The significance of the subterranean fauna in biogeographical reconstruction: examples from Cape Range peninsula, Western Australia

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Abstract

Cape Range peninsula contains a diverse troglobite (obligatory cave inhabitants) fauna, the only rich troglobite community known in Western Australia and in the semi-arid tropics. At least thirty-eight species of troglobite (or stygobiont) in this sparsely sampled area place it amongst the worlds faunistically diverse karst areas. The characteristics of the region and its subterranean fauna are broadly examined in this paper.

The area (with Barrow Island) has high generic endemism with *c.* 14 apparently endemic genera including amphipods, shrimps, snails, millipedes, schizomids, spiders, archaeognaths, thysanurans and fish.

In the context of cave biology the communities are not simple with up to seven troglobites occupying a single cave, together with many other species lacking such overt modification to cave life but seemingly out of place in a semi-arid climate. The affinities of the fauna are varied but a large element of the terrestrial fauna is derived from the humid tropics and is relictual from times when humid forest covered this region.

The cave systems in Cape Range are fossil and were clearly formed under more humid conditions, as evidenced by the cave fauna. Stalagmite growth has been extraordinary slow, suggesting that the climate was not been substantially wetter than at present over the last 170,000 years. Hence, the climate required for cave formation and forest cover predates this. However, sympatric congenors both in the range and on the coastal plain suggest that climatic/eustatic fluctuations have led to fragmentation and rejoining of populations.

Genetic distance (D) between cave populations is used naively to establish a sequence of biological events in Cape Range in order to look for consistency both within the genetic data and with other evidence. A sequential chronology is presented from the Precambrian to the present as a series of working hypotheses, *viz. D* between altitudinally separated congeneric amphipods suggests a late Miocene/early Pliocene date for the uplift of the Cape Range anticline which supports palaeontological and geomorphological evidence. *D* between partly sympatric *Stygiocaris* species suggests speciation at 5 Ma, perhaps associated with the same event. Terrestrial fauna appears to have speciated later; paradoxosomatid millipedes speciated in the Pliocene (*c.* 3 Ma) and were separated into genetic provinces by *c.* 2 Ma which, by deduction, is when the wet forest was lost from the gorges. *D* for amphipods within the range suggests that the perched water tables in the range were isolated in the early Pleistocene (*c.* 1 Ma). *D* suggests that the isolation between caves of species populations occurred during the mid to late Pleistocene both in the range and on the coastal plain, presumably associated with Pleistocene climatic and eustatic fluctuations.

Hypotheses presented lead to the following predictions: elements of the Cape Range stygofauna should be found on the coast bordering the Pilbara Craton; elements of the Cape Range terrestrial/freshwater fauna should occur along water courses that would have drained from the Pilbara Craton across the Cape Range Formation.

The conservation implications of troglobite biogeography are briefly examined.

Introduction

Until recently troglobites (obligate cave dwellers) were thought to have been isolated in caves due to the climatic changes during the Pleistocene (Vandel 1965; Barr 1968; Mitchell 1970; Sbordoni 1982). Hence, in lowland tropical areas, where such changes were minimal, troglobites should be rare. In addition, owing to aridity, the lack of pre-adapted moist litter inhabitants explained the apparent scarcity of troglobites in Australia (Moore 1964; Hamilton-Smith 1967; Barr 1973).

During the last two decades these preconceptions have been overturned (well summarised in Bellés 1991) and cave species have been found which were clearly isolated well before the Pleistocene in both tropical and marine caves (Leleup 1968; Culver 1982; Howarth 1983). In Australia troglobites have been found in previously glaciated areas of Tasmania (Eberhard *et al.* 1991) and rich assemblages discovered in both the wet (lava tubes and karst; Hoch 1990; Hoch and Asche 1989; Hoch and Howarth 1989a, 1989b, 1989c; Howarth 1988; Howarth and Stone 1990) and arid tropical regions of mainland Australia (Dalens 1992; Harvey 1988, 1991, 1992, 1993; Humphreys 1989, 1990, 1991a, 1991b, 1991c, 1991d, 1991e; Humphreys and Adams 1991; Humphreys *et al.* 1989; 1990; Humphreys and Collis 1990; Humphreys and Shear 1993; Moore and Humphreys in press; Poore and Humphreys 1992; Roth 1991; Shear 1992; Vine *et al.* 1988).

Table 1. Taxa present in cave C-118. * = Troglobites.

Annelida Oligochaeta	*Austropholochaetella kendricki* Jamieson
Mollusca: Camaeinidae: Sinumeloninae	Gen. et sp. nov.
Camaeinidae: Sinumeloninae	*Strepsitaurus rugus* (Cotton)
Pleurodontidae	*Quistrachia* sp. nov.
Crustacea: Isopoda: Armadillidae	*Buddelundia cinerascens* (Budde-Lund)
Armadillidae	*B. grisea* Dalens
Armadillidae	*B. hirsuta* Dalens
Oniscidae	*Hanoniscus* sp. nov*
Philosciidae	*Australophiloscia* sp. nov.
Philosciidae	*Laevophiloscia yalgoonensis* Wahrberg
Chilopoda: Scutigeromorpha	*Allothereuea ?leseurii*
Diplopoda: Paradoxosomatidae	*Stygiochiropus communis* Humphreys & Shear*
Chelicerata: Acari	?
Schizomida	*Draculoides vinei* (Harvey)*
Araneae: Ctenidae	Gen. et sp. nov.*
Araneae: Linyphiidae	*Chthiononetes tenuis* Millidge
Araneae: Pholcidae	*Trichocyclus* sp. nov.
Insecta: Collembola: Entomobryidae	*Lepidosira* sp.
Blattodea	*Nocticola flabella* Roth*
Psocidae	?
Orthoptera: Nemobiinae	?gen.*
Heteroptera: Reduvidae: Reduviinae	?
Heteroptera: Emersinae	*Stenolemoides* sp.
Coleoptera : Clivinini	*Clivinia* sp.
Curculionidae: Polydrosinae	*Myllocerus* sp. nov.
Carabidae: Psydritae	*Mecyclothorax* sp., flightless
Diptera: Mycetophilidae	?

In this paper I do not attempt to discuss the detailed biogeography of all or any group of animals found on the Cape Range peninsula, as such general discussion would, for the most part, be premature and this more focused discussion is the province of the specialist systematic contributions to this literature. However, I do want to discuss the general characteristics of the area, especially as they relate to cave animals, both aquatic and terrestrial, and the manner in which this may contribute to the wider biogeographical discussion.

Diversity

Cave communities are normally considered to be simple with rarely more than four or five interacting species (Culver 1982). The situation in Cape Range is more complex. For example, the small cave C-118 contains seven highly adapted troglobites and another 19 species (Table 1), some of which show some pigments loss, eye reduction or flightlessness, attributes more common in cave species (Culver 1982; Roff 1990). In the absence of detailed biological studies the interdependencies of this fauna are unclear. Certainly some of the species interact (Humphreys 1991), both within and between the troglobite and non-troglobite sections of the fauna. For example the troglobite *Draculoides vinei* frequently eats non-troglobitic philosciid isopods, but also eats the troglobitic millipede, *Stygiochiropus communis* which are themselves eaten by non-troglobitic pholcid spiders, *Trichocyclus* sp. Similar complex interactions are seen also in the stygofauna (W.F. Humphreys, unpublished).

From Cape Range and the related Barrow Island fauna, both part of the Cape Range Formation, a total of 39 troglobite or stygobiont species have or are being described from 28 families and 30 genera (10 endemic). Their distribution amongst the higher taxa is shown in Table 2. They represent 29 terrestrial and nine aquatic species; at least another six species occur in the karst system. A large number of other species are found whose association with

Table 2. List of troglobites from the Cape Range peninsula and Barrow Island (part of the Cape Range Formation). Number of genera endemic to area in parentheses. [1] Probable troglobite.

Taxon		Families	Genera	Species	Authority
Chelicerata	Pseudoscorpionida	2	2	2	Harvey 1991, 1993
	Schizomida	1	1(1)	2	Harvey 1988
	Araneae	5	6(1)	6	M.S. Harvey, pers comm.; M. R. Gray, pers comm.; Millidge 1993.
	Opiliones[1]	1	1(1)	1	G. Hunt, pers comm.
Crustacea	Thermosbaenacea	1	1	1	Poore and Humphreys 1992
	Amphipoda	1	1(1)	2	W.D. Williams, pers. comm.
	Isopoda	4	?5	7	H. Dalens, 1992, pers. comm.; Bruce and Humphreys 1993
	Decapoda	1	1(1)	2	Holthuis 1960
Diplopoda	Polydesmida	3	3 (2)	5	Humphreys and Shear 1993
	Polyzoniida	1	1	1	D.G. Black, pers comm.
	Spirobolida	1	1(1)	1	R. Hoffman, pers comm.
Insecta	Blattaria	1	1	2	Roth 1991
	Hemiptera	2	2	3	Hoch 1993
	Orthoptera	2	2(1)	2	D.C.F. Rentz, pers comm.
Chordata	Vertebrata	2	2(1)	2	Mees 1962; Whitley 1945
Total		28	30(10)	39	

Table 3. New genera from the Cape Range peninsula. [1]Troglobitic or [2]stygobiont species. [3]Genus also known from Barrow Island. [4]Genus known only from Barrow Island.

Amphipoda: Melitidae	Gen. et spp. nov.[2]	W.D. Williams, pers. comm.
Crustacea: Atyidae	*Stygiocaris*[2,3]	Holthuis 1960
Mollusca: Camaeinidae	Gen. et sp. nov.	A. Solem and S.M. Slack-Smith, pers. comm.
Camaeinidae	Gen. et sp. nov.	A. Solem and S.M. Slack-Smith, pers. comm.
Diplopoda: Polydesmida: Paradoxosomatidae	*Stygiochiropus*[1]	Humphreys and Shear 1993
Diplopoda: Polydesmida: Paradoxosomatidae	*Boreohesperus*	Shear 1992
Diplopoda: Spirobolida	Gen. et sp. nov. [4]	Hoffmann 1993
Chelicerata: Schizomida	*Draculoides*[1,3]	Harvey 1992
Pseudoscorpionida: Hyidae	*Hyella*[1]	Harvey 1993
Opiliones: Assamiidae	Gen. et sp. nov.[1]	G. Hunt, pers. comm.
Araneae: Miturgidae	Gen. et sp. nov.[1]	M.R. Gray, pers. comm.
Araneae: Filistatidae	Gen. et sp. nov.	M.R. Gray, pers. comm.
Araneae: Linyphiidae	*Chthiononetes*[1]	Millidge 1993
Archaeognatha: Meinertellidae	Gen. et sp. nov.	Sturm and Smith, in press
Thysanura: Lepismatidae	Gen. et sp. nov.	G. Smith, pers. comm.
Pisces: Perciformes: Eleotridae	*Milyeringa*[2]	Whitley 1945

the caves is largely unknown but many are clearly relicts of a wetter climate, especially the Mollusca (Slack-Smith 1993), Chelicerata and Myriapoda (Harvey *et al.* 1993). The Cape Range area contains 6.5% of the troglobite species known from the world's tropics: about 600 species of troglobites are known from the tropical areas of the world; 477 terrestrial, 115 fresh water and 57 anchialine water species (S.B. Peck, pers. comm. 1992).

Hence, despite the brief history of work in the area the troglobite fauna is already known to be exceptionally species rich. For example, *c.* 12 species of troglobites are known from the entire Nullarbor karst of southern Australia, 40 species from NE Queensland (Chillagoe karst and Undara lava tubes; Howarth 1988) and 24 species on Hawaii Island where many species have close epigean relatives (Howarth 1987). In addition many new genera have been described from the area, especially amongst the cave dwelling fauna (Table 3) and there is a high level of generic endemism.

Affinities

Little is known of the affinities, both taxonomic and regional, of most of the terrestrial invertebrates of Cape Range owing to inadequate regional collections and lack of studies on their systematics. For example, for the highly cave adapted paradoxosomatid millipedes the available generic level classification and collections are inadequate to determine either their geographical or ecosystem affinities (Humphreys and Shear 1993). Despite these shortcomings it is clear that the cave fauna of Cape Range has mixed affinities, and that part of the fauna has humid, often warm closed forest, affinities (Humphreys 1993a). Many mollusca (Slack-Smith 1993) and troglobitic chelicerates have warm humid closed forest affinities (Harvey *et al.* 1993) as does the cockroach *Nocticola flabella* (Roth 1991). Polyzonid millipedes, as well as *Lecanomerus* sp. (Coleoptera: Carabidae: Harpalitae), *Mecyclothorax* sp. and *Craspedophorus* sp. (Coleoptera: Carabidae: Panagaeitae) also have affinities with moist

Table 4. The mean number (log (n+1)) of individuals per species of Coleoptera collected in Cape Range from cave, epigean or both habitats until June 1992. Total taxa = 103. Common letters within a column denote no significant difference between the rows (Fisher's PLSD).

	x=log (n+1)	S. d.	No. species	$(10^x - 1)$
Cave	0.40a	0.159	21	1.5
Epigean	0.50a	0.304	78	2.2
Both habitats	0.95	0.405	4	7.9

forest faunas, though not necessarily warm ones (B.P. Moore, pers. comm. 1989). However, some of the troglobites have southern (cool closed) forest affinities (Harvey *et al.* 1993) so the terrestrial cave fauna clearly has a complex biogeographical history.

Coleoptera, which are a major component of the temperate cave fauna in both hemispheres (Eberhard *et al.* 1991), are poorly represented by troglobites in Cape Range. Of the species collected in Cape Range from epigean and cave habitats (Table 4), only four species were collected in both habitats which suggest a separation of the surface and cave faunas even though the species lack troglomorphies. This suggests that many species lacking overt troglomorphies may be surviving in cave habitats and supports the observation that many of the non-troglobitic species of chelicerate (M.S. Harvey, pers. comm.) and mollusca (Slack-Smith 1993) more typical of humid forest may be using caves as refugia from the arid surface conditions. Hence, species collected in caves both with and without troglomorphies may have wet forest affinities and they provide the main evidence of such vegetation in Cape Range since the Miocene.

Even within caves the collecting in Cape Range has been limited, both in diversity and extent. For example, while the most diverse fauna is found in humid caves, some of the caves are extremely dry (Humphreys 1990) and these caves have been little studied and the few taxa collected are scarce, and not troglobitic, such as the reduviid bugs *Stenolemus giraffe* Wygodzinsky (Emersinae), *Poecilosphodrus* sp. nov. (Harpactorinae) and *Centrogonus* sp. (Reduviinae). In addition many of the caves have high concentrations of carbon dioxide (>8%) and, because the caves are vertical, these more dangerous habitats have not been explored although experience suggests that a rich fauna may be found there (Howarth and Stone 1990).

Relict fauna?

In some tropical locations there is evidence that many troglobitic species are closely related to the local epigean species and thus that parapatric speciation may have occurred (Howarth 1982, 1987; Peck 1990) - hence the fauna of such areas is not relictual as is presupposed in most models of troglobite evolution.

A number of troglobitic genera are endemic to Cape Range (Table 3) and none is known to have congenors amongst the epigean fauna. Of the genera not endemic to Cape Range, few are known to be represented by both cave and epigean species (one example is the genus *Tyrannochthonius:* Pseudoscorpionida) but the genera are too poorly known to suggest their sister species (Harvey *et al.* 1993). Hence, to date there is no evidence of parapatric speciation between the surface and troglobite fauna in Cape Range and the data are compatible with the hypothesis that the cave fauna in general is relictual.

Pleistocene glaciation, considered to have played an important role in the evolution of northern temperate troglobite populations (Barr 1973; Peck 1981; Culver 1982; Delay *et al.* 1980), would have had minimal effect in tropical lowlands (Howarth 1987), such as Cape Range. The lack of evidence for parapatric speciation in Cape Range and the humid warm closed forest affinities of much of the fauna suggests that the parsimonious explanation for the rich troglobitic fauna is that the caves are refugia from the now semi-arid conditions on Cape Range. Hence the model for isolation is a sub-set of the climatic shift model (see Peck 1980), with aridity rather than cold being the isolating mechanism.

Such regional relictual faunas, present in both the aquatic (Humphreys 1993b) and terrestrial systems (Humphreys 1993a) of Cape Range peninsula, have high specific and generic endemicity. The contemporary biota of an area is made up of lineages which have arrived in the area from different sources, by various methods and especially at different times. Relict faunas are especially useful in disentangling this, often conflicting, information because they are clearly separated from contemporary events and can sometimes provide information on the age or order of the vicariant events that resulted in the relictual fauna. Surface living taxa which become relictual face extinction if the climate continues to change, a process perhaps exemplified by the demise of the palm tree *Livistona alfredii* F. Muell. in Cape Range (Humphreys *et al.* 1990). In contrast, the conditions that have allowed troglobitic species to survive often persist in caves through dramatic climatic perturbations.

Characteristics of subterranean habitats and fauna

Hypogean faunas have peculiar habits and habitats and an understanding of their biogeography is aided by having some appreciation of the nature of their habitats as well as the characteristics of the species. These are addressed in the following sections.

Adaptation to cave dwelling - definitions

The fauna found in caves is customarily divided into a number of categories. Accidentals (ac) are species which enter caves by chance, whereas trogloxenes (tx), such as bats, inhabit caves sporadically. Troglophiles are facultative cave dwelling species and this category is often divided into first level troglophiles (tp_1) which are found both in cave and epigean habitats, and second level troglophiles (tp_2) which are found only in caves. Obligate cave dwellings species are termed troglobites (tb) and they usually have significant eye and pigment reduction, elongate limbs and considerable enhancement of their non-optic sense organs. Numerous other terms and categories have been advocated to cover this range of adaptation (summarised by Camacho 1992).

These categories are based on the level of dependence on the cave system mostly deduced from their distribution within and without caves and the degree of morphological adaptation presumed to be adaptive to cave life. However, second level troglophiles may turn out to have clear adaptations to caves in non-morphological characters (e.g. physiology or reproduction; Barr 1963; H. Dalens, pers. comm. 1988). Hence, in essence these are functional definitions and allocation between these categories requires assumptions about the nature of the adaptation or detailed knowledge of the species biology. This knowledge is unavailable for the vast majority of cave species and the categories should be treated with due caution.

Characteristics of underground habitats

Most caves are themselves entranceless voids, not yet connected to the surface (Curl 1966) and may even be totally enclosed voids supporting sulphide dependent ecosystems (Sarbu

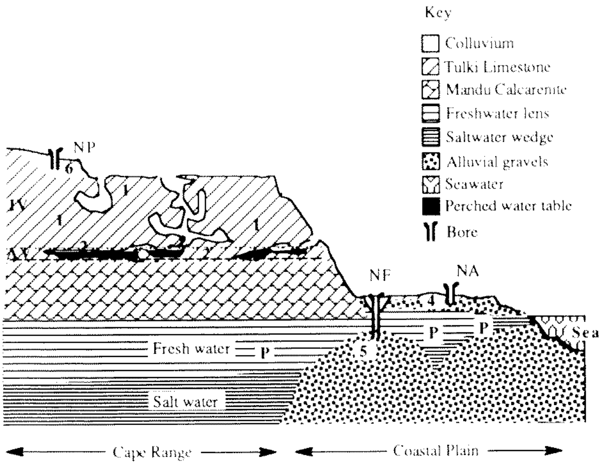

Figure 1. Diagrammatic cross section of major sub-surface habitats on the Cape Range peninsula. In caves formed by solution there are three main zones: 1) a dry upper zone, (inactive vadose, IV); 2) a periodically flooded zone (active vadose, AV); and a continuously flooded zone (phreatic, P). Non-cave subsurface habitats (4-6), are collectively called interstitial habitats to differentiate them from karstic habitats. The main interstitial habitats are 4) the gravels alongside streams and rivers (*nappes phreatiques*, NA); 5) the underflow of streams and rivers (*nappes fluviales*, NF); and subsurface habitats above the water table (*nappes perches*, NP). The 'bore' symbol indicates that these habitats are normally sampled indirectly, using various pumping devices (Bou and Rouch 1967). (Adapted from Culver 1986).

1990). Subterranean faunas do not only occur in caves but also, probably mainly, they inhabit interstitial and fissure habitats. While biologists working on the macrofauna of caves were able to divide their specimens according to the simple schema above, the range of habitats encompassed by the subterranean world is huge (Howarth 1983; Juberthie 1983). In the terrestrial realm it ranges through the essentially epigean to the endolithic, and in size from the interstitial (spaces < 1 mm diameter) to macro-caverns (> 20 cm). Where such habitats are beneath water the stygobiologists use a separate set of terms to describe their subterranean system (Botosaneanu 1986) which at its limits has some congruence with those studied by limnologists on the one hand and marine biologists on the other. These problems have led to the realisation that distinctive, but artificial, classification into facultative or obligate cave inhabitants (Peck 1990) is often misleading and that the subterranean system is better viewed as a continuum of void sizes and habitat types.

In Figure 1 I provide a schematic view of the major sub-surface karstic habitats of Cape Range peninsula. In Cape Range only caves proper (inactive vadose zone) have been extensively sampled, including the active vadose zone accessible at only four locations. Other habitats have been sampled sparsely, including the interstitial habitat via piezometric bores. On the coastal plain bordering Cape Range a freshwater lens overlies saltwater and merges into an anchialine habitat; these are sparsely accessible through bores, wells and caves (Table 5; Humphreys and Adams 1991; Humphreys 1993b).

Nature of the area

The cavernous Tulki Limestone (or Tulki-like; K.J. McNamara and G.W. Kendrick, pers. comm. 1991) of the anticlinal Cape Range Formation is exposed at Cape Range and on

Table 5. Simplified scheme of the major subsurface karstic habitats (after Culver 1986). Only those marked with an asterisk have been sampled at all on the Cape Range peninsula and Barrow Island. Interstitial habitats are likely to occur because extensive alluvial gravel deposits fan across the coastal plain from the mouths of the gorges in Cape Range (Sofoulis 1951) and through which the freshwater lens beneath the coastal areas is recharged by run off from the range (Hocking *et al.* 1987).

	Zone	Characteristics	Sampling method
Solution caves	Inactive vadose*	Dry upper zone	Direct and traps
	Active vadose*	Periodically flooded	Direct and traps
	Phreatic*	Continuously flooded	Diving and traps
Interstitial habitats	*Nappes phreatiques*	Gravels alongside streams	Pumping and traps
	Nappes fluviales	Underflow of streams	Pumping and traps
	Nappes perches	Above the water table	Pumping and traps

Barrow Island 160 km to the north-east. Whereas the elevated caves contain primarily terrestrial fauna, caves on the adjacent coastal plains contain primarily a subterranean aquatic (stygo-) fauna (Humphreys 1993a; Humphreys and Adams 1991; Knott 1993) at least partly in an anchialine habitat and hence in continuity with the waters of the North West Shelf (Humphreys 1993b).

It is the humid caves in Cape Range that contain the rich and highly adapted terrestrial troglobite fauna with some northern affinities and they are comparable to the caves of north-east Queensland studied by Howarth (1988). However, in other respects it is a very different system, being in a semi-arid area with rainfall being especially unpredictable between both seasons and years (Humphreys *et al.* 1989). This sparse rainfall occasionally, perhaps every few years, floods the caves and so provides both the humidity necessary for the cave animals (Humphreys 1990) and carries with it the organic matter which fuels the cave ecosystem (Humphreys 1991a). When caves are thus recharged the populations of cave animals in the mesocaverns move into the newly inhabitable areas and breed there. Until they are next recharged the caves slowly dry and the populations retract from the drying cave and then into the mesocaverns (Humphreys 1990, 1991a, 1991b; Humphreys *et al.* 1989; Humphreys and Shear 1993).

Resilience of the cave fauna

These characteristics lead population pulses to extend upwards from the mesocaverns at intervals like pseudopodia into the accessible areas of caves (megacaverns). Depending on the characteristics of the caves, the weather and the catchment size, these pulses of the community extend into the accessible areas of the caves with different frequencies and have different rates of decay (Figure 2). The habitable areas are dynamic, continually expanding and contracting, and are fed by unpredictable pulses of organic matter washed into the cave (see Humphreys *et al.* 1989). Hence, the caves in Cape Range contain highly dynamic troglobite communities (Humphreys 1991a) which belie the stability often associated with such systems (Poulson and White 1969).

When the caves are depleted of their fauna through lack of water or energy, it is these deep fissure habitats that are thought to sustain low populations of the cave animals and from where populations reoccupy the cave proper when they are next wetted and re-energised (Humphreys 1991a). The genetic evidence suggests that many apparently separate caves must

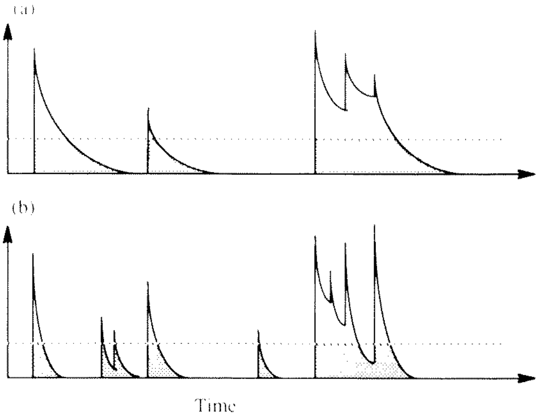

Figure 2. Hypothetical availability and depletion of resources in Cape Range caves. a) Slow drying (small entrance) cave with a small catchment; b) fast drying cave with a large catchment. The fine horizontal line denotes the resource level (energy or water) below which the populations are eliminated from the cave (shaded areas). Population responses would lag following the influx of new resources. Caves with large catchments (b) flood and are recharged with energy more frequently. Slow drying caves (a) maintain populations for longer after flooding (after Humphreys 1991a: Fig. 6).

be linked by fissure habitats, especially in the most genetically homogeneous southern part of the range (Adams and Humphreys 1993; Humphreys 1990; Humphreys and Shear 1993). This ability of the fauna to migrate both vertically and, to some extent, laterally within the karst system permits the fauna to survive local extinction caused by flooding, drought or stochastic processes; it is the essence of the resilience of the cave fauna.

Another factor contributing to the resilience of the fauna is the temperature tolerance of the troglobite species. Cave temperatures are expected to be at about the mean annual surface temperature (Wigley and Brown 1976) which in Cape Range is 27.3°C. However, the temperature of different caves containing troglobites is from 17°C to 29°C (Humphreys 1990). Hence, whereas the humidity requirements of the troglobites are exacting (Humphreys 1990) the same species is found in caves encompassing an 13°C range of temperature.

Considering these characteristics of the cave system in Cape Range, the fauna would be expected easily to survive a wide range of climatic perturbation in the region. In consequence, whilst this would have permitted long term survival of the cave fauna in the area, it does not, in itself, provide clues as to the climatic changes since the troglobites occupied the caves.

Characteristics of the aquatic system

The subterranean aquatic fauna of the Cape Range peninsula (Humphreys and Adams 1991; Humphreys 1993b; Knott 1993) can be divided into those inhabiting caves in Cape Range, where they were probably isolated by eustatic events (see below), and those inhabiting the ground waters in the fringing coastal plain. Of the latter, some are congeneric with Caribbean stygofauna (Bruce and Humphreys 1993; Poore and Humphreys 1992) and may have been vicariated by plate tectonic events following the break-up of Pangaea (Humphreys 1993b). In general there is a predominance of Tethyan elements in this fauna (Humphreys 1993b; Knott 1993) .

Coastal stygofauna

A freshwater lens overlying salt water occurs beneath the peninsula and this is recharged from Cape Range following exceptional rainfall (Hocking *et al.* 1987). Hence, the presence of Cape Range on the peninsula is an important influence permitting the presence of the rich stygofauna on the coastal plain. The present conditions preclude dispersal along the coast south of Cape Range owing to the highly saline groundwater starting at the neck of Cape Range peninsula (Carter 1902; Hocking *et al.* 1987). However, the aquatic species would have had many opportunities to move widely through the North West Shelf during periods of lowered sea level, as recently as the Holocene. This hypothesis is supported by the occurrence of *Halosbaena tulki* (Thermosbaenacea), and the troglobitic shrimp, *Stygiocaris stylifera,* the species found on the eastern shore of Cape Range, on Barrow Island, 160 km to the north-east (Humphreys and Adams 1991; Humphreys, 1993b). Indeed, such dispersal is required if those taxa of stygofauna possibly distributed by plate tectonic events, namely *H. tulki* and *Haptolana pholeta* Bruce and Humphreys (Isopoda: Cirolanidae), were to colonise the Cape Range Formation from necessarily older land such as the Pilbara Craton (Humphreys 1993b).

These processes are not directly related to climate and thus differ in essence from the processes probably leading to the isolation of the Cape Range cave fauna. While the terrestrial cave species have been isolated by aridity to Cape Range, small parts of it or even to single caves, the coastal aquatic fauna has had many opportunities to expand widely through suitable habitat on the exposed North West Shelf; it is currently almost as restricted as at any time since the Pliocene (see Wyrwoll *et al.* 1993).

Continuous and patchy habitats

Theoretically the *nappes phreatiques* and the *nappes fluviales* (Table 5) form more or less continuous habitats whereas *nappes perches* are patchy, forming isolated habitats. Hence, speciation is most likely to occur in the latter habitat and the biogeographical implications of this are apparent on the Cape Range peninsula. The fish and shrimps which inhabit the phreatic habitats on the coast form linear populations with little genetic variability (Humphreys and Adams 1991; Adams and Humphreys 1993), whereas the amphipod populations inhabiting the *nappes perches* show considerable genetic divergence between the isolated perched water tables (Table 6). However, the genetic evidence suggests that, following the separation of the Cape Range amphipods from their coastal congenors in the Pliocene, the *nappes perches* was continuous until it fragmented in the early Pleistocene (Table 10).

Table 6. Greatest Nei's genetic distance between populations of animals inhabiting different types of aquatic habitat (Table 5) on the Cape Range peninsula. Data are extracted from Humphreys and Adams (1991).

Common name	Taxon	No. of populations	Nei's Distance	Habitat	Characteristic
Blind Gudgeon	*Milyeringa veritas*	6	0.030	*Phreatiques*	Continuous
Atydid shrimps	*Stygiocaris lancifera*	4	0.015	*Phreatiques*	Continuous
Atydid shrimps	*S. stylifera*	2	0.006	*Phreatiques*	Continuous
Melitid amphipods	-	4	0.200	*Nappes perches*	Discontinuous

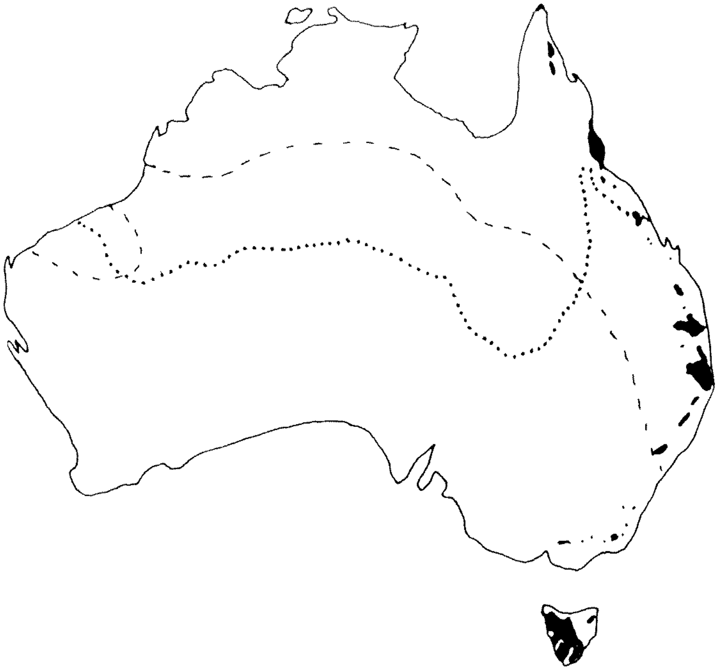

Figure 3. The current distribution of extensive coastal rainforest (black) and the southerly limit (dashed lines) of remnant coastal rainforest elements in contemporary Australia (after Webb and Tracey 1981). The former occurs in an arc through eastern Australia with a distribution similar to the Pliocene limits of forest with *Nothofagus*. The dotted line shows the known northerly extent of forest with *Nothofagus* in the Eocene; further north data are mostly lacking (after Truswell 1990).

Aridity and the origins of the cave fauna

Complex rainforest occurred on the western shoulder of Australia during the Eocene (Truswell 1990) but the 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 south-western seaboards of the continent, as exists today (Figure 3).

There is no direct evidence of tropical rainforest on Cape Range and their occurrence is primarily deduced from the faunistic affinities, especially of some cave living animals. The presence of remnant rainforest plant species in Cape Range would not by itself be evidence of continuous forest connection with source areas, as required by physico-chemically sensitive cryptozoic invertebrates, because such forest can become established in remote patches by propagule dispersal whenever suitable habitat conditions prevail (Kenneally *et al.* 1991). However, very humid adapted invertebrates probably cannot similarly disperse as they are found as separate species with small ranges (e.g. Schizomida; Harvey 1992). Similarly, the presence of highly adapted troglobites of the genera *Draculoides* (Schizomida) and *Nocticola* (Blattaria) on both Cape Range and Barrow Island is evidence of either extensive forest or continuous air-filled subterranean voids over the North West Shelf. The occurrence of

Draculoides in coastal limestones on Cape Range peninsula and in fissured limestone on Barrow Island is consistent with the latter hypothesis.

The evidence suggest that following the emergence of the Cape Range anticline from the sea, probably in the late Miocene (Wyrwoll *et al.* 1993), the area must have had a direct forest connection with some older land mass. I discuss below the possible connections.

The regional rainforest would have progressively fragmented (Webb and Tracey 1981) during the development of a more arid climate through the Miocene and Pliocene, with high pressure cells occurring to the south of the continent which was under an easterly wind pattern (Bowler 1982). Along river valleys forest persists providing potential corridors of suitable habitat between regions for humid requiring species. Indeed, such riverine remnants are implied in Truswell's (1990) palaebotanical reconstructions. The persistence of such vegetation along the Ashburton River, which flowed across the emergent North West Shelf, would have provided such a connection between the Neogene Cape Range Formation and older landmasses, especially the Pilbara Craton (see also Wyrwoll *et al.* 1993). The occurrence of *Livistona alfredii* palms on Cape Range supports this contention as the species is known elsewhere only from the Pilbara, including the Ashburton basin (Humphreys *et al.* 1990), where it is relictual in areas of superficial groundwater (G.W. Kendrick; pers. comm.).

These hypotheses lead to several predictions:

1. Elements of the ancient anchialine stygofauna present in the Cape Range Formation should occur in suitable substrates fringing the Pilbara Craton (Humphreys 1993b).
2. There should be common elements in the freshwater fauna of the Cape Range Formation and the Ashburton River basin. This would especially be expected in the subterranean waters along river courses (*nappes phreatiques* and *nappes fluviales*) as they are buffered from external conditions. The Millstream aquifer is a prime candidate for such fauna (G.W. Kendrick, pers. comm.).
3. Cavernous rocks in the Ashburton Basin, especially those close to the river, are likely to contain some elements of the terrestrial troglobite fauna found in the Cape Range Formation.

Local biogeographical implications

As conditions became more arid forest would have been progressively lost from the higher parts of Cape Range, persisting in gorges and scree slopes, as found in the Kimberley (McKenzie 1991). Hence the different karst areas would eventually be joined by corridors of remnant rainforest persisting in the gorges. Because the deeper gorges cut through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone beneath, the loss of forest would eventually preclude dispersal of cryptozoic animals between karst provinces.

Within the context of a general decline in forest cover owing to the onset of arid conditions, minor departures from this trend (Wyrwoll 1993) would have permitted forests to advance and retreat on the sides of the gorges. Hence the troglobite populations would have been periodically separated and rejoined and so offering opportunities for speciation and the subsequent sympatry of the congeneric species (Figure 4). Such changes could explain the presence in sympatry of congeneric species of the *Stygiochiropus* millipedes in C-111 (Humphreys and Shear 1993), especially as they are at the limits of the range. Similar processes, resulting from eustatic events, are suggested by the sympatry of the shrimps, *Stygiocaris* spp. on the west coast of the peninsula (Mees 1962; Humphreys and Adams 1991; Humphreys 1993b).

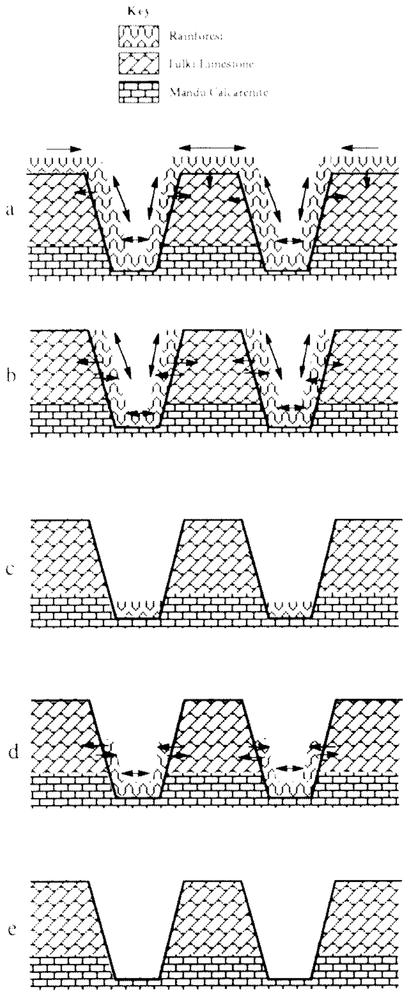

Figure 4. Schematic diagram of Cape Range showing three karst (potential genetic) provinces separated by deep gorges cutting through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone beneath. The arrows show possible movement of putative or actual troglobitic fauna between areas as rainforest advances and retreats. a) Rainforest covers the range permitting free interchange of humid dependent species within and between areas. b) Rainforest restricted to the gorges permitting interchange between the major karst provinces but not between isolated caves within a province. c) Rainforest restricted to the riverine section of gorges permitting no interchange of species within or between karst provinces; the cave restricted populations are now allopatric. The forest acts as refugia for humid dependent species. d) Rainforest advances up the gorges again permitting interchange between karst provinces. e) Rainforest lost from the gorges as the climate dries and no further interchange will be possible between the karst provinces even if the climate temporarily becomes wetter.

The timing of biogeographically pertinent events in Cape Range

Biogeography can best be understood if a reliable chronology of events of biogeographic significance can be established. In the absence of such a chronology much use can be made of a temporally sequential list, especially if relative ages can be attributed to the events. Such a chronology needs to bring together disparate and independent information so that it can be examined for internal consistency and to identify crucial periods where data are lacking so that such deficiencies can be addressed. Here I attempt a first approximation of a relative chronology for the Cape Range area and which is summarised in Table 10.

The chronology needs to cover all biogeographically pertinent periods which for Cape Range necessitates consideration of more ancient land areas and possible connections. As the stygofauna has quite clear affinities with the Caribbean and north African stygofauna (Poore and Humphreys 1992; Humphreys 1993b; Knott 1993), the chronology needs to cover pertinent plate tectonic events as well.

Regional stability

Although Cape Range is of Neogene age it lies close to the Pilbara Craton, a centre of exceptional long term stability that has undergone no major regional deformation and has been continuously emergent since the Precambrian (*c.* 600 Ma; Trendall 1990). Since the Triassic (*c.* 200 Ma) it has mainly been fringed with shallow marine environments or inland intrusions of the Tethys Sea (Hocking 1990). Hence, Mesozoic deposits abut the western

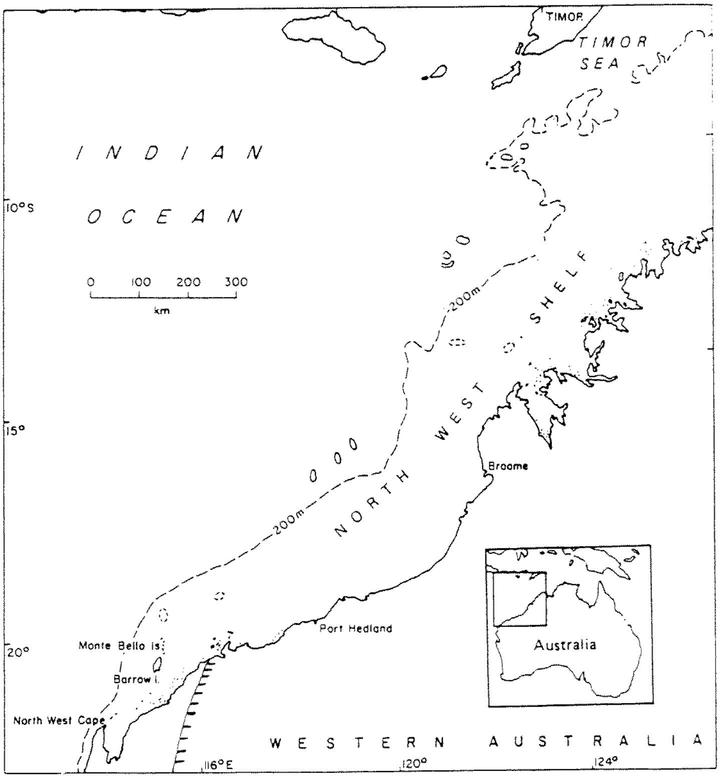

Figure 5. Locality map showing the location of features mentioned in the text. The hatched line west of the 116°E mark represents the border between the Mesozoic (100 Ma) or Tertiary (*c.* 19 Ma; Cape Range and Barrow I.) formations to the west and the Precambrian Pilbara Craton to the east. The latter has not undergone major regional deformation since 2400 Ma (Trendall 1990) and has been emergent continuously for > 600 Ma.

Table 7. The approximate latitude of the north-west of Australia from 160 Ma to the present compared with the south-west, north-east and south-east of the continent. The locations are present day Port Hedland (NW), Cape Naturaliste (SW), Townsville (NE) and Wilson's Promontory (SE). Data derived from Veevers *et al.* 1991.

Period	Latitude (°S)			
Ma	NW	SW	NE	SE
160	42	44	60	70
132	51	50	75	73
118	52	55	68	80
96	53	64	55	75
84	54	67	55	74
64	56	71	50	68
49	47	62	43	62
45	46	60	42	60
35	43	58	40	58
20	37	53	34	54
10	22	35	18	38
0	21	33	19	38
Max	56	71	75	80
Min	21	33	18	38
Range	35	38	57	42

border (Figure 5) and these are themselves fringed with Tertiary deposits including those of Cape Range.

Furthermore, the north-west is the only part of Australia to have remained north of 60°S since the Jurassic (other areas having been to latitudes >70°S; Table 7), an important period in the vicariance models proposed to explain the distribution of relictual, warm water, stygofauna, supposedly of Tethyan origin, such as *Haptolana* and *Halosbaena* (Stock and Longley 1981; Iliffe *et al.* 1984b; Hart *et al.* 1985; Wägele 1985; Cals and Boutin 1985; Wilkens *et al.* 1986; Humphreys 1993b).

Together, these factors offer an adjacent potential source area for the Cape Range fauna which has had an exceptionally long history of both geomorphological and, in an Australian context, of climatic stability.

Sea level

The Cape Range peninsula fringes the extensive and shallow North West Shelf, itself broadly contiguous with other shelves around northern Australia (Veevers 1991). On a number of occasions, during periods of lowered sea level and as recently as the Holocene, these shelves would have been emergent and formed an extensive, low coastal plain similar to those found bordering the Cape Range peninsula today (Figures 5 and 6). For example, the sea is <20 m deep between Barrow Island and the mainland and they would have been connected between *c.* 80,000-8,000 BP and for *c.* 80% of the last 0.25 Ma (estimated from Chappell and Thom 1977: fig. 1). This plain would have provided a continuous suitable habitat for the current stygofauna thus linking the Miocene formations with the Precambrian Pilbara Craton to the north-east. The occurrence of *S. stylifera* and *H. tulki* on both Barrow Island and the Cape Range peninsula is evidence for the suitability of the substrate for such dispersal.

Table 8. Mean growth rates (mm a^{-1}) for stalagmites from northern hemisphere[1] caves (calculated from Table 8.5 in Ford and Williams [1989] using mean values if a range was given). The minimal growth rate of a well developed stalagmite from cave C-126 in Cape Range is given for comparison. Some comparative data are given for Australia.

Group or age	Mean	St. Dev.	C. V.	N
All data[1]	0.116	0.114	98	18
Holocene	0.230	0.148	64	5
Post glacial	0.120	0.028	24	2
Late glacial	0.098	0.062	63	3
Interstadial	0.023	0.021	91	4
170-<80 ka	0.0007	Cape Range	-	
98-55 ka	0.020	Tasmania	Goede *et al.* 1990	
4.3-2.9 ka	0.500	Tasmania	Goede *et al.* 1990	
12.6-8.8 ka	0.233	Tasmania	Goede and Vogel 1991	

Stalagmite dates and growth

The caves in Cape Range, of which >400 are known, are currently fossil systems that were clearly formed during periods of substantially greater rainfall such as would have supported the warm moist closed canopy forests suggested by the affinities of the troglobite fauna. Some caves exhibit sparse speleothem decoration and a number of stalagmites have been dated in an attempt to determine wetter periods and growth rate examined in one older specimen (uranium series dating by Dr D. Smith, Department of Inorganic Chemistry, University of Melbourne).

Sections of a stalagmite from C-126 *c.* 65 mm apart gave dates of 170,000 (+49,000 - 35,000 years) and 80,000 (+13,500 -12,100 years). The former sample was clean (^{230}Th/^{232}Th =105) while the latter samples was contaminated with detrital material (^{230}Th/^{232}Th =1.8) so that further analysis to correct the date would yield a substantially more recent date. Taking the data at face value the growth rate of the stalagmite averaged 0.72 mm ka^{-1} (range of estimate = 0.42 to 1.59 mm ka^{-1}); the growth rate after correcting for contamination would be lower.

Growth rates of speleothem vary widely, averaging 120 mm ka^{-1} (0.12 mm a^{-1}; calculated from Ford and Williams 1989). Hence, the growth rate of the stalagmite from C-126 in Cape Range is an order of magnitude less than these reported for other areas (Table 8). However, even this stalagmite (aged < 170 ka) probably formed under more humid conditions than occur now. The period of substantially greater rainfall required to form the caves must predate 170 ka BP.

Altitudinal separation of aquatic congenors

A series of emerged and warped marine erosion terraces occur on the western side of Cape Range up to an altitude of *c.* 60 m and which were thought to have formed during periods of elevated Pleistocene sea levels with the warping indicative of Quaternary tectonism (van de Graaff *et al.* 1976). This suggestion that the Cape Range anticline had been exposed above sea level for only a short time was difficult to reconcile with the biogeography and degree of adaptation of the cave fauna. Recent palaeontological evidence suggests that the sea has not been above the Jurabi Terrace (c. +10-15 m MLWS) since the Pliocene and that the major uplift of the anticline occurred in the late Miocene- early Pliocene, 7-10 Ma ago (Wyrwoll *et al.* 1993).

Table 9. The estimated altitude of the water in the four caves known to contain standing water in Cape Range; the four caves contain melitid amphipods which are congeneric with a species on the coastal plain of the Cape Range peninsula.

Cave	Altitude (m) at entrance	Depth to water (m)	Water level (m)	Grid reference	Map Sheet 1: 50,000
C-18	265	50	215	08705425	MANDU
C-64	180	10	190	92255920	LEARMONTH
C-103	300	55	245	08275029	MANDU
C-163	255	60	195	90954740	LEARMONTH

The aquatic fauna may provide important clues as to the timing of events in Cape Range. The only known aquatic species in Cape Range (Humphreys and Adams 1991) is congeneric with a new genus of melitid amphipod that inhabits the coastal plain bordering Cape Range (W.D. Williams; pers. comm.). The two species are separated by an altitude of *c*. 200 m (Table 9) and inhabit water of very different salinity, being 0.5 ‰ in the range and *c*. 12 ‰ on the coast (Humphreys and Adams 1991). There is clearly no gene flow between them as there are 70% fixed allozymic differences between the plain and range populations (M. Adams; per. comm. 1992).

The parsimonious hypothesis is that the ancestral population of melitid amphipod became separated by altitude when the Cape Range anticline rose above sea level in the late Miocene-early Pliocene, 7-10 Ma ago (Wyrwoll *et al.* 1993). This is supported by estimates of genetic distance between the congeneric amphipod species which suggests that they have been separated for *c*. 7 Ma (Table 10).

Hence, two independent lines of evidence support an early elevation of Cape Range and thus the karst region would have been exposed throughout this time and freshwater solution would have initiated cave formation. Additional evidence is provided below, which indicates that terrestrial taxa also were speciating on Cape Range during the Pliocene. Concordance between tectonic events and isozyme analysis have been reported elsewhere in the context of cave fauna and over similar periods (Sbordoni 1982).

Genetic provinces and the timing of events in Cape Range

The troglobites in Cape Range occur within separate genetic provinces separated in part by the deeper gorges that cut through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone beneath (Humphreys 1991a; Humphreys 1993a; Humphreys and Shear 1993; Adams and Humphreys, unpublished). These discontinuities form major barriers to gene flow which, like the altitudinal separation of the amphipods, may provide clues as to the relative timing of events within Cape Range. Cave dwelling, but non-troglobitic species do not show such genetic provincialism (Humphreys 1989; Adams and Humphreys 1993).

I want to look at the nature of these genetic provinces and consider the clues they may provide as to the timing of climatic events in Cape Range. The best electrophoretic data are for the endemic genus of troglobitic millipedes, *Stygiochiropus* spp. which contains three morphospecies, two of which are known from single locations (Humphreys and Shear 1993). Allozyme electrophoretic data are available for two of these species from which genetic distance can be determined (Adams and Humphreys 1993 and unpublished).

The populations of the widespread species, *Stygiochiropus communis*, in the three genetic provinces are separated by large genetic distances, although less than between species

(Humphreys and Shear 1993; Humphreys 1993a, Adams and Humphreys 1993). For comparison it is greater than the genetic distance separating 41% of the 111 species of *Drosophila* examined by Coyne and Orr (1989). Cave populations of *S. communis* within the geomorphologically and genetically homogeneous southern genetic province differ by an

Table 10. Suggested sequence of events in the Cape Range area. Its purpose is to provide an heuristic focus for the timing of biogeographically pertinent events in Cape Range, rather than to serve as an accurate record of events. Some of these events are depicted in Figure 6.

Event	Date	≈Time	Evidence
		Thousand years	
N. W. Shelf inundated[1]	Holocene	8-0	Calculated from Chappell and Thom 1977
Wetter period	Pleistocene	14-11	Ur/Th speleothem date, C-125[2]
N. W. Shelf inundated[1]	Pleistocene	85-80	Calculated from Chappell and Thom 1977
Differentiation[12]; S. province	Pleistocene	100	*D* between millipede populations[4,10]
N. W. Shelf inundated[1]	Pleistocene	111-99	Calculated from Chappell and Thom 1977
Wetter period	Pleistocene	128	*Andara trapezi* distribution[11]
N. W. Shelf inundated[1]	Pleistocene	135-116	Calculated from Chappell and Thom 1977
Differentiation in central province	Pleistocene	150	*D* between amphipods in range[4,6]
E and W coast populations isolated	Pleistocene	200	*D* between cave fish populations[4,5, 6,7]
Atyid populations isolated	Pleistocene	200	*D* between *S. lancifera* populations[4,6]
Differentiation of populations	Pleistocene	200	*D* between *Draculoides* populations[4]
Wetter period	Pleistocene	219-68	Ur/Th speleothem date, C-126 and C-163[2]
N. W. Shelf inundated[1]	Pleistocene	222-216	Calculated from Chappell and Thom 1977
Wetter period	Pleistocene	225	*Andara trapezi* distribution[11]
Differentiation[12]; central pops	Pleistocene	300	*D* between millipede populations[4]
Differentiation[12]; northern pops	Pleistocene	350	*D* between millipede populations[4]
Barrow I. isolated from C.R.	Pleistocene	400	*D* between *S. stylifera* populations[4,8,10]
Northern cave waters isolated	Pleistocene	650	*D* between amphipods in range[4,6]
		Million years	
Southern cave waters isolated	Pleistocene	1.3	*D* between amphipods in range[4,6]
Wet forest lost from gorges	Pliocene	1.2-1.7	Deduced from * above
Northern cave areas isolated	Pliocene/Pleistocene	*1.2	*D* between millipede genetic provinces[4,10]
Southern cave areas isolated	Pliocene	*1.7	*D* between millipede genetic provinces[4,10]
Marine terraces	Pliocene	>2	Wyrwoll *et al.* 1993
Millipedes speciate	Pliocene	3.0	*D* between congeneric millipedes[4,10]
Shrimps speciate	Pliocene	3.8	*D* between congeneric atyid shrimps[4,10]
Amphipods speciate	Miocene/Pliocene	7	*D* between congeneric amphipods[4,10]
Anticline uplift	Upper Miocene	>7	Wyrwoll *et al.* 1993
Closed forest with *Nothofagus*	Miocene	>7	Truswell 1990
Cape Range limestone formed	Lower Miocene	19	Condon *et al.* 1953
Complex rainforest in vicinity	Eocene	>38	Truswell 1990
Tethys encircles Pilbara Craton	Cretaceous	118	Veevers *et al.* 1991
Eastern Gondwana fragments	Cretaceous	133-96	Veevers *et al.* 1991
Pilbara Craton emergent	Precambrian	>600	Hocking 1990

[1] Defined as Barrow Island being separated from the mainland when the sea level exceeds -20 m of present sea level. [2] 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. [3] One sample from C-126 dated 94-68 ky was excluded as the detrital contamination (^{230}Th: ^{232}Th = 1.8), if corrected, would give a much more recent date (see text). [4] Calculated from the average Nei's genetic distance (*D*) assuming *D* =1 corresponds to five million years of divergence (Nei 1987). [5] *Milyeringa veritas*. [6] Humphreys and Adams 1991. [7] Between populations on the east and west coast of the Cape Range peninsula. [8] Between populations on Barrow Island and the Cape Range peninsula. [9] Humphreys and Shear 1993. [10] Adams and Humphreys 1993, unpublished. [11] Kendrick *et al.* 1991. [12] By inference caves isolated.

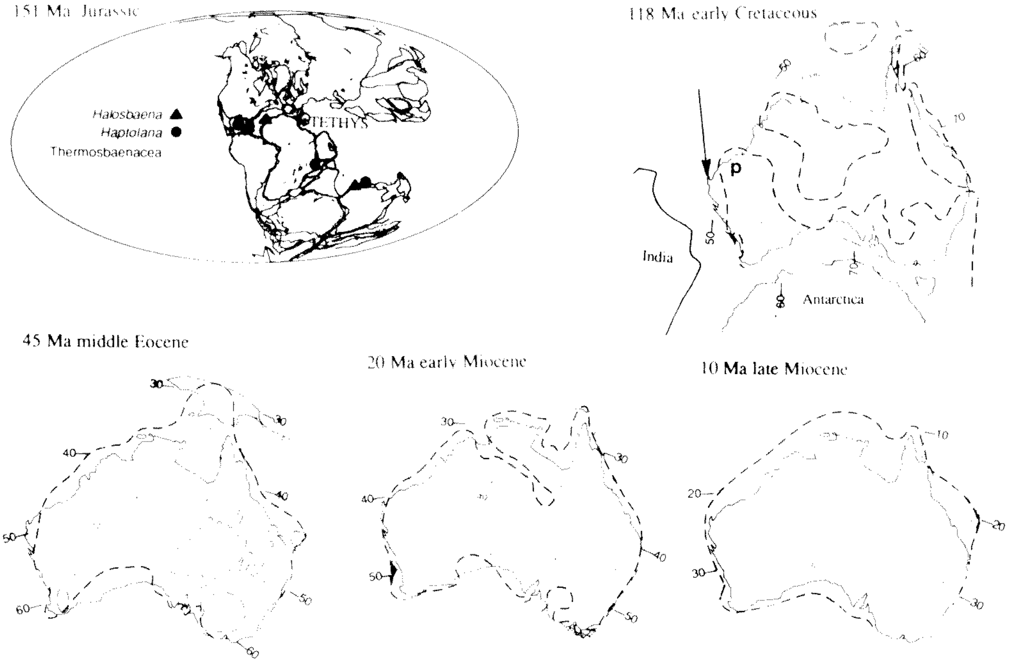

Figure 6. Composite diagram depicting some of the events recorded in Table 10. a) The relative location of the continental plates in the Jurassic (151 Ma) when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. The symbols show the known locations of the genera *Halosbaena* (Thermosbaenacea) and *Haptolana* (Isopoda: Cirolanidae). The plate map was produced using Scotese and Denham (1988). b-e) The current outline of Australia superimposed on the emergent parts of the Australian plate (dashed line) in the:- b) early Cretaceous (118 Ma), shallow seas surround the Pilbara Craton (p), arrow shows Cape Range; c) middle Eocene (45 Ma), complex rainforest in riverine and lacustrine areas across the southern half of Australia; d) early Miocene (20 Ma), complex rainforest no longer present, Cape Range limestones deposited; e) late Miocene (10 Ma), and through the Pliocene forest with *Nothofagus* retreats to eastern seaboard (Truswell 1990: Fig. 7), Cape Range anticline fully developed (Wyrwoll *et al.* 1993). The numbers on the maps show the latitude. Continental margins after Veevers *et al.* (1991); vegetation from Truswell (1990: Fig.7).

average of D =0.02, whereas in the geomorphologically more complex northern and central provinces, the cave populations differ by a mean D=0.094. The sympatric species of millipedes (*S. communis* and *S. sympatricus*) are known only from the northern province and their mean D =0.60 (0.085, 36) is greater than the mean D of 0.53 which predicts total isolation in *Drosophila* (D =0.66 for allopatric and D =0.31 for sympatric species: Coyne 1989).

On the basis of D =1 corresponding to five million years (5 Ma) of divergence (Nei 1987) then, for the paradoxosomatid millipedes, species were separated *c.* 3 Ma, genetic provinces were isolated *c.* 2 Ma, caves within the two northern provinces were isolated *c.* 1 Ma, and caves within the more homogeneous southern province *c.* 0.1 Ma. While the absolute age is questionable, the relative timing (30: 20: 10: 1 units) suggests two main periods of change separated by an order of magnitude in time; the most recent vicariance, within the southern region, can possibly be associated with Pleistocene drying conditions rather than with the geomorphological features (gorges etc.) associated with the older categories.

While troglobites can move through mesovoids in both lava and karst systems (Howarth 1987), the genetic evidence from Cape Range suggests that there is only restricted gene flow within genetic provinces and no effective gene flow across those gorges which cut through the cavernous Tulki Limestone into the Mandu Calacarenite (Humphreys and Adams 1993). These barriers of non-cavernous limestone, combined with the surface aridity, prevent panmixia (Figure 4).

If the humidity is sufficiently high, the millipedes will, even today, venture to the cave entrance. Hence, the vicariance event probably was not the cutting of the gorges, but the loss of moist forest from the gorges where it would have persisted for longest as aridity increased. This vicariant event establishing the three genetic provinces would have occurred at the temporal equivalent of a genetic distance of D=0.4, which according to Nei (1987) equates with 2 Ma.

Sequence of events

In this section I discuss some of the varied evidence for the timing of biogeographically pertinent events in Cape Range and examine the data for consistency.

Genetic evidence

1. There is a general consistency in the genetic evidence in that speciation events always predate population substructuring within species (amphipods, *Stygiocaris*, *Stygiochiropus*; Table 10).

2. Speciation events occurred during the early Pliocene (7-3 Ma) in the three terrestrial and aquatic genera examined (amphipods, *Stygiocaris*, *Stygiochiropus*; Table 10).

3. Major provincialisation of the millipede populations (Humphreys and Shear 1993; Adams and Humphreys 1993, unpublished) occurred in the late Pliocene from which it is deduced forest was lost from the area *c.* 2 Ma. All subsequent genetic fragmentation of the population occurred in the Pleistocene for both aquatic and terrestrial species (amphipods, *Stygiocaris*, *Stygiochiropus*; Table 10), possibly related to the major climatic and eustatic fluctuations known to have occurred during this period (Wyrwoll 1993; Wyrwoll *et al.* 1993). Evidence for wetter periods comes from both speleothem dating and the distribution of the estuarine mollusc *Andara trapezi* (Deshayes) (Bivalvia: Arcoida) (Kendrick *et al.* 1991).

4. Consistency is shown in that for both the millipedes and amphipods the southern karst province became genetically isolated from the central province well before the northern province.

5. Both genera expected to be affected by the uplift of the Cape Range anticline seem to have speciated early than others (? early Pliocene). The amphipods were discussed previously in relation to their altitudinal separation. *Stygiocaris stylifera* is found on Barrow Island and the northern and eastern side of the Cape Range peninsula whereas *S. lancifera* seems to be confined to the western side of the peninsula (Humphreys and Adams 1991). There seems to be no overt barrier to gene flow within the range of *S. lancifera* (Humphreys and Adams 1991) which suggests that the partial sympatry of *Stygiocaris* spp. has only recently been established following speciation that was perhaps associated with the uplift of the Cape Range anticline.

6. The deduction from the genetic evidence and local distribution of the amphipods is consistent with recent palaeontological and geomorphological evidence for the uplift of the Cape Range anticline (Table 10; Wyrwoll *et al.* 1993).

Hence, independent evidence supports the interpretation of the separation of genetic provinces within the Cape Range karst region and suggests a common factor may be at play. Namely, the onset of arid conditions and the loss of rainforest prevented the movement between karst provinces of terrestrial cave fauna, and it also lowered the perched water table resulting in the subsequent fragmentation of the aquatic fauna in Cape Range.

Conservation implications of troglobite biogeography

Troglobite and other cave inhabiting species have a number of biogeographic characteristics that make them especially vulnerable to extinction. They usually have a very limited geographical range and, terrestrial troglobites especially, are often restricted to a single cave system. They typically occur in small populations with their inherent vulnerability to extinction through the stochastic processes acting on small populations. Many cave species exhibit a reduced physiological regulatory ability (Ahearn and Howarth 1982; Humphreys and Collis 1990) and hence minor disturbance of their physico-chemical environment can have a profound effect on the viability of troglobite populations.

For similar reasons, cave faunas generally, even the terrestrial species, are vulnerable to changes in the quality or quantity of the water table (Table 11). For example *Schizomus wessoni* (Chamberlin) was eliminated from its type locality as a result of long term drying of the Santa Cruz River due to agricultural activities, and the draining of land rendered oases unsuitable for *S. joshuensis* (Rowland and Reddell 1981). Contaminants can move large distances in fractured limestone (Wilber 1969; Freeze and Cherry 1979; Iliffe *et al.* 1984a) and can thus disrupt the entire range of a cave restricted species. Because degradation occurs much more slowly in underground waters, contamination of such waters, while being invisible, is more persistent than in surface waters. Hence, it is undesirable to dump waste products, even saline water, into the superficial karst and the World Conservation Monitoring Centre has warned against such practices.

Potential disturbance of cave species (Figure 7), because it is superimposed on their innate vulnerability to extinction, needs to be given special consideration. Most troglobites are stenotopic, stenotropic, and have common physico-chemical sensitivities and so processes causing the elimination of one species may eliminate the entire community, as has been documented elsewhere (C.D. Deltshev 1989 and H. Kovacs 1989 cited in Tercafs 1992). For

Table 11: The causes of cave species becoming vulnerable, rare or endangered (extracted from Rowland and Reddell 1981 and Culver 1986).

Factor	No. species[1]
Industrial development and quarrying	2
Overuse or pollution of water	12
Flooding	1
Direct human disturbance	9
Overcollecting[2]	3

[1] They comprise arachnids (7 species), crustaceans (4), insects (1), fish (5), amphibians (2) and mammals (5).

[2] All overcollecting was of aquatic vertebrates.

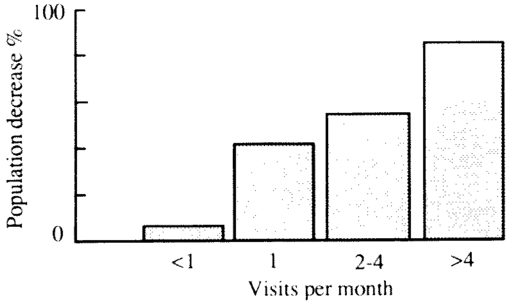

Figure 7. The effect of human disturbance on the summer colonies of the bat *Myotis griscens* in 20 caves in Alabama and Tennessee. The values given are the percentage decrease in the size of summer colonies between 1968-70 and 1976 at different levels of disturbance (number of visits by people each month; after Tuttle 1979).

this reason the underground fauna needs to be treated as a separate component of any management plan, and the emphasis placed on the underground habitat rather than the species.

Closing discussion

In this section I want to draw together the types of evidence available from the hypogean fauna of the Cape Range peninsula that makes it so suitable in biogeographical reconstruction. There are two areas of interest here. Firstly, the general utility of hypogean faunas; secondly, aspects peculiar to the fauna of the Cape Range peninsula which make it especially interesting.

Populations of animals may persist in caves long after climatic changes have eliminated, whether by cold, heat or aridity, their surface ancestors. Hence, a living echo of these past climates may be contained in the characteristics of the fauna that has become cave adapted. Simply because these populations survived past climatic changes in the area places them amongst the more ancient local taxa. As such, they are especially useful in interpreting past tectonic events in an area where the contemporary surface biota have, for the most part, been moulded by the current climatic conditions (e.g. Baynes and Jones 1993; Kendrick 1993; Keighery and Gibson 1993).

The subterranean fauna of the Cape Range peninsula is both diverse and complex, having disparate affinities. This is the case for both the terrestrial cave fauna of Cape Range itself and for the coastal stygofauna, despite their very different origins. The terrestrial fauna has affinities with moist closed forest litter faunas, such as those now associated with both tropical and temperate areas of Australia, as well as further afield, including those with eastern Gondwana distributions (Harvey *et al.* 1993). The stygofauna, however, has primarily a Tethyan affinity (Humphreys 1993b; Knott 1993) but there is also a Gondwana component.

The composition and affinities of the terrestrial troglobite fauna are consistent with it having been isolated in caves by the onset of the aridity already developing in the lower Miocene when the Cape Range Formation was deposited. With the increasing aridity elements of the humid closed forest fauna entered humid caves, initially perhaps only in the dry season, and some populations would have become permanent cave dwellers and evolved troglomorphies. These cave populations became grouped into genetically isolated provinces when the loss of humid vegetation from the gorges removed the last vestige of connection between adjacent karst areas.

The elevation of the Cape Range anticline is quite recent (*c.* 10 Ma) and hence both the terrestrial and aquatic components of the fauna have probably dispersed into the area from adjacent or distant source areas of greater antiquity. The aquatic components probably colonised the more ancient borders of Tethys (?Pilbara coastline) or persisted in the tectonic plates following the break-up of Pangaea (see Poore and Humphreys 1992; Humphreys 1993b) before dispersing to the Cape Range peninsula across the exposed North West Shelf at times of lower sea level. The terrestrial component of the fauna probably moved into the area along residual riverine forests because regional aridity, the isolating process, was already well advanced when Cape Range was uplifted. However, this fauna could have diffused across the North West Shelf, in air-filled subterranean voids, at times of lower sea level.

These hypotheses predict that elements of both the Cape Range troglobites and the coastal stygofauna will be found on the much older land masses in the vicinity of the Cape Range peninsula, especially the Pilbara Craton. The discovery of elements of both faunas on Barrow Island on the North West Shelf is consistent with these hypotheses.

Karst systems form a structurally rich habitat, even in arid areas lacking vegetation, because karst dissolution processes form essentially a continuum of voids, in both scale and space, between the epigean and aquatic habitats. Despite only periodic recharges of water and energy of only low predictability, this structure provides considerable resilience to the ecosystem as a whole. This is enhanced by the capability for limited vertical and lateral movement of the fauna through this spongework, thus allowing access to suitable conditions despite the marked surface and subsurface changes.

The geomorphological structure of the region probably makes an important contribution to the long term suitability of the karst for subterranean fauna. In particular, the depth of the cavernous limestone, and the presence of a non-cavernous (?impermeable) limestone beneath, probably enhances the long term stability of the habitat. In addition, the presence of Cape Range on the peninsula is important for the coastal stygofauna because it provides the hydraulic recharge of the fresh-water lens which overlies, in proximity to Cape Range, the saline ground waters generally occurring in the region.

The processes of karst and cave formation in Cape Range have not been studied in any depth. However, a general understanding of karst systems and processes allows predictions to be made and greatly assists in the interpretation of the data (Humphreys and Adams 1991). For example, the location of sampling sites within karst regions can have predictable effects on the characteristics of the fauna; the allozyme variation of aquatic species sampled high in the range reflects the discontinuous nature of perched water tables, whereas populations sampled on the coastal plain have much more extensive gene flow, consistent with the structure of the aquatic system.

Finally, the use of a wide range of information has led to a chronology of events pertinent to the Cape Range peninsula that has considerable internal consistency for the relative timing of events despite the uncertainties surrounding the various estimates. Such concordance between tectonic events and isozyme analysis over a similar period has been found elsewhere in much better understood systems (Sbordoni 1982).

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