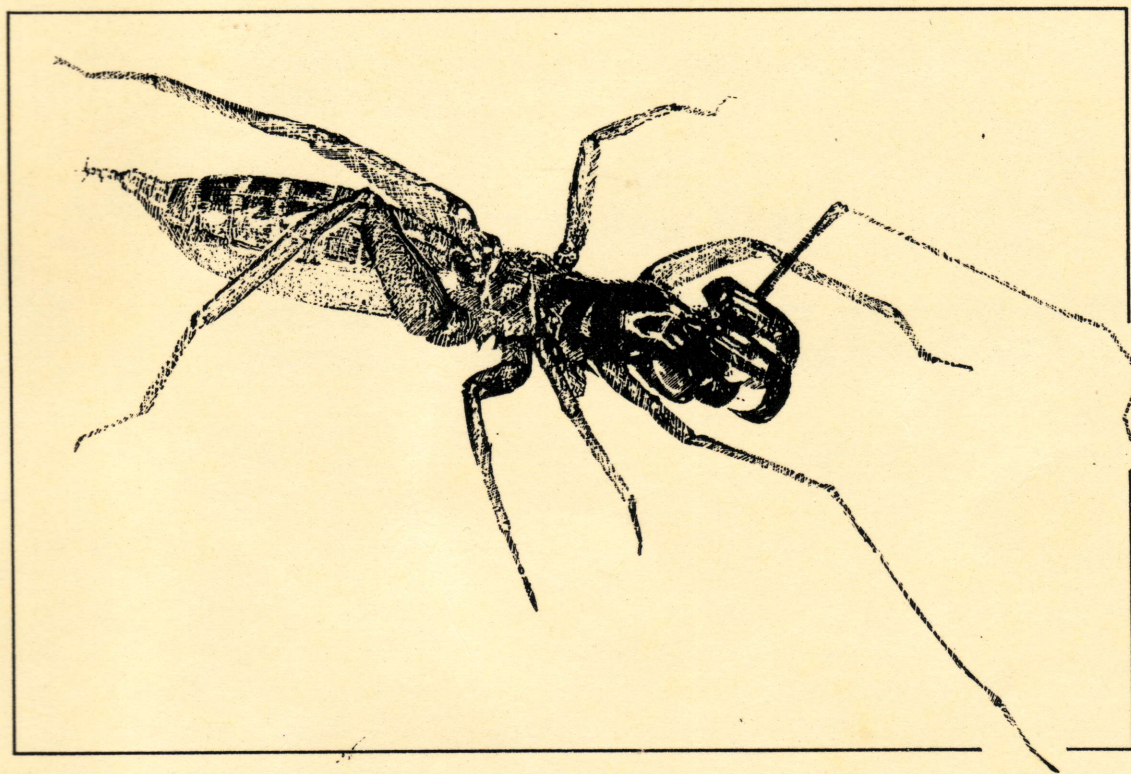


**Status of relict cave fauna of
Cape Range, Western Australia,
especially the Schizomida (Arachnida).**



**Status of relict cave fauna of Cape Range,
Western Australia, especially the Schizomida
(Arachnida).**

A report to the Australian National Parks and Wildlife Service.

May 1989

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C 203 has been renumbered C 207 [Two Hundred Cave]

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Cover picture:- the Cape Range schizomid, *Schizomus vinei* Harvey 1988

The Report

This report is presented in the form of an extended paper covering the terms of the contract with ANPWS. For completeness it incorporates also work previously and subsequently conducted on the cave faunae and their environments. The findings of the study are presented in the main body of the report while sub-reports and some extensive data are contained in appendices.

The nine subjects covered in the contract are presented below:-

1. Examine caves known to have schizomids and assess their status.
2. Design and carry out a survey to locate and examine caves for schizomids and other cave fauna.
3. Liaise with specialists in Australia and overseas who may be able to determine or describe the non-schizomid fauna of the caves.
4. Design a scheme to optimise the information obtained from regular observations of the caves with schizomids and encourage amateur cavers in the area to implement it.
5. Establish a laboratory colony of schizomids to examine their biology and assess their reproductive potential
6. Within the constraints of prudent collecting, to be determined from population assessment, examine the allozyme variation between caves to determine whether the populations are connected.
7. Compile and document published and *de novo* information on the fauna of Cape Range caves, including liaison with specialists in relevant fields.
8. Conduct those laboratory investigations on the physiology of schizomids necessary to assess their vulnerability.
9. Provide recommendations on the conservation and management of cavernicolous fauna in the area in liaison with caving societies.

Summary

1. This report details the findings of a study on the troglobitic fauna (especially *Schizomus vinei*, Schizomida, Chelicerata) in Cape Range, North West Cape, Western Australia.
2. There are three distinct troglobitic faunae on the North West Cape; one in the coastal limestone (2 fishes and 2 shrimps), one associated with water in Cape Range (amphipods), and the terrestrial fauna in Cape Range caves.
3. Cape Range contains a rich terrestrial troglobitic fauna. The taxonomic affinities of most of the species have yet to be established. The area has a tropical semi-arid climate but the species that have been examined closely mostly have affinities with inhabitants of tropical wet forest litter.
4. The terrestrial troglobitic fauna occurs in about 14 of about 212 caves known from North West Cape, mostly in Cape Range.
5. The troglobitic fauna is known from caves forming a narrow band along the eastern edge of Cape Range.
6. The terrestrial troglobites in Cape Range include *S. vinei*, two spider species, several isopod species (woodlice), a millipede, a pseudoscorpion, crickets, and a cockroach. Most species await formal taxonomic description.
7. A large number of other invertebrate species are found whose association with the caves is largely unknown but many are clearly relict populations from a wetter climate. They include many molluscs, woodlice (>5 species), earthworms, centipedes, a pseudoscorpion, spiders and many insects.
8. The troglibites are found only in caves with high relative humidities (> 90%), but the wide range of temperatures (11°K) between the various caves is not related to the distribution of the troglobites.
9. Soil water and organic carbon contents of the mud-banks in the caves together account for half of the variance in the distribution of *S. vinei* and a significant amount of the variance in the distribution of the troglobitic millipede.
10. The populations of schizomids, millipedes and amphipods are not panmictic throughout their range, but are separated genetically by the deeper canyons bisecting the limestone in which the caves occur. The only non-troglobitic species examined (an isopod) was panmictic throughout its known range.
11. The troglobites have a high rate of water loss and are unlikely to be able to move between caves across the surface.

12. The genetical data indicate that, while not all cave areas are interconnected, there are several areas where the caves apparently are connected.

13. The cave environments are quite variable and they are differentially subjected to the influx of surface water according to the characteristics of their catchment areas. Such influx supplies the organic matter which fuels the cave ecosystem. Some caves flood after only small rainfall while others require major rainfall and are probably only flooded once every few years but with very low predictability.

14. The populations of troglobites expand into recently wetted areas of caves and start to breed. Caves not flooded for several years have populations containing mostly adults.

15. Population estimates, using mark and recapture methods, suggest that the populations of some cave inhabitants, including some troglobites, are large.

16. The likely origin of the troglobites is discussed in relation to palaeoclimatic information; the troglobites provide the only evidence that rainforest has occurred in the area since the Miocene.

17. The problems associated with the management of this specialised fauna are discussed at length and a number of recommendations are made to promote their survival.

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KARST LANDFORMS
 Surface Features
 GEOMORPHIC HISTORY
 Speleogenesis
 Climatic History
 CONCLUSIONS

Appendix 8: Distances between the various caves from which samples were taken for genetical analysis.

Appendix 9: Taxa collected from Cape Range and their locality.

Appendix 10: Descriptions of the caves containing troglobites.

It is a general management objective for Cape Range National Park to 'protect and conserve indigenous and scenic resources'. There are specific management objectives to 'maintain scientific reference areas' and to 'conserve and protect ground water resources' (CALM 1987).

The entire area known to contain terrestrial troglobites on North West Cape is in a Temporary reserve for Limestone (TR5980H) under the control of the Minister for Mines.

INTRODUCTION

Until recently troglobites (obligate cave dwellers) were thought to be rare in tropical caves due to the small influence of Pleistocene climatic changes which were considered necessary to eliminate the surface populations of putative troglobites (Vandel 1965; Barr 1968, 1973b; Mitchell 1970; Sbordoni 1982). Australian caves specifically have been considered to be deficient in troglobites compared with other continents. This has been explained by the aridity of the continent and the lack of pre-adapted moist litter species (Moore 1964; Hamilton-Smith 1967; Barr 1973). No troglobites are known from Victoria (Department of Conservation, Forests and Lands 1986), and the vast Nullarbor karst region, which borders the Great Australian Bight, has only about 12 troglobitic species (seven in Nurina Cave), despite having been relatively well explored.

Both of the above presumptions have proved incorrect. Rich troglobitic faunae have been found in many tropical areas (Leleup 1968; Howarth 1983), including both wet tropical (Chillagoe in Queensland, Howarth 1988) and semi-arid tropical (Cape Range) areas in Australia.

This report is about the fauna of the semi-arid but tropical Cape Range caves in Western Australia, an area where biospeleological research has started only recently (Vine *et al.* 1988; Harvey 1988; Humphreys *et al.* 1989). Due to the impossibility of determining the degree of cave dependance of the non-troglobitic fauna (see below), the study concentrates on those species clearly troglobitic, and the more abundant species which provide them with food. As no measure of the completeness of the survey has been attempted, the study cannot claim to be comprehensive survey of the cave fauna.

Definitions

Caves and karst systems generally may be valued for a number of disparate reasons. For example they may be valued in terms of aesthetics, landforms, biology, palaeoenvironment, archaeology, mineralogy and recreation. (Department of Conservation, Forests and Lands 1986). Caves may contain fauna and flora, extant or extinct, fossil or sub-fossil. This report covers only the living fauna of the caves of Cape Range and concentrates on the more abundant troglobites, especially the schizomid.

The fauna found in caves is traditionally divided amongst:- accidentals (species entering caves by chance); troglloxenes (sporadic cave dwelling species e.g. bats); troglrophiles (facultative cave dwelling species, often divided into first level troglrophiles, found both in cave and epigean habitats, and second level troglrophiles which are found only in caves) and troglobites (obligate cave dwellings species usually with significant eye and pigment reduction and which are of considerable evolutionary interest; Hamilton-Smith 1967; Culver 1982). Various other terms and categories are used by different workers (e.g. Vandel 1965).

The categories are based on the level of dependence on the cave system (Hamilton-Smith 1971) deduced from their distribution within and without caves and the degree of morphological adaptation presumed to be adaptive to cave life. Second level troglrophiles may turn out to have clear adaptations to caves in non-morphological characters, e.g. physiological (Barr 1963).

As these are, in essence, functional definitions the classification requires assumptions about the nature of the adaptation or detailed knowledge of the species biology for allocation between these categories to be made. As this knowledge is unavailable for the vast majority of Australian cave faunae, especially the newly worked Cape Range area, in this report species are termed troglobites only if the systematist involved considers them to have cave adaptation (e.g. reduced eyes) or they are eyeless or lack pigment (in taxa normally possessing these characters). Other species are simply recorded as having been found in caves and, through lack of information on their biology and of the epigean community, are not categorised.

METHODS

Field: cave C162 (Rock Bench) was surveyed to Grade 5-3 using standard speleological methods (Ellis 1976). Temperature and relative humidity were measured using a whirling hygrometer (Brannan, England). Continuous records of temperature and humidity were made using thermohydrographs (Okawa Seiki Company Ltd., Tokyo) located at two positions in each of C118 and C162; namely at the location with troglobites closest to the cave entrance (the front) and that furthest from the cave entrance (the back) irrespective of the occurrence of troglobites. Replicate soil samples were collected from various areas within caves and associated with the faunal type and numbers. The water content of the soil was determined gravimetrically after drying at 70°C. The content of organic carbon was determined by the Walkley-Black dichromate oxidation method with glucose as a standard; the presence of CaCO₃ up to 50% of the sample volume gives no interference (Allison 1965).

The carbon dioxide levels in the atmosphere of some caves were noted from the physiological reaction of cavers (people are affected physiologically at about 3% CO₂; Williamson 1975), and sometimes by air quality monitoring equipment

(0.1-6.0% CO₂; Dräger detector tubes:- Drägerwerk ag Lübeck, Federal Republic of Germany).

Numbers of *Schizomus vinei*, millipedes and isopods were estimated by mark and recapture methods. Individuals were trapped beneath an inverted vial and the position marked with tape colour coded for species. Individuals were measured in constraining apparatus and marked with fluorescent powders (Daylight Pigments; Abel Lemon Company, Adelaide: either Horizon Blue A60, Lunar Yellow E27, Cerse T13 or Blaze GT 5/20). Different colours were used for various sectors of the mudbanks to examine movement. After the first day of sampling all individuals caught were examined for powder marks under an ultraviolet lamp (Model MS-47: Ultra-violet Products Inc. San Gabriel, California). The total length and width of individuals were measured using a x10 Lupe (Peak) fitted with a 10 mm linear graticule. Schizomids and isopods were restrained between two pieces of flexible clear plastic fitted to supporting rings, while millipedes were coerced into a narrow glass tube to keep them straight while being measured.

Laboratory: Population analysis; the background to the analysis was explained at length in Humphreys *et al.* (1989), and a brief outline only is given here. The population size was estimated from the mark and recapture data using the sequential Bayes algorithm (Gazey and Staley 1986) as was used in an earlier study of *S. vinei* (Humphreys *et al.* 1989), and where the rationale is explained in more detail. The algorithm estimates the minimum population size with 95% confidence and the mean and median population size.

Electrophoresis: cellulose acetate gel electrophoresis was conducted using standard methods (Richardson *et al.* 1986). Homogenates were made from whole, liquid nitrogen stored, individuals (from 11 to 44) of four species (*S. vinei*, millipedes, amphipods and isopods) and used to examine the allozyme variation between the populations in different caves. Samples of the four species collected from between three and ten caves were examined. For systematic purposes, the null hypothesis under test was that all populations were sampled from the same gene pool of a single species. The sample sizes per cave (3+) are entirely adequate for systematic studies on allopatric populations (Richardson *et al.* 1986). Previous data from *S. vinei* (Humphreys *et al.* 1989) were included in the analysis. From 4 to 46 enzymes and non-enzymic proteins were examined in the different species (detailed in Appendices 2 to 5) of which from 2 to 32 were scored. For each species the enzymes (and protein) examined and the number of alleles found are detailed in Appendix 6 together with their accepted names and codes; the nomenclature and conventions for referring to alleles and loci follow Richardson *et al.* (1986).

Husbandry: Animals were maintained in the laboratory in either 50 ml vials or small vivaria; in either cases the floor comprised one centimeter or more of soil from the cave of origin. The soil was kept moist with distilled water to maintain

near saturated humidity, while preventing the accumulation of solutes. Schizomids were fed weekly on live oniscoid isopods and the 'miturgids' on flour moths. Cave isopods and millipedes maintained in leaf litter from the original cave and then supplemented with litter of non-cave origin, heat sterilized to prevent contamination by other species of invertebrates and micro-organisms.

Water loss: evaporative water loss (EWL) was measured in a dry air stream of 19.6°C flowing at 50 ml min⁻¹ in a 3.9 mm internal diameter tube (except for the large 'miturgids' in which a tube of 26.7 mm internal diameter was used) and the water content of the downstream air determined by means of an electrolytic water detector (Type 26-303 moisture monitor; Consolodated Electrodynamics Corporation). The current output of the electrolytic cell was monitored with a Thurlby digital multimeter with an RS-232 interface to a Commodore 128 microcomputer. The computer logged the data at 30 sec. intervals, and calculated the EWL (mg min⁻¹), surface area specific EWL (mg cm⁻² sec⁻¹) and resistance (sec cm⁻¹). The surface area (y) was calculated from standard equations where $y = 12 (\text{body weight})^{0.67}$. Resistance to water loss (R) was calculated after Nobel (1974) as $R = dCWV/EWL$, where dCWV is the water vapour concentration deficit (mg cm⁻³) and EWL is the surface-area-specific evaporative water loss (mg cm⁻² sec⁻¹). Individuals were equilibrated in the apparatus prior to the measurement of water loss to remove adsorbed water.

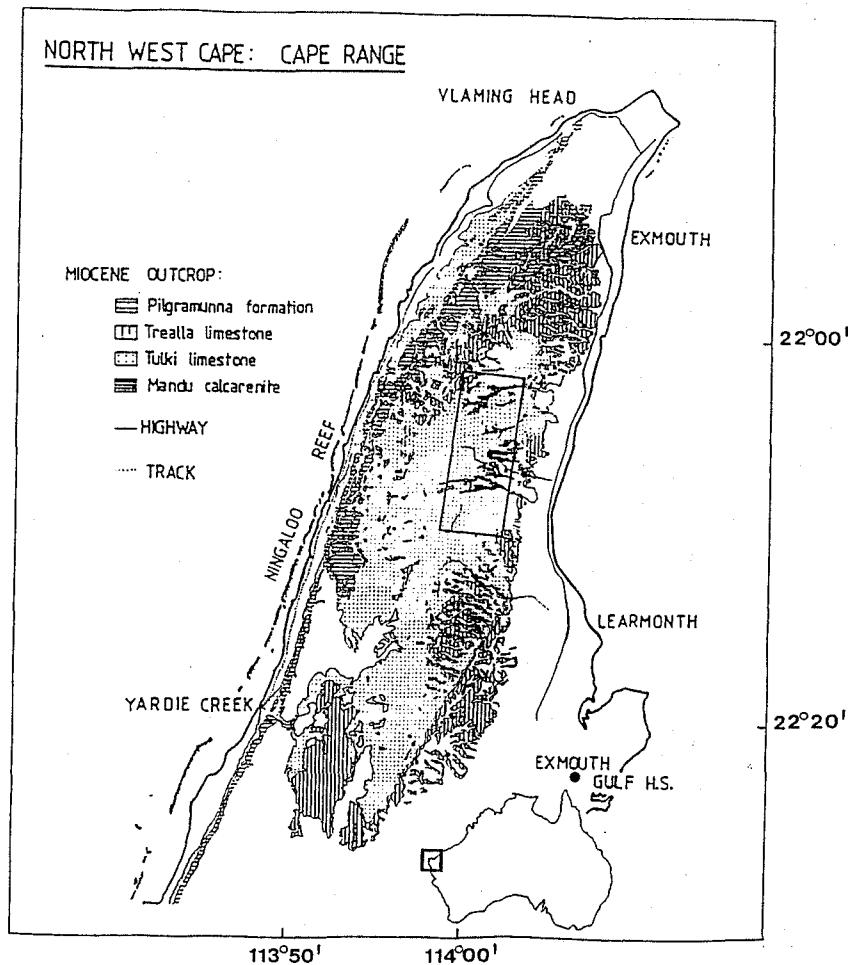
Statistics: least squares regression, one-way ANOVA with GT2 multiple comparisons at $\alpha = 0.05$, the comparison of the slopes and displacement of regression lines (ANCOVA) and correlation follow the algorithms of Sokal and Rohlf (1981). Standard analyses of the genetical data follow Richardson *et al.* (1986).

RESULTS

Regional location and geomorphology.

Cape Range forms the spine of North West Cape of Western Australia (Figure 1) and lies just within the tropics (22°S) in a semi-arid climate. The range is an anticline formed in marine limestones, the details of which are presented elsewhere (Vine *et al.* 1988, Humphreys *et al.* 1989) and amplified in Appendix 7.

Figure 1: Regional location of Cape Range on North West Cape, Western Australia and the main geomorphological features. The square outlined on the map of Cape Range includes the area of canyons seen in Figure 4.

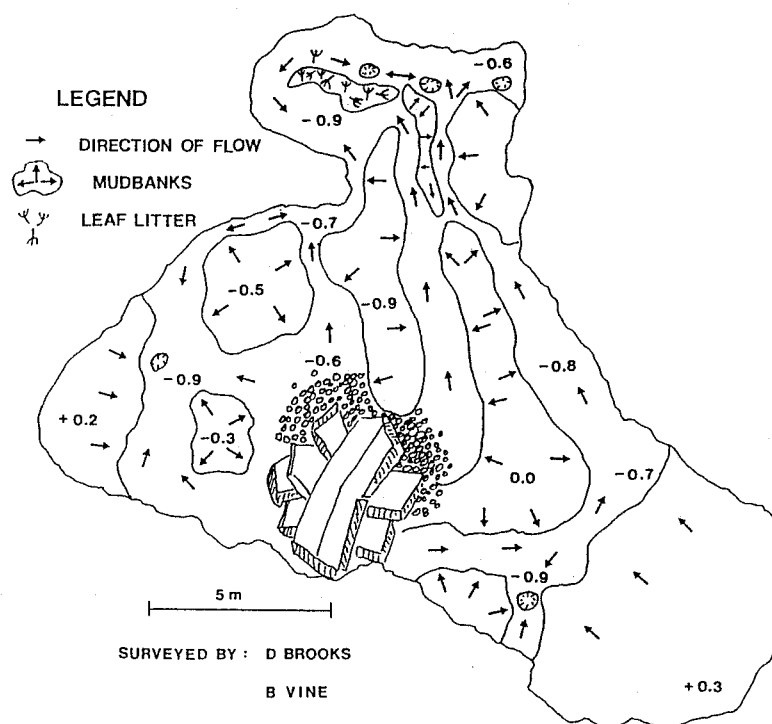


Cave morphology

The population census was conducted in caves C118 and C162. Cave C162 (Fig. 2) is broadly open to the outside and contains several large mud banks separated by gullies which lead to a number of drainage holes. The mud banks and channels occupy respectively 50% and 41% of the 195 m² cave.

In contrast the larger cave C118 opens to the surface through a narrow tunnel only about 1.5 m² in cross section (a description and plan of C118 is given in Humphreys *et al.* 1989). Brief descriptions of the other caves mentioned in the text are given in Appendix 10 and their locations in Appendix 1 and in Vine *et al.* 1988).

Figure 2: Plan of C 162 (Rock Bench) showing the location of the mudbanks and other features



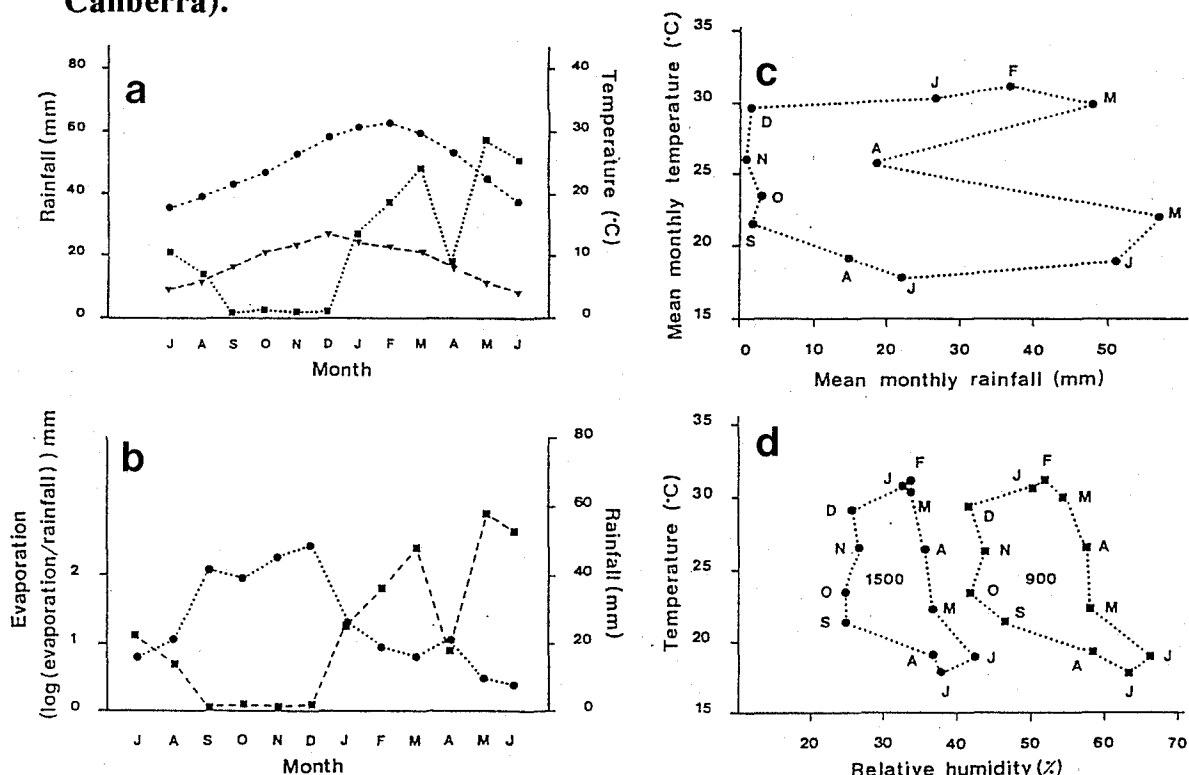
Cook (1962) believed that caves extending to sea level (300 m deep) could occur on Cape Range, with solution pipes in the hard Tulki Limestone connecting below to caverns in the friable Mandu Calcarene, none has yet been found. The change with depth in many caves from vertical solution pipes to horizontal development has been interpreted as reflecting this transition (Kendrick and Porter 1973), as were those caves with considerable lateral extension, especially C163 (Wanderer's Delight), the only cave with considerable lateral extent (*ca* 4 km to date). However, a fossil found there is *Echinolampas westralensis* (Echinoidea: Echinolampadidae) which occurs only in Tulki Limestone. It is a good marker species as different species occur in the Mandu Calcarene below and the Trealla Limestone above (K. MacNamara; pers. comm. 1989). Hence it seems that all known deep caves are in the Tulki Limestone and do not extend into the Mandu Calcarene beneath.

Climate

Cape Range is classified as semi-arid but it is situated in that area of Australia with the least predictable rainfall; both the constancy and contingency (*sensu* Colwell 1974) of the rainfall is low and the probability is low of single rainfalls sufficient to flood deeply caves (see full discussion in Humphreys *et al.* 1989). A

synopsis of the climate is presented in Figure 3 and shows clearly, despite the still harsh climate, the ameliorating effect of the coastal proximity on temperature and relative humidity.

Figure 3: Climatographic synthesis of the Cape Range area. a: Mean monthly temperature (°C) and rainfall (mm). b: Log ratio of mean monthly evapotranspiration over mean rainfall (mm). c: Hythergraph of mean monthly rainfall (mm) and temperature (°C). d: Hythergraph of mean monthly temperature (°C) and 0900 h and 1500 h relative humidity (%). The data are composite and were extracted from the available data for Exmouth, Learmonth and Exmouth (Navy) (Microfiche Climatic Averages, Australia and TABS Elements May 1986, Bureau of Meteorology, Canberra).



Fauna from the caves of Cape Range

A list of the fauna collected from the cave in Cape Range is presented in Appendix 9. To date few of the species have been formally described and taxonomists from around the world are working on the material. They are mentioned in the acknowledgements. There are a number, as yet unknown, of troglobitic species, characteristically blind, non-pigmented and long-limbed. These include the millipedes, *S. vinei*, possibly three species of isopods (H. Dalens, pers. comm. 1988), the amphipods, 'miturgid' spider, pseudoscorpion, cockroach, crickets, possibly two carab beetle species (J. Moore, pers. comm.) and a linyphiid spider. In addition a large range of species from many orders have been found with as yet no established affinities or established status as cavernicoles (Appendix 9).

Known range of the troglobitic fauna

Most of the amateur cavers in the area had concentrated their efforts in a small area of Cape Range, that within a days walk from the few access tracks. Despite this concentration of effort, on a number of occasions, even in well worked area, up to five new caves have been found on returning from well known caves. Clearly a considerable number of caves remain to be found even in these well worked areas.

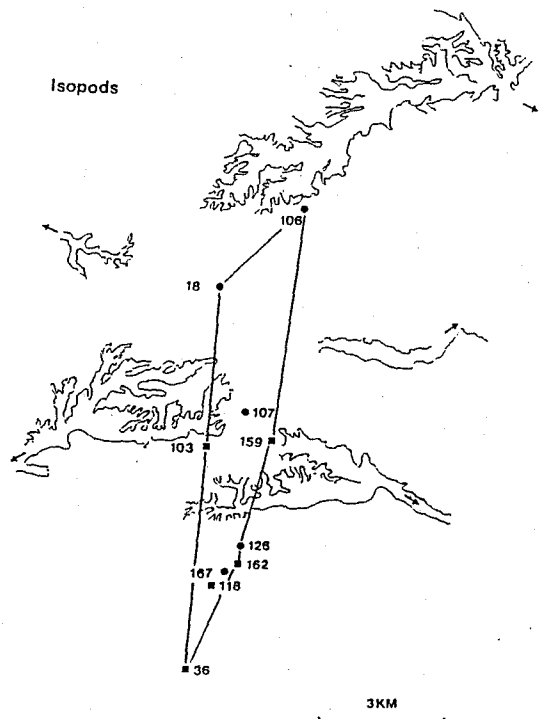
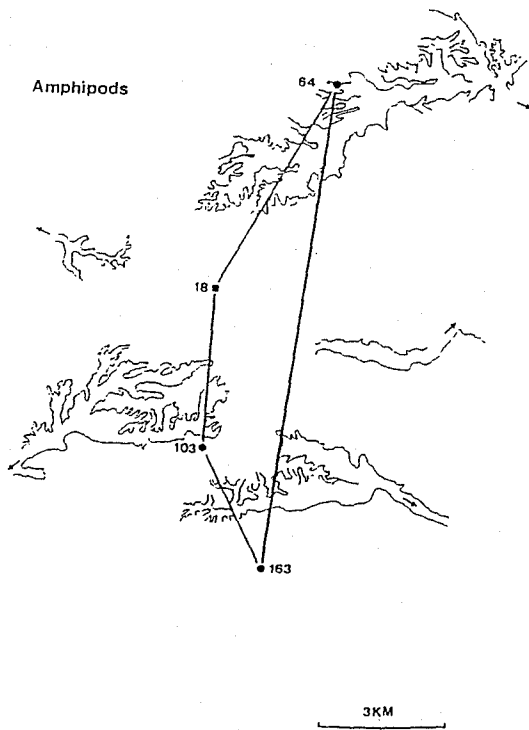
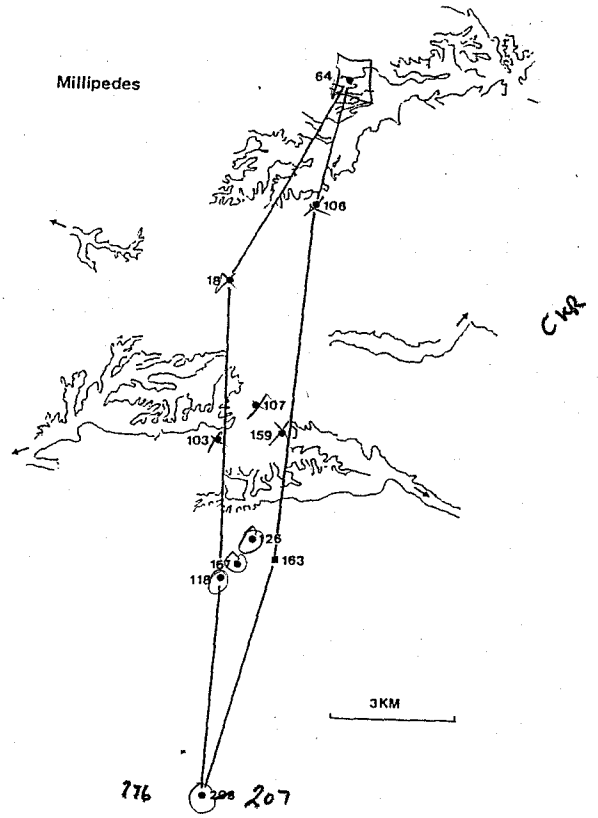
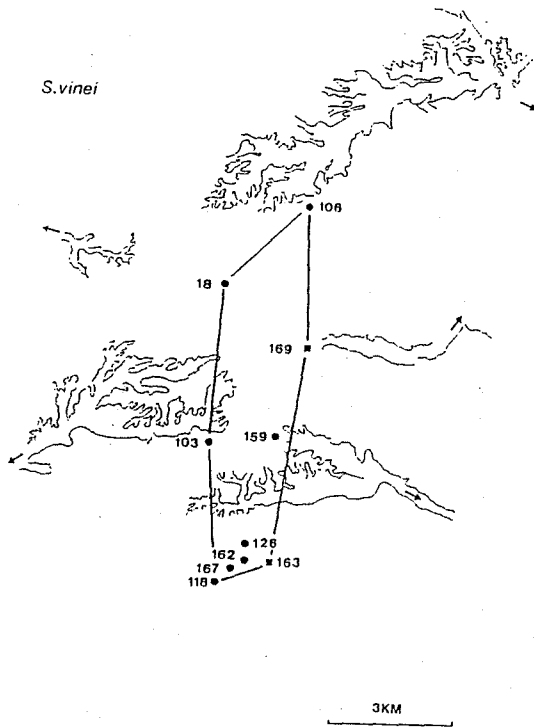
In March 1987 *Schizomus vinei* (then unnamed) was known from Cape Range only as sparse populations in two caves, C18 and C106 separated by 2.8 km (Vine *et al.* 1988). To assess the conservation status considerable effort was made to find new caves to extend the known range of the schizomid. By late 1987 the species was known from eight caves up to 9.4 km apart covering an area of 12.8 km² (convex polygon method) and with some dense populations (Humphreys *et al.* 1989). By the end of 1988 the schizomid had been described (Harvey 1988) and is now known to occur in 11 caves up to 9.9 km apart and covering 14.1 km² of Cape Range (Figure 4). To date no *S. vinei* have been found outside this core area, but in one cave remote from this core (C198) millipedes and cave crickets were seen but not collected. As 73% (11 of 15) caves with millipedes also contain *S. vinei*, and because the millipedes are far more visible than *S. vinei*, the schizomids may occur throughout the range of the millipedes.

The millipede, not previously studied, has been found in 15 caves up to 18.0 km apart (20.3 km including C198, where they were seen but not collected), covering an area of 24.8 km² (70.8 km² including C198)(Figure 4).

Walking traverses and aerial reconnaissance located several new karst areas to the west and south of the known range of *S. vinei*. Due to the rugged nature of the country and the remoteness of the areas these caves have yet to be explored.

These caves are up to 31 km south and 10 km west of the core area and potentially offer range extensions of up to 310 km². A five fold range extension to the Cape Range troglobitic fauna would add significant safeguards for their conservation in addition to the major range extensions already verified.

Figure 4: Next page. Distribution of caves containing troglobites in Cape Range (cf. Figure 1). The canyons are shown which cut through the Tulki limestone, in which the caves are formed, and into the Mandu Calcarenite below. Upper left:- *S. vinei* which is not panmictic and is divided between southern and northern populations separated by the southern canyon (however, see genetics results). Upper right:- millipedes which are not panmictic and divides into a homogeneous southern population and a heterogenous northern population with a genetical outlier population in C64 (cf. amphipods). Lower left:- Amphipods. Lower right: Isopods which are panmictic throughout the distribution shown. Symbols denote the presence of populations in a cave with circles indicating caves from which samples were taken for genetical analysis.



A schizomid with eyespots was taken recently from a litter sample collected from vine thickets on Boongarree I. (15° 05' S, 125° 13' E), in the north Kimberley District of Western Australia (B.Y. Main; pers. comm. 1988). This is the first non-troglobitic schizomid known from Western Australia; about 12 species await description from the Northern Territory and Queensland (M. Harvey; pers. comm. 1988).

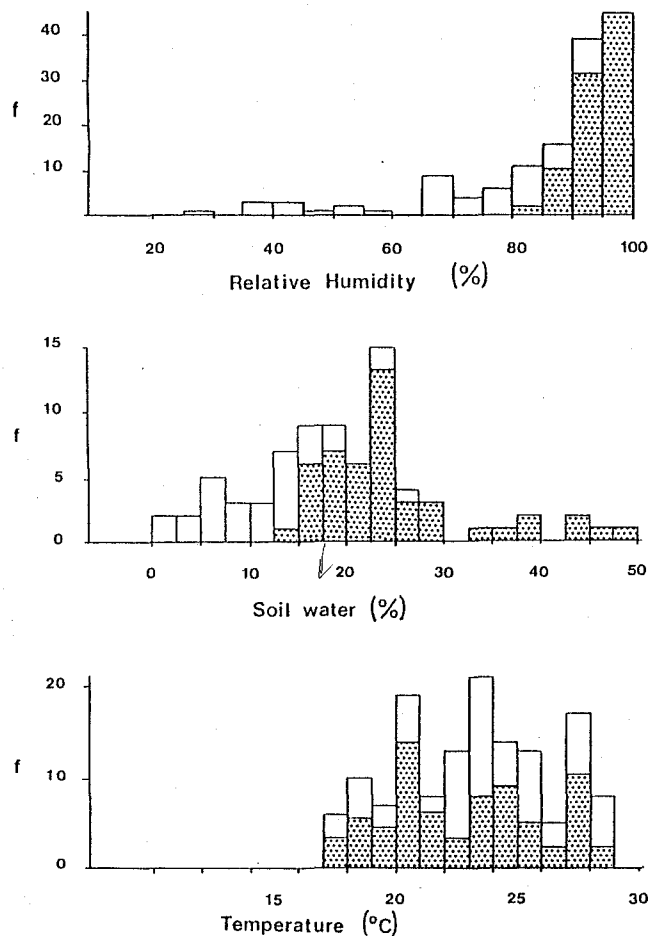
Cave environment

The typical troglobitic fauna (*S. vinei* and millipedes) occurs in only a few of the 211 caves currently known from Cape Range. The caves containing troglobitic fauna have higher relative humidities ($G_{adj} = 79.47$ with 1 d.f; $P < 0.001$) than those without the fauna, have more water in the mud ($G_{adj} = 18.15$ with 1 d.f; $P < 0.001$), but do not differ in temperature (Figure 5: $G_{adj} = 1.22$ with 1 d.f; $P = 0.269$). The troglobitic fauna occurs over the entire and very wide temperature range (11°K) found in the caves of Cape Range. However, they are restricted to areas of soil water >12% (Figure 5) and relative humidity >80% (Figure 5). Above 80% R.H. there is a strong positive correlation between R.H. and the proportion of caves containing troglobitic fauna ($r=0.981$; $P<0.05$), such that between 95-100% R.H. all caves contain troglobites (Figure 5).

Caves temperatures are generally close to the mean annual surface temperature (MAST), which at Learmonth is 27.3°C. However, the temperature in winter of different caves is between 17 and 28°C (Figure 5). Only three of the caves recorded have temperatures within 2°K of MAST (C159, C167 and C169) and the remainder group into warm caves (C103, C96, C64, C118, C157 and C207) ranging between 23.0°C (C103) and 24.7°C (C207) and cool caves (C107, C18, C106, C126, C163 and C162) with temperatures between 18.1°C (C107) and 21.5°C (C162).

While general models predict that, progressively deeper in the cave, temperatures should be less variable and approach MAST (Wigley and Brown 1971, 1976). However, this is not always the case because the upper parts of large chambers may act as heat traps or they may be close to the surface and thus be more immediately subject to external temperature cycles (e.g. C118).

Figure 5: Distribution of relative humidity (upper), soil water content (middle) and dry bulb temperature (lower) in the caves of Cape Range. Shaded area denote the occurrence of troglobites. For relative humidity and temperature ($^{\circ}\text{C}$) $n = 141$. For soil water (% dry weight) the values are the mean of from two to five samples (299 samples); mean sample number = 3.93, s.d. = 0.98; $N=76$.



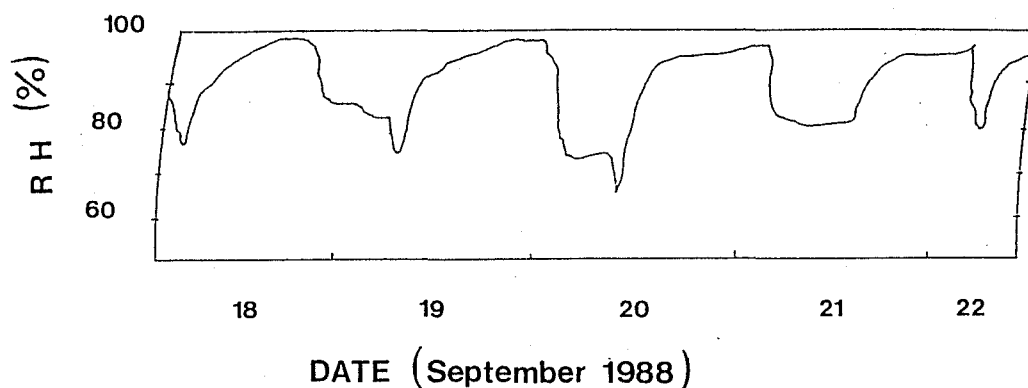
In Cape Range there is no clear reason why cave temperatures differ; caves with similar characteristics vary widely in temperature:- deep, open caves with long leads (C18, C207, C106 and C163) vary from 18.4 $^{\circ}\text{C}$ (C18) to 24.7 $^{\circ}\text{C}$ (C207); while deep caves with tight entrances cover the range 20.3 $^{\circ}\text{C}$ (C126) to 25.7 $^{\circ}\text{C}$ (C159). The two caves with considerable lateral extension range from 20.7 $^{\circ}\text{C}$ (C163) to 23.3 $^{\circ}\text{C}$ (C64). Conversely the shallow caves often have temperatures clearly related to the relative size of the opening; wide open caves vary in temperature with outside air temperature (C162 - 21.5 $^{\circ}\text{C}$), while those with tight

entrances are closer to MAST (C118 - 24.5°C). Geographical location also seems unimportant as caves C167 and C163 are only 0.9 km apart but differ in temperature by 6.9 °K.

Examining the two caves (C118 and C162) in which the population work was conducted shows that the range of temperatures and humidities in C162, as expected from its low volume to entrance size ratio (VESR), was much greater in C162 (see plan in Fig. 2) than in C118 (Table 7) which has a high VESR. The greater range at the back of C118 is due to this location being a blind collapse close to the surface (survey point 15 Fig. 1 of Humphreys *et al.* 1989); it is an area of dry soil devoid of fauna.

The range of relative humidity is much greater than previously appreciated (Humphreys *et al.* 1989) in the more open caves due to the minima occurring in the early morning (Fig. 6). The humidities are sufficiently low at night to restrict the movement of the cave fauna and one would expect, therefore, to find diurnal changes in the activity patterns of the fauna. It also means that the animals would most likely be driven deeper into the cave at night, rather than potentially moving to the humid surface; this would further restrict the possibility of above ground dispersion (see discussion in Humphreys *et al.* 1989).

Figure 6: Tracing from hydrograph record from the front thermohydrograph in C162 for the period 16-20 September 1988. This was the period of most extreme and diurnally synchronised changes in relative humidity. The maximum diurnal change in temperature at this location was *ca* 3°K.



Water vapour movement into and from caves.

While temperature *per se* is unimportant to the distribution of the troglobites in Cape Range (Figure 5), temperature indirectly can have a major influence on the water vapour pressure in the caves and hence the rate of drying of caves.

The net movement of water between caves and the outside is determined by the gradient in partial pressure of water vapour (Edney 1977). Cape Range is just within the world climatic area in which the average daily range in temperature exceeds the average monthly range (Petterssen 1958). Hence in Cape Range, as in many tropical areas (Howarth 1980), the night time temperatures often fall below the cave temperatures; this results in a net movement of water vapour out of the cave at night (tropical caves containing troglobites usually have R.H. close to 100%). This has been termed the 'tropical winter effect' (Howarth 1980, 1983) by analogy with the excessive drying of caves in colder climates in winter. Hence, all else being equal, warm caves will dry more rapidly and have shorter periods when they are suitable for troglobites. The relevance of this effect will become apparent in the discussion below in relation to the pulses in both the population sizes and the local range of the species in the caves of Cape Range.

Caves in Cape Range have deep temperatures differing by 11°K (17-28°C), mostly being in the range 17-23°C. Hence, because the cave atmospheres are almost saturated with water vapour, there will be about a two fold difference in the water vapour pressure within the faunal caves. Therefore under the same outside conditions some caves will have gradients in water vapour pressure which are the reverse of others. More detailed and long term recording, especially of the climate on the range, would be required to determine these conditions.

Table 1: The range of temperature and relative humidity recorded in the faunal area closest to the entrance and that in the location furthest from the entrance between 10.8.88 to 22.9.88.

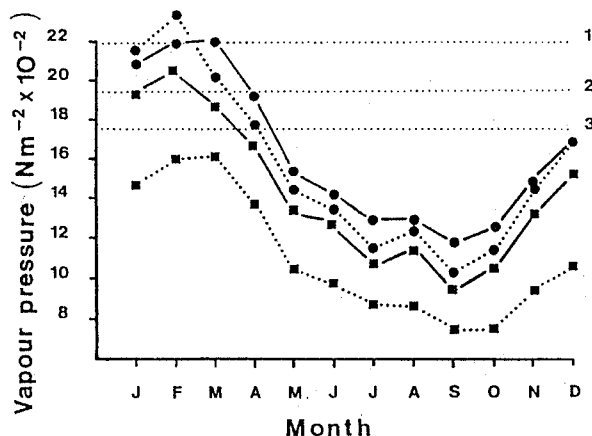
Cave	Sector	Temperature °C	Relative humidity	
			Hygrometer	Hydrograph ¹
C 118	Front	22.5 - 23.5	91 - 97	
C 118	Back	23.5 - 25.7	87 - 100	
C 162	Front	17.8 - 22.8	80 - 100	65 - 100
C 162	Back	17.8 - 22.2	92 - 99	74 - 99

¹The disparity here is due to the minimum RH reading occurring a about 0600 when no whirling hygrometer readings were taken.

The mean minimum temperature is below most cave temperatures from April through September in Cape Range and a net loss of water from the caves would be expected at night during these months. The data for August and September support this conjecture (Table 1 and Fig. 7). No data are available for diurnal changes in cave humidities for Cape Range in summer. However, despite cave temperatures being below outside temperatures throughout the day, the low surface humidities would be expected to prevent an influx of water vapour for much of the summer. The expected vapour pressure gradients, determined from meteorological data from the coastal areas of North West Cape, suggest that only

the cooler caves would gain water during the height of summer (Figure 7). However, these mean monthly values are misleading as there was clearly a diurnal change in the direction of the vapour pressure gradient in the caves in September 1988 (Fig. 7; Table 1).

Figure 7: Annual changes in the partial vapour pressure (mbars) of water on North West Cape and the water vapour pressure of caves at various temperatures and humidities. The surface data are for Learmonth and are calculated for the 0900h (solid line and circles) and 1500h (solid line and squares) meteorological readings of temperature and humidity, as well as for the mean monthly maximum (dotted line and circles) and minimum (dotted line and squares) temperatures (Vine *et al.* 1988). The horizontal lines show the partial vapour pressure of caves at the given temperatures and humidities; if the curves lie below a particular horizontal line then, under those conditions of temperature and humidity, water vapour will leave that cave and vice versa. Cave conditions:- 1) 19°C and 100% R.H.; 2) 17°C and 100% R.H.; 3) 17°C and 90% R.H.



Carbon dioxide

Many caves in Cape Range contain high levels of CO₂ as indicated by human physiological response (e.g. C66, Tetra-Dome and C69, Linda's Delight). This is particularly the case after rain, even in shallow caves such as C118 (M. East; pers. comm. 1988). Sections of caves containing troglobites have levels of CO₂ ranging from 0.06% (C126) to 0.5% (C167) with a mean of 0.18% CO₂ (s.d.=0.16, n=7) in cave areas containing troglobites. Because cavers could not sustain entry into some areas of high CO₂ levels (>>8% CO₂; off scale of indicator tube in a vertical lead in C207), it is not known whether troglobites inhabited such areas as has been reported for a few caves elsewhere. Troglobites survive high CO₂ levels (5.4%; Vandel 1965) and in Bayliss Cave, at Chillagoe in north Queensland, 75% of the 24 species of troglobites occur only in the foul air zone where CO₂ concentrations ranged from 0.6 to 6.0% (Howarth 1988).

Population biology

Population size

The estimated population densities for millipedes, *S. vinei* and isopods are given in Table 2 for the entire size range of the species and for that subset of the data including only the size range of the species actually marked (isopods were found in numbers only in C162). The pertinent posterior distributions and the cumulative posterior distributions (probabilities) against population size are given in Figure 8.

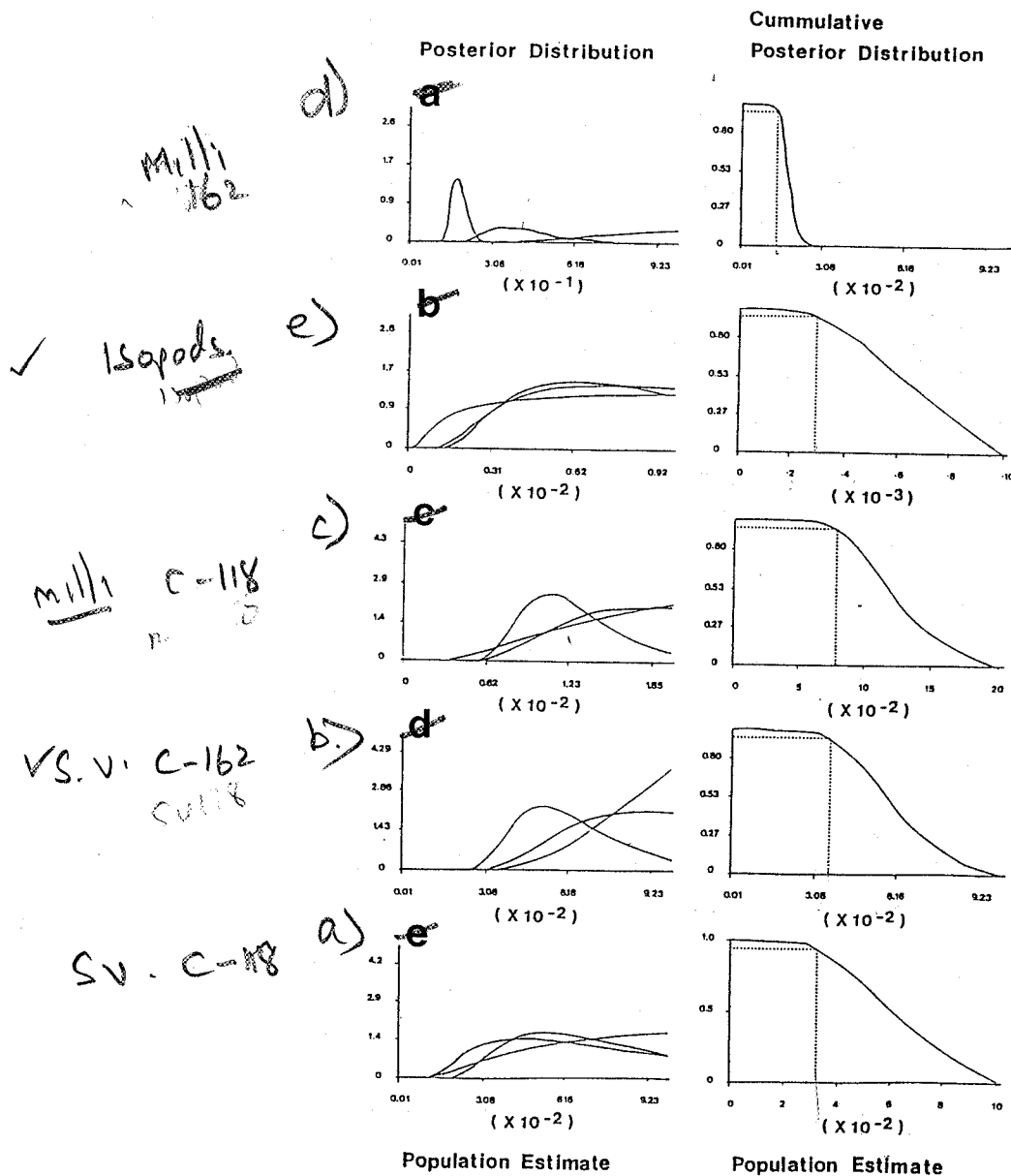
Table 2: Population size estimates from mark release recapture experiments on three species from two caves in Cape Range. Above includes the entire size range and below a restricted subset for *S. vinei* > 5 mm and millipedes > 9 mm total length. Also included are the estimates for *S. vinei* from C118 made in July 1987 (Humphreys *et al.* 1989).

Species	Cave	Population estimates:		
		Mean	Median	Minimum ¹
<hr/>				
	Entire size range			
<i>Schizomus vinei</i>	C118	858	990-1010	340
	C162	1029	990-1010	573
Millipedes	C118	1409	1485-1515	841
	C162	189	495-505	140
Isopods	C162	6397	4950-505	2892
<i>S. vinei</i> > 5 mm; millipedes > 9 mm total length.				
<i>Schizomus vinei</i>	C118	628	496-506	318
	C162	609	496-506	557
Millipedes	C118	1231	990-1011	767
	C162	184	496-506	136
Previous year				
<i>S. vinei</i> ²	C118	1987	3494-3505	1323

¹ This is the minimum population size estimated with 95% confidence using Bayes algorithm. ² Millipedes and isopods were not examined in 1987.

There had been visually an obvious marked reduction in the number of *S. vinei* in C118 from the previous year and this is reflected in the population estimate. Similarly there were visually more *S. vinei* and fewer millipedes in C162 than in C118 during 1988, again reflected in the population estimates. From the view point of conservation the statistic of most interest is the minimum population size with 95% confidence. The population sizes are large for troglobites but, from visual assessment, are not representative of many of the other species of troglobites in the Cape Range caves, most of which are known from few sightings and specimens. The most conspicuous of these is the blind 'miturgid' which seemed most abundant in C126; an attempted mark and recapture study was abandoned when only seven individuals could be found.

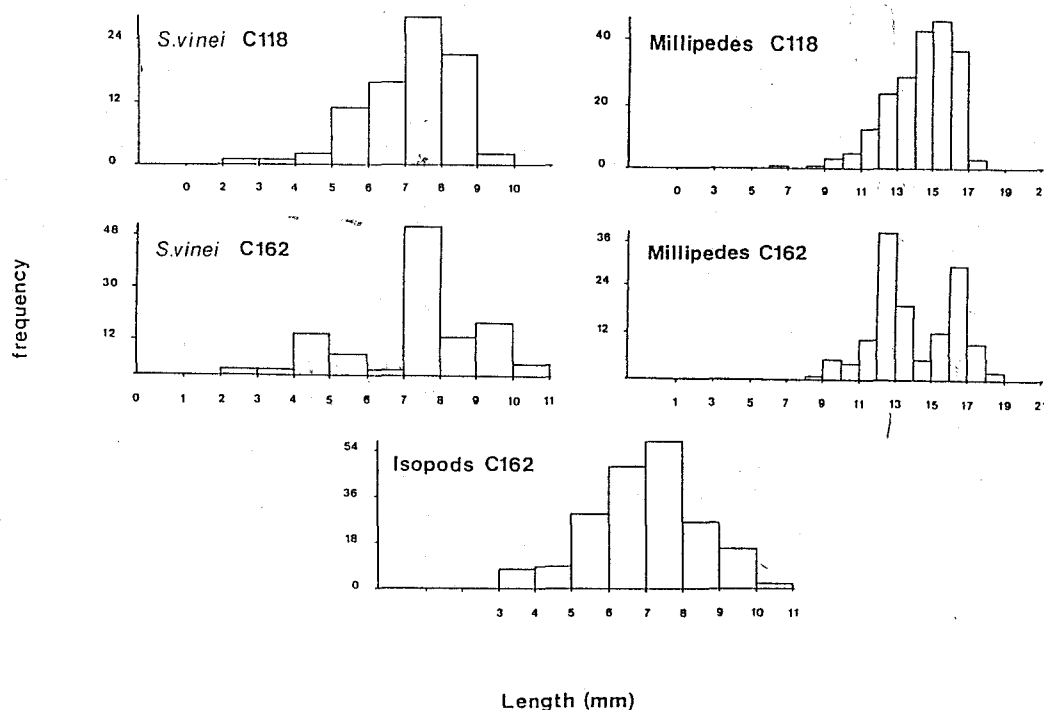
Figure 8: Statistical distributions derived from the capture-mark-release and recapture data using the Bayes algorithm (see Gazey and Staley 1986) to estimate the population sizes of three species in two caves in Cape Range. In each row the left figure shows the posterior distribution plotted against population size, while the right figure shows the cumulative posterior distribution (probability) against population size. In the latter figure the dotted line shows the minimum population size estimated with 95% confidence. a) *S. vinei* in C118; b) *S. vinei* in C162; c) Millipedes in C118; d) Millipedes in C162; e) Isopods in C 162.



Size class structure.

S. vinei in C118 had a unimodal size class structure with the mode at 7 mm, while in C162 the size class structure was polymodal with modes at 4, 7 and 9 mm (Figure 9). The millipedes in C118 had a unimodal size class structure with the mode at 15 mm, while in C162 the size class structure was bimodal with modes at 12 and 16 mm (Figure 9). The size class structure of the isopods in C162 was unimodal with a mode at 7 mm (Figure 9).

Figure 9: Size class frequency distribution (total length, mm) of:- a) *S. vinei* in C118 (n= 82); b) *S. vinei* in C162 (n=173); c) millipedes in C118 (n=205); d) millipedes in C162 (n= 134); e) Isopods in C162 (n= 196).



Despite the large reduction in numbers of *S. vinei* in C118 between 1987 (Humphreys *et al.* 1989) and 1988, the size class structure had not changed substantially in that time, and the population was still dominated by the large size classes.

Of millipedes bred in the laboratory the smallest individual seen on the surface was 6 mm in length, compared with the smallest seen in a cave of 5 mm. Hence, as with the schizomids (Humphreys *et al.* 1989), it would appear that the entire size range of surface active millipedes was sampled in the caves.

Population dynamics

In 1988 both *S. vinei* and the millipedes in C162 had cohorts of small individuals in the population, while in C118 only a single large cohort was present in both 1987 and 1988. Because C118 had not flooded (hence had received no additional organic material) since the previous year, the *S. vinei* population had not bred and no young cohort was in the population. Although no size data are available for the millipedes in 1987, their decline in numbers (visual estimate), and the lack of small cohorts, is consistent with the situation in *S. vinei*. In addition there had been a marked reduction in the number of isopods (visual estimate) in C118 over the year. From the laboratory growth rate of *S. vinei*, any surviving young produced since the sample in 1987 (Humphreys *et al.* 1989) would still have been detected by their smaller size in 1988.

As discussed in more detail below, C162 had been recently reactivated by wetting, and in both the species of troglobites examined, cohorts of smaller (assumed to be younger) individuals were present in the population. The population was contracting spatially during the 1988 study but individuals of both *S. vinei* and millipedes were caught at about the smallest free-living size. To date I have no growth rate or breeding data for the millipedes and so cannot estimate the time since last breeding nor the time to reach adult size.

It was not possible to determine the sex of *S. vinei* during the population study in the caves due to the lack of overt characters by which to distinguish the sexes (see Harvey 1988). However, the sex ratio appears to be strongly biased in the favour of females. Of 17 adults brought to Perth in 1987 only three were males and in 1988 only one of 23 adults was male; in both cases there was a significant departure from a sex ratio of parity (both $P < 0.01$). This large disparity in the sex ratio of *S. vinei* is not thought to result from biased collecting as in the laboratory there is no overt difference in the activities of the sexes. It possibly results from a shorter life span in males; in the laboratory, males often fall prey to females (Humphreys *et al.* 1989), which are larger, but it is not known whether they do so differentially from females. The biased sex ratio suggests that females may be able to store sperm for long periods; the only oviposition yet recorded was to a female which had been without male contact for at least seven months (Humphreys *et al.* 1989).

The size of *S. vinei* relative to other schizomids

Compared with any New World species of *Schizomus* (Rowland and Reddell (1979a, 1979b, 1980, 1981) the carapace length of *S. vinei* is greater (males $\times 1.35$, females $\times 1.21$; Table 3). Amongst New World schizomids there is a tendency for females to be larger than males in troglobites but vice versa in non-troglobites (Table 5). *S. vinei* fits the pattern found in New World schizomids in which there is a tendency for females to be larger than males in troglobites but vice versa in non-troglobites (Table 4; $P = 0.0037$; Fisher's Exact Test).

Table 3: The size of *S. vinei* relative to other schizomids in various families and taxonomic groups in the genus *Schizomus* in the New World. The data for *S. vinei* are from Harvey (1988) and the remainder from Rowland and Reddell (1979a, 1979b, 1980, 1981) from where the taxonomic groupings are taken. Taxa included by a common letter to the right are not significantly different (One-way ANOVA followed by the GT2 multiple comparison test within sexes). Groups with N<3 are excluded from the analysis.

Taxonomic group	Carapace length (mm)		
	Mean	s.d. ¹	N
Females			
<i>Agastoschizomus</i>	3.03	-	1
<i>S. vinei</i>	1.82	0.25	2
<i>pecki</i>	1.50	0.14	7 a
<i>briggsi</i>	1.31	0.14	7 ab
<i>Simonis</i>	1.20	0.13	8 b
<i>mexicanus</i>	1.17	0.13	11 b
Protoschizomidae	1.16	-	1
<i>brasiliensis</i>	1.12	0.17	12 b
<i>dumitrescoae</i>	1.12	0.17	8 b
other	1.10	0.16	4 b
<i>goodnightorum</i>	0.96	0.14	2
Males			
<i>Agastoschizomus</i>	2.10	0.51	2
<i>S. vinei</i>	1.82	0.25	2
<i>briggsi</i>	1.34	0.12	7 a
<i>pecki</i>	1.28	0.06	2
Protoschizomidae	1.20	0.08	2
<i>brasiliensis</i>	1.17	0.22	9 a
<i>goodnightorum</i>	1.17	0.17	4 a
<i>Simonis</i>	1.13	0.15	6 a
<i>dumitrescoae</i>	1.13	0.15	13 a
<i>mexicanus</i>	1.12	0.10	10 a
other	1.03	0.15	3

¹ The range is shown if N = 2. Females:- $F_{s6,50} = 6.556$; $P < 0.001$. Males:- $F_{s6,45} = 2.179$; $P = 0.063$.

Table 4: The relative carapace length within species of male and female schizomids from the New World, grouped according to their status as troglobites. Data from Rowland and Reddell (1979a, 1979b, 1980, 1981). Fisher's Exact Test; $P = 0.0037$.

Relative length	Troglobite?	
	Yes	No
Male > female	2	17
female > male	12	10

Table 5: The relative carapace length within taxonomic groups of male and female schizomids and the proportion of each group that are troglobitic (%T). Data from Rowland and Reddell (1979a, 1979b, 1980, 1981).

Taxonomic group	%T	Ratio female: male carapace length		
		mean	s.d.	n
Protoschizomidae	100	1.289	-	1
<i>pecki</i>	100	1.159	0.056	2
<i>mexicanus</i>	75	1.067	0.058	8
<i>dumitrescoae</i>	63	1.023	0.047	8
<i>briggsi</i>	14	0.975	0.025	7
<i>Simonis</i>	0	1.097	0.220	5
<i>brasiliensis</i>	0	1.019	0.055	6
other	0	1.044	0.084	3
goodnightorum	0	0.867	0.062	2

Rainfall to flood

The cave fauna depends on allochthonous organic matter for its energy source. Hence the amount of rain required to cause water to flow strongly into caves in Cape Range is important because it brings with it most of the organic matter required to fuel the cave ecosystem. Humphreys *et al.* (1989) calculated that minor inflows could occur into some caves after 25 mm of rainfall which should occur on average every 5.4 months, but with very low predictability; deep flooding could occur on average every 56 months.

The history of work in some caves provides additional clues, both to the amount of rain required to flood caves, as well as to the problems associated with attempting to predict wetting cycles of caves. Rainfall is defined as the cumulative rainfall separated by no more than two dry (or trace) days.

Rainfall of 156 mm was recorded at Learmonth (not 230.8 mm as reported in Vine *et al.* 1988 which was the months total rain in May 1984) and resulted in C106 flooding to a depth of 27 m and deep flooding also in C18. Rainfall of 236 mm caused water to flow from Shothole Tunnel (C64; the only known outflow cave in Cape Range) but 100 mm of rainfall was insufficient to make it flow (B. Vine; pers. comm. 1988). The 24 mm of rain recorded at Learmonth during cyclone Herbie (21 May 1988) resulted in only trivial inflow into C171, yet an adjacent doline (diameter 25 m) contained 15 cm of water (H. Tomlinson; pers. comm. 1988).

Table 6: Soil water content (% dry weight) in July 1987 and August 1988 at the same sites in C118. Probabilities are based on one way ANOVA within rows.

Area	1987			1988			P
	Mean	s.d.	N	Mean	s.d.	N	
1	19.2	0.79	6	13.65	0.65	5	<0.001
2	11.4	2.42	6	7.26	1.64	5	<0.001
3	15.0	1.30	6	12.77	0.86	3	0.033
4 ¹	20.4	1.53	6	19.61	2.55	3	0.570

¹ This area contained the most abundant fauna in 1988.

High carbon dioxide levels tend to occur in tropical caves as a result of biogenic CO₂ production (Vandel 1965) which occurs mostly after the influx of water and organic matter into caves. C118 had noticeable CO₂ levels on 17 July 1986 (M. East; pers. comm. 1988) and was presumably then much wetter as no high CO₂ levels have been recorded subsequently. C118 was studied in detail in July 1987 at which time there had been no recent influx of water (Humphreys *et al.* 1989). It was studied in detail again from August to September 1988. No influx of water had occurred during the year (pigment silhouettes from the 1987 marking were still present throughout the cave) and the cave had dried significantly except around the drain holes (Table 6), and the fauna was more sparse (see above). In August 1988 rainfall of 39 mm was recorded at Learmonth but this was insufficient to cause an inflow of water into this cave or into C162. The most recent rainfall greater than 39 mm occurred in February 1986 (97 mm) and the previous heavier rainfall was the big fall in May 1984 mentioned elsewhere (Table 9). The high CO₂ levels in C118 in July 1986 suggest that the 97 mm of rain in February 1986 was sufficient to flood the cave, and that since that date it had been drying continuously for a period of 30 months (i.e. until the work in 1988; Table 6). While there were significant site differences in the soil water content in C118, there was no significant drying within sites between 10 August and 19 September 1988 (Table 7); this is consistent with the cave type, namely a large cavern with a very small entrance hole.

Table 7: Soil water content (% dry weight) on two dates in 1988 at two locations in C118.

Area	10 August			19 September		
	Mean	s.d.	N	Mean	s.d.	N
1	13.65	0.646	5	14.42	1.37	3
2	23.37	1.197	5	23.65	0.654	3

A two-way factorial ANOVA showed no significant interaction between time and site ($F_{s1,12} = 0.229$; $P = 0.229$). There was no change in soil water content with time ($F_{s1,13} = 1.095$; $P = 0.31$) but there was a strong between site difference ($F_{s1,13} = 386.4$; $P < 0.001$).

C162: this cave was dry when first entered (20 August 1987) except for a one m² damp patch at the back of the cave where schizomids were found. When next entered on 20 May 1988 the cave had clearly been flooded as the mud throughout the cave was wet and there had been some redistribution of the sediments (M. East; pers. comm. 1988, and photographs). The flooding had reactivated the fauna as is evident from the smaller cohorts in the populations of both millipedes and schizomids (see above). This cave dries rapidly; on 10 August 1988 the mud banks in C162 were uniformly wet ($P = 0.129$; Table 8). From then until 22 September 1988 the soil water content declined significantly in all areas of the cave (Table 8), but more so closest to the entrance ($P < 0.001$). This cave is broadly open to the surface (Fig. 2) and a small area even receives direct sunlight for some of the day. Hence there is a strong gradient in drying with distance from the entrance which results in the significant interaction between time and location in the cave (Table 8).

Table 8: Soil water content (% dry weight) on two dates in 1988 at three locations in C162. The means are ordered with increasing distance from the cave entrance. $N=5$ for each sample. Probabilities are given separately for each row and column¹.

Area	10 August		22 September		P
	Mean	s.d.	Mean	s.d.	
1	22.71	3.24	9.09	0.524	$P < 0.001$
2	23.19	1.62	16.91	1.718	$P < 0.001$
3	25.38	0.72	23.54	1.42	$P = 0.032$
$P = 0.129$			$P < 0.001$		

¹ A two-way factorial ANOVA showed strong interaction between time and site ($F_{2,24} = 67.07$; $P < 0.0001$); hence the rows and columns were analysed separately using one way ANOVA.

Sometime between 20 August 1987 and 20 May 1988 C162 was flooded. However, no rainfall >10 mm was recorded at Learmonth in the intervening period (Table 9). Rainfall of 39 mm recorded in August 1988 did not result in either C118 or C162 receiving an influx of water. Observations show that heavy rain in Cape Range is often localised and while it is clear that this period provided substantial water to the catchment of C162, no water flowed into C118 only 0.85 km away. The biological indicators (the size of individuals in the younger cohorts of schizomids and millipedes) suggest that the influx of water into C162 must have happened towards the start of this period, otherwise there would have been insufficient time for them to grow to the size recorded in late 1988, judging by the growth rate of *S. vinei* in the laboratory (Humphreys *et al.* 1989).

Table 9: Maximum single rainfall events for each month at Learmonth for the period 1984-1988. A rainfall event is the total rainfall for a period when rain (excluding traces), separated by no more than two dry days, was recorded. Source:- Commonwealth Bureau of Meteorology.

Year	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
1984	0	55	15	5	156	11	83	7	1	10	0	1
1985	0	18	0	31	50	51	65	1	0	2	0	0
1986	2	97	29	0	9	27	8	3	8	2	0	0
1987	0	33	1	2	9	50	16	1	0	0	0	0
1988	0	0	10	8	24	9	13	39	0	-	-	-

Soil water and faunal density

Different areas of individual caves vary considerably in water content at the same time (C118, $F_{s15,32} = 36.08$, $P < 0.001$; C162, $F_{s23,44} = 26.21$, $P < 0.001$), even over short distances; e.g. from 3.6 to 19.5% between the top and bottom of a 60 cm high mudbank in C207. Wetting and drying of the mud banks in the caves is associated respectively with expansion and contraction of the populations of cave fauna (see above). The drying of C162 between 10 August and 22 September 1988 was associated with a contraction of the fauna into about half the cave area - those parts still with the wettest soils. In addition, in cave C118 between July 1987 and September 1988, there was a four fold reduction in the minimum population size of *S. vinei*, from 1323 to 318 individuals.

Organic carbon

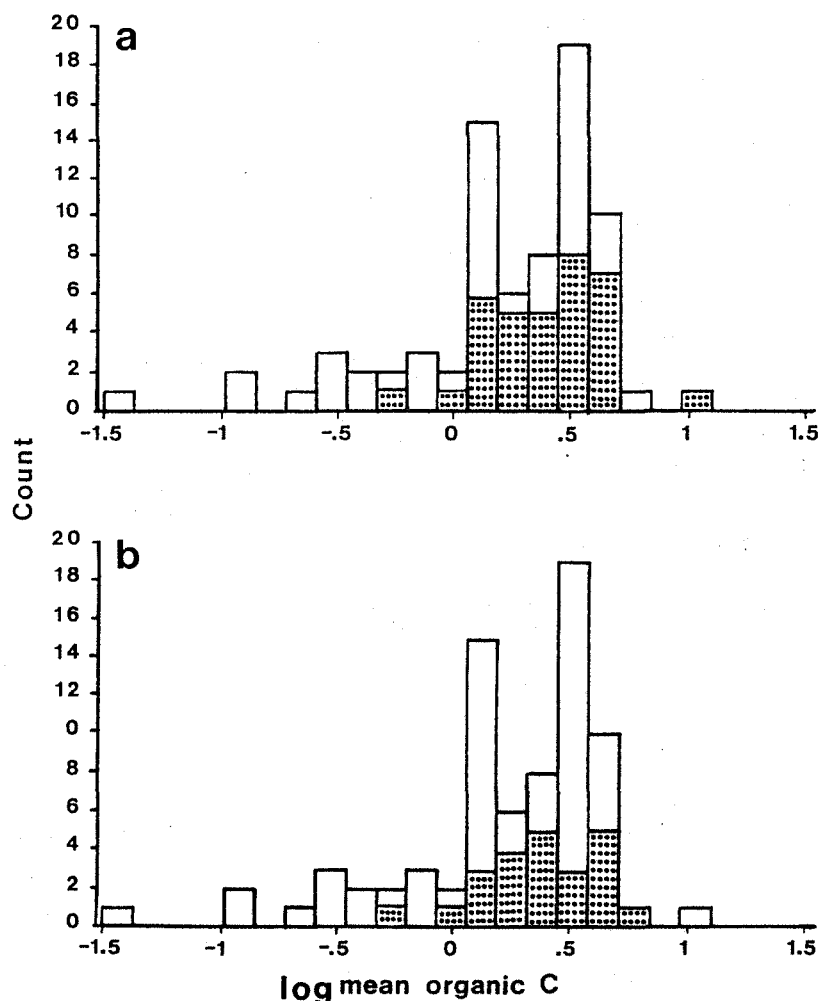
The mean organic carbon content of the cave soils is 2.4 % (s. d.=1.75; N= 227; range 0.04-11.4). There are considerable differences in the organic carbon content of the soils in different caves ($F_{s11,62} = 18.1$, $P < 0.001$) which vary between 0.07% in C169 to 4.09% in C106. Within caves organic carbon also differs between areas, ranging from 0.14% to 1.84% in C118 ($F_{s15,32} = 19.4$, $P < 0.001$), and between 2.3% and 5.7% in C162 ($F_{s23,44} = 6.15$, $P < 0.001$). Over all caves the mean water content (X) is positively correlated with the content of organic carbon ($C = 0.02 X - 0.15$; $r^2 = 0.19$, $F_{s1,74} = 17.17$, $P < 0.001$). However, within caves water and organic carbon content may be closely related (C118: $r = 0.655$, N= 49, $P < 0.001$) or show no association (C162: $r = 0.02$, N=69, $P = 0.89$). The distribution of *S. vinei* and the millipedes varies with both the contents of organic carbon and water in the mud-banks (Table 10).

Table 10: Mean organic carbon and water content in samples from numerous caves and their relationship to the presence and absence of troglobitic fauna. Within columns rows with common letters do not differ significantly.

Group	log Mean Organic C	Mean Water %
No fauna	0.028a	14.79a
Millipedes	0.324ab	17.35a
<i>S. vinei</i>	0.422b	26.17b

The presence of *S. vinei* in caves is closely associated with the amount of organic carbon (C%: Figure 10) and water (H₂O%) in the mud-banks, which together account for half the variance in their occurrence ($Y = 0.40C + 0.017 H_2O + 0.084$; $F_{s2,41} = 22.25$, $P < 0.001$, adj. $r^2 = 0.497$). However, only the amount of organic carbon is associated with the occurrence of millipedes ($Y = 0.421C + 0.316$; $F_{s1,42} = 9.56$, $P < 0.001$, adj $r^2 = 0.171$) and this agrees with the general field observation that millipedes are found in drier areas than those in which *S. vinei* are found.

Figure 10: The frequency distribution of organic carbon (%) in soils from caves in Cape Range. The shaded area shows the occurrence of *S. vinei* (a) and millipedes (b).



Comparative data are available for C118 from the same sampling points in both 1987 (Humphreys *et al.* 1989) and 1988 during which time the cave had not been recharged by flooding with organic material. Of the five areas compared all had mean organic carbon contents lower than in the previous year, three of them significantly so (Table 11). Below I examine the relevance of the loss of organic carbon from the cave.

Table 11: The amount of organic carbon in the mud of C118 in 1987 and 1988, during which time the cave had not flooded.

Area of cave ¹	Mean organic C (%)		F-test	d.f.	P
	1987	1988			
All samples	1.517	1.323	2.38	1,76	0.126
A	1.78	1.29	8.94	1,13	0.010
B	1.85	1.40	11.66	1,7	0.011
C	2.04	1.69	1.39	1,7	0.276
D	1.50	1.27	0.64	1,7	0.450
E	0.42	0.15	27.74	1,7	0.001

¹These areas are shown in Humphreys *et al.* 1989

The mudbanks in C118 occupy *ca* 100 m² of the cave (Humphreys *et al.* 1989). The soil samples included the top 4 cm of soil, were *ca* 10 cm² and on the main mud-banks had a mean dry weight of 28.8 g (s.d. 5.1, n=15). Between 1987 and 1988 there was a mean reduction of 0.44% in the organic carbon content of the mud-banks containing the fauna (Table 11, A-C); this is *ca* 12500 g organic carbon, equivalent to *ca* 140 MJ. In order to determine whether this loss of carbon from the mud-banks is of any meaning I give below a rough energy calculation for the population of the top predator in the cave, *S. vinei*.

The mean population of schizomids was estimated to be *ca* 3500 in 1987. The respiration rate of *S. vinei* is low, about 0.2 $\mu\text{l mg}^{-1} \text{hr}^{-1}$ (unpublished data). If we assume a mean individual weight of 10 mg then the annual respiration is *ca* 61 litres of O₂. Using an oxycaloric equivalent of 20 J ml⁻¹ oxygen, this is equivalent to respiration of *ca* 1.2 MJ. The production efficiency for the animals will be *ca* 0.3 (Humphreys 1979) so the assimilation of the populations will be *ca* 1.75 MJ, or *ca* 1.3% of the estimated loss of organic carbon from the mud-banks.

Some rough calculations are made to determine where the rest of the carbon is going. There were probably in the order of 20000 millipedes and isopods in the cave, which on the same basis as above would account for an additional *ca* 7.5% loss of organic carbon, making *ca* 9% in total. The caves contains at least two additional top predators, a large troglobitic spider and a pholcid spider, as well as

troglobitic crickets and cockroaches; all appear to be in low densities. However, judging by the worm casts, the cave contains a substantial but unknown population of earthworms of considerable mass relative to the other species in the cave. These are probably responsible for considerable incorporation of organic detritus into the soil, as well as making a network of tunnels just beneath the surface. Rats (*Rattus rattus*) have occurred in C118 and, although they probably feed on the surface and there is no evidence of food importation by them, they may die in the cave (a skeleton was recovered in 1987). *R. rattus* weighs *ca* 150 g and a single carcass would contribute *ca* 1 Mj of energy to the cave, namely about the same as the annual energy flow through the *S. vinei* population.

Three factors of importance arise from this analysis. First, given that it is a crude approximation, the loss of organic carbon from the system is much greater than the estimated loss through the schizomids; were it *vice versa* the assumption that no energy had been imported through the year would need questioning. Second, the analysis suggests that the major contributors to the energy flow in the cave have not been examined; earthworms and micro-organisms probably have a substantially larger biomass than the populations considered and they could account for the remainder of the loss of organic carbon. Third, it suggests that during a period without any influx of detritus, such as occurred in C118 between 1987 and 1988, that a detailed analysis of the organic carbon content of the mud could be a short cut method of examining the energetics of the cave ecosystem. Given the difficulty of enumerating cave populations such an approach may be the only feasible method to examine the system as a whole.

The annual reduction in organic carbon in C118 was 0.44% between 1987 and 1988. At this rate of reduction the level of organic carbon in 1987 would fall below the level at which troglobites were found in any cave (0.5%; Figure 10) in 5 years. Hence, it would seem that *S. vinei* would require the cave to be recharged with organic matter resulting from major inflows of water within this period. It was estimated that major flooding would occur every 56 months (4.7 years) but with very low predicatability (Humphreys *et al.* 1989). In addition it has been deduced that in 1988 there had probably been no major flooding of C118 for five years (since May 1984). Assuming the rate of organic carbon reduction occurred at the same rate over this period, then the level of organic carbon after the 1984 flooding would have been *ca* 3.2%, which is about the mode level found in caves containing troglobites (Figure 10) and similar to the value of a recently flooded cave (C162; mean 3.49, s.d. 0.83, n=68).

The above calculations provide further weak but consistent evidence that the flooding frequency of the caves, the organic carbon recharge and depletion rates, and the population events are tightly connected.

Population pulses

As suggested previously (Humphreys *et al.* 1989), the caves must be linked at a level below which cavers can reach. In these levels, relatively devoid of energy, there must be a low population of the cave animals. When caves are wetted and reenergised by the influx of organic matter these population move upwards into the newly inhabitable areas and breed there (see C162). Until the next influx of water the caves dry out slowly and the populations retract towards the less dry parts of the cave and then leave entirely those parts of the cave accessible to cavers.

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 size of the cave and its opening to the outside. Hence C162 receives an inflow after relatively low rainfall but then dries rapidly. In contrast, C118 obtains an inflow after only heavy rainfall but thereafter dries very slowly.

Hence, the evidence suggests that there is an inaccessible cave community within Cape Range which extends upwards at intervals like pseudopodia into the accessible areas of caves. 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. 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). This is in strong contrast to the accepted view of cave communities and environments, which are considered to be more or less stable (Poulston and White 1969).

Water loss

The mean values for water loss and the weights of the six species examined are presented in Table 12, where water loss is presented relative to individuals, to surface area and as resistance.

Analysis of variance was conducted on the regressions of water loss ($\log \mu\text{g hr}^{-1}$) on body weight (mg) for all samples of the same species from different caves (millipedes from C162 and C106 and *S. vinei* from C106, C118, C159 and C162). None was found to differ significantly from the others and the samples were pooled.

Comparison of the regressions for the six species showed that the slopes were not parallel ($F_{5,73} = 4.327$; $P=0.002$). Removal of *O. moreletii* data results in parallel lines for the remaining five species ($F_{5,48} = 1.063$; $P=0.385$) with a common slope of 0.555 (Figure 11), but which are significantly displaced ($F_{5,42}$

= 92.900; $P < 0.001$, Table 13). The GT2 multiple comparison test shows that the 'miturgids' have a lower rate of water loss than *S. vinei* and that both have lower rates than all other species ($P < 0.05$; Table 13). The ratios for the 'miturgids', *S. vinei*, millipedes, epigean isopods and cave isopods are 1.0 : 3.14: 6.81 : 8.00 : 11.07.

Table 12: Mean weight and rates of evaporative water loss (EWL) from *S. vinei* and 'miturgid' spiders from caves, and millipedes (*Ommatoiulus moreletii*) and isopods from cave and non-cave habitats. The data are presented as mass and area-specific rates together with the whole body resistance (R). The value in parentheses is the standard deviation of the mean.

Species	N	Weight (mg)	Water loss: ($\text{mg g}^{-1} \text{ min}^{-1}$) ($\text{mg cm}^{-2} \text{ h}^{-1}$)		Resistance (cm sec^{-1})
Cave millipedes	19	10.46 (3.27)	1.668 (0.613)	0.507 (0.205)	40.88 (17.21)
<i>O. moreletii</i>	11	54.47 (22.82)	0.043 (0.013)	0.023 (0.009)	878.13 (284.35)
<i>Schizomus vinei</i>	20	8.15 (3.36)	0.836 (0.180)	0.228 (0.039)	76.58 (12.91)
Cave isopods	19	14.21 (5.59)	2.279 (0.450)	0.742 (0.092)	22.36 (2.83)
Garden isopods	10	10.54 (11.23)	2.210 (0.962)	0.570 (0.164)	31.61 (8.65)
cave 'miturgids'	6	50.68 (69.98)	0.310 (0.319)	0.072 (0.047)	303.99 (132.19)

Figure 11: Regressions of water loss ($\log \mu\text{g hr}^{-1}$) on body weight for six species. The plotted regression lines for all species, except *O. moreletii*, have been adjusted to their common slope. 'Miturgids' (X), *S. vinei* (squares), cave millipedes (+), cave isopods (triangles), epigean isopods (o closed) and *O. moreletii* (O open).

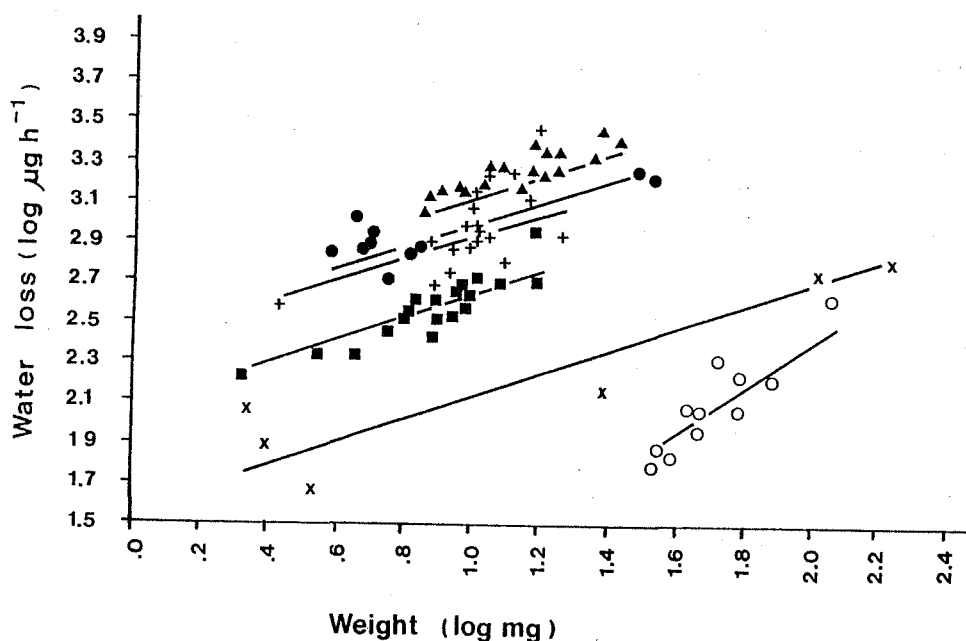


Table 13: Analyses of the regressions of water loss (log $\mu\text{g hr}^{-1}$) on weight (log mg) for six species determined by a water monitor (see methods). T and N denote troglolithic and epigeal species respectively. Lines (excluding the portuguese millipede, *O. moreletii*) with common letters show that the adjusted mean Y values for a common slope of 0.56 are not significantly different.

Species		b	a	N	r	Ts	P	Mean Y
'Miturgids'	T	0.500	1.646	6	0.921	4.717	0.009	2.133
<i>S. vinei</i>	T	0.716	1.939	20	0.898	8.651	<0.001	2.630
Millipedes	T	0.826	2.146	19	0.663	3.656	0.002	2.966a
Isopods	N	0.429	2.576	10	0.844	4.451	0.002	3.036ab
Isopods	T	0.559	2.622	19	0.880	7.651	<0.001	3.177b
<i>O. moreletii</i>	N	1.437	-0.370	11	0.918	6.962	<0.001	-
ANOVA								
All six species:-		Slopes; $F_{5,73} = 4.327$; $P = 0.002$						
Minus <i>O. moreletii</i> :-		Slopes; $F_{5,65} = 1.352$; $P = 0.260$						
		Intercepts; $F_{5,69} = 120.975$; $P < 0.001$						

Cave millipedes have water loss rates 41 times that of the epigeal millipedes (*O. moreletii*) of a given size (ANOVA slopes; $F_{5,26} = 2.987$, $P = 0.096$: intercepts; $F_{5,27} = 143.17$; $P < 0.001$) and the rate of water loss is directly proportional to body weight (common slope = 1.023).

Cave isopods have water loss rates 1.52 times that of epigeal isopods of a given size (ANOVA slopes; $F_{5,25} = 1.174$, $P = 0.289$: intercepts $F_{5,26} = 34.244$, $P < 0.001$) and the rate of water loss is proportional to body weight^{0.47}.

The regressions for all cave species have a common slope of 0.568 ($F_{3,56} = 1.698$; $P = 0.178$) and all four species differ significantly in their rate of water loss, with the ratio 'miturgids', *S. vinei*, millipedes and isopods being 1.0 : 3.16 : 6.84 : 11.07.

The resistance reported here for *S. vinei* is considerably higher (76.6 cm sec⁻¹) than that previously reported (15.2 cm sec⁻¹; Humphreys *et al.* 1989) for a smaller sample, despite the flow rate used here being *ca* 4.7 times greater (7 cm sec⁻¹) than that previously used. It probably results from the inclusion of adsorbed water in the earlier study due to a shorter period of equilibration (*ca* 15 min compared with 33.5 min. (s.d. = 14.7). This is supported by multiplying the rate of water loss during the measurement period by the total time the individual was in the apparatus; this accounted for between 26 and 49% of the gravimetrically determined water loss, with no significant correlation with individual weight in any species.

Genetics

Six criteria need to be met to conduct adequate genetical work at the species level (Richardson *et al.* 1986). Namely, 1) six polymorphic loci are required; 2) samples should be drawn from the smallest and most homogeneous population units possible; 3) replicate samples at the smallest scale; 4) sample over some geographical distance including the extremities and intermediate locations; 5) three animals in each group are sufficient for species work as the probability of not collecting a heterozygote is $(0.5)^n$; 6) need preliminary estimate of the value of P, the proportion of loci polymorphic. Caves make ideal sampling units for work of this type and three of the species examined meet all but the last criteria and *S. vinei* has only three polymorphic loci.

A summary of the genetical analysis is given, together with detailed notes, in Table 14 and the data in Appendices 1-5. The enzymes examined for each species are shown in Appendix 6.

Millipedes: In contrast to the schizomid and isopod data below, there is unequivocal evidence that the populations have not been taken from a single gene pool (Appendix 4 a-c). Two major genetic groupings emerge (Figure 4); Group I (which includes the southern caves C118, C207, C126 and C167), and Group II (which includes the northern caves C159, C107, C103, C18, C106 and C64). These two groups differ at an average of 19% of loci. Unless these two groupings follow a major geographic dichotomy, then it is likely that they represent two distinct species.

The four populations in Group I, south of Mt Hollister, are genetically homogeneous. In contrast there is one significant indication of divergence amongst the Group II populations. Population C64 is the most divergent, differing at several loci from the other populations within this group (Figure 12). The caves included in Group I and Group II are separated by a major canyon almost bisecting Cape Range (Figure 4) and which cuts through the Tulki limestone, in which the caves are formed, into the Mandu Calcarene below (Figure 1). Cave C64 is separated from the remainder of the northern group of caves by another deep canyon (Shothole Canyon).

***S. vinei* :** The eight populations (Figure 4) are genetically similar and the data are consistent with the presence of a single biological species (Appendix 5 a-d). The sample sizes are inadequate to conduct proper statistical comparisons. However, the allele and genotype frequencies suggest that the cave sample sets are not taken from a single panmictic population. The strongest evidence for this suggestion comes from the Mdh-2 data, in which the C159 population exhibits a fixed allelic difference from all other populations. On a null hypothesis that all individuals have come from a single panmictic population, then the chance of not observing an Mdh-2ab heterozygote in 44 cases (for a population with allele frequencies $a = 0.09$, $b = 0.91$) is $(1 - 2 \times 0.91 \times 0.09)^{44} = 0.000381$. Of course it is

unwise for a number of reasons to use a single marker to form unequivocal genetic conclusions (see Richardson *et al.* 1986). The data for Est and Pgm provide weak support for the idea that the cave samples do not come from a single gene pool.

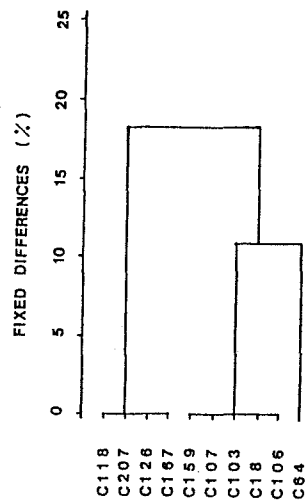
Table 14: Summary of the genetical information.

Attribute	<i>S. vinei</i> ⁹	Millipedes ⁶	Isopods	Amphipods ⁴
# caves sampled	8	10	5	3
# individuals	44	40	23	11
# enzymes examined	37	46	43	49
# enzymes scored	22	27	32	25
# loci invariable (%)	19 ⁸ (86)	9 (33)	17 (53)	15 (60)
# polymorphic loci (%)	3 (14)	18 (67)	15 (47)	10 (40)
H-W Equilibrium	Yes	Yes	Yes	Yes
Panmictic population	No	No ⁶	Yes	No ¹
? more than one species ²	No	Yes	No ⁵	Yes
Geographic explanation ³	Yes ⁷	Yes	-	Yes
Troglobite	Yes	Yes	No	Yes

¹ No gene flow between caves. ² Genetic differences indicate the possibility of sibling species. ³ The genetic differences are in accord with major geomorphological features. ⁴ The three populations are divided by the same geomorphological features which separate the Groups in the phenogram of genetic differences between the populations of millipedes. ⁵ One individual from C106 had no demonstrable activity for most loci. However, for the three loci which were scorable (Acon-2, Gpi and Pep-D2), this individual exhibited fixed allelic differences from all other isopods. This individual clearly represents a different species from the other 15 sampled and it was not included in the above analysis. ⁶ There are two major genetic groupings differing at an average of 19% of loci:- Group I - C118, C203, C126 and C167; Group II- C159, C107, C103, C18, C106 and C64. The four populations in Group I are genetically homogeneous. In Group II the population from C64 is the most divergent. The three groups are divided by major geomorphological features in the form of deep canyons which cut through the limestone strata in which the caves are found. ⁷ The gene frequencies of two (Mdh-2 and Pgm) of the three polymorphic loci differ significantly when the data are divided into two according to geomorphological features (respectively $P=0.0071$ and $P=0.0009$; Fishers Exact test). In addition the population from C159, for the Mdh-2 data, has fixed allelic differences from the other populations. ⁸ Ten of which were not active in all samples. ⁹ Two loci dropped from previous study (Humphreys *et al.* 1989).

On the hypothesis that the same geomorphological features separating the millipedes will affect all troglobites, the data were divided into two groups representing the northern and southern areas (Figure 4). The gene frequencies of two (Mdh-2 and Pgm) of the three polymorphic loci differ significantly between areas (Table 15).

Figure 12: UPGMA phenogram showing the genetic relationships between the populations of millipedes in ten caves.



Isopods: The five populations are genetically very similar and the allele and genotype frequencies are consistent with each cave sample being obtained from a single gene pool, i.e. they are panmictic (Figure 4). Of the four species studied, the isopod, which was the only non-troglobite examined, displayed the highest levels of within-population polymorphism. The most striking example of this is at the Mpi locus (Appendix 3a), where nine alleles were found in 22 individuals.

Table 15: Gene frequencies at the three polymorphic loci in *S. vinei* from caves to the north and south of the main canyon (see text).

Locus Allele	<u>Est</u>		<u>Mdh-2</u>		<u>Pgm</u>	
	b	a	b	a	b	a
Northern area	43	5	40	8	12	36
Southern area	36	4	40	0	0	38
Fishers Exact P	0.7759		0.00706		0.00085	

Amphipods: In contrast to the data for *S. vinei* and the isopod, there is unequivocal evidence that each of the three populations is genetically isolated from the other two (Appendix 2 a-c). Ignoring allele frequency differences, there are five fixed genetic differences between C163 and the others, whilst C64 and C103 differ at three loci. Such multiple fixed differences indicate that there is no gene flow between any of the three caves. The genetic differences observed between cave populations are at the higher end of the range normally observed for allopatric populations of a single species; taxonomic work is required to determine whether these population represent sibling species.

Distance between caves

Examination of the distribution of the distance between all pairs of caves from which genetical samples were taken, shows that the mean distance between caves is similar in Group I and Group II but is significantly greater between the caves in different Groups (Table 16).

Table 16: The distance (km) between all pairs of caves in the southern (Group I) and northern (Group II) sectors and the correlation (Spearman's Rank) between distance of separation of caves and both the Fixed Differences (%) and Nei's Distance for millipedes. Common letters within columns denote no significant difference (ANOVA with GT2 multiple comparison test), while an asterisk denotes significant correlation.

Comparison	Distance (km) ¹			Nei's ² Mean	FD% ³ Mean	Correlation with distance	
	Mean	S.D.	N			Nei's	FD%
Within Group I	3.4a	2.88	6	13.5	-0.30a	0.86*	- 4
Within Group II	4.6a	2.69	15	98.7	0.15a	0.46*	0.43
Between groups	7.8	4.28	24	288.3	1.27	0.38*	0.15

¹ $F_{s, 2, 42} = 5.401$; $P = 0.008$. ² Nei's Distance: - $F_{s, 2, 42} = 96.63$; $P < 0.001$.

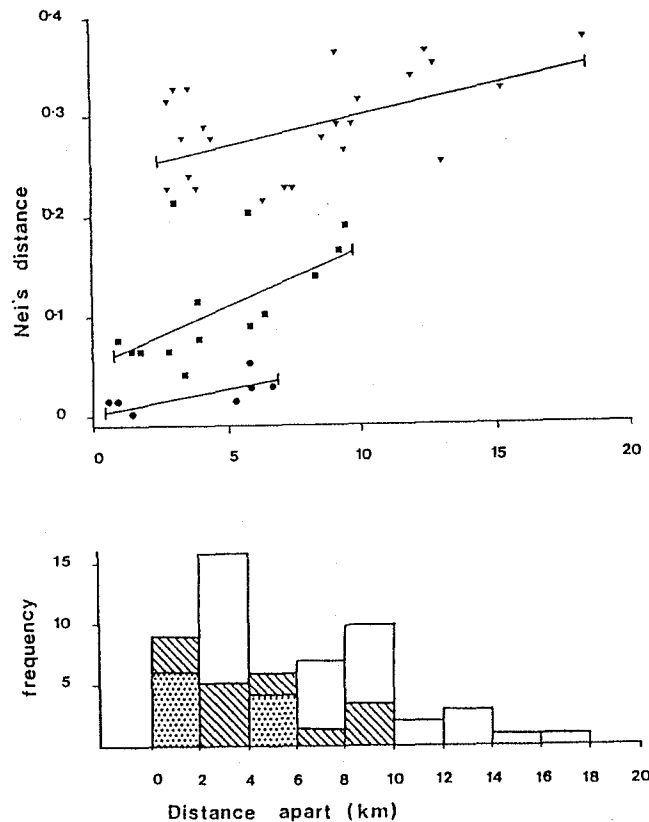
³ Fixed Differences % ($\text{Log}(X + 0.5)$): - $F_{s, 2, 42} = 60.77$; $P < 0.001$. ⁴ No variation.

The data for the metric distance between caves, Fixed Differences and Nei's Distance were divided into three groups:- all pairs of caves in either the southern (Group I) or the northern area (Group II), and all pairs of caves between Groups I and II. For the millipedes, which have the best genetical data base, the mean value of Nei's Distance differs significantly between the three groups, being lowest in the more homogeneous southern area and greatest between areas (Table 16). The proportion of Fixed Differences is similar for comparisons of caves within groups but significantly higher for caves between groups (Table 16).

There is significant correlation between the distance of separation of the caves and Nei's Distance, for both within and between Group comparisons (Table 16; Fig. 13). Clearly the genetical distance is dependent on both the area from which the samples were taken ($t_{s42} = 11.26$; $P < 0.001$) and the distance apart of the caves ($t_{s42} = 3.71$; $P < 0.001$); together they explain 83% of the variance. Nei's Distance can be viewed as an estimate of the number of DNA base differences per locus between populations (Richardson *et al.* 1986).

Conversely Fixed Differences do not correlate with the distance apart of the caves either within or between Groups, but do so if all cave pairs are compared ($r_{s43} = 0.49$; $P < 0.05$ - Spearman's Rank Correlation). The sparse data available for the other three species show no significant correlation between the indices and the distance between caves.

Figure 13: Graph of Nei's Distance between samples from each pair of caves plotted against the distance (km) separating the caves. Symbols denote data from different Groups of caves; circles and dotted = Group I, squares and hatched = Group II, and triangles and open box = between Group comparisons. The regression lines for the separate data sets are shown. The histogram below shows the distribution of distances between caves.



Various hypotheses predict that the proportion of loci polymorphic (**P**) and the proportion of loci heterozygous (**H**) should be respectively lower or higher in cave species than their epigeal counterparts. Neutralist arguments generally predict lower **H** in cave population as **H** is positively correlated with population size (as is the time since a population bottleneck). The parallel selectionist argument predicts the same due to the lower spatial and temporal heterogeneity in caves, but another predicts the opposite due to ecological release (see Culver 1982). Culver (1982, Table 5.2) analysed the data available and found trends for lower **P** and **H** in the data for terrestrial cave dwellers and for fish, but the reverse for aquatic invertebrates. **H** was significantly lower for terrestrial troglobitic arthropods and **H** was significantly higher for aquatic troglobitic arthropods compared with their non-cave counterparts.

Adding the mean values of my millipede and amphipod data (Table 14) to the appropriate data sets used by Culver (ibid.) results in a significantly lower value of **H** in the terrestrial troglobitic arthropods ($F_{s1,31} = 5.238$; $P = 0.029$), and makes **H** not significantly different ($F_{s1,12} = 1.964$; $P = 0.186$) for aquatic troglobitic arthropods, compared with their non-cave living counterparts. It makes **P** for troglobitic arthropods not significantly different ($F_{s1,31} = 3.259$, $P = 0.081$) for

aquatic troglobitic arthropods, and does not make significant the aquatic troglobitic arthropods ($F_{s1,12} = 0.011$, $P = 0.917$), compared with their non-cave living counterparts. Despite the general trends still holding, as foreshadowed by Culver (1982), the addition of a single data set has changed the statistical conclusions.

TABLE 17: Mean heterozygosity (H) of the populations of four species in each cave from which they were sampled.

Species	cave												H		
	18 II	64 II	103 II	106 II	107 II	118 I	126 I	159 II	162 I	163 I	167 I	207 I	Mean	s.d.	N
Millipede ¹	.17	.07	.06	.06	.17	.04	.05	.13	-	-	.04	.06	0.083	0.052	10
<i>S. vinei</i> ²	.02	-	.00	.01	-	.00	.00	.04	.00	-	.00	-	0.009	0.015	8
Amphipod	-	.02	.04	-	-	-	-	-	-	.08	-	-	0.048	0.029	3
Isopod ³	.08	-	-	.09	.07	-	.07	-	-	-	.10	-	0.082	0.011	5

¹ H is lower in Group I than in Group II ($F_{s1,8} = 8.867$; $P = 0.018$, log transformed data). ² Group I has lower (zero) variance than Group II. ³ Groups I and II have equal H ($F_{s1,3} = 0.146$; $P = 0.728$).

Culver (1982, Table 5.3) has shown that mean H may vary between species within a cave from 0.008 to 0.228. In the Cape Range samples mean H varies between species ($F_{s3,22} = 7.452$; $P = 0.0013$) and is towards the lower end of this range (Table 17). In addition H is lower in millipedes from the southern, than the northern, group of caves (Table 17; $F_{s1,8} = 8.867$; $P = 0.018$, log transformed data). This is true also if the outlier cave C64 is excluded from the northern Group ($F_{s1,7} = 8.352$; $P = 0.023$).

It is clear that no generalization can be made concerning the relative change in H of troglobitic populations and that specific cases must be examined. Four theories have received support in various studies.

T1. Small effective population size coupled with genetic drift result in low genetic variation in cave populations (neutralist hypothesis).

T2. Differences in time since a genetic bottleneck account for differences in genetic variation among cave populations (neutralist hypothesis).

T3. The relative environmental uniformity of caves results in low heterozygosity (selectionist hypothesis).

T4. Reduced species diversity allows ecological release and high heterozygosity (selectionist hypothesis).

H is low in the four populations examined from Cape Range, irrespective of whether or not they are troglobites. All the populations are large for cave populations, even assuming no connection with other caves. For the four species studied the mutation rates required to produce the observed heterozygosity is less than from 1×10^{-5} to 2×10^{-6} for populations of 1000 or more (applying the formula of Maruyama and Kimura 1978). As the population sizes are certainly adequate and the rates of mutation reasonable, this study is consistent with T1. However, the southern populations of millipedes are genetically homogeneous. Hence, gene flow between caves must occur making the effective population size larger than in the heterogeneous northern populations for which there is evidence of restricted gene flow. Despite this the mean **H** for the southern cave millipedes is significantly lower than that for the northern group, which is inconsistent with T1.

T2 is unlikely to be supported as isolation in the cave in Cape Range probably resulted from increasing aridity; the close proximity of the caves and their similarity in altitude makes it unlikely that isolation occurred over a considerable range in time.

T4 is not supported because the caves in Cape Range have, for caves, a high species diversity but low **H** irrespective of whether the species are or are not troglobites. This leaves T3 to be considered. The cave in Cape Range shows environmental uniformity relative to the current external climate but may not be uniform relative to the tropical rainforest from which the fauna probably was derived. In addition, not only is the cave fauna fueled by pulses of organic matter being washed into the caves which are unpredictable in quantity and timing (see climate), but there is evidence that the Cape Range cave fauna undergoes major expansion and contraction in population size, range and breeding rate depending on the state of hydration of the cave and available food supply. Hence, the evidence to date from the Cape Range studies does not fit comfortably with any of the hypotheses proposed.

Husbandry and reproduction

All species except the millipedes survived well on their laboratory maintenance regime.

One *S. vinei* laid nine eggs in captivity. The eggs were carried on the elevated abdomen but she failed to retain them.

Most millipede cultures failed to thrive in captivity and had died out within three months. Young appeared in one batch and survived well on the supplemented food. Future cultures should survive on the new regime.

The isopods were reared easily in captivity and bred readily on both cave litter and supplemented heat sterilized.

The 'miturgids' would initially not feed in the laboratory but ate readily when fed flour moths. Future cultures should survive readily on the new regime. No moths have been observed in the caves but non-cave Miturgidae also feed readily on moths while ignoring many other prey items.

Growth

Growth rates in the laboratory for *S. vinei* have been presented elsewhere (Humphreys *et al.* 1989) and are known to be low. No growth rate information has been gained from the field, nor is it possible so to do during the field season due to the slow growth rates and small individual size.

Origins of cave faunae

There is general consensus that for terrestrial species in northern temperate zone caves that the immediate ancestors of currently troglobitic species are forest soil and litter-dwelling species that were isolated in caves during the Pleistocene interglacials (Barr 1968, Peck 1981a). There are five principle lines of evidence for this (Culver 1982):- 1. Caves in glaciated areas have depauperate or no terrestrial fauna. 2. The closest surface relatives of many cave-limited species are to be found in the litter of boreal forests. 3. Those regions most affected by the Pleistocene, but not ice-covered, have the largest number of terrestrial troglobites. 4. Regions lacking forests throughout the Pleistocene have a depauperate terrestrial cave fauna. 5. Estimates of the time of divergence of closely related species are consistent with isolation during the Pleistocene (Delay *et al.* 1980).

It is considered that the more general hypotheses concerning Pleistocene effects are probably of little relevance to areas in the lowland tropics, in which Cape Range lies, as such effects would have been less severe (Culver 1982). It has been argued that such effects may have been sufficiently great in some lowland caves (Reddell 1981), but this has been disputed (Mateu 1980). Probably because people think of the lowland tropics as comprising rainforest they have been unable to derive parsimonious explanations as to the method of isolation. This has led to explanations depending on refugia from biotic pressure, such as predation or competition (Culver 1982). Such propositions are probably not testable and so have little heuristic value.

The terrestrial component of the Cape Range troglobitic fauna was probably derived in manner directly analogous to the glacial relict fauna of the northern temperate region, with aridity, rather than low temperature, causing the regional extinction of the original habitat (rainforest) of the ancestors of the troglobitic species. In the next section I will explore the evidence for when this may have occurred.

Climatic History

Information on the age of the cave systems in Cape Range is lacking and evidence of the likely age of the systems must be deduced from the fauna and palaeoclimatic data, in itself sparse for Western Australia.

At present Cape Range has a semi-arid climate and the caves contain a troglobitic fauna whose affinities lie with species from humid tropical and sub-tropical forests. These cave species (*S. vinei*, millipedes, pseudoscorpions and 'miturgids') exhibit high rates of for water loss (Humphreys *et al.* 1989 and unpublished) and are derived presumably from a period when rainforest covered Cape Range. As this troglobitic fauna provides the only evidence that rainforest has occupied Cape Range since the Miocene, when the Tulki Limestone was formed, then palaeoclimatic information on rainfall must be examined for clues.

The caves are experiencing presently an erosive rather than a depositional cycle. Nonetheless, there is evidence of two major periods of cave formation which may not have been simultaneous. The evidence of more extensive calcite deposition in caves (White; Appendix 7) and the presence of latisols in the area (Wyrwoll, pers. comm. 1988), some overlying karst features, indicate wetter conditions in the past but do not quantify the degree of wetness or when it occurred (White; Appendix 7). A tentative uranium series dating of some speleothem material indicates that one such wetter period has occurred within the last million years (T. Hamilton, pers. comm. 1988), but more accurate dates have still to be determined.

There is no reliable dating of the start of the present arid conditions in the region but Humphreys *et al.* (1989) argued, on the basis of archaeological data (Morse 1988), that the area has been as arid as the present back to 25000 years before the present (k yr BP). As the Tulki Limestone, in which the caves occur, is of Middle Miocene age (Condon 1968; Playford *et al.* 1975a,b), say 13×10^6 yr BP, we need to find evidence of substantially wetter periods (and preferably of fossil rain forest) between 13000 and 20 k yr BP.

In southern Australia lakes were greatly expanded from 50-20 k yr BP followed by drying and accentuated aridity until about 13 k yr BP (Bowler and Wasson 1984). However, the extensive alluvial deposits ("Red Alluvium") in the Gascoyne and Geraldton districts of Western Australia were formed between 120 and 40 k yr BP and indicate "semi-arid conditions with intense rainfall events occurring more frequently than today...". Following this deposition intense aridity characterized regional climate until an amelioration set in during the Early Holocene (Wyrwoll 1977, 1979).

Kendrick (pers. comm. 1989) recently compiled a large body of data on contemporary Pleistocene fossil distribution of *Anadara trapezi* (Deshayes)(*Bivalvia*: *Arcoida*) which he argues require open estuarine condition.

Should laterites covered with soil →
containing water-worn pebbles in the
base of a gorge indicate that
forest covered the Cape Range after
the gorges had formed?

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Its occurrence in certain deposits indicate such conditions from Shark Bay north to the Lyndon River during both of the last two interglacials. This evidence suggests a more humid climate in the region during the Pleistocene isotopic substages 5e and 7c (following Shackleton and Opdyke 1973; Bowen 1978). While we know nothing of the intensity of these wetter periods it seems that at the earliest rainforest elements could have been supported is either 128 or 225 k yr BP.

The genetical information is consistent with the capture of the now troglobitic fauna by the caves prior to the erosion of the deep canyons which bisect the Tulki limestone in Cape Range. This was overlaid by the Vlaming sandstone which is of Pliocene age (5-1.8 m yr BP).

There is a significant subterranean marine fauna on the coastal plain adjoining Cape Range which has no members in common with the Cape Range cave fauna. As the amphipod from Cape Range is of marine origin (B. Knott; pers. comm. 1988) and is not known to occur on the coastal plain, it would seem that an earlier marine invasion of the Cape Range caves occurred, possibly before the Cape Range anticline was uplifted.

Whatever the actual period of rainforest at or before 128 k yr BP, the significance of this period is that at the youngest the troglobitic fauna of Cape Range is probably older than terrestrial troglobites usually studied. In the northern temperate areas, most terrestrial cave species were isolated in caves during one of the warming periods of the Pleistocene interglacials (Barr 1960, 1965), most recently during the Early Holocene, about 10 k yr BP (Culver 1982).

Aquatic cave species are considered to have been isolated in caves for longer periods than terrestrial species, up to 2000 k yr BP (Hobbs and Barr 1972) or even earlier (Holsinger 1978). [Note that of the species examined from Cape Range the aquatic amphipods genetically are the most dissimilar between caves]. Some other groups are considered to have been isolated more recently; < 10 k yr BP in the Mexican characin *Astyanax mexicanus* (Mitchell *et al.* 1977) and between 20 and 0.09 k yr BP for the diverse Hawaiian lava tube fauna, but this may be complicated by the ability of the species to move between caves (Howarth 1972). Peck (1980, 1981b) has suggested pulses in the rate of isolation of putative troglobites in caves of the Grand Canyon during Pleistocene interglacials, namely >350, 320-275, 235-185, 150-90 and <15 k yr BP.

Culver (1982) generalised that the time of isolation in caves are between 10^4 and 10^5 years for terrestrial species and between 10^5 and 10^6 years for aquatic species. Clearly the Cape Range terrestrial fauna lies at earliest in the top order of magnitude of this estimate. The long period of isolation of the Cape Range troglobites is supported by the very high degree of cave adaptation found in some species, e.g. *Nocticola* sp. nov.

Zoogeography

The lack of major surveys of the terrestrial fauna and flora on North West Cape prevents any serious assessment of the biogeographic affinities of the area. I give below a synopsis of what is known of the area.

The recent mammal fauna of the area is best examined from sub-fossil deposits and from which two elements can be identified: a wet-dry tropical (Torresian) element, consisting of *Dasyurus hallucatus*, *Planigale maculata* and *Mesembriomys macrurus*, for which North West Cape represents a westerly limit; and an arid zone (Eyrean) element composed of the rest of the ground dwelling mammal species which were originally all widespread in suitable habitats in the arid zone. For some of the southern arid zone species such as *Leporillus apicalis* and *Pseudomys fieldi*, if it is correctly identified, North West Cape represents a northerly range limit, probably made possible by the moderating effect on the climate of the west coast summer sea breezes (A. Baynes and B. Jones, unpublished).

Conservation and management

Background

The karst area on North West Cape is of international significance. Most of the caves known from Cape Range are in the Cape Range National Park established in 1964 and extended in 1969 to cover 50581 ha.

In 1976 the National Park was proclaimed Crown Land thereby allowing for oil and gas exploration within the National Park under the guidelines laid down by the Environmental Protection Authority (EPA). The EPA's recommendations for the park's extension were endorsed by Cabinet, but rescinded in 1979.

The CALM Act (1984) requires 'the protection of indigenous fauna and the preservation of any feature of archaeological ... or scientific interest' (CALM 1987).

It is a general management objective for Cape Range National Park to 'protect and conserve indigenous animals and their habitats' as well as the 'physical, cultural and scenic resources'. There are specific management objectives to 'maintain scientific reference areas' and to 'conserve and protect ground water resources' (CALM 1987).

A temporary limestone reserve (TR5980H), under the control of the Minister for Mines, covers a large proportion of the eastern half of Cape Range. This reserve includes all the caves known to contain terrestrial troglobites and much of the coastal area from which the aquatic subterranean fauna is known.

These conservation recommendations are concerned with the biological, but not the speleological, aspects of conservation, although both have much in common. In addition they deal primarily with the caves in Cape Range and do not cover in detail the coastal caves and bore holes which contain a different rare and aquatic subterranean fauna about which little is known, but which is under the greatest pressure from development. This system is not part of a river as believed by Whitley (1945) but is an extensive network of waterways within the limestone and subject to the influence of diurnal oceanic tides (Mees 1962).

Type localities and other significant sites:-

1. There are two distinct subterranean faunae on North West Cape, one in the coastal limestone and the other in the caves of Cape Range. The coastal fauna is distinct from that in Cape Range, having no species in common. The four species known from the coastal limestone co-occur (Hamilton-Smith 1967).
2. Most of the caves in Cape Range, and all those known to contain troglobites, lie within Cape Range National Park or in the proposed southern and eastern extension of the National Park.
3. Many of the caves in Cape Range, and all those known to contain troglobites, lie within the temporary limestone reserve (TR5980H), under the control of the Minister for Mines.
4. Most of the caves containing the coastal subterranean aquatic fauna lie outside the current boundaries of Cape Range National Park, on pastoral property, defence establishment land and the Exmouth town site. This entire fauna is at risk because development of the area is proceeding apace and none of the species in the system is specifically or generally protected by legislation.
5. Cape Range National Park is on the Register of the National Estate, together with the adjoining Ningaloo Marine Park.
6. C21 (Monajee):- the skull of a thylacine (*Thylacinus cynocephalus*, Marsupialia: Dasyuridae) was reported (Kendrick and Porter 1973).
7. C24 (Milyering Well) is the type locality of the Blind or Cave Gudgeon, *Milyeringa veritas* Whitley 1945 (Perciformes: Eleotridae) (Whitley 1960, Allen 1982). This is classified as rare and total protection has been recommended (Michaelis 1985).
8. C26 (Tantabiddi Well) is the type locality of The Blind Cave Eel, *Anommatophasma candidum* (Mees 1962) (Synbranchiformes: Synbranchidae). It is classified as vulnerable (Michaelis 1985). An eel was seen in Kubra Well (C27) in 1973 and in C105, south of the proposed marina in Exmouth, on 29 May 1988 (M. East; pers. comm.), the only sighting in more than a decade.

9. Kudumurra Well is the type locality of *Stygiocaris lancifera* Holthuis and of *S. stylifera* Holthuis (Crustacea: Decapoda) (Holthuis 1960).
10. C106 (Shot Pot) is the type locality of *Schizomus vinei* Harvey 1988 (Chelicerata: Schizomida).
11. C6 is the type locality of *Austropholochaetella kendricki* Jamieson 1971 (Oligochaeta)(see also Humphreys *et al.* 1989).
12. C118 is the type locality of *Nocticola* sp. (Blattodea; Roth ms.), a very highly cave adapted species..
13. C18, C163, C103 and C64 contain an amphipod of marine origin and part of the *Victoriapisa* complex (Gammaridae; B. Knott; pers.comm. 1988). One of the caves will be designated the type locality.
14. A unknown number (>15) of undescribed genera and species, both epigeal and of varying dependence on caves, including troglobites, are in the process of being described from caves in Cape Range. One cave for each species will be designated the type locality and paratypes will probably be allocated from other caves. Some of these species are of considerable biogeographic significance as they have affinities with faunae from distant parts of Australia, as well Papua New Guinea, Africa and India.
15. There are significant sites of human occupation in the caves at the foot of the scarp of Cape Range, few of which have been examined. Mandu Mandu rockshelter was occupied back to 25000 BP (carbon dates) and contains representatives of the contemporary and extinct fauna as sub-fossils (Morse 1988). Padjari Manu (formerly Bunbury Cave) contains engravings and deposits (Site Reference P0267) and rock shelters nearby (P0751) contain some art and sparse deposits. These sites are being managed on the basis of only limited or specialist access (P. Randolph; pers. comm. 1989).
16. The caves in Cape Range are mostly vertical and unsuited to occupancy by humans. However, there is evidence from some caves of human usage of the area; marine shells used as utensils were apparently discarded by aboriginal people in a deep solution hole (C21, Monajee; Kendrick and Porter 1973). A rock shelter at C193 has a blackened roof and was possibly utilized by aboriginal people; this will be examined during the 1989 field season.
17. Bats (Chiroptera) do not commonly enter vertical caves of the type found in Cape Range. Bats have been seen but not collected in C192, C194, C200. Webb (1981) saw two species in C64. Several species have been identified from bone material in caves, namely *Chalinolobus gouldii*, *Eptesicus finlaysoni*, *Tadarida australis*, *Taphozous georgianus* and *Pteropus scapulatus*.

18. There are significant deposits of sub-fossil bones in many caves, some of which are contained in deep deposits of roof fall material (>3 m in C144). The cave deposits have led to significant extensions of the known range of some species of recent mammals. Material collected during the study shows *Dasycercus cristicauda* to be present in sub-fossil deposits (C4; The Owl Roost) and confirmed the presence of *Notomys longicaudatus* (A. Baynes and B. Jones, unpublished) which was doubtful in a previous study (Kendrick and Porter 1973). North West Cape is clearly an important area for the study of the pre-European zoogeography of mammals. However, in order to make substantial further progress an order of magnitude more cave surface material from a number of deposits is required (A. Baynes and B. Jones, unpublished). Thirty-two species of modern mammals have been recorded from bones and sub-fossil deposits in caves, mostly from C4 (A. Baynes and B. Jones; pers. comm.), namely *Dasyurus hallucatus*, *Dasycercus cristicauda*, *Phascogale calura*, *Antechinus rosamondae*, *Pseudantechinus macdonnellensis*, *Planigale maculata*, *Sminthopsis longicaudata*, *Sminthopsis macroura*, *Thylacinus cynocephalus*, *Isodon auratus*, *Perameles* sp., *Trichosurus vulpecula*, (??*Potorous platyops*), *Bettongia lesueur*, *Petrogale*, *Macropus robustus*, *Notomys alexis*, *N. longicaudatus*, *Leporillus apicalis*, *Pseudomys desertor*, *P. fieldi*, *P. hermannsburgensis*, *P. nanus*, *Mesembriomys macrurus*, *Zyzomys pedunculatus*, *Rattus tunneyi*, *Canis familiaris*, *Chalinolobus gouldii*, *Eptesicus finlaysoni*, *Tadarida australis*, *Taphozous georgianus*, *Pteropus scapulatus*. *et al.*

19. The karst system *per se* is an important palaeoclimatic site and there are potentially important palaeoclimatic sites in some caves in the form of stratified mud banks, some with numerous layers especially in C18, C103, C106 and C118, and in the speleothems.

20. The palaeosols obvious around some dolines are indicators of potential palaeoclimatic significance (Appendix 7 and K-H. Wyrwoll, pers. comm. 1988).

21. The troglobitic fauna as a whole is significant due to its endemism, its zoogeographical affinities and as a palaeoclimatic indicator.

22. Those caves containing standing water (C18, C64, C103 and C163) are significant sites for the sampling of deep water bodies within Cape Range for assessment of the nature of the water bodies. *C119?*

23. There are major fossil localities outcropping in the karst area, especially Miocene sites, rich in echinoids, in the Tulki Limestone 1 km south of Charles Knife Road (McNamara and Philip 1984).

Disturbance

Due to the relatively recent exploration of the Cape Range karst there has been little damage to caves in the area. C10 has been blocked with concrete rubble, C90 was deliberately plugged with concrete and C9 contains rubbish and has been silted by the erosion of an area cleared of vegetation during oil exploration (M. East; pers. comm. 1989). ^{THE} Owl's Roost (C4) is the most visited tourist cave and contains some rubbish; this is a shallow and scenic cave easily entered down the roots of a fig tree and it contains significant bone deposits (Kendrick and Porter 1973; A. Baynes and B. Jones, unpublished).

Some coastal caves (known locally as wells), which were major water sources for aboriginal people (Carter 1902), have been heavily utilized for water by pastoralists, Exmouth Town (e.g. C27, Kubura Well, which contained the Blind Cave Eel, *A. candidum*; Mees 1962) and the shire and other authorities. Bores throughout the area draw on the coastal ground water and bore fields along the eastern scarp draw water for Exmouth and the military facilities.

Quarry works south of the Exmouth town site have exposed some underground caverns, including C23 (Dozer Cave) which is adjacent to and connects with C105 which contains *A. candidum* (M. East; pers. comm. 1989). The location of rubbish dumps close to the coastal limestone is a potential source of contamination for the coastal ground water system.

The caves

By 1988 about 212 caves have been recorded from North West Cape, including the coastal regions. Formal surveys of their structure have been made of C29 (Bell), C163 (Wanderer's Delight; part), C118 (Humphreys *et al.* 1989), C18 (Vine *et al.* 1988) and C161 (Star Chamber; part).

The main energy input into the caves is vegetable matter washed into caves by the influx of water associated with mass flow of surface water following unpredictable heavy rainfall (Humphreys *et al.* 1989; Vine *et al.* 1988). This provides nutrients for fungal growth and saprophages, the former supporting the fungivores. Both in turn support the predators (schizomids and spiders); the schizomids are not known to consume any items breeding outside the caves. It is not known what the much rarer 'miturgid' spiders eat; in the laboratory they are adept at catching small moths and have never taken other food offered including many of the cave species, except other 'miturgids'. However, observation suggests that accidentals are not an important component of the cave fauna.

The caves are vulnerable to outside inputs which may be considered under two categories. A) direct effects on the caves and B) indirect effects on the caves.

A) Direct effects:

Owing to the nature of the caves their ecosystems are vulnerable to changes induced internally by a number of factors. These fall into four categories. 1) pollutants, 2) disturbance 3) atmospheric and 4) surface activity.

1. Pollutants: a container of pressurized domestic insecticide or insect repellent dropped intact into a deep cave will eventually corrode and the entire contents would be released at once. Such an episode would effectively fumigate a large volume of the cave. Air movement in some caves is minimal and this would exacerbate the local lethal effect. A surface contact insecticide would have a much longer term effect. Because flies are a nuisance in Cape Range, insect repellants are more likely to be dropped deliberately or accidentally into caves.

People entering caves are likely to contaminate the caves with general rubbish, which while unsightly, is unlikely to disrupt the ecosystem. Of more concern are the nutrient supplement resulting from organic wastes, especially food and faeces. The latter are of most concern as they may attract from a distance a range of coprophilic organisms. Of specific concern is rubbish which may breakdown releasing toxic materials, especially heavy metals, which may persist in the cave. These are mainly associated with lamps (carbide from acetelene lamps, and cadmium, mercury and lead from batteries). While responsible cavers remove all material from caves, even members of major caving clubs have been known to leave such material in caves.

2. Disturbance: people entering caves can physically disturb the fauna by trampling and by moving stones. This is especially true on the mud-banks which are the preferred area of movement of cavers, and areas where the fauna is most prone to crushing.

3. Atmospheric: the entry of large numbers of people can significantly change the gas composition and the humidity in caves, as can the enlargement of cave entrances to facilitate access. However, most caves on Cape Range ~~caves~~ are poor in decoration and otherwise unsuited to mass use such as would occur in a tourist cave.

4. Nearby surface activity: dumping of anything into or near a cave, either garbage, rubble or soil, may alter the drainage into or within the cave (e.g. block current exits), change its nutrient status or pollute it.

1. Oil exploration is continuing apace around Cape Range both onshore and offshore and interest has been expressed in further exploring Cape Range itself. This can have a number of effects in addition to the more general effects discussed above:-

a) Roughly graded tracks for seismic exploration can disrupt the pattern of water

flow and lead to increased erosion and hence sediment transport by water.

b) Gas or oil leaks from exploration or production wells in the karst area could permeate through large parts of the cave system, eliminating the fauna and presenting a major hazard to cavers.

2. Roads through the karst area: a number of tracks were constructed in Cape Range during the period of oil exploration in the 1950's. These tracks have permitted access to some of the karst area and are unsealed.

The Environmental Protection Authority is currently drawing up general environmental guidelines for oil exploration in Western Australian National Parks. Specific guidelines need be drawn up for oil exploration in Cape Range (see above).

B) Indirect effects:

Owing to the epigeal origin of the energy input into the caves changes at the surface within the water catchment of the cave may have a considerable impact on the cave ecosystem. This needs to be considered in any management procedures on the range. These fall into three categories:- 1) pollutants, 2) drainage pattern, 3) vegetation changes and 4) changes to the water table.

1) **Pollutants:** because the main influx of water is derived from the run-off associated with exceptionally heavy rainfall, surface pollutants are likely to be carried into the cave from throughout its catchment. However, as such water flow tends to be massive the pollutants are likely to be considerably diluted. Hence, unless the pollutant is in high concentration or highly toxic, run-off pollution is probably of no great concern.

More insidious are the long term changes resulting from changes to the catchment of a given cave.

2) **Drainage pattern:** changes to the drainage pattern of the catchment may change the humidity, detritus influx and sedimentation rate of the cave. The drainage pattern may be changed in the long term through, for example, road construction, or in the short term by temporary features associated with construction sites or mineral exploration. Such changes will be temporary only if the vegetation and the landform of the sites are restored on completion of the work. Both changes will influence the cave environment by changing the long term mean levels of energy or humidity and by changing the periodicity of the energy input.

Periodicity *per se* may be crucial as the cave ecosystem receives a pulsed input of energy associated with unpredictable heavy rainfall. Hence, changes to the periodicity and pulse size, especially lengthening the mean period between

pulses, may disrupt finely tuned life cycle adaptations to the mean pulse length and frequency. Such interactions generally are little understood and are the focus of current research. Local extinction would be predicted if there was sufficient interruption to the input of organic matter, initially of the predators and later of the detritivores. Minor silting eliminate the pools of water inhabited by the amphipods in C18. Sedimentation is important as many of the cave organisms are most prolific on, or found only in, the mud-banks in the caves which retain water and buffer changes in cave humidity.

3) **Vegetation changes:** burning or clearing vegetation will also alter the long term mean energy input into a cave and its periodicity, even in the absence of changes to the drainage pattern. The effects will be similar to changes in drainage pattern.

The consequences to the cave ecosystem of minor changes to the drainage pattern or vegetation cannot be predicted other than that there will be some change. However, total disruption to energy input will eliminate the cave fauna, and reduction of the mean relative humidity below 90%, will probably eliminate the troglobitic fauna as it is found only in caves with high humidities (this report; Vine *et al.* 1988; Humphreys *et al.* 1989).

The caves in Cape Range are of importance other than for the conservation of fauna. Caves and karst areas have wide ranging values covering the fields of aesthetics, landform, biology, hydrology, limnology, paleoenvironment, archaeology, minerology and recreation. Management plans for the karst area should take into account these other values when drawing up strategies for faunal protection.

Water Table

The existence of aquatic fauna in some of the caves is dependent on the current water table. Lowering of the water table in the range will eliminate populations from within the explorable regions of caves. In addition it may lower the cave humidity and, in consequence, affect adversely the terrestrial cave fauna, especially the schizomids. At this stage little is known of the water bodies within Cape Range other than, as the fauna has no species in common, they are separate from those of the coastal plains. The genetical evidence from the aquatic amphipods suggests that the major canyons separate not only the populations, but also the water bodies they inhabit.

Cave faunae generally, and schizomids in particular, are vulnerable to change in the water table. *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 oases were rendered unsuitable for *S. joshuensis* by draining (Rowland and Reddell 1981).

Considerable quantities of bore water are drawn from the foothills of Cape Range and the surrounding coastal plain to supply human needs. Additional draw off has recently been committed to supply tourist and management facilities at Milyering and more is proposed to service new tourist facilities all around North West Cape.

The Geological Survey of Western Australia consider there is a shallow fresh water lens beneath Cape Range rising to no more than 5 m above MSL, that this is recharged after exceptional rain, and that the coastal areas are recharged by run off from the range. It is considered that the water drawn from the aquifers by the water supply authorities in the area represents recharge water and not fossil water, but there is no direct evidence to support this assertion and no detailed examination of the bore logs has been undertaken.

Of particular concern, in the absence of a faunal survey, is the proposal to cut a marina through the coastal limestone to the south of Exmouth. This will force the salt water wedge further inland and potentially bisect the known distribution of the Blind Cave Eel (*Ophisternon candidum*). The coastal plain has unique fauna of aquatic animals (Cawthorn 1953) including two species of fish, *O. candidum*, and the Blind or Cave Gudgeon (*Milyeringa veritas*), classified respectively as vulnerable and rare (Michaelis 1985). Knowledge of the distribution of this coastal fauna is sparse and fragmentary and a survey of its distribution and abundance is needed urgently. This is undoubtedly the most threatened ecosystem on North West Cape, and about which least is known

Little is known about the water bodies in and around Cape Range. Management of the water supply should aim to monitor the bores for the level of the saline layer so as to provide advanced warning of over use of the ground water. In addition hydrological work should be conducted to identify the water bodies involved, both within and around Cape Range, so that their degree of integration can be determined and the implications of drawing ground water established. Over the last ten years, two known springs have ceased to flow (Appendix 7) and some bores to the north of Exmouth have dried up (L. Banfield, pers. comm. 1988), both suggestive of recent lowering of the water table.

Are the caves Interconnected?

Examination of the current evidence (see above) suggests that the caves are much bigger than indicated by the dimensions of the individual caves alone. That is, with respect to the dispersion abilities of the fauna, the caves, or certain subsets of the caves, probably form a continuous network of galleries.

The evidence for connections (see Humphreys *et al.* 1989).

1. Apparent similarity of the communities within the caves.
2. Apparently much larger populations present than are observed within those sections of the caves accessible to humans.
3. Caves that have lost their fauna after deep flooding are recolonized in a time period inconsistently short with respect to the growth rate of the species.
4. Caves with very confined populations due to dryness are widely occupied after the cave has been wetted by shallow flooding.
5. There is genetic homogeneity (at the species level) of the fauna separated by long distances but which are not separated by major canyons. Within these groups genetic distance is correlated directly with distance of separation between caves.

The evidence against connections (see Humphreys *et al.* 1989).

1. Many caves have high levels of carbon dioxide and there is a general lack of obvious air movement ("breathing"); this is inconsistent with barometrically induced air flow to be expected in extensive cave systems.
2. There is no direct evidence that any caves are linked; the extensive leads in C163 have approached but not so far reached any other cave *i.e.* those caves with extensive lateral development do not pass beneath adjacent known caves.
3. The only evidence to data that there is any discontinuity in the water body along the length of Cape Range known to be occupied by troglobites is the genetical evidence from the amphipods. However, the range water is clearly distinct from that of the coastal limestone (Humphreys *et al.* 1989) and they contain no species in common.
4. There is strong genetical evidence that there is no interbreeding between populations of troglobites in caves separated by the deep canyons which dissect the limestone in which the caves are formed *i.e.* there is genetic discontinuity across the major geomorphological hiatuses.

Conclusions

Assuming that the troglobites cannot move across the surface between caves or as part of the epigean fauna (see above and Humphreys *et al.* 1989):-

1. Caves in the southern group are interconnected below ground but there is some restriction of gene flow between the caves.

2. Caves in the northern group (excluding C64) are interconnected below ground but there is greater restriction of gene flow between the caves than between those in the southern group.

3. Caves in the northern and southern group and C64 are probably not interconnected below ground even indirectly.

Uncertainty

Uncertainty about the extent of the interconnection between the known caves would complicate considerably potential management of the karst region. However, knowledge that there are connections between some caves and no connections between others has considerable management implications that differ in the two cases.

Interconnection means that the populations are extensive and the loss of the populations in a single cave would not result in serious depletion of the genetic stock. However, interconnection also means that serious pollution of a single cave could effect the entire cave system and result in the loss of the entire genetic stock.

Lack of interconnection (as between the northern and southern cave groups) has the converse management implications:- damage to a single cave could result in the loss of an entire genetic stock (whether this would be at the species level has yet to be determined), but serious pollution would be limited to that cave and not spread through the entire system.

Clearly the southern group of caves needs to be managed as a whole as the caves are interconnected, however tenuously. The northern group (excluding C64) contains more heterogenous populations and more genetical information is required to determine whether individual caves should be managed separately (especially C159 for *S. vinei*). C64, the only known cave containing troglobites north of Shothole Canyon, should be managed separately.

Implications

This information has serious management implications as the effective management for conservation of single caves requires only the protection of the cave and its catchment, however, those caves that are interconnected requires that the karst area needs be managed as a whole.

Recommendations

Knowledge of the caves in Cape Range is both recent and very limited; the only mention in the Management Plan (CALM 1987) of caves in Cape Range is in

reference to vertebrate fossil material. The following recommendations are made solely in terms of the conservation of the troglobitic fauna without consideration of other factors.

A) Of the 212 caves known from North West Cape, about 16 in Cape Range are currently known to contain the characteristic terrestrial troglobitic fauna. For the catchment areas of those caves (namely C18; C76; C64; C103; C106; C107; C118; C126; C159; C162; C163; C167; C169; C190; C198; and C207):-

1. Foot tracks and roads should not pass close the caves to reduce the possibility of accidental pollution (e.g. insecticide containers).
2. The catchment area and drainage pattern should not be disrupted in any way that may alter the drainage characteristics or runoff rate. Hence, roads should not pass through cave catchments (they alter drainage patterns and hydrocarbons from road making materials and vehicle waste may pollute the caves), nor should the vegetation be cleared (it accelerates runoff and changes sediment loads).

A new road traversing the range is planned and two routes have been proposed with a preferences for a link between Shothole Canyon to Milyering (CALM 1987). Both routes tranverse the known distribution of the caves containing troglobites.

B) For any major development on Cape Range, such as the proposed road making, mineral exploration, alteration to road surfaces and buildings (CALM 1987):-

1. A survey for caves should be conducted on foot by competent cavers on the proposed site or route and they should be examined for cave fauna.
2. If significant cave fauna is found they should be treated as in A) above.
3. Hydrocarbons should not be sprayed on roads to bind them.

C) Access to the caves is mostly dependent on local knowledge of their locations. This knowledge is being rapidly disseminated and direct human pressure on the caves will increase. As most caves require technical climbing gear, casual visits are mostly precluded. Nonetheless, a number of instances of irregular cavers using irregular equipment have been observed. Officially, permission is required from the management authority to cave in the National Park (for reasons of safety rather than management) but there is no effective control due to the location of the main cave area in relationship to the management personnel. The effects of human usage of caves on troglobitic fauna is little understood but there are indications that caution should be exercised in their management. Two caves in Australia (Phoenix Cave and Bunangonia Cave) contained numerous cave

crickets and silverfish (*Thysanura*) when they were first discovered. Three years later (1977) a long term study on the crickets started and this was followed by a steady decline in numbers. The cave entrance was then blocked for six months and the number of crickets started to increase (Smith 1978). This experience does not demonstrate cause and effect but raises a note of caution about the potential sensitivity of troglobitic fauna to disturbance.

Due either to the characteristics of their entrances or to their remoteness it would be impracticable to restrict access, by the construction of gates, to many of the fauna caves (e.g. C167, C118, C103) for the purpose of faunal conservation, nor at present could it be warranted. However, the situation should be kept under review and overt pressure on the faunal caves may require direct action to prevent degradation. If this arises it is entirely practicable to gate and barrier the access tracks to much of the karst area to prevent unauthorized vehicle entry. Such action would deter all but the most determined cavers and the presence of vehicles at the gates would alert rangers to unauthorized entry.

6. The management authority should establish a regular working group to liaise with local cavers, caving clubs, biospeleologists and other informants to monitor the use of and degradation to cave systems. The working group should be invested with the power to recommend specific actions (e.g. gating) and to monitor their implementation and effectiveness.

7. A number of major facilities are proposed which require water and waste disposal; they include a camp site 600 m from Milyering Well, the type locality of *Milyeringa veritas* (Fig. 6 in CALM 1987). Although composting toilets will be utilized wherever possible within the Cape Range National Park (CALM 1987), it is recommended that borehole toilets not be constructed in the coastal limestone on North West Cape until there is some understanding of the distribution and genetics of the coastal subterranean fauna.

8. A survey of the subterranean fauna characteristic of the coastal limestone should be undertaken as a matter of priority because it is little understood and is potentially vulnerable to the development projects underway or planned. Initially the genetics of the populations on either side of North West Cape should be examined to establish whether management needs consider a single population or genetically distinct populations; the implications of this are discussed above in reference to the caves in Cape Range.

Summary recommendations

1. The catchment areas of caves that contain troglobitic fauna (C18, C¹⁵~~76~~, C64, C103, C106, C107, C118, C126, C159, C162, C163, C167, C169, C190, C198 and C207; see Appendix 10), and any caves subsequently discovered to contain troglobitic fauna (hereafter called the caves), should be mapped and protected according to the guidelines specified above.

2. The subterranean fauna on the coastal plain of North West Cape should be surveyed, as to their distribution and genetic heterogeneity, as a matter of priority.
3. All caves containing troglobites should be protected from any disturbance that will affect their functioning as a natural system.
4. Foot tracks and roads should not pass close the caves.
5. No clearing, alteration, deposition, removal or construction should occur within the catchments of the caves.
6. Proposed clearing, alteration, deposition, removal or construction (including access tracks) within the karst area should be preceded by a full cave survey by competent biospelologists on foot. New caves containing significant fauna should be treated as above.
7. Hydrocarbon contamination from construction, vehicles, exploration and road surfaces should be prevented within the catchments of the caves.
8. The precise locations of caves should not be widely disseminated until effective monitoring and management of the karst area is established.
9. The management authority should establish a working group with powers to make specific management recommendations, to monitor their implementation and effectiveness, and to recommend nomination of specific caves which should be given explicit statutory protection of their structure and contents.
10. Long term lowering of the water table (either coastal or within Cape Range), or changes to the characteristics of the water, will alter the nature of the cave systems. The management authority, in conjunction with those authorities with responsibilities or interests in ground water, should establish a working group to implement a thorough and detailed assessment of the ground water on North West Cape. This should determine the nature of the water bodies, their connectedness, characteristics, rate of replenishment and rate of draw off (both natural and artificial). Subsequent water management should aim to draw off recharge water only, leaving fossil water bodies intact.
11. The management authority, in conjunction with other competent authorities, should draw up a management plan specifically for the karst areas of the national park. The current management plan makes little mention of the karst areas and has no recommendations specifically applicable to these areas.
12. The management authority should provide information on, and interpretation of, cave heritage within the National Park. While the caves are covered by the

general policy, of both caving clubs (through the Australian Speleological Federation), and national parks, that all refuse must be removed respectively from caves and national parks, the information needs reinforcing for caves as removal should include human excrement, and the guidelines should emphasise the problems associated with, and sources of, heavy metal pollution.

13. The temporary limestone reserve (TR5980H), vested in the Minister for Mines, should be rescinded.

14. The proposed route of the trans-range road should be surveyed comprehensively on foot for caves and their contents by competent biospeleologists; the final route should avoid the catchments of caves containing troglobites.

15. Until the subterranean fauna in the coastal plains has been examined adequately, all new toilet facilities established in the area should be of the composting type.

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APPENDICES

Appendix 1: Coordinates¹, names and numbers of karst features from Cape Range mentioned in the text. The C prefix denotes caves from the Cape Range karst province allocated by the Australian Speleological Federation (Matthews 1985). The coordinates were determined from the grid references on the 1:50000 Series R712 maps: Mandu (Sheet 1653-I); Tantabiddi (Sheet 1654-II); Yardie Creek (Sheet 1653-II); Learmonth (Sheet 1753-IV) and North West Cape (Sheet 1754-III).

CAVE#	NAME	LATITUDE	LONGITUDE
C4	The Owl Roost	22° 11' 03"S	113° 59' 03"E
C18	Dry Swallett	22° 05' 24"S	113° 59' 30"E
C24	Milyering Well	22° 01' 06"S	113° 55' 39"E
C26	Tantabiddi Well	21° 56' 09"S	113° 57' 45"E
C28	Bundera Sinkhole	22° 24' 51"S	112° 45' 51"E
C36	The Twin Holes	22° 10' 24"S	113° 59' 09"E
C64	Shot-Hole Tunnel	22° 02' 39"S	114° 01' 06"E
C94	Unnamed	21° 49' 54"S	114° 04' 06"E
C96	Anomaly Cave	22° 00' 06"S	113° 57' 21"E
C103	Trionomo Cave	22° 07' 27"S	114° 59' 21"E
C105	Unnamed	21° 58' 58"S	114° 07' 22"E
C106	Shot Pot	22° 04' 21"S	114° 00' 39"E
C107	Unnamed	22° 07' 00"S	113° 59' 54"E
C118	Unnamed	22° 09' 21"S	113° 59' 27"E
C126	Unnamed	22° 08' 45"S	113° 59' 54"E
C144	Unnamed	22° 10' 45"S	113° 58' 57"E
C149	Tulki Well	22° 05' 30"S	113° 53' 48"E
C159	Gullet Cave	22° 07' 23"S	114° 00' 18"E
C162	Rock Bench Cave	22° 09' 00"S	113° 59' 51"E
C163	Wanderer's Delight Cave	22° 09' 06"S	114° 00' 12"E
C167	Spiral Cave	22° 09' 09"S	113° 59' 39"E
C169	Unnamed	22° 06' 12"S	114° 00' 27"E
C186	Unnamed	22° 07' 09"S	114° 00' 09"E
C187	Unnamed	22° 07' 18"S	114° 00' 18"E
C188	Unnamed	22° 07' 09"S	114° 00' 08"E
C189	Unnamed	22° 06' 45"S	114° 00' 03"E
C190	Unnamed	22° 06' 36"S	114° 00' 06"E
C191	Unnamed	22° 07' 57"S	113° 57' 06"E
C192	Unnamed	22° 13' 24"S	113° 57' 09"E
C193	Unnamed	22° 13' 56"S	113° 56' 45"E
C194	Unnamed	22° 13' 57"S	113° 56' 51"E
C195	Unnamed	22° 13' 24"S	113° 57' 19"E
C196	Unnamed	22° 13' 21"S	113° 57' 21"E
C197	Unnamed	22° 12' 51"S	113° 56' 54"E
C198	Unnamed	22° 12' 51"S	113° 56' 54"E

C199	Unnamed	22° 12' 39"S	113° 00' 59"E
C200	Unnamed	22° 13' 30"S	114° 00' 36"E
C203	Unnamed	22° 26' 15"S	113° 54' 36"E
C204	Unnamed	22° 26' 15"S	113° 54' 36"E
C205	Unnamed	22° 23' 48"S	113° 55' 24"E
C206	Unnamed	22° 22' 48"S	113° 54' 30"E
C207	Two Hundred Cave	22° 12' 15"S	113° 59' 12"E
C209	Death Adder	22° 09' 12"S	113° 59' 48"E

¹Grid references have deliberately been omitted from this report to protect better the location of the caves.

Appendix 2: Genetics data for the amphipods (determined by M. Adams, Evolutionary Biology Unit, South Australian Museum).

a: Genetic profiles of individual amphipods
b: Allele frequencies for the four populations of amphipods.
c: Genetic distance matrix for populations of amphipods.

Appendix 2a: Genetic profiles of individual amphipods (assuming autosomal loci in a diploid organism). Allozymes are designated alphabetically, in order of increasing electrophoretic mobility. (- not scorable).

EBU#	Cave	Fdp	Gapd	Got1	Gpi	Hk	Idh	Ldh	Mdh1	PepD	Pgam	Pgm1	Pgm2
A01	C163	b	b	b	c	ab	a	a	a	c	a	c	a
A02	C163	b	b	b	c	a	ab	a	a	b	a	c	a
A03	C163	b	b	b	c	a	b	a	a	c	a	c	a
A04	C163	b	b	b	bc	b	a	a	-	bc	b	c	a
A05	C164	b	a	a	a	b	b	a	a	b	ab	b	a
A06	C164	b	a	a	a	ab	b	a	a	ab	ab	b	a
A07	C164	b	a	a	a	b	b	a	a	a	b	b	-
A08	C164	b	a	a	a	b	b	-	a	a	b	b	-
A09	C64	a	a	b	a	b	b	-	a	b	b	ab	a
A10	C64	a	a	b	a	b	b	a	a	b	ab	b	a
A11	C64	a	a	b	a	b	b	-	-	b	b	b	-

[illegible]

**Appendix 2b: Allele frequencies for the four populations of amphipods.
Maximum sample size per cave in brackets.**

LOCUS	allele	C163 (4)	C164 (4)	C64 (3)
<u>Fdp</u>	b	100	100	
	a			100
<u>Gapd</u>	b	100		
	a		100	100
<u>Got1</u>	b	100		100
	a		100	
<u>Gpi</u>	c	87		
	b	13		
	a		100	100
<u>Hk</u>	b	37	87	100
	a	63	13	
<u>Ldh</u>	b	37	100	100
	a	63		
<u>PepD</u>	c	62		
	b	38	37	100
	a		63	
<u>Pgam</u>	b	25	75	83
	a	75	25	17
<u>Pgm1</u>	c	100		
	b		100	83
	a			17
<u>Tpi</u>	c			100
	b		100	
	a	100		
Invariant loci:- <u>Acon1</u> , <u>Acon2</u> , <u>Enol</u> , <u>Got2</u> , <u>Gp1</u> , <u>Gp2</u> , <u>Gpt</u> , <u>Lap</u> , <u>Ldh</u> , <u>Mdh1</u> , <u>Mdh2</u> , <u>Mpi</u> , <u>PepA</u> , <u>Pgm2</u> and <u>Pk</u> .				

Appendix 2c: Genetic distance matrix for populations of amphipods.
Lower matrix - % fixed difference
Upper matrix - Corrected Nei's D (x 1000)

	C163	C164	C64
C163	-	296	297
C164	20	-	148
C64	20	12	-

Appendix 3: Genetics data for the isopods (determined by M. Adams, Evolutionary Biology Unit, South Australian Museum).

- a: Genetic profiles of individual isopods.
 b: Allele frequencies for the four populations of isopods.
 c: Genetic distance matrix for populations of isopods.

Appendix 3a: Genetic profiles of individual isopods (assuming autosomal loci in a diploid organism). Allozymes are designated alphabetically, in order of increasing electrophoretic mobility. (-- not scorable).

####	Cave	Acon1	Acon2	Adh1	Adh2	Dia	Enol	Fdp	Gapd	Got1	Got2	Gp1	Gp2	Gpi
I01	C18	aa	aa	aa	aa	bb	bb	aa	aa	bb	ab	aa	aa	aa
I02	C18	aa	aa	bc	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I03	C18	aa	aa	bb	ab	bb	bb	bb	aa	bb	bb	aa	aa	aa
I04	C18	aa	aa	bb	aa	bb	bb	bb	--	bb	bb	aa	aa	aa
I05	C18	aa	aa	aa	aa	bb	bb	a	aa	bb	bb	aa	aa	aa
I06	C18	aa	aa	ab	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I07	C18	aa	aa	aa	aa	bb	bb	ab	aa	bb	bb	aa	aa	aa
I08	C18	aa	aa	bb	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I09	C126	aa	aa	aa	aa	bb	bb	ab	aa	bb	bb	aa	aa	aa
I10	C126	aa	aa	ab	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I11	C126	aa	aa	ab	aa	ab	bb	bb	aa	bb	bb	aa	aa	aa
I12	C126	aa	aa	bb	aa	bb	bb	ab	aa	bb	bb	aa	aa	aa
I13	C106	aa	aa	aa	aa	bb	bb	ab	aa	bb	bb	aa	aa	aa
I14	C106	aa	aa	aa	aa	bb	bb	ab	aa	bb	bb	aa	aa	aa
I16	C106	ab	aa	bb	aa	ab	bb	ab	aa	bb	bb	aa	aa	aa
I17	C107	aa	aa	bb	aa	bb	bb	ab	aa	bb	bc	aa	aa	aa
I18	C107	aa	aa	bb	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I19	C107	aa	aa	ab	aa	bb	bb	ab	--	bb	ab	aa	aa	aa
I20	C107	aa	ab	ab	aa	bb	bb	bb	aa	bb	bb	aa	aa	aa
I21	C167	aa	aa	aa	aa	bb	bb	ab	aa	ab	bb	aa	aa	aa
I22	C167	--	aa	bb	aa	bb	bb	bb	--	ab	bb	aa	aa	aa
I23	C167	--	aa	aa	aa	bb	bb	bb	--	bb	bb	aa	aa	aa
I24	C167	--	aa	bb	aa	bb	ab	ab	--	bb	bb	aa	aa	aa

####	Cave	Gpt	Lap	Ldh	Mdh	Mpi	PepB	PepD1	PepD2	Pgd	Pgam	Pgm1	Pgm2
I01	C18	aa	aa	aa	aa	ce	bb	aa	aa	aa	aa	bb	bb
I02	C18	aa	aa	aa	aa	ff	bb	aa	aa	aa	aa	bb	bb
I03	C18	aa	aa	aa	aa	gg	ab	aa	aa	aa	aa	bb	ab
I04	C18	aa	aa	--	aa	fg	bb	aa	aa	ab	aa	bb	bb
I05	C18	aa	aa	aa	aa	cc	bb	aa	aa	aa	aa	bb	bb
I06	C18	aa	aa	aa	aa	cg	bc	aa	aa	aa	aa	bb	bb
I07	C18	aa	aa	aa	aa	--	bb	aa	aa	ab	aa	bb	bb
I08	C18	aa	aa	--	aa	fh	bb	aa	aa	ab	aa	bb	ab
I09	C126	aa	aa	aa	aa	eh	bb	aa	aa	aa	aa	bb	bb
I10	C126	aa	aa	aa	aa	bh	bb	aa	aa	aa	aa	bb	bb
I11	C126	aa	aa	--	aa	df	bb	aa	aa	aa	aa	bb	bb
I12	C126	aa	aa	aa	aa	ee	ab	aa	aa	aa	aa	ab	bb
I13	C106	aa	aa	aa	aa	eg	bb	aa	aa	aa	aa	bb	bb
I14	C106	aa	aa	aa	aa	eh	ab	aa	aa	aa	aa	bb	bc
I16	C106	aa	aa	aa	aa	ah	bb	aa	aa	--	aa	bb	bb
I17	C107	aa	aa	aa	aa	ii	bb	aa	aa	aa	aa	bb	bb
I18	C107	aa	aa	aa	aa	hh	bb	aa	aa	aa	aa	bb	bb
I19	C107	aa	aa	aa	aa	fg	bb	aa	aa	aa	aa	bb	bb
I20	C107	ab	aa	--	aa	fh	bb	aa	aa	aa	aa	bb	bb
I21	C167	aa	aa	aa	aa	ei	bb	aa	aa	ab	aa	bb	ab
I22	C167	aa	aa	aa	aa	ei	bb	aa	aa	aa	aa	bc	ab
I23	C167	aa	aa	aa	aa	hh	bb	aa	aa	aa	aa	bb	ab
I24	C167	aa	aa	aa	aa	ee	bb	aa	aa	ab	aa	bb	bb

All individuals were aa for Ald, Ap, Glo, Pk1, Pk2, Sordh, and Tpi.

Appendix 3b: Allele frequencies for the four populations of isopods. Maximum sample size per cave in brackets.

LOCUS	allele	C18 (8)	C126 (4)	C106 (3)	C107 (4)	C167 (4)
<u>Acon-1</u>	b			17		
	a	100	100	83	100	100
<u>Acon-2</u>	b				12	
	a	100	100	100	88	100
<u>Adh-1</u>	c	6				
	b	50	50	33	75	50
	a	44	50	67	25	50
<u>Adh-2</u>	b	6				
	a	94	100	100	100	100
<u>Dia</u>	b	100	87	83	100	100
	a		13	17		
<u>Enol</u>	b	100	100	100	100	87
	a					13
<u>Fdp</u>	b	75	75	50	75	75
	a	25	25	50	25	25
<u>Got-1</u>	b	100	100	100	100	75
	a					25
<u>Got-2</u>	c				12	
	b	94	100	100	75	100
	a	6			13	
<u>Gpt</u>	b				12	
	a	100	100	100	88	100
<u>Mpi</u>	i				25	25
	h	7	25	33	37	25
	g	28		17	13	
	f	29	12		25	
	e	7	38	33		50
	d		12			
	c	29				
	b		13			
	a			17		
<u>Pep-B</u>	c	6				
	b	88	87	83	100	100
	a	6	13	17		
<u>6Pgd</u>	b	19				25
	a	81	100	100	100	75

<u>Pgm-1</u>	c					12
	b	100	87	100	100	88
	a		13			

<u>Pgm-2</u>	c			17		
	b	87	100	83	100	62
	a	13				38

Invariant loci: Ald, Ap, Gapd, Glo, Gp-1, Gp-2,
Gpi, Lap, Ldh, Mdh, Pep-D1, Pep-D2, Pgam, Pk-1,
Pk-2, Sordh and Tpi.

Appendix 3c: Genetic distance matrix for the isopod populations.

Lower matrix - % fixed difference

Upper matrix - Corrected Nei's D (x 1000)

	C18	C126	C106	C107	C167
C18	-	1	1	2	0
C126	0	-	0	0	0
C106	0	0	-	4	0
C107	0	0	0	-	0
C167	0	0	0	0	-

Appendix 4: Genetics data for the millipedes (determined by M. Adams, Evolutionary Biology Unit, South Australian Museum).

a: Genetic profiles of individual millipedes.

b: Allele frequencies for the four populations of millipedes.

c: Genetic distance matrix for populations of millipedes.

Appendix 4a: Genetic profiles of individual millipedes (assuming autosomal loci in a diploid organism). Allozymes are designated alphabetically, in order of increasing electrophoretic mobility. (- not scorable).

####	Cave	Acon	Ada	Adh1	Ald	Dia	Fdpa	Fum	Got2	Gpi	Gsr	Hk	Idh	Lap
M01	C18	ac	c	b	a	a	b	a	b	ab	a	-	-	c
M02	C18	ac	c	b	a	a	b	a	b	a	a	a	a	c
M03	C18	c	c	-	-	a	b	a	b	a	a	a	-	c
M04	C18	c	c	-	a	b	b	a	b	b	a	a	-	c
M05	C106	c	c	b	a	ab	b	a	b	be	a	a	a	cd
M06	C106	c	c	b	a	b	b	a	b	bd	a	a	a	d
M07	C106	c	c	b	a	b	b	a	b	bd	a	a	-	d
M08	C106	c	c	b	a	a	b	-	b	b	-	-	-	d
M09	C64	d	c	b	a	a	a	a	b	c	a	b	a	d
M10	C64	d	c	b	a	a	a	a	b	bc	-	b	-	cd
M11	C64	d	c	b	a	a	a	a	b	bc	a	b	a	d
M12	C64	d	c	b	a	a	a	a	b	c	a	b	a	cd
M13	C126	c	b	a	a	a	b	a	b	b	a	b	a	c
M14	C126	c	a	a	a	a	b	a	b	ab	a	b	a	cd
M15	C126	c	ab	a	a	a	b	a	b	b	a	b	a	c
M16	C126	c	b	a	a	a	b	a	b	b	a	-	a	c
M17	C167	c	b	a	a	a	b	a	b	b	a	b	a	c
M18	C167	c	ab	a	a	a	b	a	b	ab	a	b	a	c
M19	C167	c	b	a	a	a	b	a	b	b	a	b	a	c
M20	C167	c	b	a	-	a	b	a	b	b	a	b	a	c
M21	C159	b	c	b	a	a	b	a	b	b	a	-	-	c
M22	C159	bc	c	b	a	a	b	b	ab	bc	-	-	a	cd
M23	C159	b	c	b	a	a	b	a	ab	b	-	-	-	d
M24	C159	b	c	b	a	a	b	a	ab	b	-	-	-	cd
M25	C118	c	ab	a	a	a	b	a	b	b	a	b	a	c
M26	C118	c	b	a	a	a	b	a	b	b	a	b	a	c
M27	C118	c	ab	a	-	a	b	a	b	b	a	b	a	c
M28	C118	c	a	a	a	a	b	a	b	b	a	b	a	c
M29	C103	e	c	b	a	a	b	ab	ab	c	a	a	a	d
M30	C103	ce	c	b	a	a	b	a	a	bc	a	-	-	cd
M31	C103	cd	c	b	a	a	b	a	a	c	-	-	-	de
M32	C103	c	c	b	-	a	b	a	a	c	-	-	-	d

M33	C107	c	cd	b	a	a	ab	a	b	cd	a	a	a	cd
M34	C107	ab	cd	b	a	ab	b	a	ab	cd	a	-	a	bd
M35	C107	c	c	b	a	b	ab	a	b	bc	a	a	a	ae
M36	C107	c	c	b	a	ab	b	a	b	bc	a	a	a	cd
M37	C20 ⁷ 3	c	a	a	a	a	b	a	b	b	a	b	-	c
M38	C20 3	c	a	ab	a	a	b	a	b	b	a	b	-	c
M39	C20 3	c	a	a	a	a	b	a	b	b	a	b	-	c
M40	C20 3	c	a	a	a	a	b	a	b	b	a	b	-	c

Cave Mdh2 Ldh PepD Tpi Pgam PepA PepB Mpi Mdh1 Got1 Gp1 Enol Pk Ap

M01	C18	ab	a	b	ab	b	b	b	ab	a	a	a	a	a
M02	C18	b	a	b	b	ab	b	bc	a	a	a	a	a	a
M03	C18	b	a	b	b	b	b	b	ab	a	a	a	a	a
M04	C18	ab	a	b	b	bc	b	c	b	a	a	a	a	a
M05	C106	b	a	b	b	b	b	b	ab	a	a	a	a	a
M06	C106	b	a	b	b	b	b	b	b	a	a	a	a	a
M07	C106	b	a	b	b	b	b	b	ab	a	a	a	a	a
M08	C106	b	a	b	b	b	b	b	-	a	a	a	a	a
M09	C64	b	a	b	c	c	b	b	ab	a	a	a	a	a
M10	C64	b	a	b	b	c	b	b	ab	a	a	a	a	a
M11	C64	b	a	b	b	cd	b	b	a	a	a	a	a	a
M12	C64	b	a	-	b	c	b	b	ab	a	a	a	a	a
M13	C126	c	a	b	b	b	b	a	a	a	a	a	a	a
M14	C126	c	a	b	b	be	b	a	a	a	a	a	a	a
M15	C126	c	a	b	b	b	b	a	a	a	a	a	a	a
M16	C126	c	a	b	b	be	b	a	a	a	a	a	a	a
M17	C167	c	a	b	b	b	b	a	a	a	a	a	a	a
M18	C167	c	a	b	b	b	b	a	a	a	a	a	a	a
M19	C167	c	a	b	b	b	a	a	a	a	a	a	a	a
M20	C167	c	a	b	b	be	b	a	a	a	a	a	a	a
M21	C159	b	a	b	b	b	b	b	a	a	a	a	a	a
M22	C159	b	a	b	b	b	b	b	a	a	a	a	a	a
M23	C159	b	a	b	b	b	b	b	a	a	a	a	a	a
M24	C159	b	a	b	b	b	b	b	a	a	a	a	a	a
M25	C118	c	a	b	b	be	b	a	a	a	a	a	a	a
M26	C118	c	a	b	b	be	b	a	a	a	a	a	a	a
M27	C118	c	a	b	b	be	b	a	a	a	a	a	a	a
M28	C118	c	a	b	b	b	b	a	a	a	a	a	a	a
M29	C103	b	a	b	b	b	b	b	a	a	a	a	a	a
M30	C103	b	-	b	b	b	b	b	a	a	a	a	a	a
M31	C103	b	a	b	b	b	b	b	a	a	a	a	a	a
M32	C103	b	-	b	b	b	b	b	a	a	a	a	a	a
M33	C107	b	a	b	b	ab	b	b	ab	a	a	a	a	a
M34	C107	b	a	b	b	b	b	b	ab	a	a	a	a	a
M35	C107	b	ab	b	b	b	b	b	b	a	a	a	a	a
M36	C107	b	a	b	b	ac	b	b	ab	a	a	a	a	a
M37	C203	c	a	b	b	e	b	a	a	a	a	a	a	a
M38	C203				c	a	b	b	e	b	a	a	a	a
M39	C203	c	a	b	b	e	b	a	a	a	a	a	a	a
M40	C203	c	a	b	b	b	b	a	a	a	a	a	a	a

Group I - C118, C203, C126 and C167

Group II - C159, C107, C103, C18, C106 and C64.

Appendix 4b: Allele frequencies for the ten populations of millipedes. Maximum sample size per cave in brackets.

[illegible]

<u>Ldh</u>	b						12				
	a	100	100	100	100	100	88	100	100	100	100
<u>Tpi</u>	c			25							
	b	87	100	75	100	100	100	100	100	100	100
	a	13									
<u>Pgam</u>	e							25	12	37	75
	d			12							
	c	12		88			12				
	b	75	100		100	100	63	75	88	63	25
	a	13					25				
<u>PepA</u>	b	100	100	100	100	100	100	100	75	100	100
	a								25		
<u>PepB</u>	c	37									
	b	63	100	100	100	100	100				
	a							100	100	100	100
<u>Mpi</u>	b	50	67	37			62				
	a	50	33	63	100	100	38	100	100	100	100

Invariant loci: Ald, Ap, Enol, Got1, Gp1, Gsr, Mdh1, PepD and Pk.

Appendix 4c: Genetic distance matrix for populations of millipedes.
 Lower matrix - % fixed difference
 Upper matrix - Corrected Nei's D (x 1000)

	C18	C106	C64	C126	C167	C159	C118	C103	C107	C203	7
C18	-	49	201	214	221	72	221	105	30	249	
C106	0	-	203	275	291	77	289	89	8	326	
C64	11	15	-	343	366	153	352	185	138	371	
C126	19	19	26	-	0	218	-4	310	268	22	
C167	19	19	26	0	-	230	5	326	284	46	
C159	0	0	12	15	15	-	226	52	63	260	
C118	19	19	26	0	0	15	-	327	278	12	
C103	0	0	11	19	19	0	19	-	56	367	
C107	0	0	7	19	19	0	19	0	-	308	
C203	15	15	23	0	0	12	0	15	15	-	

Appendix 5: Genetics data for *Schizomus vinei* (determined by M. Adams, Evolutionary Biology Unit, South Australian Museum).

- a: Genetic profiles of individual *S. vinei*.
 b: Allele frequencies for the four populations of *S. vinei*.
 c: Genetic distance matrix for populations of *S. vinei*.
 d: Genotype frequencies at the three polymorphic loci of *S. vinei*.

Appendix 5a: Genotypes for all individuals of *Schizomus vinei* at the three polymorphic loci (assuming autosomal loci in a diploid organism).

####	CAVE	Est	Mdh-2	Pgm
S1	C18	bb	bb	ab
S2	C18	bb	bb	ab
S3	C18	bb	bb	ab
S4	C18	bb	bb	bb
15 (87)	C18	bb	bb	ab
16 (87)	C18	bb	bb	aa
17 (87)	C18	bb	bb	ab
18 (87)	C18	bb	bb	bb
S5	C103	bb	bb	aa
S6	C103	bb	bb	aa
S7	C103	bb	bb	aa
S8	C103	bb	bb	aa
S10	C106	ab	bb	aa
S11	C106	bb	bb	aa
S12	C106	ab	bb	aa
S9	C106	bb	bb	aa
23 (87)	C106	bb	bb	aa
24 (87)	C106	bb	bb	aa
26 (87)	C106	bb	bb	aa
31 (87)	C106	bb	bb	aa
S13	C118	ab	bb	aa
S14	C118	bb	bb	aa
01 (87)	C118	bb	bb	aa
02 (87)	C118	bb	bb	aa
06 (87)	C118	ab	bb	aa
10 (87)	C118	aa	bb	aa
S15	C126	bb	bb	aa
S16	C126	bb	bb	aa
S17	C126	bb	bb	aa
S18	C126	bb	bb	aa
07 (87)	C126	bb	bb	--
08 (87)	C126	bb	bb	aa
S19	C159	ab	aa	aa
S20	C159	bb	aa	aa
S21	C159	aa	aa	bb
S22	C159	bb	aa	ab

S23	C162	bb	bb	aa
S24	C162	bb	bb	aa
S25	C162	bb	bb	aa
S26	C162	bb	bb	aa
S27	C167	bb	bb	aa
S28	C167	bb	bb	aa
S29	C167	bb	bb	aa
S30	C167	bb	bb	aa
Overall allele frequencies (%):		b=90 a=10	b=91 a=9	b=14 a=86

Appendix 5b: Allele frequencies for the *Schizomus vinei* populations. Genotypes were assigned assuming autosomal loci in a diploid organism. Allozymes are designated alphabetically, in order of increasing electrophoretic mobility. Maximum sample size per cave in brackets. The results of the 1987 and 1988 studies have been integrated.

Locus allele	CAVE						
	C18 (8)	C103 (4)	C106 (8)	C118 (6)	C126 (6)	C159 (4)	C162 C167 (4) (4)
<u>Est</u>	b	100	100	87	67	100	62 100 100
	a			13	33		38
<u>Mdh-2</u>	b	100	100	100	100		100 100
	a					100	
<u>Pgm</u>	b	56				37	
	a	44	100	100	100	63	100 100

Invariant loci: Ald, Enol, Gapd, Gp, Hex, Hk, Ldh, Pk, and Tpi.

Invariant (not all samples active): Acon, Ada, Got, Gpi, Idh, Mdh-1, Pep-1, Pep-2, Pga and Pgk.

Appendix 5c: Genetic distance matrix for the *Schizomus vinei* populations.
Lower matrix - % fixed difference
Upper matrix - Corrected Nei's D (x 1000)

	C18	C103	C106	C118	C126	C159	C162	C167
C18	-	14	14	18	14	62	14	14
C103	0	-	0	3	0	68	0	0
C106	0	0	-	0	0	63	0	0
C118	0	0	0	-	4	59	3	3
C126	0	0	0	0	-	68	0	0
C159	5	5	5	5	5	-	68	68
C162	0	0	0	0	0	5	-	0
C167	0	0	0	0	0	5	0	-

Appendix 5d: Genotype frequencies at the three polymorphic loci of *S. vinei* - pooled data.

Locus	Genotype	Observed Frequency	Expected Frequency
<u>Est</u>	bb	37	35.6
	ab	5	8.0
	aa	2	0.4
<u>Mdh-2</u>	bb	40	36.4
	ab	0	7.2
	aa	4	0.4
<u>Pgm</u>	bb	3	0.
	ab	6	10.4
	aa	34	31.8

Appendix 6: The enzymes (and protein) used to examine the variation between the populations of the four species from the caves of Cape Range:- the number denotes the number of alleles found in each species, normal type = invariate locu, bold type = variate locus and italic type = invariate locus but not all samples were active.

	Millipedes	Amphipods	<i>S. vinei</i>	Isopods
Aconitate hydratase (ACON, E.C. 4.2.1.3)	1	2	<i>1</i>	2
Adenosine deaminase (ADA, E.C. 3.5.4.4)	1	-	<i>1</i>	-
Alcohol dehydrogenase (ADH, E.C. 1.1.1.1)	1	-	-	2
Aldolase (ALD, E.C. 4.1.2.13)	1	-	1	1
Alkaline phosphatase (AP, E.C. 3.1.3.1)	1	-	-	1
Diaphorase (DIA, E.C. 1.6.*.*)	1	-	-	1
Enolase (ENOL, E.C.4.2.1.11)	1	1	1	1
Esterase (EST, E.C. 3.1.1.1)	-	-	1	-
Fructose-1, 6-diphosphatase (FDP, E.C. 3.1.3.11)	1	1	-	1
Fumarate hydratase (FUM, E.C. 4.2.1.2)	1	-	-	-
Glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.2)	-	1	1	1
Lactoyl-glutathione lyase (GLO, E.C. 4.4.1.5)	-	-	-	1
Aspartate aminotransferase (GOT, E.C. 2.6.1.1)	2	2	-	2
General protein (GP),	1	2	1	2
Glucose-phosphate isomerase (GPI, E.C. 5.3.1.9)	1	1	<i>1</i>	1
Alanine aminotransferase (GPT, E.C. 2.6.1.2)	-	1	-	1
Glutathione reductase (GSR, E.C. 1.6.4.2)	1	-	-	-
Hexosaminidase (HEX, E.C. 3.2.1.30)	-	-	1	-
Hexokinase (HK, E.C. 2.7.1.1)	1	1	1	-
Isocitrate dehydrogenase (IDH, E.C. 1.1.1.42)	1	1	<i>1</i>	-
Leucine amino peptidase (LAP, E.C. 3.4.11 or 13)	1	1	-	1
Lactate dehydrogenase (LDH, E.C. 1.1.1.27)	1	1	1	1
Malate dehydrogenase (MDH, E.C. 1.1.1.37)	2	2	2	1
Mannose-phosphate isomerase (MPI, E.C.5.3.1.8)	1	1	-	1
Peptidases (PEP, E.C. 3.4.11 or 13.*)	3	2	2	4
Phosphoglycerate mutase (PGAM, E.C. 2.7.5.3)	1	1	<i>1</i>	1
6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44)	-	-	-	1
Phosphoglucomutase (PGM, E.C. 2.7.5.1)	-	2	1	3
Phosphoglycerate kinase (PGK, E.C. 2.7.2.3)	-	-	<i>1</i>	-
Pyruvate kinase (PK, E.C. 2.7.1.40)	1	1	1	2
L-idoitol dehydrogenase (SORDH, E.C. 1.1.1.14)	-	-	-	1
Triose-phosphate isomerase (TPI, E.C. 5.3.1.1)	1	1	1	1

Appendix 7: Report on the geomorphic development and history of the karst features of the Cape Range, North West Cape, Western Australia.

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The area of the North West Cape is a semi arid Tertiary limestone peninsula on the north west coast of Western Australia. The peninsula has a central 16km wide spine of folded Miocene limestones rising to an altitude of 311m and is fringed by coastal plains (Vine *et al.* 1988). The lithologies are Miocene limestones and Quaternary limestones and calcareous sand-stones as described by Condon 1968, Playford *et al.* 1975a,b, van de Graaff *et al.* 1980. The youngest Tertiary formation, the Trealla Limestone and most of the Quaternary deposits have been eroded of the top of the sequence, exposing the older Tulki Limestone and Mandu Limestone.

The major landforms of the main range have been initially controlled by tectonic structures; the range coincides with the major anticlinal structures (van de Graaff *et al.* 1980). The coastal plains which fringe this main range consist predominantly of the shallow marine and aeolian Pleistocene Bundera Calcarene which shows some local facies and depositional variation expressed as the Jurabi, Tantabiddi and Mowbowra Conglomerate members. As well, superficial deposits of lateritic material, colluvium, aeolianite and clay pan materials are common on the surface, especially, but not exclusively, of the coastal plains. The Pleistocene to Recent depositional history has been one of shoreline terrace deposition followed by emergence. Reef building is occurring at present and the evidence of reef material on the emerged shoreline terraces indicates this has occurred throughout at least the Pleistocene. Lagoonal and coastal dune deposits are currently important on the coast.

Calcretization has occurred extensively in the various calcareous sediments. Solutional processes are and have been important in the development of the landforms. Caves and other solutional features are common in all the calcareous sediments.

KARST LANDFORMS

In 1985 about 120 caves were documented from Cape Range (Matthews, 1985) but extensive exploration since then has discovered many more caves and shows that despite its semi-arid climate, the area is intensely caverniferous (B. Vine, pers. comm.).

About 209 caves have now been documented from the Cape Range area. Most of these are vertical solution pipes in the Tulki Limestone but there are a few e.g. C64 (Shot Hole Tunnel) and C163 (Wanderer's Delight) which show horizontal development. There are four types of cave found in what can be described as a karst province:

1. Vertical solution pipes with or without modification from collapse in folded Miocene limestone. These caves are variable in size and depth but appear to terminate at similar levels in the range, possibly at a previous water table, although more analysis needs to be done to confirm or deny this. They are often modified by collapse with large vertically aligned chambers. The entrances are often large and some e.g. Shot Pot (C106) bifurcate vertically. These caves show a lot of evidence of modification by large amounts of water at irregular intervals, and have possibly formed at joint intersections.

2. Horizontal systems in the main range usually, but not always, have vertical entrance pipes in the folded Miocene limestones. These systems are less well known as very few have been found and examined. However, more exploration will probably find more. The most extensive are Wanderer's Delight (C163) and Shot Hole Tunnel (C64), both of which show extensive low, horizontal, joint controlled passages with stream deposits on the floor. They appear to be formed at the top of a higher water table and have undergone more than one period of solution and deposition.

3. Small horizontal shallow caves in the coastal limestones sometimes leading to permanent water e.g. Milyering Cave (unnumbered). These caves are more similar to, but generally smaller than the caves of southwest Western Australia.

- 4 Rock shelters along the escarpments and gorges in the folded limestones. These have not been extensively looked at to determine levels of development but this is perhaps an area of further interest especially as they are important archaeologically.

The first two cave types listed show extensive evidence of further modification after their initial formation. Most of the vertical caves have large solution entrances which have been modified by collapse, and as well many have rock pile floors. The rubbly and perforated (extensive "phreatic" preparation) nature of much of the Tulki Limestone in which they form, enhances this modification. Evidence of large amounts of water entering the caves at times of intense rainfall can be found in the floor sediments. Stream bedload material of well rounded cobbles or coarse sand is found in a number of caves e.g. Wanderer's Delight, (C163) and in some of the important faunal caves e.g. Shot Pot (C106), stratified mud banks have formed the floor. Streams have cut into these mudbanks in some cases. In many cases rock piles have been removed by water action and may form some of the bedload material although this is hard to ascertain.

The horizontal caves on the whole have vertical entrances either as a pothole e.g. Wanderer's Delight (C163) or the steep sided gorge e.g. Shot Hole Tunnel (C64) has acted as the access to the horizontal systems.

Many caves have calcite speleothem deposits. Very little is currently active, not even intermittently, and most is either covered with mud e.g. Wanderer's Delight (C163), or being eroded back e.g. Anomaly (C96) and especially Owl's Roost (C4). The speleothems are predominantly wall and roof decoration often with high detrital content.

Surface Features

The centripetal drainage commented on by Condon (1968) is an important component of the surface karst features of the range. It is an essential factor in the concentration of water into the caves and solution pipes. The closed depressions so created are often large in area and rather shallow, so maximizing water collections in times of rainfall, an important factor in arid climates.

There are some solution features such as karren on the well cemented surfaces of the Tulki Limestone but this is not as extensive as in more tropical areas such as the Kimberleys.

GEOMORPHIC HISTORY

The geomorphic history of such a karst area is closely related to the climatic history of the area. Unfortunately relatively little work has been done into the Cainozoic history of Western Australia and some of that has been constrained within the dating ranges of ^{14}C . Dating of speleothems using uranium series dating may enlighten us on some of these problems.

The caves are located in limestones of mid-Miocene age which were subjected subsequently to tectonic action with the formation of the Cape Range Anticline and the corresponding synclinal feature of the Exmouth Gulf (van der Graaff *et al.* 1980). The development of the caves post dates the uplift and initial deformation of the area.

Speleogenesis

Cave development implies subaerial conditions for the solution and redeposition of calcite speleothems as such deposition occurs in the vadose zone. The horizontal systems formed at the top of a water table must have been above the water table for calcite precipitation. This is indirect evidence of lowering of water tables in the areas, perhaps related to the emergence of the coastal terraces. These horizontal systems should correlate with the emerged coastal terraces on the western side of the range (White, in prep.).

The development of the vertical caves has occurred as a consequence of the development of the centripetal drainage and is initially unrelated to the development of the horizontal passages at the top of the water table.

Subsequently in many places, the two independent systems have connected: the vertical potholes creating access to horizontal systems and leading to modification of those caves by the irregular inflow of quite large amounts of water.

Climatic History

The importance of establishing more accurate dating of the onset of aridity in Australia is offset by the difficulty in obtaining datable material. Theoretically arid conditions resulting in less water, vegetation and soil carbon dioxide result in poorly developed karst and evidence from the Nullarbor supports this as a general idea (Jennings, 1985). However extensive systems can still develop under such conditions than just the existence of caves. The development of the horizontal cave systems cannot therefore be regarded as evidence of wetter periods *per se*, although they show other evidence of wetter conditions. Even the vertical caves and the large closed depression catchments for them do not indicate substantially wetter periods than now as rainfall which arrives as intense cyclonic storms can result in large amounts of water entering the caves. Indeed, mud levels on the walls and the humidity levels in the cave air indicate that the vertical caves take and store water in such times which probably would otherwise evaporate.

On the other hand, the precipitation of calcite speleothems in the amounts present would require slower seepage of water through the soil and rock pore spaces and joints and cave environments which were wetter than at present. Although there is high air humidity and occasional underground stream conditions, neither of these are conducive to calcite deposition in the flowstone forms present. These present conditions are actually more erosive rather than depositional, and the presence of old flowstone in many caves is an indicator of wetter conditions. This is supported by the absence of much freshly precipitated calcite and the covering of thick mud over most of the speleothems. However very tentative initial Uranium series dating of some material indicates that one such wetter period has occurred within the last million years (T. Hamilton pers. comm. 1988), but more accurate dates have still not been determined.

The reporting of the a latisol over part of the Tertiary sequences (Vine *et al.* 1988) is also such evidence. Remnants of similar iron rich soil profiles can be observed in several of the dolines containing caves and a systematic search for such soil profiles may be very useful in determining evidence for previous climatic regimes.

The development of the caves on the coastal plain may not be related to either of the other two major speleogenetic phases. In all cases the position of the water table is crucial to the movement of water and its behaviour. The horizontal passages indicate periods of higher water tables and the emerged terraces indicate that the water table would have lowered corresponding to the relative lowering of the sea level. Over the last ten years, two known springs have ceased to flow, also indicating a more recent lowering of the water table.

CONCLUSIONS

There is evidence of two major periods of cave formation which may or may not be simultaneous. The evidence of more extensive calcite deposition in caves and the presence of latisols indicate wetter conditions in the past but do not quantify the degree of wetness or when it occurred. The present conditions are that of semi arid climate with occasional episodes of intense cyclonic rainfall which is effectively drained into the caves so providing conditions of extreme fluvial activity for short periods of time. How long each cave is affected by such water appears to be cave specific. There is no evidence of rising water tables at such time, only storage of surface runoff which may bank up and be slow to drain away. This in turn may affect the humidity of particular caves.

Appendix 8: Distances (km) between the various caves from which samples were taken for genetical anlysis.

[illegible]

Appendix 9: Taxa collected from Cape Range and environs. Some important species recorded in the literature are noted also. Numbers with the prefix C represent cave numbers from the Cape Range karst region.

ANNELIDA

Austropholochaetella kendricki Jamieson 1971. C6

MOLLUSCA (det. S.M. Slack-Smith¹ and the Camaeinidae by A. Solem)

Chondrinidae

Gastrocopta sp. cf *G. pilbarana*

Pupillidae

Pupoides sp.²

C107; 167

Punctidae

Discocharopa sp.

C21 (Kendrick & Porter 1973).

Subulinidae

Pseudopeas interioris Tate 1894³

C103, C159, C167

Eremopeas sp.

C21 (Kendrick & Porter 1973).

Camaeinidae⁵

Sinumeloninae⁸

New genus⁸

C107, C118

New genus⁸

C144

Strepsitaurus sp. nov.

C103, C107, C159

Strepsitaurus rugus (Cotton 1953)

C18, C366, C96⁷, C103, C118, C159, C162

Pleurodontidae

Rhagada sp. nov.⁹

C96, C106, C159

Subfamily position uncertain

Quistrachia sp. nov.¹⁰

C18, C96, C103, C107, C118, C167

¹ The identifications are tentative; most species are endemic to the Cape Range peninsula (pers. comm.; S.M. Slack-Smith 1988) ² May prove to be endemic species to the Cape Range peninsula (pers. comm. S.M. Slack-Smith 1988)

³ Normally found in rainforest litter. ⁵ Identified by A. Solem; all the species are restricted endemics to Cape Range. ⁶ In rock crevices near cave. ⁷ From doline outside cave. ⁸ Biogeographically the Sinumeloninae occur from North West Cape, south-westwards through the arid and semi-arid regions to the Eyre Peninsula in South Australia and no species are known from wet tropical areas; both the new genera are monotypic and restricted but *Strepsitaurus* has three Cape Range species (A. Solem, pers. comm. 1989.). ⁹ Restricted to North West

Cape; Biogeographically *Rhagada* extends from Mitchell Plateau in the Kimberley District (monsoonal tropics) to Shark Bay to the south of Cape Range; *ca* 25 species are known (A. Solem, pers. comm. 1989.). ¹⁰ Restricted to North West Cape; *Quistrachia* has *ca* 10 species extending from the Napier-Oscar Ranges in the south Kimberley District to Warroora (100 km south of Cape Range) and one species from Black Mt., near Boulia in West Queensland (A. Solem, pers. comm. 1989.).

CRUSTACEA

Atyidae

Stygiocaris stylifera Holthuis (1960) C25 (Kudumurra Well), C24 (Milyering Well) (Holthuis 1960), C27 (Kubura Well) (Cawthorn 1963).

Stygiocaris lancifera Holthuis (1960) C25 (Kudumurra Well), C24 (Milyering Well) (Holthuis 1960).

Amphipoda

Undescribed species³. C18²; C64¹; C103¹; C163¹.

¹Specimens from this cave used in genetics study. ²This cave now contains no accessible water. ³Populations from different caves are not panmictic; see genetics results and discussion.

Isopoda

Armadillidae¹

Beddelundia spp.

Philosciidae¹

Australophiloscia sp. nov. (close to *A. nicholli*). C18; C103

¹There are several species in each group some of which are troglobites (H. Dalens; pers. comm. 1988). Their status has yet to be determined.

Genetics were conducted on *Australophiloscia* sp. from C18; C106; C107; C126; C167

- C156 Post cellon milled-ped.
- 0447 C15
C62

DIPLOPODA (det. W.A. Shear)

Craspedosomida?⁴

Paradoxosomatidae

New genus¹ C185; C645; C76 (Lowry); C642; C1035; C1065;
C1075; C1185; C1265; C1595; C162; C163; C1675; C169; C1903;
C1983; C2075.

¹ "It is a new genus of the family Paradoxosomatidae, one which is highly modified for a troglobitic existence, probably more strongly so than anything I have ever seen in this family. The new genus is closely related to an epigean one, *Antichiropus*, which seems to be endemic to Western Australia" (W.A. Shear; pers. comm. 1988).

² Found in this cave for the first time in 1988 despite it having been known for many years and being one of the most visited caves in Cape Range. ³ Seen and not collected. ⁴ This family is found in rainforest of eastern Australia and is probably a relict rainforest species. ⁵ Specimens from this cave used in genetics study.

CHILOPODA (det. J.M. Waldock)

Scolopendromorpha

Scolopendridae

Scolopendrina morsitans. Learmonth camp; Five Mile Well (dead on water)

Cormocephalus westangelasensis C107; C167

Cryptopidae

Cryptopidae C107

Geophilomorpha

Geophilomorpha C103

Scutigleromorpha

Allothreuea ?leseurii C18; C207

Allothreuea sp. C94; C96; C169

Lithobiomorpha C18

ARACHNIDA (det. J.M. Waldock)

SCORPIONES

Buthidae

Lychas alexandrinus Learmonth camp

ACARINA (det. J.M. Waldock)

Ixodidae

?Amblyomma sp. From human leg after caving

Argassidae

K Ornithodoros gurneyi From people after caving in Cape Range

PSEUDOSCORPIONIDA (det. M.S. Harvey)

Vachonidae

Gen. et sp. nov.¹

C103

CHTHONIDAE

Tyrannochthonius sp.²

C103 / C15 / C167

SYARINIDAE
Gen. nov. C167/C15

¹Several species of the genus *Indohya*, previously known only from India, were collected in remnant rain forest in the Kimberley in 1988. *Indohya* most likely belongs to the family Vachonidae together with the new genus from C103 in Cape Range. Hence biogeographically this is consistent with a local, epigeal genus in the general area of the cavernicolous form cf. millipedes (M. Harvey; pers. comm. 1988). As *Indohya* is found in rainforests, the new genus is probably a rainforest relict. ² This is a common genus of which several are cavernicolous (M. Harvey; pers. comm. 1988).

SCHIZOMIDA

Schizomus vinei Harvey C18¹; C103¹; C106¹; C107; C118¹;
C126¹; C159¹; C162¹; C163; C167¹;
C169. ~~+ C15~~

¹Specimens from this cave were used in genetics study.

Specimen

* C186 Part cellar * C147 C15

ARANEAE

Miturgidae

'Miturgidae' (cave) C162, C163 (seen) C15 (no adults)

blind, pale, very high water loss.

Miturgidae (non-cave) Camp

Filistatidae

Not blind but cave adapted? but found also outside caves?

Pholcidae

not blind.

Linyphiidae

New genus; blind - C15

Clubionidae C167 (Spiral Cave) 13/8/1962. P. Cawthorn^e and WASG leg. Depigmented with regressed eyes (Lowry 1980), , possibly derived from *Chiracanthium* but lack claw tufts (BYM pers. comm.)¹.

¹ Possibly the 'miturgid' as only recently separated and fits description.

INSECTA

~~PROTURA~~ DIPLOURA

Japygidae

? Camptodeidae C15

THYSANURA

Being examined by G. Smith in Sydney C15

COLLEMBOLA (det. P. Greenslade).

Entomobryidae

Lepidosira sp. C126; C203; C162; C118; C190.

BLATTODEA (m, male; f, female; n, nymph)

Nocticola n. sp. Roth ms. C103 (2f,n); C118 (m,n); C126 (m); C167 (mf); C169 (fn).

ORTHOPTERA (det. D. C. F. Rentz).

Nemobiinae: unknown cricket (nymphs, f). C118, C159, C167, C190.

?*Endocusta* sp. nymph (Phalangopsinae) Padjari Manu (Bunbury Cave).

Gryllacrididae immature Camp.

HEMIPTERA (det. M. Malipatil)

Heteroptera

Reduviidae

Reduviinae

Reduviinae sp. nypmh

C118 / c15

Centrogonus sp. nymph¹

C94

Emersinae

Ploiaria sp.(Emersinae) nymph²

C113; C144; C203.

Stenolemoides sp.; (Emersinae).

C118 Just inside cave

Harpactorinae

Poecilosphodrus sp. nov. 2³

Coreidae

Cletus sp (Coreidae)

Coreidae

Coreidae

Coreidae

Scutelleridae

Scutelleridae

Other

Pentatomidae nymphs

Lygaeidae

Genus ? sp. (Lethaeini).

C207

¹ Appear to be the same species collected in Chillagoe Caves, Queensland.

² Similar species occur in Chillagoe Caves, Queensland.

³ He has more specimens of this species on loan from WAM and hopes to describe it shortly.

COLEOPTERA (Det. T.A. Weir).**Carabidae***Carenum* sp. (Scaritini).**C18; C126***Clivina* sp. (Clivinini).**C118** This genus burrows into mud on river banks.**Staphylinidae***Pinophilus* sp. (Paederinae)**C18; C106; C107****Pselaphidae**

Genus ? sp. (Brachyglutini).

C18**Scarabaeidae***Onthophagus alquirta* Matthews (Scarabaeinae). **C144**

Genus ? sp. (Melolonthinae).

C116**Tenebrionidae***Gonocephalum* sp. (Opatrini).**C18****Cerambycidae****Lamiinae.****C103****Curculionidae***Mylocerus* n. sp? (Polydrosinae) **C118; C169** (Prey of Pholcid).

Genus ? sp. (Cryptorhynchinae).

C207**Carabidae****Harpalitae***Lecanomerus* sp.¹**C18; C106.** Fully developed

hindwings therefore probably a troglophile; other species are known from caves in various parts of Australia and there are many from surface habitats in the wetter parts (B.P. Moore; pers. comm. 1989).

Psydridae

Mecyclothorax sp.¹

C118. This is the only flightless *Mecyclothorax* sp. known from caves, although the fully winged *M. punctipennis* (Macl.) is found, as a casual, in such habitats; other flightless species are mostly restricted to wet mountain forests of eastern Australia and Pacific islands, but *M. punctatus* (Sloane) is known from drier habitats (B.P. Moore; pers. comm. 1989).

Panagaeitae

Craspedophorus sp.¹

C126. Shell only. *Craspedophorus* species are essentially insects of the surface under open woodland although a few occur in wetter forests. All other Australian species are orange or yellow spotted (i.e. aposematic) but this species is immaculate and more slenderly built than most. *C. macleayi* (Sloane), an orange spotted species, is known from the north-west at King Sound (B.P. Moore; pers. comm. 1989).

¹ The affinities are clearly with wet forests faunae, though not necessarily tropical ones. Their status as cavernicoles is uncertain because there is no information on the surface fauna and they still have small but functional eyes (B.P. Moore; pers. comm. 1989).

MISCELLANEOUS

Livistona Palm, *Livistona alfredii* (F. Muell.) (det. R.N. Rodd). First specimens from south of the Pilbara Block; they are known elsewhere only from Millstream, 340 km ENE in the Fortescue basin, and from Duck Creek, 280 km to the east in the Ashburton basin; both are in the Pilbara Block.

Bats seen in C192; C194; C200 (B. Vine).

Bones seen in C192, C200 (B. Vine).

'Worms' seen in C64 (B. Vine). and C163 (M. East, pers., comm.).

Springtails seen in C190; C198 (B. Vine).

Spiders seen in C190 (B. Vine).

Crickets seen in C190 (B. Vine).

Skink (*Morethia ruficauda exquisita* Storr 1973; from C207, lacking characteristic vertebral stripe).

**Known species of troglobitic animals from the Caves of
Cape Range and North West Cape.**

Schizomus vinei Harvey 1988

'Miturgid' (undescribed)

Linyphiid (new genus)

Cricket (> 1 spp.)

Cockroach, *Nocticola* n. sp. Roth ms. Very highly cave adapted.

Diplopoda: Craspedosomatidae, new genus (otherwise found in leaf litter of
moist forests of eastern Australia. Most cave adapted.

Amphipods (1+ spp.)

Isopods (2+ spp.)

Pseudoscorpion

The Blind or Cave Gudgeon, *Milyeringa veritas* Whitley 1945
(Perciformes: Eleotridae).

The Blind Cave Eel, *Anommatophasma candidum* (Mees 1962)
(Synbranchiformes: Synbranchidae).

Stygiocaris lancifera Holthuis (Crustacea: Decapoda) (Holthuis 1960).

Stygiocaris ~~*Stylifera*~~ Holthuis (Crustacea: Decapoda) (Holthuis 1960).

Carab beetles

Appendix 10: Descriptions of the caves containing troglobites.

C4 The Owl Roost: a solution pipe entrance containing a large fig tree. The roots can be free climbed down to the top of a rubble slope at 5-6 m. This slope leads down *ca* 10 m into a large a spacious horizontal chamber. A very nice column to the left of the cave and some good helictites in the upper right corner. Small tunnel can be followed *ca* 12 m into the upper right of the cave. A small chamber (The Basement) *ca* 4 m below the floor of the cave. Entrance of which is difficult to find.

C18 Dry Swallet (called Gaping Gill by Cawthorne 1962): A large diameter solution pipe with a second much smaller entrance leading to a ledge 6 m below and from which the cave is entered by a 28 m abseil. A very large chamber below with a flat floor covered in large algal covered boulders. A tunnel leads off one side into a moist crawl containing many troglobites. A pool which used to contain amphipods is now filled with gravel. From the other side of the main chamber a tunnel leads upwards into a large dry chamber. Total depth *ca* 41 m. Map in Vine *et al.* (1988).

C28 Bundera Sinkhole: type section for the Bundera Calcarenite. A water filled collapse or cenote.

C36 The Twin Holes: a vertical solution pipe of 13.7 m is joined through a squeeze to a sinkhole (freeclimb).

C64 Shot-hole Tunnel: a low horizontal cave about 300 m long into the side of a gorge. Flowing water from the cave with a ~~sump~~^{SYPHON} towards the middle. h

C94 (unnamed): single large flat chamber with two entrances; eastern one a circular solution pipe *ca* 3.5 m deep, the other a collapse. Very dry.

C96 Anomaly Cave: a collapse entrance to an extensive horizontal cave; shelter for goats and bats.

C103 Trionomo Cave: entered by vertical solution pipe into a large chamber with a second pitch from the base of which a passage leads to a third pitch and further passages. A fourth free climb pitch leads to three crawl passages, one of which ends at a pool with amphipods.

C106 Shot Pot: a large sinkhole in a valley with an 18 m entrance pitch into a chamber with a short tight crawl at the bottom. On the north side is a stoop passage above the main chamber entered by a 23 m pitch and always very damp; plan in Vine *et al.* (1988).

C107 (unnamed); a large inflow cave with a large fig tree growing in the entrance. A crawl passage in one wall extends at least 30 m. A crawl from the back wall leads to a damp chamber with tree roots on the wall.

C118 (unnamed): collapse doline and inflow cave entered by a short passage leading to a 17 m pitch. Plan in Humphreys *et al.* (1989).

C126 (unnamed): an inflow cave with a long and narrow slot entrance leading to a large diameter solution pipe about 54 m deep. Horizontal development at the bottom (*ca* . 300m).

C144 (unnamed): a sinkhole with an 18 m entrance pitch to a half-bell shaped chamber containing a large unstratified mud-bank rich in sub-fossil bone material.

C159 Gullet Cave: narrow slot entrance *ca* 3.6 m long leads to a 6 m pitch (free climb). Total depth *ca* 25 m with a small damp chamber at the bottom.

C162 Rock Bench Cave: inflow solution pipe *ca* 10 m deep with a cavern at the bottom with a mud floor, damp in parts. Surveyed in September 1988.

C163 Wanderer's Delight Cave: a large open entrance taking inflow. From the base (*ca* 46 m) develops an extensive multilevel horizontal system which has been surveyed to *ca* 3.9 km (September 1988). A gate has been erected near the base.

C167 Spiral Cave: a very large entrance appears like a blank sinkhole but small holes can be entered which lead to a tunnel ending in a pitch. A series of pitches lead to a fairly extensive horizontal system at *ca* 39 m. A very humid cave.

C169 (unnamed): small solution pipe with a small, well decorated, chamber at the bottom (*ca* 39 m). Very humid.

