

## CAVE FAUNA IN SEMI-ARID TROPICAL WESTERN AUSTRALIA: A DIVERSE RELICT WET-FOREST LITTER FAUNA

by

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### INTRODUCTION

This paper introduces the cave fauna of the highly cavernous Cape Range karst province in the north-west of Western Australia; the area is currently arid to semi-arid and experiences highly unpredictable rainfall (HUMPHREYS *et al.*, 1989). The system has a rich and highly adapted troglobite fauna, much of it a relict rainforest fauna in this now semi-arid area (HUMPHREYS *et al.*, 1989). It is comparable in richness to the species rich caves of the humid tropics of north-east Queensland (HOWARTH, 1988). However, in other respects it is a very different system, being a relictual fauna in a semi-arid region, having high population densities that undergo irregular catastrophic reduction in numbers (HUMPHREYS, 1990, 1991a; HUMPHREYS *et al.*, 1989; HUMPHREYS and SHEAR, 1993).

### I - THE NATURE OF THE AREA

The Cape Range Formation is an anticline of Lower Miocene limestones one of which, the Tulki Limestone, is highly cavernous on Cape Range (> 450 caves known). The caves are mostly vertical (up to 100 m deep) with a lateral extent in the same order; one cave has > 5000 m of passage. In certain caves, where water saturated warm (up to 30°C) exhalant air leaves the cave, a condensation zone permits troglobitic species to exploit the very entrance to the cave, unlike other tropical caves (HOWARTH, 1987).

The caves occur in the deeply dissected Cape Range and the troglobitic fauna relies on organic matter and water entering the caves from intermittent and unpredictable flooding. The frequency of water influx into a given cave depends on the occurrence of significant rainfall and on the nature and size of the catchment area of the cave. The rate of drying of a given cave depends on the relative size of the cave and its opening to the outside.

Caves may take inflow after relatively low rainfall (every few months) but then dry rapidly (in a few months). In contrast some caves take inflow only after heavy rainfall (every few years) but thereafter dry very slowly (over several years: HUMPHREYS *et al.*, 1989; HUMPHREYS, 1991b).

When caves are recharged by water and its contained organic matter the populations 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 towards the less dry parts of the cave and then into the mesocaverns (HUMPHREYS, 1991a). The caves receive few of the major energy inputs often associated with cave systems (bats, cave crickets, roots or root exudates) and hence lack the fauna characteristic of such caves (HARRIS, 1973; NORTON *et al.*, 1975; KANE *et al.*, 1975; KANE and POULSON, 1976; STUDIER and LAVOIE 1990).

Hence, the evidence suggests that the populations in the mesocaverns extend upwards 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 (Fig. 1). The habitable areas are dynamic

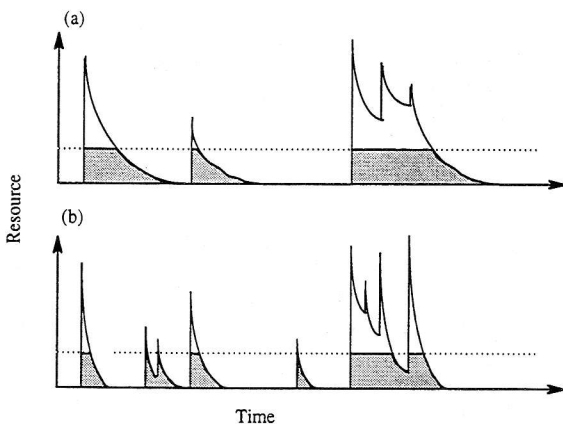


Fig. 1 - Hypothetical availability and depletion of resources in Cape Range caves. a) Slow drying (small entrance) cave with a small catchment. b) Fast drying cave with a large catchment. The fine horizontal line denotes the resource level (energy or water) below which the populations are eliminated from the cave (shaded areas). Population responses would show a lag after the influx of new resources. Caves with a 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).

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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 have highly dynamic troglobite communities (HUMPHREYS, 1991a) which belie the stability normally associated with such systems (POULSTON and WHITE, 1969).

## II - THE FAUNA OF THE CAPE RANGE FORMATION

### II.1 - Number of species

A total of 37 troglobite species have or are being described from 26 families and 27 genera (Tabl. 1) and they are distributed amongst the higher taxa as follows:- Chelicerata: Pseudoscorpionida (3 families, 3 genera, 3 species), Schizomida (1, 1, 2), Araneae (6, 6, 6). Crustacea: Thermosbaenacea (1, 1, 1), Amphipoda (1, 1, 2), Isopoda (4, ?5, 7), Decapoda (1, 1, 3). Diplopoda (3, 3, 5). Insecta: Blattaria (1, 1, 2), Hemiptera (2, 2, 3), Orthoptera (2, 2, 2). Chordata: Vertebrata (2, 2, 2). They represent 28 terrestrial and 9 aquatic species; at least another 6 species occur in the karst system. A large number of second level troglaphiles occur (e.g. four in the Arachnida alone) as well as other species whose association with the caves is largely unknown but many are clearly relicts of a wetter climate.

Tabl. 1 - The higher level classification of troglobitic and stygobiont species from the North West Cape peninsula (including Cape Range) and Barrow Island.

		Families	Genera	Species
Chelicerata	Pseudoscorpionida	3	3	3
	Schizomida	1	1	2
	Araneae	6	6	6
Crustacea	Thermosbaenacea	1	1	1
	Amphipoda	1	1	2
	Isopoda	4	5	7
	Decapoda	1	1	2
Myriapoda	Diplopoda	3	3	5
Insecta	Blattaria	1	1	2
	Hemiptera	2	2	3
	Orthoptera	2	2	2
Vertebrata	Pisces	2	2	2
		27	28	37

Hence, despite the brief history of work in the area it is known already to be exceptionally species rich. For example: ca 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 epigeal relatives (HOWARTH, 1987).

### II.2 - Numbers of individuals

Some of the species in the caves have high populations and thousands of individuals are estimated to occur in small caves for a period after flooding (HUMPHREYS *et al.*, 1989; HUMPHREYS, 1990; HUMPHREYS and SHEAR, 1993). However, these are probably not representative of the great majority of species, most of which are known from few sightings and specimens and thus are more typical of troglobite populations in general.

### II.3 - Affinities

The troglobite fauna inhabits the karst of the Cape Range Formation both in Cape Range, on the North West Cape peninsula, and on Barrow Island, 160 km to the north east (HUMPHREYS, 1991c). It has affinities mostly with rainforest litter fauna of northern and north-eastern Australia (HUMPHREYS, 1991c), as well as affinities with wet temperate forests of south-eastern Australia. The Barrow Island troglobite fauna is less diverse and contains both related species and unique faunal elements.

Some taxa show clear speciation between Barrow Island and Cape Range (*Draculoides*, *Nocticola*), or within Cape Range (paradoxosomatid millipedes), whereas others form distinct genetic provinces within Cape Range (paradoxosomatid millipedes, *Draculoides vinei*, melitid amphipod; HUMPHREYS and ADAMS, 1991). No troglobite species is known to have epigeal congeners in the area.

While the cave fauna of Cape Range has mixed affinities it clearly has a large wet tropical forest element. Many taxa have affinities with the wet tropics of northern and eastern Australia (nocticolid cockroaches), or wet forest (symphytognathid spiders; Tenebrionidae, Diplopoda: Polyzoniida and Spirobolida). *Pseudopeas interioris*

Tate (Mollusca: Subulinidae) is normally found in rainforest litter (A. SOLEM, pers. comm., 1989). The genus *Ideoblothrus* (Chelicerata: Pseudoscorpionida) is found in rainforests while *Tyrannochthonius* spp. (Pseudoscorpionida) have tropical and sub-tropical affinities; a new hyd genus (Pseudoscorpionida) belongs to a family found only in rainforest patches (Kimberley, India, Madagascar and Indonesia; M.S. Harvey; pers. comm.). Schizomida are primarily confined to the tropical and sub-tropical regions of the world. The ctenid (Araneae) is a clear indication of tropical affinity and which has close relatives in North Queensland (Undarra Caves; M. R. GRAY, pers. comm.). *Nocticola flabella* has affinities with species in north-east Queensland (ROTH, 1991). *Lecanomerus* sp. (Coleoptera: Carabidae: Harpalitae), *Mecyclothorax* sp. and *Craspedophorus* sp. (Coleoptera: Carabidae: Panagaeitae) have affinities with wet forest faunae, though not necessarily tropical ones (B.P. MOORE; pers. comm. 1989).

As shown above a section of the troglobitic fauna is clearly derived from a humid tropical forest litter fauna and provides the only evidence of such vegetation in Cape Range since at least the Miocene - the region is now separated by the Great Sandy Desert, about 3500 km from the closest possible source area (Fig. 2). While complex rainforest occurred in the western shoulder of Australia during the Eocene (TRUSWELL, 1990) there has been a progressive retreat eastwards so that extensive complex rainforest is now found only along the eastern seaboard of Australia (Fig. 2).

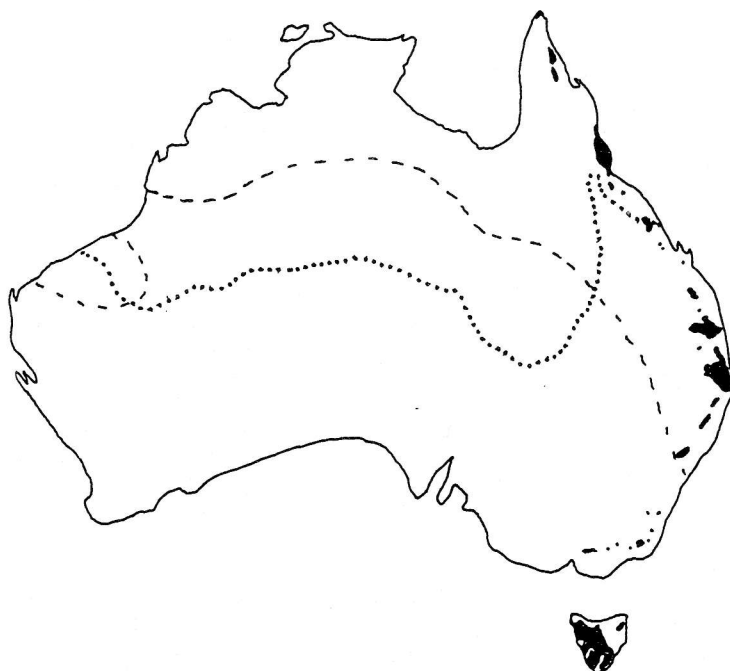


Fig. 2 - The current distribution of extensive coastal rainforest (black) and the southerly limit (dashed lines) of remnant coastal rainforest elements in contemporary Australia (after WEBB & TRACEY, 1981). The former occurs in an arc through eastern Australia with a distribution similar to the Pliocene 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).

### III - ORIGINS OF CAVE FAUNA

There is evidence of fine scale allopatric speciation (either side of gorges) in the paradoxosomatid millipedes in Cape Range (HUMPHREYS and SHEAR, 1993), the only group examined in detail. Allozyme electrophoretic data for two other troglobites (*Draculoides vinei* and the melitid amphipod) are consistent with this finding but the only cave dwelling non-troglobite examined (*Australophiloscia* sp., Isopoda: Philosciidae) is panmictic throughout the range (HUMPHREYS and ADAMS, unpublished). To date there is no evidence of parapatric speciation occurring between the surface and troglobite fauna in Cape Range, although such occurrences are common in Hawaiian troglobites where many species have close extant surface relatives and are thus not relicts (HOWARTH, 1982, 1987).

The effects of 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), are not applicable to lowland tropical areas (HOWARTH, 1987), such as Cape Range. However, the parsimonious explanation for the rich troglobitic fauna of Cape Range, in light of the lack of evidence for parapatric speciation and the northern affinities of much of the 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, with aridity rather than cold being the isolating mechanism.

#### IV - TIME OF SEPARATION

Three species of paradoxosomatid millipedes are known from Cape Range, two are known only from single caves, one isolated and one sympatric with a widespread and common species (HUMPHREYS and SHEAR, 1993). On the basis of allozyme electrophoretic data the latter shows considerable genetic divergence and the populations can be separated into three major genetic provinces (Fig. 3; W. F. HUMPHREYS and M. ADAMS, unpublished). These genetic discontinuities are associated with the deep gorges that cut through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone beneath HUMPHREYS and SHEAR (1993). The genetic differences between these provinces are large (Tabl. 2) and similar to about the mean genetic distance between species of *Drosophila* (Fig. 4). No consistent morphological character has been found to differentiate these populations.

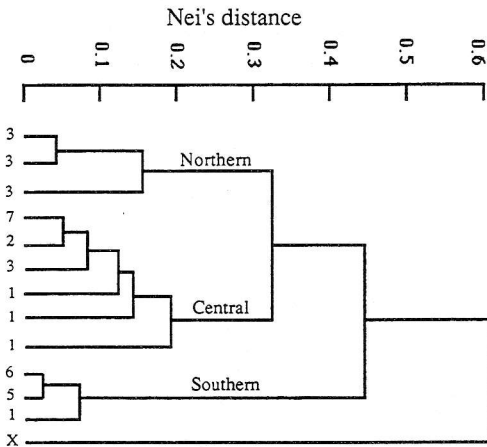


Fig. 3 - Phenogram (UPGMA) of the genetic distances (Nei's  $D$ ) between 36 cave populations of the widespread paradoxosomatid millipede in Cape Range (after HUMPHREYS and SHEAR, 1993). Only the major clusters are shown and the numbers denote the number of cave populations in that branch. X denotes a sympatric congeneric species of millipede in Cave C-111.

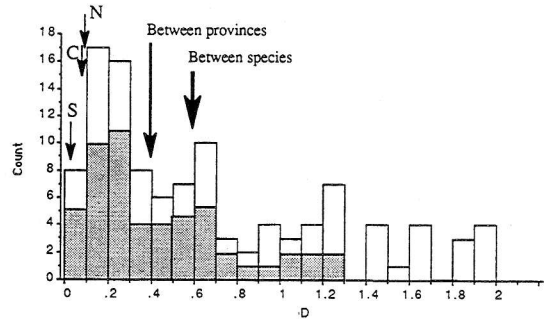


Fig. 4 - Nei's genetic distance ( $D$ ) between pairs of *Drosophila* species in sympatry (shaded) and allopatry (unshaded; data from COYNE and ORR, 1989). The arrows denote the mean  $D$  between cave populations of the widespread paradoxosomatid millipede within the northern (N), central (C) and southern (S) genetic province, between the genetic provinces and between species as defined by HUMPHREYS and SHEAR (1993).

On the basis of the index of genetic divergence  $D = 1$  corresponding to five million years (5 Ma) of divergence (NEI, 1987) then the sympatric species has been separated from the widespread species for 3 Ma, populations of the widespread species have been isolated into the three genetic provinces for *c.* 2 Ma, cave populations of the widespread species within the two northern provinces for *c.* 1 Ma and cave populations within the more homogeneous southern province *c.* 0.1 Ma.

Tabl. 2 - The mean Nei's distance between populations of the widespread paradoxosomatid millipede from 36 caves within and between genetic provinces. N is the number of comparisons made between cave populations (number of caves). The statistics refer to the comparison of means for both the within and between genetic province comparisons. Common letters following the mean denote no significant differences between the means (ANOVA with GT2 multiple comparison test). #As each point represents a comparison between two of  $n$  populations and there are  $n(n-1)/2$  points. As these are not statistically independent the degrees of freedom in the above analyses are based on  $n$  caves rather than  $n(n-1)/2$  comparisons.

	Mean	SD	CV	N# (caves)	df	Fs	P
Within genetic province							
South	0.021	0.028	131.0	60 (12)			
Central	0.090a	0.065	73.1	105 (15)			
North	0.100a	0.067	66.8	36 (9)			
All	0.070	0.065	94.1	207 (36)	2,33	6.767	0.003
Between genetic provinces							
South / Central	0.389	0.041	16.5	180 (27)			
South / North	0.518	0.073	14.1	108 (21)			
Central / North	0.320	0.085	26.5	135 (24)			
All	0.400	0.105	26.2	423 (36)	2,69	40.608	<0.001

The absolute age may be suspect but it gives a relative duration respectively of 30: 20: 10: 1 units of time. Thus, while the vicariance event for the first three categories occurred within the same order of time, those

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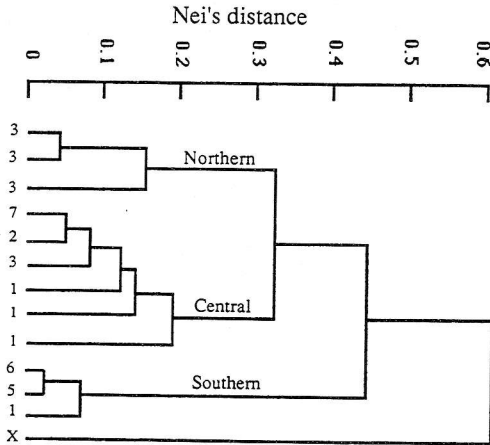


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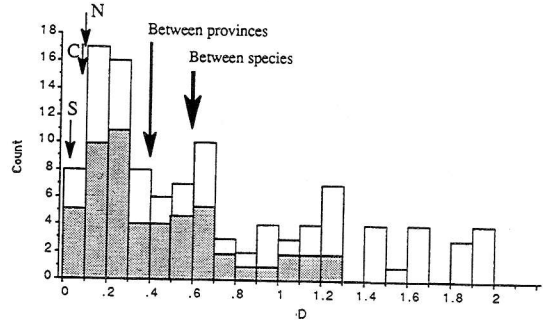


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in the southern region are an order of magnitude more recent and can probably be associated with Pleistocene drying conditions rather than the geomorphological features (gorges etc.) associated with the first three categories. These estimates of divergence time are interesting because recent evidence suggests that, rather than the Cape Range anticline being partly submerged in the Pleistocene (Van de GRAAFF *et al.*, 1976), that there has been no marine transgression greater than a few metres at least since the Pliocene (G. W. KENDRICK, pers. comm., 1992).

The occurrence of at least seven species of troglobites in 100 year old Hawaiian lava tubes suggests that species can readily move through the mesovoids in the lava (HOWARTH, 1987). However, the genetic evidence from Cape Range suggests that there is great restriction of gene flow even within genetic provinces and no effective gene flow between genetic provinces. Hence, in Cape Range the rather small gorges which cut through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone, combined with the surface aridity, essentially prevent gene flow. Given that the milipedes will come to the surface even today, the vicariance event was probably not the cutting of the gorges, but the loss of rainforest from those gorges where they would have persisted longest. The temporal equivalent of a genetic distance of  $D = 0.4$  is when rainforest was lost from the area.

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### ABSTRACT

The anticlinal Cape Range Formation of Tertiary limestones is exposed in the Cape Range and at Barrow Island in the semi-arid tropics of Western Australia. The highly cavernous Cape Range contains a diverse terrestrial troglobite fauna which in part represents a relict wet tropical forest litter fauna, isolated by aridity. There is a related fauna on Barrow island, 160 km away, a fauna containing also novel elements.

The ecosystem is dependent on the influx of water and organic matter often at long and highly unpredictable intervals, perhaps once every five years. After each influx the water and organic matter declines in a cave and the fauna retreats to the mesocaverns, to reappear in the caves following natural or experimental influxes. The system is highly unstable unlike classical karst systems.

The limited work on the karst province has yielded a diverse fauna of at least 38 species of highly adapted troglobites which belong to 28 genera in 27 families in the Diplopoda, Pseudoscorpionida, Schizomida, Araneae, Isopoda, Amphipoda, Blattaria, Hemiptera and Orthoptera. There are many more second level troglaphiles than troglobites and a large number of species of uncertain ecological status.

Deep gorges reaching a lower non-cavernous limestone are associated with major discontinuities between genetic provinces; this is found in both the terrestrial and aquatic troglobites but not in the epigeal species. Recent parapatric speciation seems not to have occurred and the fauna can be considered as relictual with aridity having eliminated the surface ancestors.

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