | coastal plain of Cape Range peninsula |
| Pseudoscorpionida | | |
| Hyidae | ∗***Hyella*** *humphreysi* | Cape Range |
| | ∗*Hyella* sp. nov. | coastal plain of Cape Range peninsula |
| Chthoniidae | ∗*Tyrannochthonius butleri* | Cape Range |
| Opilionida | | |
| Assamiidae | ∗*Anjolus* sp. (undescribed) | Cape Range |
| Phalangodidae | ∗Gen. indet.[3] | 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 | *Trichocyclus septentrionalus* | |
| Symphytognathidae | ∗*Anapistula troglobia* | Cape Range |
| Theridiidae | ∗*Steatoda* sp. 1. (Harvey et al., 1993) | Cape Range |
| | ∗*Pholcomma* sp. (Harvey et al., 1993) | Cape Range |
| Linyphiidae | ∗*Dunedinia occidentalis* | Cape Range |
| | ∗*Chthiononetes tenuis* | Cape Range |
| *MYRIAPODA* | | |
| Polyzoniida | | |
| Siphonotidae | ∗Gen. & sp. indet. | Cape Range |
| Polydesmida[4] | | |
| Paradoxosomatidae | ∗***Stygiochiropus*** *communis* | Cape Range |
| | ∗*Stygiochiropus isolatus* | Cape Range |
| | ∗*Stygiochiropus sympatricus* | Cape Range |
| | ∗*Stygiochiropus peculiaris* | coastal plain of Cape Range peninsula |
| Spirobolida | | |
| Pachybolidae | ∗***Speleostrophus*** *nesiotes* | Barrow Island |
| *INSECTA* | | |
| Diplura | | |
| Japygidae[5] | *Indjapyx* n. sp. 1 | Cape Range |
| | *Indjapyx* n. sp. 2 | Cape Range |
| | **Gen. nov.** & sp. nov. 1 | Cape Range |
| | Gen. nov. & sp. nov. 2 | 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[1] | Locations |
|---|---|---|
| Thysanura | | |
| Nicoletiidae: Atelurinae | **Trinemura troglophila* | Cape Range |
| Blattodea | **Nocticola flabella* | Cape Range |
| | **Nocticola* sp. nov. | Barrow Island |
| Orthoptera | | |
| Nemobiinae | ****Ngamarlanguia*** *luisae* | Cape Range |
| Coleoptera | | |
| Curculionidae: Polydrosinae | *Myllocerus* sp. 1[6] | Cape Range |
| Hemiptera | | |
| Meenoplidae | **Phaconeura proserpina* | coastal plain of Cape Range peninsula |
| | **Phaconeura* sp. nov. 1 (H. Hoch, pers. com.) | coastal plain of Cape Range peninsula |
| | **Phaconeura* sp. nov. 2 | Cape Range |
| Cixiidae | *?gen. | Cape Range |
| *CRUSTACEA* | | |
| Isopoda | | |
| Philosciidae | *Gen. & spp. indet. >2 | coastal plain of Cape Range peninsula;<br>Cape Range |

[1] 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.
[2] Only genus of Schizomida endemic to Australia.
[3] First blind Phalangodidae in Australia, though usual in European caves (G. Hunt, pers. comm., 1994).
[4] *Antichiropus humphreysi* and *Boreohesperus capensis* are also found in caves but are well adapted to outside conditions.
[5] J. Pagés, pers. comm., 1994–95.
[6] *Myllocerus* 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 troglobitic 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[1]

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

[1] About half of this fauna has been found since 1991.

[2] 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[1]

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

[1] These taxa may not constitute part of the stygofauna proper. However, a number of stygofaunal species are also known from the same habitats.
[2] The references denote the source of determinations.
[3] 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[1] | Exit Cave[1] | Vanishing Falls[1] | Kubla Khan[1] | New South Wales[2,3] | 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 |

[1] Locations in Tasmania. Data from Knott (1993), after Eberhard (1992).
[2] Data from A.P. Spate and S.M. Eberhard (pers. commun., 1995).
[3] 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

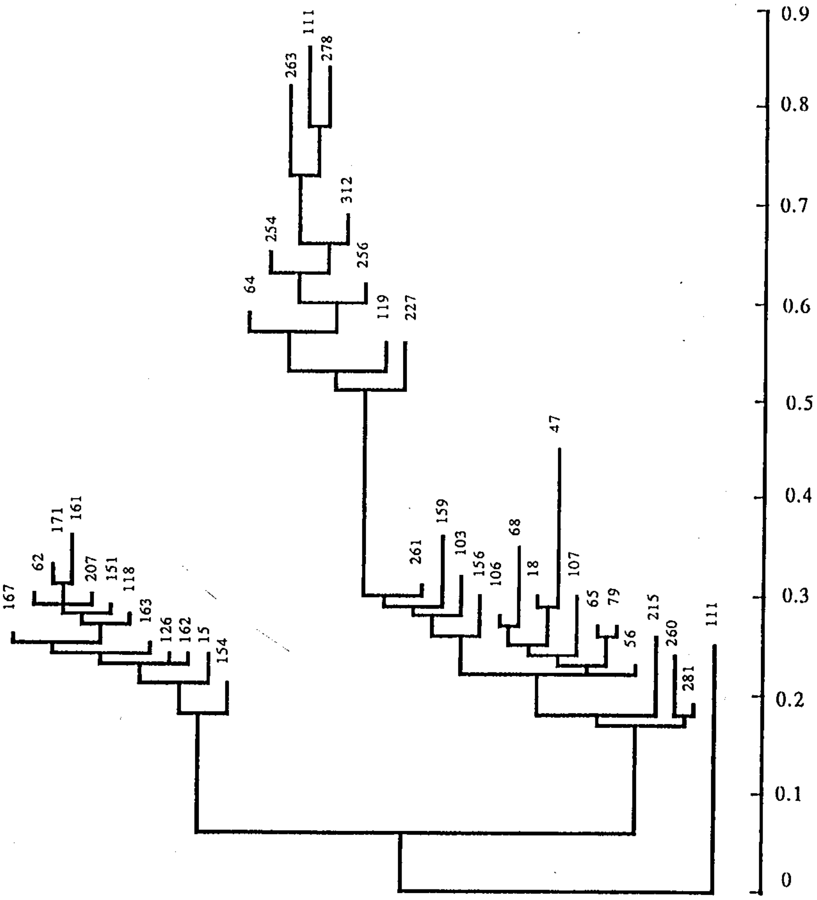

Fig. 30.5. Tree of the troglobitic millipede populations *Stygiochiropus communis* from the 38 caves numbered, produced by a Distance Wagner Analysis on the matrix of Rogers' Genetic Distance (Humphreys, 1991d) rooted on sympatric *S. sympatricus* from C-111.

Table 30.5

Number of troglobitic species of arachnids and myriapods in five regions of Australia[1]

| Region | Number of species |
|---|---|
| Nullarbor | 8 |
| Chillagoe | 14 |
| Tasmania[2] | 34 |
| New South Wales[3] | 8+ |
| Cape Range | 23[4] |

[1] Data from Harvey et al. (1993).

[2] Thirty karst regions combined.

[3] Forty-eight karst regions combined; the figure given is of genera.

[4] 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 $\mu$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 seaboards 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 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.

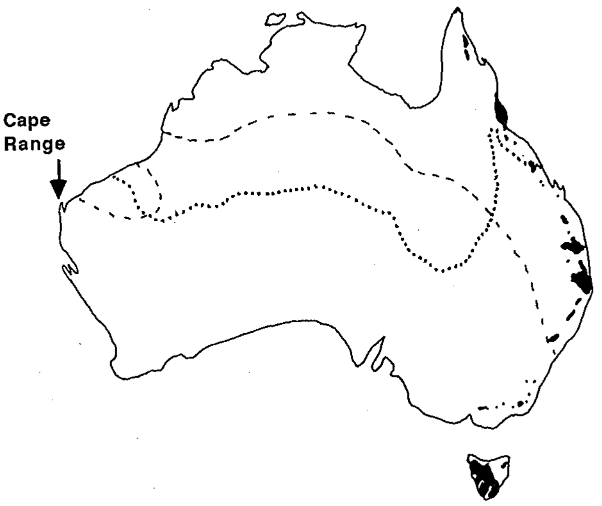

Fig. 30.6. The current distribution of extensive coastal rainforest (black) and the southerly limit (dashed lines) of remnant coastal rainforest elements in contemporary Australia (after Webb and Tracey, 1981). The former occurs in an arc through eastern Australia, with a distribution similar to the 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).

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

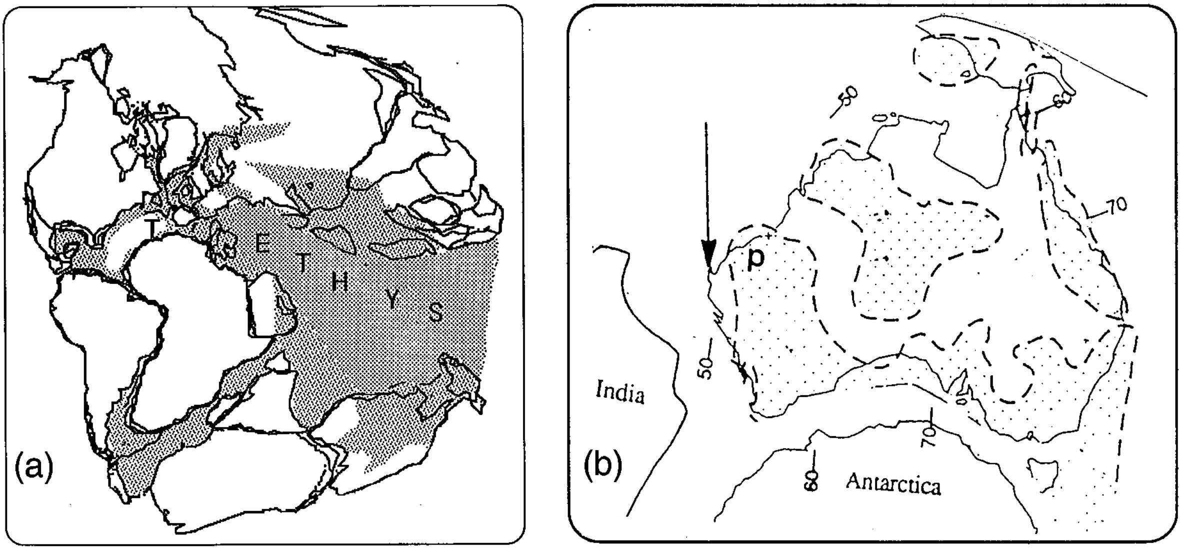

Fig. 30.7. (a) The relative location of the continental plates in the Jurassic (151 Ma ago) when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. Even with this reconstruction the genera *Halosbaena* (Thermosbaenacea), *Haptolana* (Isopoda: Cirolanidae) and *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[1]

| Event | Period | Date | Evidence |
|---|---|---|---|
| **1000 years ago** | | | |
| N.W. Shelf inundated[2] | Holocene | 8–0 | calculated from Chappell and Thom (1977) |
| Wetter period | Pleistocene | 14–11 | U/Th speleothem date, C-125[4] |
| E and W coast populations isolated | Pleistocene | 25 | *D* between *Stygiocaris stylifera* populations[3,5] |
| Differentiation of populations | Pleistocene | 30 | *S. stylifera*[5] |
| N. W. Shelf inundated[2] | Pleistocene | 85–80 | calculated from Chappell and Thom (1977) |
| Differentiation[6]; southern province | Pleistocene | 100 | *D* between millipede populations[5,7,14] |
| N.W. Shelf inundated[2] | Pleistocene | 111–99 | calculated from Chappell and Thom (1977) |
| Wetter period | Pleistocene | 128 | *Anadara trapezia* distribution[9] |
| N.W. Shelf inundated[2] | Pleistocene | 135–116 | calculated from Chappell and Thom (1977) |
| Differentiation in central province | Pleistocene | 165 | *D* between amphipods in range[5,7,10,15] |
| Differentiation of populations | Pleistocene | 200 | *D* between *Draculoides* populations[7] |
| Atyid populations isolated | Pleistocene | 205 | *D* between *S. lancifera* populations[7,10] |
| Wetter period | Pleistocene | 219–68 | U/Th speleothem date, C-126 and C-163[4] |
| N.W. Shelf inundated[2] | Pleistocene | 222–216 | calculated from Chappell and Thom (1977) |
| Wetter period | Pleistocene | 225 | *Anadara trapezia* distribution[9] |
| Differentiation[6]; central populations | Pleistocene | 400 | *D* between millipede populations[5,7] |
| E and W coast populations isolated | Pleistocene | 315 | *D* between cave fish[11] populations[5,7,10,12] |
| Differentiation[6]; northern populations | Pleistocene | 350 | *D* between millipede populations[5,7] |
| Barrow Island isolated from Cape Range | Pleistocene | 380 | *D* between *S. stylifera* populations[5,7,13] |
| Schizomid populations diverge | Pleistocene | 450 | *D* within *Draculoides vinei* populations[5,7] |
| Within-province differentiation | Pleistocene | 550 | *D* within millipede genetic provinces[5,7,14] |
| Northern cave waters isolated | Pleistocene | 650 | *D* between amphipods in range[5,7,10,15] |
| Southern caves isolated from rest | Pleistocene | 800 | *D* between millipede populations[5,7,14] |
| **1 000 000 years ago** | | | |
| Wet forest lost from gorges | Pleistocene | 4.3–1.6 | Deduced from genetic distances above |
| Southern cave waters isolated | Pleistocene | 1.3 | *D* between amphipods in range[5,7,10,15] |
| Northern cave areas isolated | Pleistocene | 1.6 | *D* between millipede genetic provinces[5,7] |
| Cape Range fully emergent | Pliocene | >2 | Marine terraces; Wyrwoll et al. (1993) |
| Southern cave areas isolated | Pliocene | 2.2 | *D* between millipede genetic provinces[5,7,14] |
| Shrimps speciate | Pliocene | 4.0 | *D* between congeneric atyid shrimps[5,7] |
| Millipedes speciate | Pliocene | 4.3 | *D* between congeneric millipedes[5,7,14] |
| Anticline uplift | Miocene/Pliocene | 7 | *D* between amphipod genera[5,7,10,15] |
| Indian and Pacific Oceans isolated[16] | Late Miocene | 7 | Kennett et al. (1985) |
| Anticline uplift | Late Miocene | >7 | Malcolm et al. (1991) |
| Closed forest with *Nothofagus* | Miocene | >7 | Truswell (1990) |
| Cooling sea and land | Miocene | 8–6 | MacFadden and Cerling (1994) |
| Indian and Atlantic Oceans separate[17] | 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[18] | 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[19] | 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[8] | Early Carboniferous | 340 | Hocking et al. (1987) |
| Pilbara Craton emergent | Precambrian | >600 | Hocking et al. (1987) |

[1] 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).

[2] 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.

[3] "*D*" is Nei's (1987) genetic distance.

[4] 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.

[5] Adams and Humphreys (1993), unpublished.

[6] By inference, caves isolated.

[7] Calculated from the average Nei's genetic distance ($D$) assuming $D = 1$ corresponds to five million years of divergence (Nei, 1987).

[8] Moogooree Limestone.

[9] Kendrick et al. (1991).

[10] Humphreys and Adams (1991).

[11] *Milyeringa veritas.*

[12] Between populations on the east and west coast of the Cape Range peninsula.

[13] Between populations on Barrow Island and the Cape Range peninsula.

[14] Humphreys and Shear (1993).

[15] 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).

[16] Diversion of North Equatorial Current from the Indian Ocean to the North Pacific.

[17] Tropical connection only.

[18] 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).

[19] 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[1] | Terrestrial | Groundwater |
|---|---|---|
| Vicariant event | aridity | plate tectonics |
| | eustatic | eustatic |
| | orogenic | orogenic |
| Relictual taxa | | |
| global | Hyidae | many stygofauna spp. |
| regional | Schizomida | amphipods |
| local | *Stygiochiropus* | amphipods in Cape Range |
| Relic taxa | e.g., Remipedia, Thermosbaenacea, Atyidae | |
| Refugium | caves | freshwater |
| | crevicular habitats | anchialine |

[1] See definitions in Glossary, p. 6.

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