The Cave Fauna of Cape Range: specific analyses

A report to the
Australian National Parks and Wildlife Service

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Cover picture: The Cape Range cockroach *Nocticola flabella* Roth 1991 (Blattaria: Nocticolidae).

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Summary

More than 400 caves an karst features are known from Cape Range, North West Cape peninsula, Western Australia. The caves in Cape Range occur in Tulki Limestone which overlies the non-cavernous Mandu Calcarenite. The area is semi-arid and has highly unpredictable rainfall.

The peninsula contains three unrelated troglobite faunae: a subterranean aquatic fauna which occurs on the coastal plain and which contains the entire known vertebrate troglobite fauna of Australia; an aquatic fauna in Cape Range; and a very rich terrestrial fauna in Cape Range which is partly derived from a wet tropical rainforest litter fauna. The terrestrial troglobites occur in caves throughout the exposed Tulki Limestone whenever the caves are sufficiently humid. Broadscale survey sampling has revealed the extent of the fauna and an indication of its richness.

Allozyme studies have indicated that the coastal fauna is essentially a linear system around the peninsula and that the populations are not interrupted by the geological discontinuities. Two species of atyid shrimps are confirmed in the fauna but not their sympatry. A model suggests that the critical areas for habitat continuity may be up against the scarp where the fauna is difficult to sample.

Within Cape Range all four caves with water contain an undescribed amphipod. Allozyme electrophoretic data suggest the presence of a single species showing genetic discontinuities through its range.

Allozyme studies on a highly adapted troglobitic millipede show at least two species to be present. The remaining samples separate into three major groups each having many fixed differences. This characteristic enables Cape Range to be divided into three genetic provinces each separated from the other at clear geomorphological hiatuses, namely, the deep gorges that cut through the cavernous Tulki Limestone into the non-cavernous Mandu Calcarenite beneath. Exhaustive analysis dispels the initial impression that the populations conform to the isolation by distance model:- the discrete sub-population model should be applied to the populations.

Allozyme studies on *Schizomus vinei* (Chelicerata, Schizomida, Hubbardiidae) show one species to be present and that the overall genetic variation is much lower than that seen in the millipedes. However, the detailed pattern of genetic variation in the schizomids, unlike the millipedes, is not solely interpretable by geographical area or from geomorphological features.

Carbon dating of the upper samples from the sedimentary sequence in cave C-118 is 236 ± 66 years BP.

Uranium series dating of speleothem material (123,014 yr BP; 72,128-173,900) is consistent with other evidence for a wetter period at that time. More recent wetter periods are indicated by Holocene dates (12,555 yr BP; 11,000-14,300).

The fauna as a whole is presented with discussion of the conservation status of the species and their habitats and recommendations made as to management of the region..

The degree of genetic variation between even closely adjacent caves means that individuals should not be transported between caves within Cape Range, even within the genetic provinces. Long term changes to the ground water system could radically alter the subterranean environment of the North West Cape peninsula and the groundwater need to be studied with reference to the cave fauna.

On the North West Cape peninsula the troglobite areas are currently under a range of land uses and land tenure. The cave faunae, including the subterranean aquatic fauna, will be best protected if the entire karst area is treated as a natural unit under common management.

Acknowledgments

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This report builds on previous and contemporary work which has been variously funded by volunteers, the Western Australian Museum, the Australian National Parks and Wildlife Service and the Australian Heritage Commission and the Western Australian Heritage Committee.

The Report

The report covers the terms of the contract with the Australian National Parks and Wildlife Service and is presented in the form of a discursive summary, the supporting evidence being provided in a series of Appendices (distinguished by letters). These Appendices are in the form of papers and the detailed evidence is contained in their own Appendices (distinguished by numbers). For completeness it incorporates also some of the work previously and subsequently conducted on the cave faunae and their environments.

The six subjects covered in the consultancy agreement are:-

1. Analyse and report on the genetic separation between caves and cave regions of three selected troglobite species.

2. Analyse and report on samples of speleothems using Ur.Th dating to determine the age of the cave system in Cape Range.

3. Analyse and report on the genetic separation of two species in the coastal subterranean fauna to determine their genetic continuity.

4. Examine and report the age of the sedimentary sequence in one cave through carbon dating.

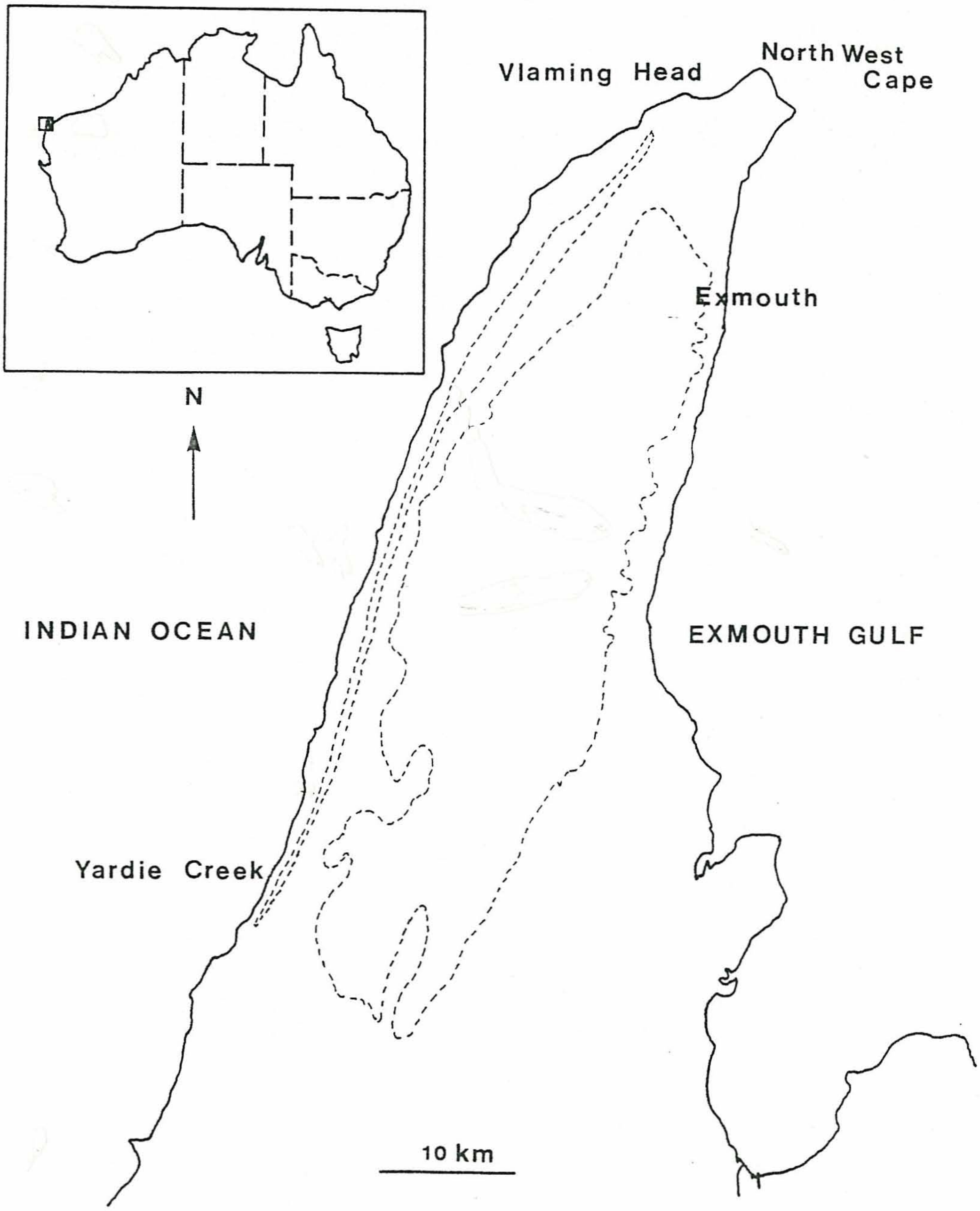
5. Collate and report on this new information and the previous data on the biology of the troglobites in Cape Range.

6. Recommend management protocols for sub-sections of Cape Range karst to accord with genetic knowledge.

Introduction

In the last few years the troglobite fauna of Cape Range, North West Cape peninsula, Western Australia, has been the subject of considerable research (Humphreys 1989, 1990, 1991a, 1991b, 1991c; Humphreys & Adams, M. in press; Humphreys, Adams & Vine 1989; Humphreys, Brooks & Vine 1990; Humphreys & Collis 1990; Vine, Knott & Humphreys 1988). Cave exploration in the area is recent (since the 1950's) and that cave research very young (since 1986; Humphreys 1991a) and the information available represents the early stages in understanding the biology of the troglobites of the Cape Range karst and of the adjacent, but unrelated, coastal plains. It is the first major karst area in Australia, and perhaps the world, where the majority of caves have been found and explored as an integrated program of cave exploration and scientific research. In addition, it is the first area for which a considerable body of background information has been assembled prior to the area becoming generally utilized. Indeed, so little caving had been done in the area that the only mention of caves in the Management Plan for Cape Range National Park is in reference to vertebrate fossils (CALM 1987).

Figure 1. Regional location of Cape Range and the North West Cape peninsula.



Background

Cape Range is a limestone anticline on the semi-arid North West Cape peninsula of Western Australia (Fig 1). It has been found to be highly cavernous and the caves contain important and species rich communities of animals. Many of these are clearly derived from animals of a wet tropical forest floor and their relatives are in north-east Queensland and the Northern Territory. These animals provide the only evidence that wet forest has covered the area since the Miocene when the limestones were deposited. In addition, a separate troglobitic fauna occurs in the surrounding coastal plain that contains all the known vertebrate troglobites of Australia (Appendix C).

The caves contain large populations of troglobitic animals (obligatory cave inhabiting species usually lacking eyes and pigment; Appendix H)) relying on imported energy for their existence (Humphreys 1991c). Such populations may represent animals that have invaded caves but which are closely related to nearby surface species, or they may represent populations that are relicts of populations that formerly occupied the surface but which are now extinct on the surface in the region. The evidence for Cape Range is that they are relict populations from times when wet tropical forest covered Cape Range. In addition caves have often accumulated significant palaeoclimatic information such as speleothem materials, stratified sediments and accumulations of fossils.

Fauna found in caves is traditionally divided amongst:- accidentals (species entering caves by chance); trogloxenes (sporadic cave dwelling species e.g. bats); troglophiles (facultative cave dwelling species, often divided into first level troglophiles, found both in cave and epigean habitats, and second level troglophiles 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).

These 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 troglophiles may turn out to have clear adaptations to caves in non-morphological characters, e.g. physiological (Barr 1963, H. Dalens, pers. comm. 1988). 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. This knowledge is unavailable for the vast majority of Australian cave faunae, especially the newly worked Cape Range area.

Recent work (Humphreys 1991b) has shown that the troglobitic fauna of Cape Range occurs over the full extent of the exposed Tulki Limestone, even in outlying segments (Appendices A and B). The fauna extends near to the following:- Milyering in the West, Learmonth in the east, Exmouth to the north and pastural country in the south. One cave contains elements of both the cave fauna from Cape Range, and of elements of the subterranean coastal fauna (C -215), previously considered to be entirely separate. Note, however, that although the systems physically connect, there are no elements of the fauna in common, even at the Order level, to both ecosystems. This cave is of considerable importance to any work seeking to understand why the millipedes have not invaded the coastal system.

Schizomus vinei are genetically conservative compared with the millipedes. Both taxa, previously known only from a narrow band of caves traversing the eastern boundary of Cape Range National Park, are now known to be widely distributed across Cape Range and to occur in 36 and 55 caves respectively (Appendices A and B).

The Caves

The genetic evidence supports the view that within three sub-areas some caves are connected either by the finer extensions of the caves formed during the karstification, or through the superficial underground compartment (milieu souterrain superficiel: Juberthie 1983). The former is considered the more likely as there is no evidence to support the latter (Appendix A).

Some seemingly small caves with tight opening have strong air movement. For example C-15 in winter has an outflow of air; because the cave air is saturated with moisture and is warmer than the outside air it condenses as it vents, forming a damp zone at the entrance. This provides a rich source of organic matter (algae) on which the troglobitic millipedes feed. The airflow indicates that the cave is much larger than is apparent and it must be connected to a much more extensive system. An adjacent deep cave has recently been found (C-402: D. Brooks, pers. comm. April 1991) proving that there are deep caves in the immediate area. Such outflowing air in winter from warm caves is characteristic of caves with openings at different levels and occurs at the upper opening (Mangin & Andrieux 1988); the airflow should reverse in summer. Some of the caves in Cape Range are cold and thus are probably not connected by passages to a larger system (cold drainage; C-18) while others a very hot but at the temperature expected from the mean annual surface temperature (Humphreys 1989, 1990, 1991a). Some parts of caves are hot from rising warm air being trapped in avens (C-118; see Mangin & Andrieux 1988).

The caves consists of two components, a relict upper layer, most of the caves in Cape Range, and a more active horizontal tunnel system probably formed on a previous water table. Many of the big solution pipes now lack a catchment as they open on high ground (e.g. C-207); other caves have been cut through by gorges (e.g. C-222) which deeply dissect Cape Range. However, others, including the horizontal systems, are in conformity with the current relief and probably reflect a later formation. The evidence for this comes from the only extensive tunnel system known from Cape Range (C-163) where the main leads are in agreement with the current relief; this system appears to connect with both the eastern and western drainage (Mandu Mandu Creek) from Cape Range. There is no superficial allochthonous drainage in Cape Range.

The dating of the cave system will provide information relevant to both the palaeoclimate of the north-west of Australia and provide the framework on which to construct the development of the troglobitic system and the loss of wet tropical rainforest from this now semi-arid region.

Adequacy of faunal sampling

The cave fauna in Cape Range comprises large populations of relatively conspicuous animals (*S. vinei*, millipedes and some isopods) and a sparse or very inconspicuous component that is very species rich (Appendix H). Considerable superficial survey sampling has been conducted in the caves of Cape Range as well as limited intensive sampling in several caves. While this has extended the geographical range of the fauna by an order of magnitude it has not adequately sampled the rare fauna. This is shown, for example, in the pseudoscorpion data where the 18 specimens collected represented six undescribed species and an undescribed genus (M.S. Harvey, pers. comm. 1991) with up to three species per cave (Table 1).

Table 1: The number of genera and species of pseudoscorpions in caves in Cape Range. Note that six undescribed species resulted from 18 specimens.

Number of:-		
species	genera	caves
1	1	6
2	2	2
3	3	1

The pseudoscorpions are the most fully described higher taxon from Cape Range and illustrate the species richness of the area. Appropriate extrapolation of the pseudoscorpion data indicates that detailed work on 100 caves could yield 15.5 species of pseudoscorpions with progressively fewer being added as more caves are sampled. This analysis is probably relevant to the fauna as a whole. More detailed collecting, especially the use of long term baits, should reveal a much greater array of species than is yet suspected.

Genetical studies

Aquatic

The quickest way to determine whether a target taxon is functioning as a unit whole or as several sub-populations or even species is to conduct a limited genetic screening from across its distributional range. Taxonomic classification is a primary determinant of management priorities for endangered species (Daugherty *et al.* 1990).

In Appendix C a detailed account is presented of the aquatic fauna of the North West Cape peninsula, both the fauna in Cape Range and the subterranean aquatic fauna that occurs on the coastal plain. A summary of the results is given here.

Since previous publications on the area the range of all four subterranean aquatic species has been considerably extended and an amphipod added to the known fauna. The fauna includes the only vertebrate troglobites known from Australia.

The Blind Cave Eel, *Ophisternon candidum* , has been seen for the first time in more than a decade and from the east coast of the peninsula where it was previously unknown. Allozyme electrophoretic data show that the Blind Gudgeon, *Milyeringa veritas*, is not panmictic within its known range. The overt geological discontinuities along the coast of the North West Cape peninsula do not constitute genetic barriers between the gudgeon populations.

Allozyme electrophoretic data confirm that two species of atyid shrimps occur but the species were found on opposite sides of the peninsula. Analysis suggests that the species composition on the east coast is different from that on the west coast.

The relationship between genetic and metric distance between the populations suggests that the coastal fauna is essentially linear along the coast and does not spread beneath Cape Range.

Within Cape Range all four wells with water contain an undescribed amphipod. Allozyme electrophoretic data suggest the presence of a single species showing genetic discontinuities through its range.

There is a cline in the water chemistry, with most parameters increasing from the mid-east coast, round the north coast and south along the west coast of the peninsula. All coastal species seem to occupy the full range of water chemistries sampled. There is a lack of effective monitoring of the quantity and quality of the water. Examination of diverse evidence from a number of sources suggests that the water table is declining and becoming more saline. Potential disruption of the habitat is discussed and a model presented which indicates that the critical areas for conservation may be close to the scarp where, owing to the absence of wells, the fauna has not been sampled.

Terrestrial

Millipedes (Appendix A)

Highly cave adapted troglobitic millipedes (*gen. et sp. nov.* : Craspedosomida: Paradoxosomatidae) occur throughout Cape Range wherever caves occur in the Tulki Limestone. They occur only in caves of high relative humidity and with damp soil. No formal taxonomy of the species has yet been completed. Millipedes were collected from 36 caves in Cape Range and were examined for allozymes at 18 polymorphic loci using gel electrophoresis. The allozymes indicate at least two species of millipedes occur as there are two very distinct types occurring sympatrically in cave C-111. The remaining samples separate into three major groups each differing by many fixed differences. This characteristic enables Cape Range to be divided into three genetic provinces each separated from the other at clear geomorphological hiatuses; these are deep gorges that cut through the cavernous Tulki Limestone into the non-cavernous Mandu Calcarenite beneath.

The three genetic provinces have different characteristics; the southern province is genetically much more homogeneous that the northern or central provinces. Exhaustive analysis dispels the initial impression (Humphreys 1989) that the populations conform to the isolation by distance model:- the discrete sub-population model should be applied to the populations.

The high degree of genetic variation between provinces and even closely adjacent caves means that individuals should not be transported between caves, especially between genetic provinces.

Schizomus vinei (Chelicerata, Schizomida, Hubbardiidae) (Appendix B)

All Australian Schizomida belong to the family Hubbardiidae (formerly Schizomidae, Reddell & Cokendolpher 1991), the Protoschizomidae being restricted to Mexico and U.S.A. (Rowland & Reddell 1979). *Schizomus vinei*, a troglobitic Schizomida occurs throughout Cape Range wherever caves occur in the Tulki Limestone. They occur only in caves of high relative humidity and with damp soil. Schizomids were collected from 18 of the 36 caves known to contain schizomids. The samples were examined for allozymes at the only four detectable polymorphic loci using gel electrophoresis.

Overall the genetic variation in the schizomids is much lower than that seen in the millipedes (Appendix A) and the amphipods (Appendix C). The allozymes indicate that although there is only one species of schizomid while the fixed genetic differences (4-7%) mean that the populations do not interbreed between some of the cave areas. However, the detailed pattern of genetic variation in the schizomids, unlike the millipedes, is not interpretable by geographical area or from geomorphological features. Nonetheless, the major genetic variation is, for the most part, also associated with the major geomorphological features, the deep gorges which cut through the cavernous Tulki Limestone into the Mandu Calcarenite below. Within extensive areas there is scarcely any genetic distance between the schizomid populations from different caves and yet these caves represent all three millipede genetic provinces; this includes C-15, C-103, C-107, C-126, C-156 , C-162, C-167 and C-278.

The degree of genetic variation between even closely adjacent caves means that individuals should not be transported between caves, even within the genetic provinces defined from the millipede data.

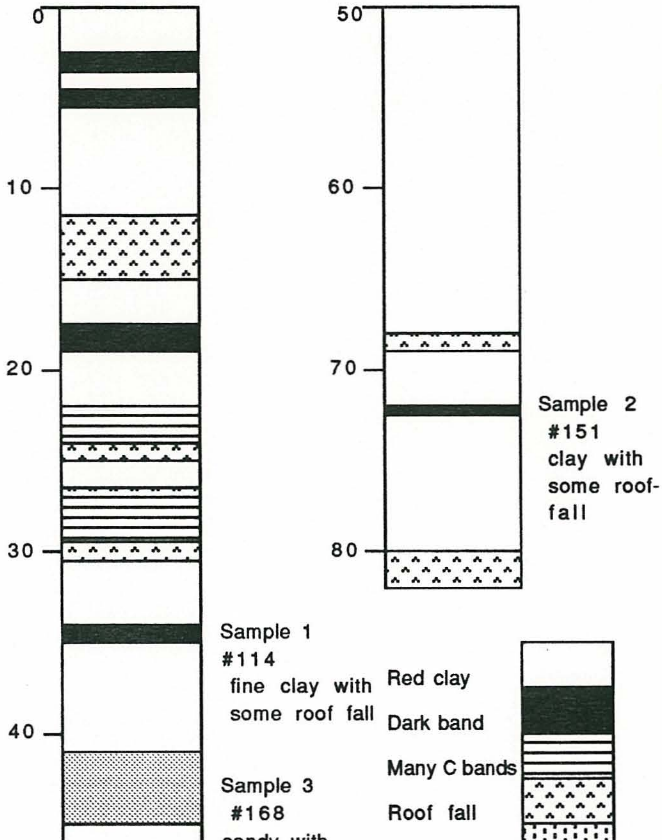
Sedimentary sequence

Cave C-118 (22° 09' S; 113° 59' E) is an inflow cave in a doline with a double entrance. A short passage at the bottom of the doline leads to a 17.3 m pitch into a large cavern below; total depth of the cave is 23.3 m. The cave, in which much biological work has been conducted, contains deep mud-banks with many well defined strata including dark bands and one major hiatus defined by a deep pale sandy layer (Fig. 2). It was proposed to date above and below the hiatus and, having established the period represented by the mud-bank, to resample in detail for additional dating to be tied in with sediment analysis. The rationale was that the banding of the sediment would contain details of both the flooding frequency of the cave as well as the natural burning frequency of the area. Detailed analysis of the dates and sediments in C-118 would establish the practicality of such work which could then be extended to further caves to build up a picture of the palaeoclimate in the area.

Some of the black banding was clearly associated with bulk charcoal and material was collected above and below the pale sandy layer in 1988 for carbon dating; these samples are not available (Dr K.H. Wyrwoll, pers. comm. 1990). Additional material was collected in 1989 but large pieces of charcoal could not be found and samples of what was thought to be finely particulate material were collected from the locations shown in Fig. 2. The lower sample was found not to be carbon (it is magnetic and is presumably an iron compound) and so no dating of the lower boundary has been completed. The loss of the earlier material has prevented the completion of this project. It is proposed to collect additional material if possible. The sediment analysis has not been conducted as it is of no value without the dating.

Only the upper sample was adequate for analysis and was dated at 236 ± 66 years BP (Appendix E). Hence the mean minimum rate of deposition of the mud banks has been 1.44 mm a^{-1}. As the estimated current flooding frequency is once every 56 months (4.7 years; Humphreys, Adams & Vine 1989), then the mean deposition of sediment on the bank each flood is about 6.8 mm, assuming no erosion of the bank surface. These rates may seem surprisingly high but they are in accord with observations made on occasion in Cape Range.

Figure 2: Schematic profile of the eastern mud-bank in C-118. Depth from surface of mud-bank in cm. This natural erosion section is between locations c and p in the cave diagram (Fig. 1; Humphreys, Adams & Vine 1989).



The mud-banks in C-162 were redistributed soon after the cave was found (M. East, pers. comm. and photographs, 1988). The pool containing amphipods in C-18 was open in 1987, completely occluded in 1988, but again open in 1989; this was accompanied by large scale accumulation of gravel. Hence, even in the current semi-arid climate, the influx of water into the caves can be both massively erosive or depositional. These events are coupled with the destruction and recolonisation of the populations of troglobites in the caves (Humphreys 1991c).

At least 17 overt strata occur from the surface to the dated layer (Fig. 2) indicating at least 17 changes in the nature of the sediment accumulation over the 236 years, one change every 14 years. This compares with the estimated current flooding frequency of once every 4.7 years which should occur after a single rainfall event of >150 mm (Humphreys, Adams & Vine 1989), an estimate supported when the cave flooded (D. Brooks; pers. comm.) after a rainfall of 140 mm in January 1990 (W.F. Humphreys, unpublished).

At least four of the upper sedimentary layers are associated with carbon layers and thus probably with fire giving a minimum fire frequency of every 64 years.

Hence the cave potentially contains significant climatic information which, if analysed in conjunction with similar sedimentary sequences in other caves, could yield independent estimates of burning and flooding events with Cape Range.

Dating of the speleothem material from caves

The caves

The karst index to Cape Range has reached C-402 (D. Brooks, pers. comm. April 1991). The deepest cave known in Cape Range is C-277 which is 82 m deep and also contains the deepest pitch in Western Australia (59.0 m). The longest cave in Cape Range has been surveyed to c. 3900 m (C-163) and much more passage awaits survey.

The bulk of the vertical cave development in Cape Range must be considered as relictual from a wetter period. There are several lines of evidence to support this. To the northern end of the exposed Tulki Limestone the gorges have intercepted cave passages so that they now hang high up the sides of the valley (e.g. C-222). Extensive cave decoration (speleothems) are present in many of the caves but most are no longer active. Much speleothem material is being buried and current conditions are erosional (e.g. C-4 and C-96; S. White in Humphreys 1989).

There is clear evidence that the area used to be much wetter than today. There are massive sink holes leading from areas without major current catchments or situated close to the greatest elevation (e.g. C-207). The water table has clearly fluctuated between stable levels as is evident from the extensive hanging floors (e.g. C-207), and well defined layers of cave coral growing on previous speleothem. However, there has been major water flow carrying large amounts of rubble since the caves stopped producing speleothem as is seen by decoration emerging from fluvial rubble. Clearly large amounts of water have flowed though the passages at times with stream bedload material of well rounded cobbles or coarse sand (e. g. Wanderer's Delight; C-163). There is considerable collapse of entrances and of roof fall within many caves.

In addition the fauna itself is evidence of previously much wetter conditions as many of the troglobites have their closest affinities with species of the forest floor of the wet tropics.

Why date?

Dating of the speleothems in Cape Range was proposed to determine the minimum time of isolation of the troglobites in the cave system. Detailed work, beyond the immediate scope of this project, should lead to a great improvement in our understanding the palaeoclimate of the north-west of Australia, an area for which palaeoclimatic data are lacking.

While various methods are available to determine age (e.g. palaeomagnetism, electron spin resonance decay, ^{14}C, and thermoluminescence), uranium series dating has been most widely used on speleothem materials. In the United Kingdom U-series dating has shown that there are ten peaks in speleothem abundance between 20,000 and 220,000 yr BP, the peaks reflect local palaeoclimate (Gorden *et al.* 1989) and occur during interglacial periods. In addition global climatic changes are also imprinted in the speleothem record (Kashiwaya, Atkinson & Smart 1991). The speleothem record matches well the insolation curves especially after 70,000 yr BP and before 100,000 yr BP (Kashiwaya, Atkinson & Smart 1991). Hence, variation in the abundance of speleothems through time is useful for reconstructing palaeoenvironmental changes.

Speleothem growth is controlled by a number of environmental and climatic factors, especially water availability, vegetation cover and temperature (Atkinson 1983, Atkinson *et al.* 1978, 1986; Hennig, Grun & Brunnacker 1983). Plant cover alters water percolation while plant productivity controls the amount of carbon dioxide in the ground water: well developed, dense and productive vegetation encourages speleothem growth (Cape Range is now semi-arid and spinifex covered with low cover and low productivity). Vegetation development itself is closely related to average temperature thus temperature may indirectly influence speleothem production.

Speleothem abundance is influenced by water availability and is greatest when groundwater is abundant. Evaporation rates, as well as precipitation, influence water availability (current evaporation rates in Cape Range are an order of magnitude greater than precipitation). In addition, water chemistry and dissolved $CO2$ are temperature dependent (Ford & Williams 1989); the partial pressure of $CO2$ in water is an important determinant of the rate of dissolution of limestone and the degassing of $CO2$ on the deposition of calcium minerals (Ford & Williams 1989).

Cape Range is not noted for its beautiful highly decorated caves. However, although much of the speleothem is small and heavily discoloured, some is massive; speleothem materials of one form or other is generally available in the caves (Table 2).

Table 2: The percentage of a sample of 77 caves examined during the 1989 field season with various forms of decoration (speleothems).

Attribute	% of caves
Stalagmites	45
Stalactites	56
Flowstone	66
Shawls	52
Gour pools	18
Oolites	5
Straws	35
Helictites	5
Columns	1
Other	5

Growth rates of speleothem vary widely depending on the climate, season or section of the cave; flowstone thickening rates are generally less than stalagmite extension rates, by up to an order of magnitude (Ford & Williams 1989). Average values from a limited range of speleothem forms show a mean rate of growth of 0.12 mm a^{-1} but with the standard deviation $\approx$ mean (Table 3a). Grouping the data according to major climatic events reduces the coefficient of variation only slightly (Table 3a). Within the bounds of the mean growth and its standard deviation (Table 3b) a 2m long stalagmite may be from 10^3 to 10^5 years old; hence, size alone is a poor indicator of age.

Table 3: Growth rates of stalagmites. a) Mean growth rates (mm a^{-1}) for stalagmites from northern hemisphere caves (calculated from Table 8.5 in Ford & Williams [1989], using mean values if a range given). b) length reached in time period at mean growth rate ± one standard deviation.

a)

Group	Mean	St. Dev.	C. V.	N
All data	0.116	0.114	98	18
Holocene	0.230	0.148	64	5
Post glacial	0.120	0.028	24	2
Late glacial	0.098	0.062	63	3
Interstadial	0.023	0.021	91	4

b)

Period (years)	Length (m) reached in time period mean	minimum	maximum
10^2	0.1	0.002	0.231
10^3	1.16	0.022	2.307
10^4	11.64	0.219	23.065
10^5	116.42	2.189	230.650
10^6	1164.19	21.888	2306.501

Dates

Uranium series dates were determined by Dr D. Smith, Department of Inorganic Chemistry, University of Melbourne on material collected at various stages by S. White, W.F. Humphreys and D. Brooks.

Samples dated were from the following areas:- C-125 (22° 06' S; 114° 01' E) is a small blank solution pipe 9.8 m deep. C-163 (Wanderer's Delight: 22° 09' S; 114° 00' E) has a large open entrance which takes a lot of in-flow - at a depth of 46m is an extensive, multi-level, horizontal system surveyed to about 4000 m by 1991 and containing an extensive canal system; a slight breeze blows through most of the tunnels.

Superficial floor material from the horizontal development area of C-163, by far the most extensive cave known from Cape Range, was dated (Appendix D) at 123,014 yr BP (72,128-173,900).

The mid-section of small stalagmite from C-125 was dated (Appendix D) at 12,555 yr BP (11,000-14,300).

While the results give a general date for the different materials, the error bounds are so large as to be of little help in interpreting palaeoclimatic events. The large error bounds result from the very low concentrations of uranium found in the samples from Cape Range and partly due to contamination of the samples.

Discussion

The dates give a minimum longevity for the cave systems in Cape Range (72,128-173,900 yr BP) and shows that some activity occurred in the speleothem material as recently as 11,000-14,300 yr BP.

Kendrick (pers. comm. 1989) compiled a large data set on the contemporary and Pleistocene fossil distribution of *Andara trapezi* (Deshayes)(Bivalvia: Arcoida) which, he argues, requires open esturine conditions. Its occurrence in certain deposits indicates such conditions from Shark Bay northwards to the Lyndon River (at the foot of the North West Cape peninsula) 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 Shackelton & Opdyke 1973; Bowen, 1978). While we know nothing of the intensity of the wetter periods it seems that wetter periods may have occurred at 128 and 225 k yr BP, the former being consistent with the date for the superficial floor material from C-163.

The Holocene date for the mid-section of a small stalagmite from C-125 indicates that even in the middle of a very dry period (Humphreys, Adams & Vine 1989) limited speleothem activity occurs, as it still does today in a few places.

Clearly a more precise dating method is required for the Cape Range speleothems and a major project examining many samples will be required to understand the genesis of the cave systems as well as the climate associated with that genesis. Samples are being sent to Canada for examination by Professor D.C. Ford at McMaster University using different methods.

Protect troglobite species individually or their habitat?

It is common practice in the United States of America to declare species endangered or threatened and then determine and protect Critical Habitats required for the persistence of the declared species (Endangered Species Act 1973, U.S.A.). This legislation has been invoked for troglobitic species. A proposed rulemaking to designate the Kauai Cave Wolf Spider (*Adelocosa anops*) as Endangered and the Kauai Cave Amphipod (*Spelaeorchestia koloana*) as Threatened considered the limited distribution (three caves), declining populations and adverse habitat modification (human visitation and quarrying); all thee caves were proposed as Critical Habitat (Anonymous. 1978).

Such powerful legislation is non-existent in Western Australia where, for instance, it is not illegal to destroy the habitat of an protected species if by so doing the species is not directly harmed.

The two species of fish (*Ophisternon candidum* and *Milyeringa veritas*) in the subterranean coastal fauna of the North West Cape peninsula have recently been included in Schedule 1 of the Wildlife Conservation Act 1950 (Government Gazette, WA 16 November 1990 pp 5696-5697). While this protects the species it provides no protection for their habitat, most of which is outside Cape Range National Park (Appendix C: on land controlled by Exmouth Town, Exmouth Shire, Department of Defense, or on leasehold rangeland). Cave faunae generally, and schizomids in particular, are vulnerable to change in the water table. For example, *Schizomus wessoni* (Chamberlin) was eliminated from its type locality as a result of long term drying of the Santa Cruz River due to agricultural activities, and draining rendered oases unsuitable for *S. joshuensis* (Rowland & Reddell 1981).

At first sight the caves and their contents within Cape Range National Park seem well protected as they are covered by the CALM Act (1984) which requires 'the protection of indiginous .... fauna and the preservation of any feature of archaeological ... or scientific interest` (CALM 1987). In addition, it is a general management objective for Cape Range National Park to 'protect and conserve indiginous .... animals and their habitats` as well as the 'physical, cultural and scenic resources` [hence caves] and there are specific management objectives to 'maintain scientific reference areas` and to 'conserve and protect ground water resources' (CALM 1987).

In practice the protection status of the caves, even those within Cape Range National Park, is uncertain. The National Park was 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 this was rescinded in 1979. Furthermore a temporary limestone reserve (TR5980H), under the control of the Minister for Mines and preceding the CALM Act, covers a large proportion of the eastern half of Cape Range. This reserve includes about 80% of the caves known to contain terrestrial troglobites and much of the coastal area from which the aquatic subterranean fauna is known.

Caves are highly susceptible to changes detrimental to their fauna. The most careful people entering caves do physical damage to the cave and its occupants, they change the gaseous composition of the air (especially CO2), they change the temperature and humidity of the air and they introduce numerous organic solvents (especially acetone and ethanol) from their expired air (Andrieux 1988, 1990). In addition they compact the surface on which they walk and displace larger particles beneath which fauna may live. In combination these factors may effect immediately the cave biology and, in the long term, change the entire physiochemical balance of the system preventing or enhancing speleothem formation. Opening up cave entrances or placing barriers changes the ventilation patterns and rates within caves and hence the entire dynamics of the system. They are often exploited for water, minerals, or waste disposal and karst systems are, often unintentionally, contaminated by sewage (e.g. Mammoth Cave Sytem in USA, the world's longest cave system).

It is clear that species protection would be inadequate to ensure their persistence. Protection of any cave species requiring it should be achieved by the protection of its habitat (*sensu lato*) with appropriate management and legislation to prevent the habitat itself being degraded.

Management of the genetic sub-provinces

Previous work indicated that within genetic sub-provinces of Cape Range (as determined from allozyme electrophoresis) that the isolation by distance model was appropriate. The implication of this was that within sub-provinces, the caves has some tenuous links below ground through which the populations moved and interbred (i.e. that panmixia occurred within the sub-provinces but not between them - Humphreys 1989, 1991b). As such management of the area merely needed to protect a section of each sub-province to maintain the genetic diversity of the area. The more detailed examination, presented here, of the genetic affinities of the populations in a much larger set of caves has shown this to be false.

Previously the common pattern found in the three species of troglobites examined (sub-populations separated by deep gorges) and panmixia in the non-troglobite (Humphreys 1989; Humphreys, Adams & Vine 1989) suggested that troglobites could be treated as a class with a common cause for the substructuring of the populations. However, it is now clear that the populations of *S. vinei* and of the millipedes are not necessarily isolated by the same mechanisms and so the presumption above cannot be applied to troglobites as a class. Secondly, within sub-regions the isolation by distance model is not applicable and so the deduction (Humphreys 1989; Humphreys, Adams & Vine 1989, Humphreys 1991c) cannot be supported that the caves are generally interconnected within sub-provinces.

As no common pattern of separation can now be deduced, each cave must be treated as a separate conservation unit as the faunal assemblage may be unique - because most species are known from few specimens, and as very many caves are known to support troglobites, much more detailed work is required to establish a communality of troglobitic species between caves.

As indicated elsewhere (Appendix G), normal sensible management practices should suffice to protect in the medium term (decades) the fauna in caves covered by Cape Range National Park, unless dramatic change occur in the area. However, long term changes, especially to the ground water system, could radically alter the subterranean environment of the North West Cape peninsula and, if the cave fauna are considered important, human impacts on the groundwater need to be studied.

On the North West Cape peninsula the cave fauna, including the subterranean aquatic fauna, will be best protected if the entire karst area is treated as a natural unit under common management, preferably by inclusion in Cape Range National Park.

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APPENDIX A

Genetics of the troglobitic millipedes (*gen. et sp. nov.* : Craspedosomida: Paradoxosomatidae) from Cape Range, Western Australia.

Summary

Highly cave adapted troglobitic millipedes (*gen. et sp. nov.* : Craspedosomida: Paradoxosomatidae) occur throughout Cape Range wherever caves occur in the Tulki Limestone. They occur only in caves of high relative humidity and with damp soil. No formal taxonomy of the species has yet been completed. Millipedes were collected from 36 caves in Cape Range and were examined for allozymes at 18 polymorphic loci using gel electrophoresis. The allozymes indicate at least two species of millipedes occur as there are two very distinct types occurring sympatrically in cave C-111. The remaining samples separate into three major groups each differing by many fixed differences. This characteristic enables Cape Range to be divided into three genetic provinces each separated from the other at clear geomorphological hiatuses; these are deep gorges that cut through the cavernous Tulki Limestone into the non-cavernous Mandu Calcarenite beneath.

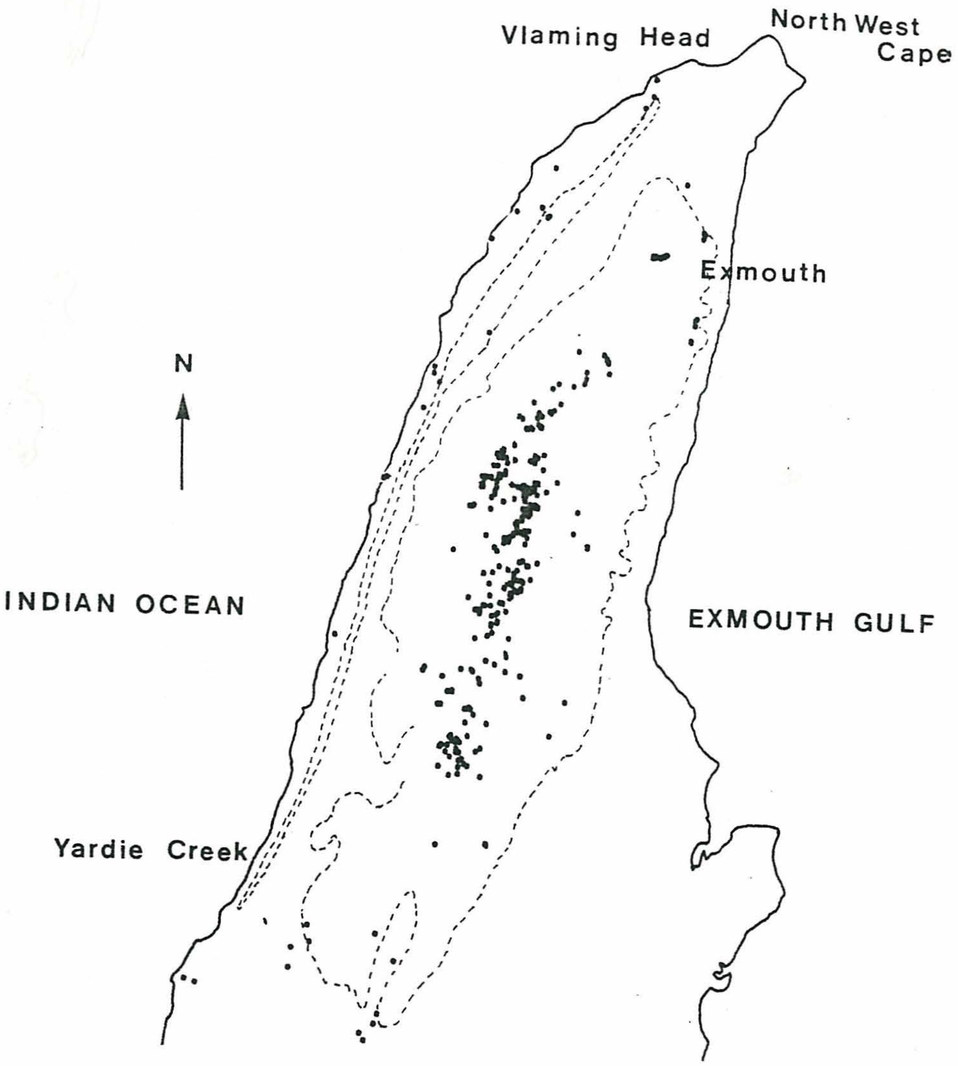
The three genetic provinces have different characteristics; the southern province is genetically much more homogeneous that the northern or central provinces. Exhaustive analysis dispels the initial impression that the populations conform to the isolation by distance model:- the discrete sub-population model should be applied to the populations.

The high degree of genetic variation between provinces and even closely adjacent caves means that individuals should not be transported between caves, especially between provinces.

Introduction

The rich troglobite fauna of Cape Range (North West Cape peninsula, Western Australia) is dominated by an undescribed genus of paradoxosomatid (Craspedosomida) millipedes. This domination is both numerical and distributional with the family known from 55 caves, covering about 500 km^2 of Cape Range; this is a twelve-fold increase in the known range of the millipedes over 1988 and is highly significant for the species conservation as they were known previously only from a narrow band of caves traversing the border of Cape Range National Park. There is clear morphological evidence that speciation has occurred amongst the different cave areas in the range. The millipede populations occupy quite varied cave habitats (Humphreys 1989), show considerable genetic variability and have many polymorphic loci (Humphreys 1989). Combined with the large populations these characteristics make the millipedes the most suitable study organisms to understand the nature of the cave systems in Cape Range - the continuity of cave systems is crucial to their management.

Figure 1: : The location of caves in Cape Range on the North West Cape peninsula. Cape Range encompasses all the outcropping Tulki Limestone (dashed lines) in which the caves containing troglobites are found; the one cave outside this area is also in Tulki Limestone but it is superficially covered by other deposits. Troglobites are also found in the narrow band of Tulki Limestone close to the western coastal plain.



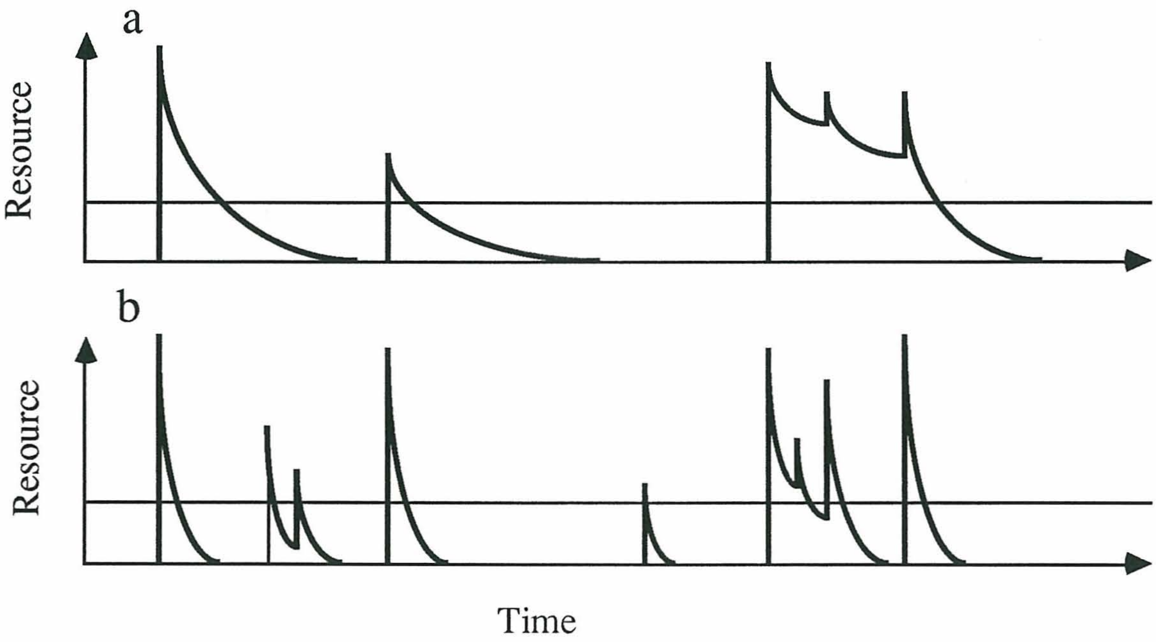
Background

The regional, climatic and biological setting has been described in detail elsewhere (Humphreys, 1989; 1990; in press; Humphreys & Adams, in press; Humphreys, Adams & Vine, 1989; Humphreys & Collis, 1990; Vine, Knott & Humphreys, 1988). Sufficient information is given here to aid understanding of this system.

Cape Range lies just within the semi-arid tropics of Western Australia (Fig. 1). Australia is a continent of unpredictable rain; Cape Range lies in the area of least predictable rainfall - both the seasonality and the between year variation in the rainfall being high (Humphreys, Adams & Vine 1989). The caves occur in the deeply dissected Cape Range and contain a rich troglobitic fauna (obligate cave dwelling species). The fauna relies on organic matter and water entering the caves from intermittent flooding which reactivated the cave fauna - the populations widely occupy the cave and breed (Humphreys in press).

The interval between flooding depends on the characteristics of the cave and its catchment as well as the rainfall of the area. Some caves flood after 25 mm of rain and dry quickly, while others flood only after >156 mm rain and dry slowly (Humphreys, Adams & Vine 1989; Humphreys 1989). Hence wetting and drying cycles many vary from a month to several years and in consequence there are pulses in the population numbers which expand and contract in the caves throughout Cape Range with varying frequency and amplitude (Fig. 2)(Humphreys in press) and not necessarily in synchrony. Hence the caves in Cape Range have highly dynamic troglobite communities and belie the stability normally attributed to such systems.

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



A pilot study indicated that three troglobitic species in Cape Range have non-panmictic populations whereas the one non-troglobitic species examined has panmictic populations throughout the range (Humphreys 1989). The genetic discontinuities appear to be associated with major geomorphological boundaries; gorges which cut through the cavernous Tulki Limestone into the non-cavernous Mandu Limestone. Within sub-regions the genetic distance was correlated directly with metric distance. Hence the cave system appears to be broken by the gorges and that between gorges there is gene flow between caves, albeit restricted.

Methods

Samples collected from throughout the karst area in 1989/90 were preserved in liquid nitrogen with replicate material preserved in alcohol.

Electrophoresis: cellulose acetate gel electrophoresis was conducted using standard methods (Richardson, Baverstock & Adams 1986). Homogenates were made from whole individuals and used to examine the allozyme variation between the populations in Cape Range. Samples were available from 36 caves. For systematic purposes, the null hypothesis under test was that all populations were sampled from the gene pool of a single species. A pilot study (Humphreys 1989) examined 46 enzymes and non-enzymic proteins of which 27 were scorable and 18 were polymorphic (Table 1). Only these latter loci were examined in this larger study.

Table 1: Summary of the genetical information.

Attribute	Millipedes [1]
# caves sampled	10
# individuals	40
# enzymes examined	46
# enzymes scored	27
# loci invariate (%)	9 (33)
# polymorphic loci (%)	18 (67)
H-W Equilibrium	Yes
Panmictic population	No[2]
? more than one species [3]	Yes
Geographic explanation [4]	Yes
Troglobite	Yes

[1] There are two major genetic groupings differing at an average of 19% of loci:- Group I - C-118, C-203, C-126 and C-167; Group II- C-159, C-107, C-103, C-18, C-106 and C-64. The four populations in Group I are genetically homogeneous. In Group II the population from C-64 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. [3] Genetic differences indicate the possibility of sibling species. [4] The genetic differences are in accord with major geomorpological features.

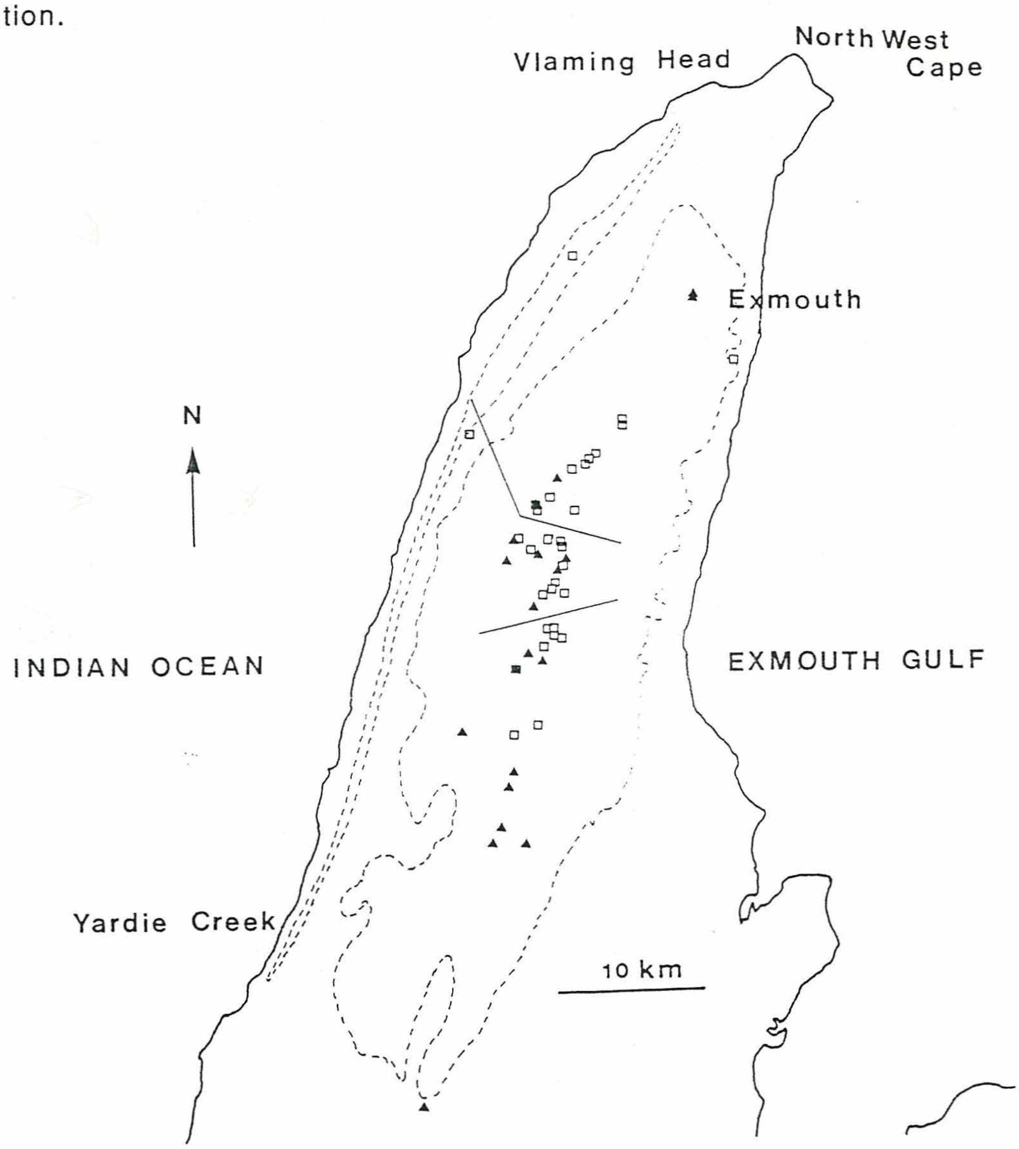
The enzymes used are as follows:- aconitate hydratase (ACON, E.C. 4.2.1.3), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), diaphorase (DIA, E.C. 1.6.99.?), enolase (ENOL, E.C. 4.2.1.11), fructose-1, 6-diphosphatase (FDP, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), hexokinase (HK, E.C. 2.7.1.1), malate dehydrogenase (MDH, E.C. 1.1.1.37), peptidases (PEP, E.C. 3.4.11.? or 3.4.13.?), and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). The nomenclature and conventions for referring to alleles and loci follow Richardson, Baverstock & Adams (1986).

The species meets the criteria for adequate genetic work at the within-species level (Richardson, Baverstock & Adams 1986) in that there were at least six polymorphic loci; the samples could be drawn from the smallest and homogeneous population units (caves) and they were sampled over some geographical distance including the extremities and intermediate locations.

Results

The troglobitic millipedes are known from 55 caves in Cape Range, *Schizomus vinei* from 36 caves and 31 of these caves are in common. The electrophoretic data for the millipedes represents the data from 36 populations from 35 caves. The samples for electrophoresis provide a good regional coverage of the distribution of schizomids in Cape Range (Fig. 3).

Figure 3: The location of Cape Range on the North West Cape peninsula and the distribution of caves and caves with millipedes. Cape Range encompasses all the outcropping Tulki Limestone (dashed lines) in which the caves containing troglobites are found; the one cave outside this area is also in Tulki Limestone but it is superficially covered by other deposits. The points denote caves from which millipedes have been recorded; the open points being the locations of samples used for the allozyme study. The solid lines across the range denote the boundaries between the three major subregions as indicated by the electrophoretic work. The sympatric populations occur in cave C-111 at the extreme north-west of the distribution.



There is unequivocal evidence that the populations have not been taken from a single gene pool (Appendix 1 a-c). Four major genetic groupings emerge (Figure 4); a southern group (which includes caves C-15, C-62, C-118, C-126, C-151, C-154, C-161, C-162, C-163, C-167, C-171 and C-207), a northern group (which includes caves C-64, C-111, C-119, C-227, C-

254, C-256, C-263, C-278 and C-312) and a central group (which includes caves C-18, C-47, C-56, C-65, C-68, C-79, C-103, C-106, C-107, C-156, C-159, C-215, C-260, C-261 and C-281). In addition there is a lone outlier population in C-111 which has 38% fixed differences from the other groups, including a sympatric population in C-111; this population

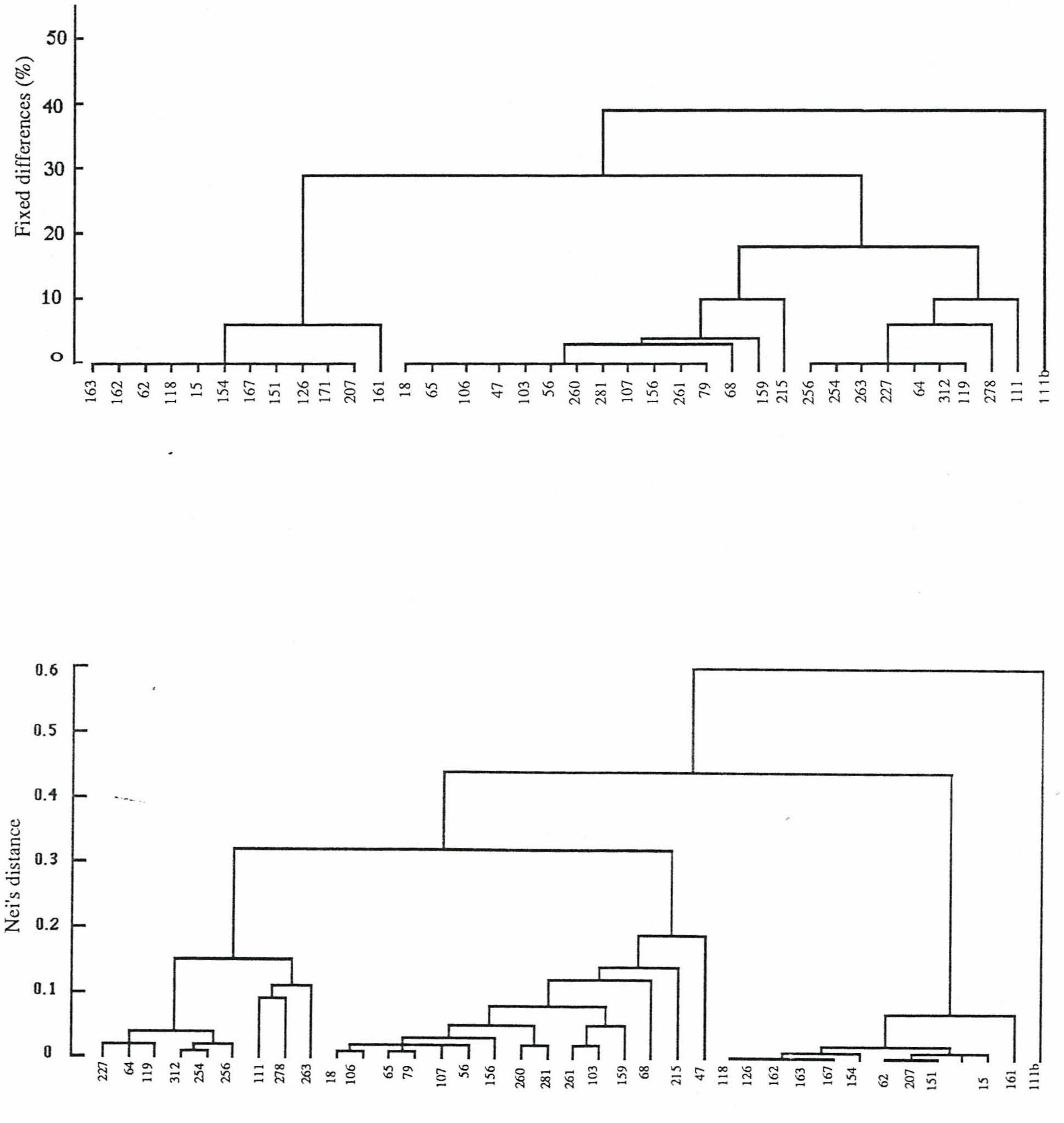
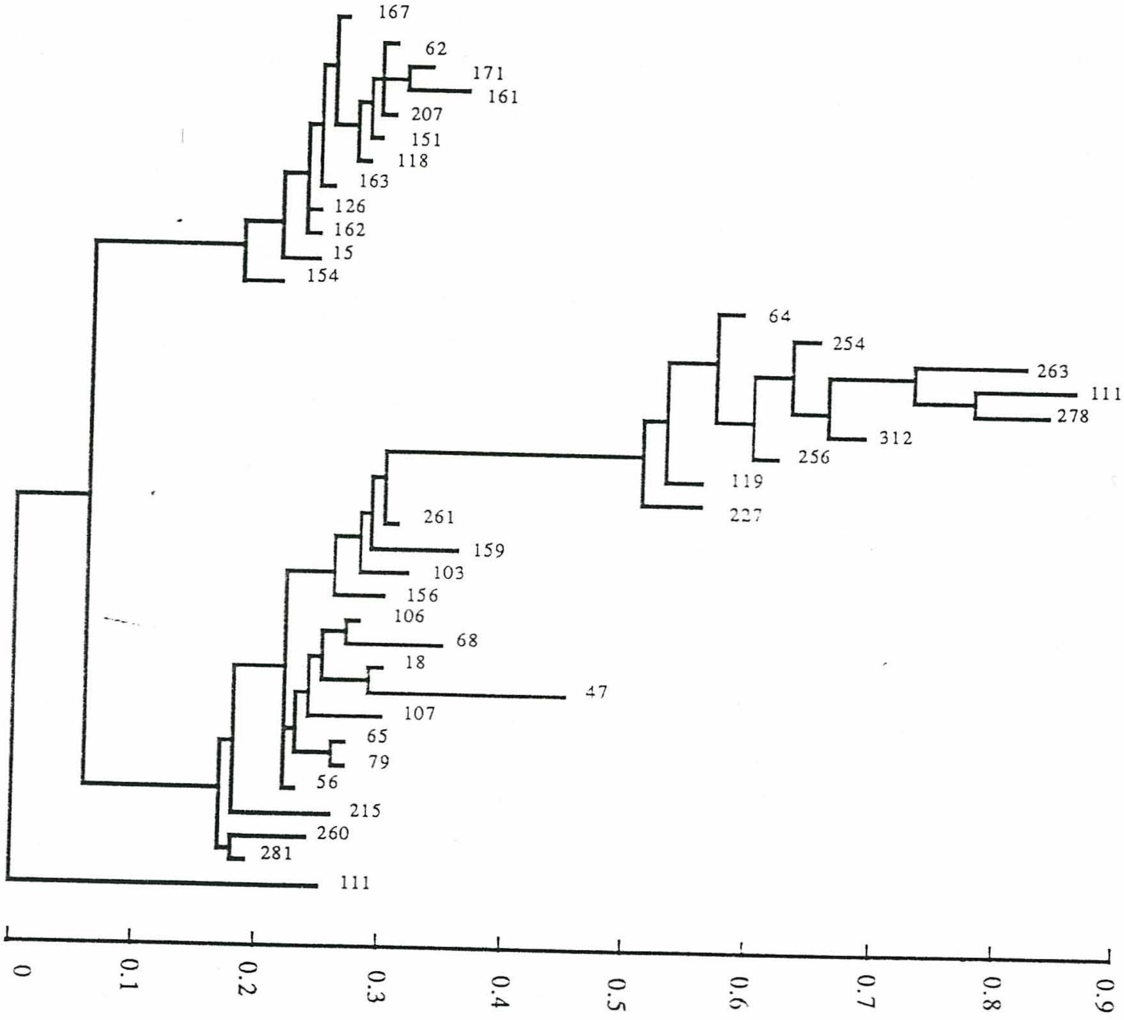


Figure 4: UPGMA phenograms showing the genetic relationships (a) % fixed differences; b) Nei's distance corrected for small sample size) between populations of millipedes from 36 caves in Cape Range.

A phylogenetic method (Distance Wagner) was used to see whether the topology of the four main subregions differed from those found in the phenograms presented above (Fig 4). Examination of the Wagner tree (Fig. 6) shows that the branching order of the four major subregions is not different from that shown in the phenograms. However, the relationship between caves is shown more succinctly in the Wagner tree. It is clear that the south contains the most genetically homogeneous subgroup and that the central and northern groups are more heterogenous. The northern group has diverged strongly from the central group and is the most heterogenous subgroup.

Figure 6: Tree of the millipedes produced by a Distance Wagner Analysis on the matrix of Rogers' Genetic Distance rooted on sympatric species from C-111.



Distance between caves

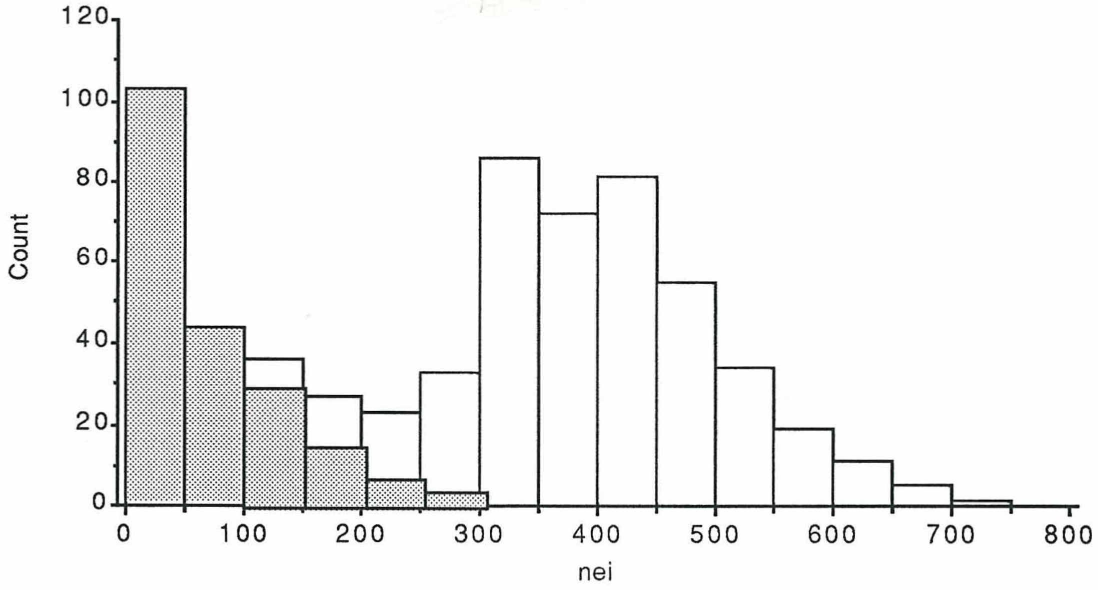
The mean distance separating caves within the three groups does not differ significantly (Table 2) but the between group distances are much greater (Table 2). The minimum distances separating caves containing millipedes of the three genetic groups are small, 1.23 Km between the northern and central groups, and 2.36 km between the northern and central groups. These distances are very small compared with the mean distance between caves within Groups (Table 2). Hence the evidence suggests that the genetic areas have distinct boundaries.

Table 2: The distances, both metric (km) and genetic (% fixed differences and corrected Nei's distance x 1000) between all pairs of caves from which millipede electrophoretic samples were derived in the southern, central and northern genetic sectors of Cape Range. Common letters within columns denote no significant difference (ANOVA followed by Fisher's PLSD).

Comparison	Distance (km)			F.D.%	Nei's
	Mean	S.D.	N		
Within Southern Group	3.51a	2.5	66	0.92	21.1
Within Central Group	4.10a	2.88	105	2.59	94.4a
Within Northern Group	5.24a	4.88	36	3.06	100.5a
Between Groups	10.55	5.58	423	25.58	399.6

ANOVA's#: **Distance**:- $Fs_{3,32} = 79.67$, $P<0.001$. **Fixed differences** (log +1 transformation):- $Fs_{3,32} = 803.6$, $P<0.001$- follow-up test is Fisher's PLSD based on log transformed data. **Nei's distance**:- $Fs_{3,32} = 577.9$, $P<0.001$. #As each point represents a comparison between two of n populations and there are n(n-1)/2 points. As these are not statistically independent the degrees of freedom in the above analyses are based on n caves rather than n(n-1)/2 comparisons.

Figure 7: Nei's distance (x1000) between all pairs of caves from which millipede genetical samples were taken. Stippled bars denote within area and open bars denote between area genetic distances.



Fixed differences (%FD):- there is a trend of increasing %FD, and thus within group heterogeneity, from south to north (Table 2) and all the groups differ significantly. However, the %FD between groups is much greater than that within groups (Table 2).

Nei's distance:- mean Nei's distance in the southern group is lower than in either the central or northern group and shows again that this population is genetically more homogeneous (Table 2). As is the case for %FD, the between group Nei's distance is substantially greater than that within groups (Table 2 and Fig. 7).

Together these data suggest that the southern group of caves is more connected than either the central or the northern group; this will be discussed below.

Metric and genetic distance

For both within and between group data sets there is a significant direct regression for both measures of genetic distance on the distance separating the caves (Table 3). This suggests that an isolation by distance model (IBDM) may be applicable to the data and this is discussed further below.

Table 3: The relationship between two measures of genetic distance and the metric distance (km) between all cave pairs. The caves are grouped according to the groups defined by the principal coordinate analysis (Fig 3).

Index	Group	Slope	Intercept	No. caves	D.F.*	Fs	P
Fixed differences (%)	South	0.27	0.03	12	1,10	6.73	<0.05
Nei's distance (x1000)	South	4.47	5.40	12	1,10	12.54	<0.01
Fixed differences (%)	North	0.68	-0.49	9	1,7	29.58	<0.001
Nei's distance (x1000)	North	7.45	61.48	9	1,7	14.09	<0.01
Fixed differences (%)	Central	0.99	-1.77	15	1,13	68.21	<0.001
Nei's distance (x1000)	Central	8.42	55.76	15	1,13	16.13	<0.001
Fixed differences (%)	All	1.44	5.72	36	1,34	410.97	<0.001
Nei's distance (x1000)	All	18.77	133.40	36	1,34	353.52	<0.001

* As each point represents a comparison between two of n populations and there are n(n-1)/2 points. As these are not statistically independent the degrees of freedom in the above analyses are based on n caves rather than n(n-1)/2 comparisons. Tests marked thus '*' in the text are treated in the same manner.

Is the isolation by distance model appropriate?

From the contingency table analysis comparing all caves with each other, the southern group clearly comprises three sub-groups, namely:- a) 161; b) 15, 62, 171, 207; c) 118, 126, 151, 154, 162, 163, 167. Only sub-group is large enough to test and it is inconsistent with IBDM (regression of Nei's Distance on metric distance; *Fs $_{1,5}$ = 1.59, P>0.25).

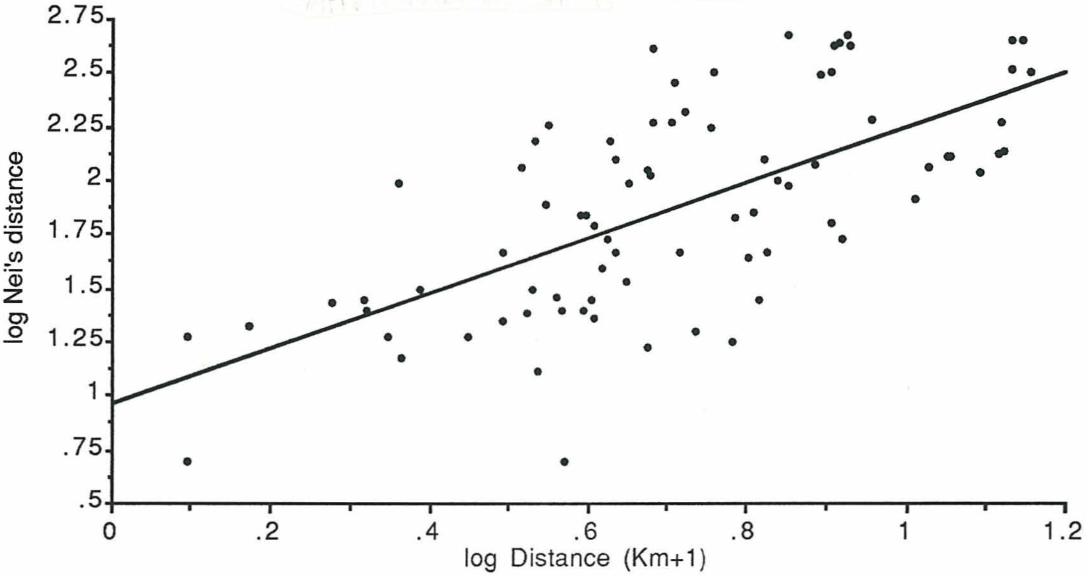
Table 4: Regressions for single caves which are consistent with the isolation by distance model.

Group	Cave	Nei	Km	D.F.	F	P	slope	intercept
South	154	lin	lin	1,9	8.764	0.016	9.51	9.04
South	163	lin	lin	1,9	7.524	0.023	6.90	-2.03
Central	79	log	log	1,6	10.446	0.018	0.8	1.48

Fixed differences imply that there is effectively no genetic exchange between populations, hence caves showing fixed differences should be excluded from the analysis. Having removed data for caves having populations of millipedes showing fixed differences within a group then neither the southern (*P>0.25), nor the northern groups (*P>0.1) show overall support for IBDM but examining caves individually shows three caves consistent with IBDM (Table 4).

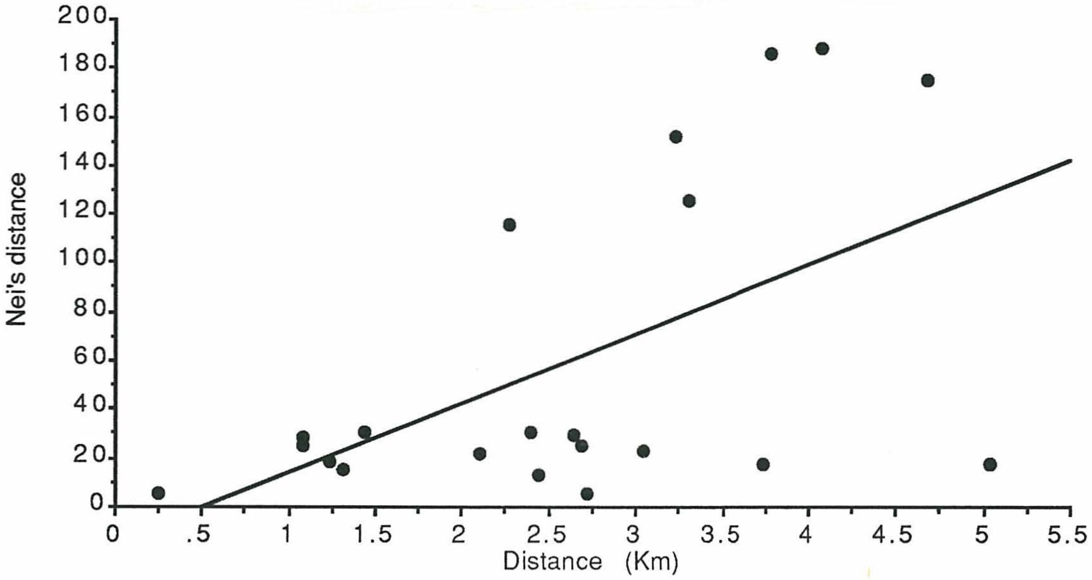
The central group appears to be consistent with IBDM as there is a strong positive regression of Nei's distance on the distance (Km) separating the caves (Fig. 8: *Fs 1,13 = 60.91, P<0.001).

Figure 8: The relationship between Nei's distance and the distance separating the caves in the central area.



However, subdividing the data further into the clear genetic sub-groups identified in the Wagner tree (Fig. 6), the largest sub-group includes eight caves (18, 47, 56, 65, 68, 79, 106, 107). Again there is a significant effect of distance (*Fs 1,6 = 7.94, P<0.05) but clearly there are two different relationships (Fig. 9) with all the upper points representing data including C-47. Exclusion of these data shows no support for IBDM (*Fs1,5 = 0.005, P>0.75).

Figure 9: The relationship between Nei's distance and the distance separating the caves in the largest sub-group in the central area.



In summary, on closer analysis none of the general relationships is consistent with IBDM and the data from only three of 36 caves (8%) support IBDM. Thus it seems that the relationships occur by chance rather than reflecting agreement with IBDM.

The nature of the populations

The work in Cape Range aimed to determine the degree of genetic divergence between cave populations in order to define the genetic provinces within Cape Range (Humphreys 1989). The current work aimed to better define the genetic provinces and, within provinces, to assess the degree of connection between caves permitting interbreeding. The rationale for this is examined below.

Caves within a region can be connected (in terms of allowing movement of troglobites) by fine leads joining adjacent caves but inaccessible to cave exploration. Else, they may have no direct connections resulting from the karstification, but may be connected by larger spaces in the rocks just beneath the soil layer - the superficial underground compartment (milieu souterrain superficiel: Juberthie 1983). Both these types of cavities potentially may permit migration of troglobites between adjacent caves within a karst province or even between karst provinces (Juberthie 1983). The amount of migration permitted by the combination of both routes is a measure of the permeability of the system to troglobites - I will term this bio-connectance.

The bio-connectance of the caves should be reflected in the degree of genetic similarity between caves. The working hypothesis was developed that within genetic provinces the amount of movement of troglobites should decrease with the distance separating the caves. In other words that Cape Range is a relatively undifferentiated spongework inhabited by troglobites and that one is sampling this spongework when collecting those individuals that have entered the larger caverns.

This hypothesis must be rejected because the isolation by distance model, discussed at length above, has been rejected. With it is rejected random dispersal and the concept of a spongework within Cape Range occupied by troglobites.

The model more appropriate for the millipede populations is the discrete sub-population model. This model assumes that the populations consist of a series of sub-populations within which mating occurs at random. Sub-populations are separated from each other by environmental or behavioural barriers that allow only very limited amounts of migration between them (Richardson, Baverstock & Adams 1986).

Discussion

Bio-connectance

Any fixed differences imply that gene flow does not occur between the populations (Richardson, Baverstock & Adams 1986). The millipede populations in Cape Range differ by up to 48% fixed differences (C-118 and C-256). Excluding the clearly sympatric species in C-111, the three genetic groups along Cape Range have a large number of fixed differences and clearly represent discrete populations that do not interbreed. The borders between the groups are associated with geomorphological barriers to movement between caves in different areas (the gorges that cut through the Tulki Limestone into the Mandu Calcarenite below). However, while there are few fixed differences within areas, they do occur between some cave pairs as discussed below.

In the southern group only cave C-161 has fixed differences from all other caves. Of the caves for which millipede genetical data are available, C-161 is the only one lying in a valley draining to the west in the southern part of the group area. In the northern group C-111 and C-278 have fixed differences from all others. C-111 is the only cave sampled north of the deep gorge of

Tantabiddy Creek which cuts through the Pilgramunna Formation into Tulki Limestone. C-278 is the only cave in the northern sector that lies south of some of the branches of Shothole Canyon. In the central group C-68, C-159 and C-215 have fixed differences from all others. C-68 is the only cave sampled which lies in the drainage basin of the creek that reaches the west coast just to the north of Tulki Well (22o 05' S). C-159 is the cave most closely associated with the complex branching gorges between Mt Hollister and Charles Knife Road, gorges that cut through the Tulki Limestone into the Mandu Calcarenite below. C-215 is the only cave in this group on the west coast and is well remove spatially from the other caves. It is separated from them by deep gorges which cut through the Pilgramunna Formation into Tulki Limestone.

Hence, it seems that fixed differences within groups may result from isolation by distance (C-215 and C-111), isolation within a catchment (C-68 and C-161) or isolation by geomorphological features (C-159 and C-278) such as deeply dissected country (similar to the more overt isolation between groups).

Management Implications

In Cape Range the genetic evidence suggests that there are three independent areas for both the terrestrial and aquatic components of the fauna (evidence from electrophoretic work on millipedes, schizomids and amphipods), that areas can and should be managed independently, and that all three areas need to be maintained to sustain the very great genetic diversity of the area.

Nonetheless, the three areas may require different management philosophies. The southern area is much more genetically homogeneous than the other areas and the greatest genetic diversity is in the central area where the caves, despite their close proximity, are well isolated from each other. One can predict that extinction of the populations in one cave in the southern region would be followed by relatively rapid repopulation, whereas the elimination of a local population in the central region may be permanent.

The alignment of the proposed road across Cape Range (CALM 1987) between Shot Hole Canyon and Milyering should be reconsidered as it traverses the boundary between the northern and central genetic areas. Hence, any adverse effects will impinge on two distinct faunistic areas. In addition the road would facilitate cavers access to and movement between two genetic provinces and thus increase the change of inadvertent transport of individual troglobites between genetic provinces.

Acknowledgments

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APPENDICES

Appendix 1: Genetical data for the millipedes from 36 caves in Cape Range.

Appendix 1a: Genetic profiles of individual millipedes (assuming autosomal loci in a diploid organism). Allozymes are designated alphabetically in order of increasing electrophoretic mobility. - denotes not scorable.

Code	RnGrp	Acon	Ada	Adh	Dia	Enol	Fdp	Fum	Got1	Got2	Gpi	Hk	Mdh1	Mdh2	PepA	PepB	PepC	PepD	Tpi
31791	B 1	cc	bd	bb	bb	aa	cc	bb	aa	cd	cc	cc	bb	ee	bb	bb	bb	dd	bb
31822	B 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	cd	bb
31850	B 1	cc	cd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
31881	B 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cd	--	bb	ee	bb	bb	bb	dd	bb
31911	B 1	cc	ad	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	dd	bb
31942	C 1	cc	dd	bb	bb	aa	cc	bb	aa	cd	cc	cc	bb	ee	bb	bb	bb	dd	bb
31972	C 1	cc	dd	bb	bb	aa	cc	bb	aa	dd	cc	cc	bb	ee	bc	bb	bb	dd	bb
32003	C 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	dd	bb
32095	D 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
32125	D 1	cc	de	bb	bb	aa	cc	bb	aa	cd	cc	cc	bb	ee	bb	bb	bb	dd	bb
21185	D 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
118-01	A 1	cc	de	bb	bb	--	cc	--	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
126-01	A 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
126-02	A 1	cc	dd	bb	bb	aa	cc	bb	aa	--	cc	cc	bb	ee	bb	bb	bb	--	bb
126-03	A 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	--	bb
126-04	A 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
126-06	C 1	ac	de	bb	bb	aa	cc	bb	aa	cc	bc	cc	bb	ee	bb	bb	bb	dd	bb
126-07	C 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
126-08	C 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	ab	bb	bb	dd	bb
126-09	E 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	dd	bb
126-10	E 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	dd	bb
126-11	E 1	cc	de	bb	bb	aa	cc	bb	aa	cc	bc	--	bb	ee	bb	bb	bb	dd	bb
126-12	E 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	--	bb	ee	bb	bb	bb	dd	bb
126-13	E 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	ab	bb	bb	dd	bb
151-01	C 1	bc	de	--	bb	aa	--	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
151-06?	C 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
154-01	A 1	cc	--	bb	bb	aa	cc	bb	aa	ac	cd	bb	bb	ee	bb	bb	bb	--	bb
154-02	A 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
154-03	A 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
154-04	A 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
154-05	A 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	bb	bb	bb	--	bb
154-06	A 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
154-07	A 1	cc	--	bb	bb	aa	cc	bb	aa	cc	cc	bc	bb	ee	bb	bb	bb	--	bb
161-01	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-02	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-03	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-04	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-05	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-06	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-07	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-08	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
161-09	C 1	cc	dd	aa	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
162-01	D 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
162-02	D 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	ab	bb	bb	dd	bb
162-03	D 1	cd	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	ab	bb	bb	dd	bb
162-04	D 1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
162-05	D 1	bc	de	bb	bb	aa	cc	bb	aa	cc	ad	cc	bb	ee	bb	bb	bb	dd	bb
162-06	D 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	bc	cc	bb	ee	bb	bb	bb	dd	bb
162-07	D 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	ab	bb	bb	dd	bb
163-01	B 1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
163-02	B 1	cc	de	bb	bc	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
163-03	B 1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb

Appendix 1a continued

163-04	B	1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
163-05	E	1	cc	ee	bb	bb	aa	cc	bb	aa	cc	bc	cc	bb	ee	ab	bb	bb	dd	bb
163-06	E	1	cc	de	bb	bb	aa	cc	bb	aa	cd	cd	cc	bb	ee	bb	bb	bb	dd	bb
163-07	E	1	cc	ee	bb	bb	aa	cc	bb	aa	cc	bc	cc	bb	ee	bb	bb	bb	dd	bb
163-08	E	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cd	--	bb	ee	bb	bb	bb	dd	bb
163-09	E	1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cd	cc	bb	ee	ab	bb	bb	dd	bb
163-10	E	1	bc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
167-01	A	1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	ab	bb	bb	--	bb
167-02	A	1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
167-03	A	1	cc	de	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	--	bb
167-04	A	1	cc	ee	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	ab	bb	bb	--	bb
167-05	B	1	cc	de	bb	bc	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
167-06	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
171-01	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	--	bb	ee	bb	bb	bb	dd	bb
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171-05	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	--	bb	ee	bb	bb	bb	dd	bb
171-06	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	--	bb	ee	bb	bb	bb	dd	bb
171-07	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	--	bc	ee	bb	bb	bb	dd	bb
171-08	B	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	--	bb	ee	bb	bb	bb	dd	bb
171-09	B	1	cd	bd	aa	bb	aa	cc	bb	aa	cc	cc	--	bc	ee	bb	bb	bb	dd	bb
207-01	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-02	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-03	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-04	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-05	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-06	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-07	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-08	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-09	D	1	cc	dd	bb	bb	aa	cc	bb	aa	bc	cc	cc	bb	ee	bb	bb	bb	dd	bb
207-10	D	1	cc	dd	bb	bb	aa	cc	bb	aa	cc	cc	cc	bb	ee	bb	bb	bb	dd	bb
21915	A	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	--	bb	ce	bb	dd	bb	--	cc
21946	A	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ce	bb	dd	bb	--	bc
21975	A	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ee	bb	dd	bb	--	cc
111-05	B	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	dd	--	bb	ee	--	dd	bb	aa	bb
111-06	B	2	cc	ff	cc	bb	aa	bb	bb	aa	--	dd	--	bb	ee	--	dd	bb	aa	bb
119-01	A	2	dd	ff	--	bb	aa	bb	--	aa	cc	cd	cc	bb	cc	bb	dd	bb	--	cc
227-01	C	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ee	bb	dd	bb	ab	bc
227-01	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ce	bb	dd	bb	aa	cc
227-02	C	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ce	bb	de	bb	aa	bc
227-02	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cc	cc	bb	cc	bb	de	bb	aa	bc
227-03	C	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ce	bb	dd	bb	aa	bc
227-03	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ee	bb	dd	bb	ad	bb
227-04	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ce	bb	de	bb	ad	cc
227-05	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ce	bb	de	bb	aa	bb
227-06	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cc	cc	bb	cc	bb	dd	bb	aa	bc
227-07	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cc	cc	bb	cc	bb	dd	bb	aa	bb
227-08	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	cc	bb	dd	bb	ad	bb
227-09	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ee	bb	dd	bb	aa	bb
227-10	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	ac	bb	ff	bb	dd	bb	dd	bb
254-01	D	2	dd	ff	cc	bb	aa	bb	bb	aa	--	dd	--	bb	cf	bb	dd	bb	aa	cc
254-02	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	bd	cc	bb	cf	bb	dd	bb	aa	bc
254-03	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	ad	cc
254-04	D	2	dd	ff	cc	bb	aa	bb	aa	aa	cc	dd	cc	bb	ef	bb	dd	bb	aa	ac
254-05	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	--	bb	ff	bb	dd	bb	aa	ab
254-06	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cd	dd	cc	bb	ff	bb	dd	bb	ad	ac
254-07	D	2	dd	ff	cc	bb	aa	bb	ab	aa	cc	dd	cc	bb	ff	bb	dd	bb	ad	cc
254-08	D	2	dd	ff	cc	bb	aa	bb	ab	aa	cc	dd	cc	bb	ff	bb	dd	bb	aa	bc
254-09	D	2	dd	ff	cc	bb	aa	bb	ab	aa	cc	dd	cc	bb	ff	bb	dd	bb	aa	bc
256-01	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	ab	cc

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256-02	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	cf	bb	dd	bb	ab	cc
256-03	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	cf	bb	dd	bb	bb	bc
256-04	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	ab	cc
256-05	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	ac	bb	ff	bb	dd	bb	ab	cc
256-06	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	cf	bb	dd	bb	ab	bc
256-07	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	aa	cc
256-08	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	ab	cc
256-09	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	bb	cc
256-10	D	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	ab	cc
263-01	E	2	dd	ff	cc	bb	aa	bb	bb	aa	dd	cc	cc	bb	ff	bb	dd	bb	aa	bb
263-02	E	2	cc	ff	cc	bb	aa	bb	bb	aa	dd	cd	cc	bc	cf	bb	dd	bb	aa	bb
263-03	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cd	dd	cc	bb	df	bb	df	bb	aa	bb
263-04	E	2	cd	ff	cc	bb	aa	aa	bb	aa	dd	dd	cc	bb	ff	bb	dd	bb	aa	bc
263-05	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cd	dd	bc	bb	ff	bb	df	bb	aa	bb
263-06	E	2	cc	ff	cc	bb	aa	ab	bb	aa	dd	dd	cc	bb	cf	bb	dd	bb	aa	bb
263-07	E	2	cc	ff	cc	bb	aa	ab	bb	aa	dd	dd	cc	bb	ff	bb	df	bb	aa	bc
263-08	E	2	cc	ff	cc	bb	aa	aa	bb	aa	dd	cd	cc	bb	ff	bb	df	bb	aa	bc
263-09	E	2	dd	ff	cc	bb	aa	bb	bb	aa	dd	cd	cc	bb	ff	bb	dd	bb	aa	bb
263-10	E	2	cc	ff	cc	bb	aa	ab	bb	aa	dd	dd	cc	bb	ff	bb	dd	bb	aa	bb
263-11	E	2	cc	ff	cc	bb	aa	bb	bb	aa	dd	dd	cc	bb	cf	bb	df	bb	aa	bc
278-01	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cd	bb	bb	ff	bb	dd	bb	ab	bb
278-02	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cc	bb	bb	ff	bb	dd	bb	ab	bc
278-03	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	bb	bb
278-04	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cd	bc	bb	cf	bb	dd	bb	aa	bc
278-05	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	cf	bb	dd	bb	ab	bb
278-06	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cd	--	bb	ff	bb	dd	bb	ab	bb
278-07	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	dd	ac	bb	ff	bb	dd	bb	ab	bb
278-08	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ff	bb	dd	bb	ab	bc
278-09	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cc	cc	bb	ff	bb	dd	bb	ab	bb
278-10	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	cd	bc	bb	cf	bb	dd	bb	ab	bb
278-11	E	2	cc	ff	cc	bb	aa	bb	bb	aa	cc	dd	bc	bb	ff	bb	dd	bb	bb	bb
312-01	B	2	dd	ff	cc	bb	aa	aa	bb	aa	cd	cd	cc	bb	af	bb	dd	bb	aa	bc
312-02	B	2	dd	ff	cc	ab	aa	bb	bc	aa	cc	cd	cc	bb	ff	bb	dd	bb	aa	bb
312-03	B	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ff	bb	dd	bb	aa	bc
312-04	B	2	dd	ff	cc	bb	aa	bb	bc	aa	cd	dd	cc	bb	ef	bb	dd	bb	aa	bc
312-05	B	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	dd	cc	bb	ff	bb	dd	bb	aa	bc
312-06	B	2	dd	ff	cc	bb	aa	bb	bc	aa	cc	bd	cc	bb	ef	bb	cd	bb	aa	cc
312-07	B	2	dd	ff	cc	ab	aa	bb	bb	aa	cc	bd	cc	bb	ef	bb	dd	bb	aa	cc
312-07	E	2	dd	ff	cc	bb	aa	bb	bb	aa	cd	cd	cc	bb	ef	bb	dd	bb	aa	cc
312-08	E	2	dd	ff	cc	bb	aa	bb	ab	aa	cc	dd	cc	bb	cf	bb	cd	bb	aa	bc
312-09	E	2	dd	ff	cc	bb	aa	bb	bb	aa	cc	cd	cc	bb	ee	bb	dd	bb	aa	cc
31794	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	bc	bb	bb	cc	bb	dd	bb	--	bb
31825	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bc	bb	cc	bb	dd	bb	--	bb
31853	A	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb
31884	A	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	bc	bb	bb	cc	bb	dd	bb	--	bb
31914	B	3	cc	ff	cc	ad	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	ab	dd	bb
31945	B	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	bc	bc	bb	cc	bb	dd	bb	dd	bb
31975	B	3	cc	ff	cc	ad	aa	cc	bb	aa	cc	cd	bc	bb	cc	bb	df	bb	dd	bb
32006	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bc	bb	bb	ac	bb	dd	bb	dd	bb
32037	C	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cc	bc	bb	ac	bb	df	bb	dd	bb
32067	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	dd	bb
32098	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bc	cc	bb	ac	bb	dd	bb	dd	ab
32128	C	3	cc	ff	cc	bc	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
018-13	E	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	bb	bb	bb	ac	bb	dd	bb	dd	bb
018-14	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bc	bb	bb	cc	bb	dd	ab	dd	bb
15706	B	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	bb	bb	bb	cc	bb	dd	aa	dd	bb
15737	B	3	cc	ff	cc	ac	aa	cc	bb	aa	cc	bb	bc	bb	bc	bb	dd	ab	dd	bb
15796	B	3	cc	ff	cc	aa	aa	cc	bb	aa	cc	bb	cc	ab	cc	bb	dd	aa	dd	bb
15826	B	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	bd	cc	bb	cc	bb	dd	aa	dd	bb
15857	B	3	cc	ff	cc	cc	aa	cc	bb	aa	cc	bb	cc	bb	cc	bb	dd	aa	dd	bb
15887	B	3	cc	ff	cc	aa	aa	cc	bb	aa	cc	bd	cc	bb	cc	bb	dd	aa	dd	bb

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15918	B	3	cc	ff	cc	aa	aa	cc	bb	aa	cc	bb	cc	bb	cc	bb	dd	aa	dd	bb
15949	B	3	cc	ff	cc	aa	aa	cc	bb	aa	cc	bb	cc	bb	bc	bb	df	aa	dd	bb
15979	B	3	cc	ff	cc	aa	aa	cc	bb	aa	cc	bb	cc	bb	bc	bb	dd	aa	dd	bb
18993	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bc	--	bb
19024	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	--	bb
19053	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	--	bb
19084	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	--	bb
19114	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	--	bb
22281	C	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
22312	C	3	cc	ff	cc	bc	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
22340	C	3	cc	ff	cc	ad	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
22371	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
22401	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
22432	C	3	cc	ff	cc	cd	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
22462	C	3	cc	ff	cc	ad	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
22493	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
22524	C	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
23376	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	cc	--	bb
23407	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bc	--	bb
23436	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	cc	--	bb
23467	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bc	--	bb
27394	C	3	cc	ff	cc	cd	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
27425	C	3	cc	ff	cc	ad	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
27453	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
27484	C	3	cc	ff	cc	cc	aa	cc	bb	aa	cc	ee	bb	bb	cc	bb	dd	bb	dd	bb
27514	C	3	cc	ff	cc	cc	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
27545	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	de	bc	bb	cc	bb	dd	bb	dd	bb
27575	C	3	cc	ff	cc	ac	aa	cc	bb	aa	cc	cd	--	bb	cc	bb	dd	bb	dd	bb
27606	C	3	cc	ff	cc	ac	aa	cc	bb	aa	cc	bd	bb	bb	cc	bb	dd	bb	dd	bb
27637	C	3	cc	ff	cc	cc	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	dd	bb
27667	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	bc	bb	bb	cc	bb	dd	bb	dd	bb
27698	C	3	cc	ff	cc	ac	aa	cc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bc	dd	bb
103-01	B	3	bd	ff	cc	bb	aa	cc	bb	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-02	B	3	de	ff	cc	bb	aa	cc	bb	aa	aa	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-03	B	3	bc	ff	cc	bb	aa	cc	bd	aa	ac	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-04	B	3	cc	ff	cc	bb	aa	cc	bd	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-05	C	3	de	ff	cc	bb	aa	cc	bb	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-06	C	3	ce	ff	cc	bb	aa	cc	bb	aa	aa	cc	bb	bb	cc	bb	dd	bb	dd	bb
103-07	C	3	bd	ff	cc	bb	aa	cc	bb	aa	ac	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-08	C	3	cd	ff	cc	bb	aa	cc	bb	aa	aa	cc	bb	bb	cc	bb	dd	bb	dd	bb
103-09	E	3	bd	ff	cc	bb	aa	cc	bb	aa	aa	cc	bb	bb	cc	bb	dd	bb	dd	bb
103-10	E	3	cd	ff	cc	bb	aa	cc	bd	aa	aa	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-11	E	3	bd	ff	cc	bb	aa	cc	bb	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-12	E	3	be	ff	cc	bb	aa	cc	bd	aa	aa	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-13	E	3	cc	ff	cc	bb	aa	cc	bb	aa	aa	dd	bb	bb	cc	bb	dd	bb	dd	bb
103-14	E	3	bd	ff	cc	bb	aa	cc	dd	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-15	E	3	bc	ff	cc	bb	aa	cc	bb	aa	aa	cd	bb	bb	cc	bb	dd	bb	dd	bb
103-16	E	3	cc	ff	cc	bb	aa	cc	bd	aa	aa	dd	bb	bb	cc	bb	dd	bb	dd	bb
106-01	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	--	bb
106-02	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cf	bb	bb	cc	bb	dd	bb	--	bb
106-03	A	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb
106-04	A	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	ce	bb	bb	cc	bb	dd	bb	--	bb
106-05	B	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cc	--	bb	cc	bb	dd	bb	dd	bb
106-06	B	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	dd	bb
106-07	B	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
106-08	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	dd	bb
106-09	E	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cf	bb	bb	cc	bb	dd	bb	dd	bb
106-10	E	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	dd	bb
107-01	A	3	cc	ff	cc	--	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bc	--	bb
107-02	A	3	cc	ff	cc	bb	aa	bc	bb	aa	cc	de	bb	bb	cc	bb	dd	bb	--	bb
107-03	A	3	cc	ff	cc	bb	aa	bc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb

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107-04	A	3	cc	ff	cc	bb	aa	bc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	--	bb
107-05	A	3	bc	ff	cc	--	aa	bc	bb	aa	cc	dd	bb	bb	cc	bb	dd	bb	--	bb
107-06	A	3	ac	ff	cc	dd	aa	bc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb
107-07	A	3	cc	ff	cc	dd	aa	bc	bb	aa	cc	de	bb	bb	cc	bb	dd	bb	--	bb
107-08	A	3	cc	ff	cc	bd	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb
156-01	A	3	bc	ff	cc	bd	aa	cc	bb	aa	ac	dd	bb	bb	cc	bb	dd	bb	--	bb
156-02	A	3	cc	ff	cc	bd	aa	cc	bb	aa	ac	cd	bb	bb	cc	bb	dd	bb	--	bb
156-03	A	3	bb	ff	cc	bb	aa	cc	bb	aa	ac	dd	bb	bb	cc	bb	dd	bb	--	bb
156-04	A	3	cc	ff	cc	bb	aa	cc	bb	aa	aa	dd	bb	bb	cc	bb	dd	bb	--	bb
156-05	A	3	bc	ff	cc	bb	aa	cc	bb	aa	ac	dd	bb	bb	cc	bb	dd	bb	--	bb
156-06	A	3	bc	ff	cc	bd	aa	cc	bb	aa	ac	cd	bb	bb	cc	bb	dd	bb	--	bb
156-07	A	3	bc	ff	cc	bb	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	--	bb
156-08	A	3	cc	ff	cc	dd	aa	cc	bb	aa	cc	cc	bb	bb	cc	bb	dd	bb	--	bb
156-09	A	3	cc	ff	cc	bb	aa	cc	bb	aa	ac	cc	bb	bb	cc	bb	dd	bb	--	bb
159-01	A	3	bb	ff	cc	bb	aa	cc	bb	aa	ac	cc	--	bb	cc	bb	dd	bb	--	bb
215-01	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-02	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	--	bb	aa	bb	dd	bb	dd	bb
215-03	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	--	bb	aa	bb	dd	bb	dd	bb
215-04	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-05	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	--	bb	aa	bb	dd	bb	dd	bb
215-06	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-07	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-08	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-09	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
215-10	D	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bb	bb	bb	aa	bb	dd	bb	dd	bb
260-01	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bc	dd	bb	cc	bb	dd	bb	dd	bb
260-02	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bd	bd	bb	ac	bb	cd	bb	dd	bb
260-03	C	3	bc	ff	cc	bb	aa	cc	bb	aa	cc	dd	bd	bb	ac	bb	dd	bb	dd	bb
260-04	C	3	cc	ff	cc	ab	aa	cc	bb	aa	cc	bd	bd	bb	aa	bb	cd	bb	dd	bb
260-05	C	3	cc	ff	cc	bb	aa	cc	bb	aa	--	bd	--	bb	--	bb	cd	bb	dd	bb
260-06	C	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bd	bd	bb	ac	bb	cd	bc	dd	bb
261-01	A	3	--	ff	--	bb	aa	cc	--	aa	--	cd	--	bb	cc	ab	dd	bb	--	bb
281-01	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cc	bb	bb	ac	bb	cd	bb	dd	bb
281-02	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cd	bb	bb	cc	bb	dd	bb	dd	bb
281-03	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	bd	dd	bb	ac	bb	dd	bb	dd	bb
281-04	E	3	cc	ff	cc	bb	aa	cc	bb	aa	cc	cd	bb	bb	ac	bb	cd	bb	dd	bb
999-01	B	4	ee	ee	bb	bb	aa	bb	bb	aa	cc	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-02	B	4	ee	eg	bb	bb	aa	bb	bb	aa	cc	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-03	B	4	ee	ee	bb	bb	aa	bb	bb	aa	ac	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-04	B	4	ee	ee	bb	bb	aa	bb	bb	aa	cc	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-07	B	4	ee	ee	bb	bb	aa	bb	bb	aa	ac	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-08	B	4	ee	ee	bb	bb	aa	bb	bb	aa	ac	dd	bb	cc	ff	bb	aa	bb	dd	bb
999-09	B	4	ee	ee	bb	bb	aa	bb	bb	aa	ac	dd	bb	cc	ff	bb	aa	bb	dd	bb

Appendix 1b: Allele frequencies of the 36 populations of millipedes.

Appendix 1b/1

LOCUS	Allele	015	062	118	126	151	154	161	162	163	167	171	207	064	111
Acon	e														
	d								7			12		100	
	c	100	100	100	96	75	100	100	86	95	100	88	100		100
	b					25			7	5					
	a				4										
	N=	10	1	1	12	2	7	9	7	10	6	8	10	3	2
Ada	g														
	f													100	100
	e	10		50	54	25	90		57	70	50				
	d	75	100	50	46	75	10	100	43	30	50	94	100		
	c	5													
	b	5										6			
	a	5													
	N=	10	1	1	12	2	5	9	7	10	6	9	10	3	2
Adh	c													100	100
	b	100	100	100	100	100	100		100	100	100	83	100		
	a							100				17			
	N=	10	1	1	12	1	7	9	7	10	6	9	10	3	2
Dia	d														
	c									5	8				
	b	100	100	100	100	100	100	100	100	95	92	100	100	100	100
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
Enol	a	100	100	**	100	100	100	100	100	100	100	100	100	100	100
	N=	10	1		12	2	7	9	7	10	6	9	10	3	2
Fdp	c	100	100	100	100	100	100	100	100	100	100	100	100		
	b													100	100
	a														
	N=	10	1	1	12	1	7	9	7	10	6	9	10	3	2
Fum	d														
	c														
	b	100	100		100	100	100	100	100	100	100	100	100	100	100
	a			**											
	N=	10	1		12	2	7	9	7	10	6	9	10	3	2

Appendix 1b/1 continued

LOCUS	Allele	015	062	118	126	151	154	161	162	163	167	171	207	064	111
Got1	a	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
Got2	d	25								5					
	c	75	100	100	100	100	93	100	100	95	100	100	95	100	100
	b												5		
	a						7								
	N=	10	1	1	11	2	7	9	7	10	6	9	10	3	1
Gpi	f														
	e														
	d	20			17		14		15	15				100	100
	c	80	100	100	75	100	86	100	71	75	100	100	100		
	b				8				7	10					
	a								7						
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
Hk	d														
	c	100	100	100	100	100	79	100	100	100	100		100	100	
	b						21								
	a											**			**
	N=	9	1	1	10	2	7	9	7	9	6		10	2	
Mdh1	c											11			
	b	100	100	100	100	100	100	100	100	100	100	89	100	100	100
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
Mdh2	f														
	e	100	100	100	100	100	100	100	100	100	100	100	100	67	100
	d														
	c													33	
	b														
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
PepA	c	5													
	b	95	100	100	92	100	100	100	79	90	83	100	100	100	
	a				8				21	10	17				**
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	

Appendix 1b/1 continued

LOCUS	Allele	015	062	118	126	151	154	161	162	163	167	171	207	064	111
PepB	f														
	e														
	d													100	100
	c														
	b	100	100	100	100	100	100	100	100	100	100	100	100		
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
PepC	c														
	b	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2
PepD	d	95	100		100	100		100	100	100	100	100	100		
	c	5													
	b														
	a			**			**							**	100
	N=	10	1		8	2		9	7	10	2	9	10		2
Tpi	c													83	
	b	100	100	100	100	100	100	100	100	100	100	100	100	17	100
	a														
	N=	10	1	1	12	2	7	9	7	10	6	9	10	3	2

Appendix 1b/2

LOCUS	Allele	119	227	254	256	263	278	312	018	047	056	065	068	079	103
Acon	e														13
	d	100	100	100	100	23		100							28
	c					77	100		100	100	100	100	100	100	34
	b														25
	a														
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
	f	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	e														
	d														
	c														
	b														
	a														
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Adh	c		100	100	100	100	100	100	100	100	100	100	100	100	100
	b														
	a	**													
	N=		13	9	10	11	11	10	14	9	5	9	4	11	16
Dia	d								32			28	100	9	
	c								3	17		11		45	
	b	100	100	100	100	100	100	90	54	11	100	33		14	100
	a							10	11	72		28		32	
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Enol	a	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Fdp	c								100	100	100	100	100	100	100
	b	100	100	100	100	68	100	90							
	a					32		10							
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Fum	d														22
	c							15							
	b		100	72	100	100	100	80	100	100	100	100	100	100	78
	a	**		28				5							
	N=		13	9	10	11	11	10	14	9	5	9	4	11	16
Got1	a	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16

Appendix 1b/2 continued

LOCUS	Allele	119	227	254	256	263	278	312	018	047	056	065	068	079	103
Got2	d			6		91		15							
	c	100	100	94	100	9	100	85	100	100	100	100	100	100	6
	b														
	a														94
	N=	1	13	8	10	11	11	10	14	9	5	9	4	11	16
Gpi	f														
	e													13	
	d	50	54	88	100	77	59	65	10	11	60	83	12	55	62
	c	50	46	6		23	41	25	61		40	17	88	23	38
	b			6				10	29	89				9	
	a														
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Hk	d														
	c	100	96	100	95	95	60	100	21	83				5	
	b					5	35		79	17	100	100	100	95	100
	a		4		5		5								
	N=	1	13	7	10	11	10	10	14	9	5	9	4	10	16
Mdh1	c					5									
	b	100	100	100	100	95	100	100	100	94	100	100	100	100	100
	a									6					
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
Mdh2	f		8	83	85	81	86	60							
	e		42	6				30							
	d					5									
	c	100	50	11	15	14	14	5	86	83	100	100	100	100	100
	b									17					
	a							5	14						
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
PepA	c														
	b	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	a														
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
PepB	f					23			7	6					
	e		15												
	d	100	85	100	100	77	100	90	93	94	100	100	100	100	100
	c							10							
	b														
	a														
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16
PepC	c										10		75	5	
	b	100	100	100	100	100	100	100	93	6	90	100	25	95	100
	a								7	94					
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16

Appendix 1b/2 continued

LOCUS	Allele	119	227	254	256	263	278	312	018	047	056	065	068	079	103
PepD	d		19	17					100	100		100		100	100
	c														
	b		4		55		55								
	a	**	77	83	45	100	45	100			**		**		
	N=		13	9	10	11	11	10	10	9		9		11	16
Tpi	c	100	35	61	90	18	14	65							
	b		65	22	10	82	86	35	96	100	100	100	100	100	100
	a			17					4						
	N=	1	13	9	10	11	11	10	14	9	5	9	4	11	16

Appendix 1b/3

LOCUS	Allele	106	107	156	159	215	260	261	281	111b
Acon	e									100
	d									
	c	100	88	67		100	92		100	
	b		6	33	100		8			
	a		6					**		
	N=	10	8	9	1	10	6		4	7
Ada	g									7
	f	100	100	100	100	100	100	100	100	
	e									93
	d									
	c									
	b									
	a									
	N=	10	8	9	1	10	6	1	4	7
Adh	c	100	100	100	100	100	100		100	
	b									100
	a							**		
	N=	10	8	9	1	10	6		4	7
Dia	d	35	42	28						
	c									
	b	65	58	72	100	100	92	100	100	100
	a						8			
	N=	10	6	9	1	10	6	1	4	7
Enol	a	100	100	100	100	100	100	100	100	100
	N=	10	8	9	1	10	6	1	4	7
Fdp	c	100	62	100	100	100	100	100	100	
	b		38							100
	a									
	N=	10	8	9	1	10	6	1	4	7
Fum	d									
	c									
	b	100	100	100	100	100	100		100	100
	a							**		
	N=	10	8	9	1	10	6		4	7

Appendix 1b/3 continued

LOCUS	Allele	106	107	156	159	215	260	261	281	111b
Got1	a	100	100	100	100	100	100	100	100	100
	N=	10	8	9	1	10	6	1	4	7
Got2	d									
	c	100	100	56	50	100	100		100	71
	b									
	a			44	50			**		29
	N=	10	8	9	1	10	5		4	7
	Gpi	f	10							
	e	5	13							
	d	10	56	61			50	50	37	100
	c	75	31	39	100		8	50	50	
	b					100	42		13	
	a									
	N=	10	8	9	1	10	6	1	4	7
Hk	d						60		25	
	c									
	b	100	100	100		100	40		75	100
	a				**			**		
	N=	9	8	9		7	5		4	7
Mdh1	c									100
	b	100	100	100	100	100	100	100	100	
	a									
	N=	10	8	9	1	10	6	1	4	7
Mdh2	f									100
	e									
	d									
	c	100	100	100	100		50	100	62	
	b									
	a					100	50		38	
	N=	10	8	9	1	10	5	1	4	7
PepA	c									
	b	100	100	100	100	100	100	50	100	100
	a							50		
	N=	10	8	9	1	10	6	1	4	7

Appendix 1b/3 continued

LOCUS	Allele	106	107	156	159	215	260	261	281	111b
PepB	f									
	e									
	d	100	100	100	100	100	67	100	75	
	c						33		25	
	b									
	a									100
	N=	10	8	9	1	10	6	1	4	7
PepC	c		6				8			
	b	100	94	100	100	100	92	100	100	100
	a									
	N=	10	8	9	1	10	6	1	4	7
PepD	d	100				100	100		100	100
	c									
	b									
	a		**	**	**			**		
	N=	6				10	6		4	7
Tpi	c									
	b	100	100	100	100	100	100	100	100	100
	a									
	N=	10	8	9	1	10	6	1	4	7

Invariant loci: Ald, Ap, Enol, Got1, Gp1, Gsr, Mdh1, PepD and Pk (1988 data).

Appendix 1c: Genetic distance matrix.

upper - corrected Nei's D (x1000).
lower -% fixed differences.

Cave	015	062	118	126	151	154	161	162	163	167	171	207	064	111	119	227	254	256	263
015	-	6	0	10	1	36	66	12	17	10	8	5	492	434	525	442	589	628	463
062	0	-	0	18	0	52	57	21	30	14	2	0	521	470	533	453	616	657	529
118	0	0	-	0	0	0	71	0	0	0	0	0	584	445	550	466	645	702	524
126	0	0	0	-	3	9	79	0	0	0	20	18	476	424	507	429	576	613	500
151	0	0	0	0	-	25	58	3	9	0	0	0	490	463	499	425	588	628	521
154	0	0	0	0	0	-	118	9	3	12	53	52	506	378	534	419	573	599	451
161	6	6	7	6	6	6	-	83	91	73	42	57	521	470	533	453	616	657	529
162	0	0	0	0	0	0	6	-	0	0	23	22	468	427	500	423	571	607	507
163	0	0	0	0	0	0	6	0	-	1	32	30	484	432	516	436	585	623	499
167	0	0	0	0	0	0	6	0	0	-	15	14	516	455	528	448	615	656	526
171	0	0	0	0	0	0	0	0	0	0	-	2	537	466	566	462	644	685	565
207	0	0	0	0	0	0	6	0	0	0	0	-	523	472	536	455	619	659	527
064	29	35	40	29	35	29	35	24	29	35	31	35	-	126	29	26	36	33	177
111	31	38	38	31	38	27	38	31	31	38	38	38	7	-	274	115	169	211	135
119	40	40	43	40	40	40	40	33	40	40	36	40	0	23	-	28	55	52	229
227	28	28	33	28	28	29	28	22	28	28	24	28	0	6	0	-	46	70	139
254	28	28	33	28	28	29	28	22	28	28	24	28	0	6	0	0	-	19	120
256	39	44	47	39	44	35	44	33	39	44	41	44	0	13	0	0	0	-	158
263	33	33	33	33	33	29	33	33	33	33	35	33	0	6	0	0	0	0	-
278	33	33	33	33	33	29	33	33	33	33	35	33	6	6	7	6	6	6	0
312	33	33	33	33	33	29	33	28	33	33	29	33	0	6	0	0	0	0	0
018	22	22	27	22	22	24	22	22	22	22	24	22	12	19	20	11	11	17	11
047	22	28	33	22	28	24	28	22	22	28	29	28	12	19	20	11	11	17	11
056	29	29	33	29	29	24	29	29	29	29	25	29	18	13	27	18	18	18	6
065	28	28	33	28	28	24	28	28	28	28	24	28	18	19	27	17	17	22	11
068	35	35	40	35	35	29	35	35	35	35	31	35	24	20	33	24	24	24	12
079	22	22	27	22	22	24	22	22	22	22	24	22	12	19	20	11	11	17	11
103	28	28	33	28	28	24	28	28	28	28	24	28	12	19	20	11	11	17	11
106	28	28	33	28	28	24	28	28	28	28	24	28	18	19	27	17	17	22	11
107	29	29	33	29	29	24	29	29	29	29	25	29	12	7	20	12	12	12	0
156	29	29	33	29	29	24	29	29	29	29	25	29	18	13	27	18	18	18	6
159	31	31	36	31	25	31	31	25	25	31	31	31	19	27	21	13	13	19	13
215	33	33	40	28	33	29	33	28	28	33	29	33	29	25	40	28	22	33	22
260	28	28	33	28	28	24	28	28	28	28	24	28	18	19	27	17	17	22	11
261	25	25	27	25	25	25	25	25	25	25	25	25	8	18	17	8	8	8	8
281	28	28	33	28	28	24	28	28	28	28	24	28	18	19	27	17	17	22	11
111b	33	44	47	33	39	29	50	33	33	39	35	44	41	44	47	33	33	39	28

Appendix 1c continued.

Cave	278	312	018	047	056	065	068	079	103	106	107	156	159	215	260	261	281	111b
015	428	536	320	440	371	397	504	400	450	346	422	413	384	395	322	329	304	563
062	443	561	322	449	386	418	498	414	483	347	436	437	389	405	339	362	311	602
118	436	551	373	542	418	497	555	494	575	401	483	484	425	476	397	381	375	702
126	421	530	308	418	361	386	494	388	458	337	410	411	383	375	307	321	293	511
151	438	532	314	443	378	411	492	408	457	338	426	415	333	398	329	346	310	557
154	380	492	319	475	343	399	466	402	463	339	390	386	383	394	330	344	302	501
161	443	561	322	449	386	418	498	414	483	347	436	437	389	405	339	362	311	711
162	431	524	315	426	369	394	506	396	458	344	418	416	376	381	313	314	302	510
163	429	536	311	418	368	390	496	389	459	341	415	414	381	379	312	326	299	503
167	438	558	311	435	378	405	484	398	478	336	426	429	380	398	331	332	305	554
171	454	583	284	474	317	353	431	357	409	281	365	364	372	342	288	363	258	526
207	445	562	324	451	388	419	500	416	481	348	438	437	388	407	341	362	313	603
064	157	22	329	410	300	319	497	344	335	359	263	314	314	394	293	270	313	611
111	90	140	275	409	157	240	346	271	337	279	124	192	322	288	222	235	230	591
119	187	44	313	443	307	351	482	365	340	332	267	325	262	476	346	223	344	697
227	118	26	271	373	233	303	381	315	302	291	198	246	197	363	273	164	268	593
254	119	7	382	464	322	383	521	408	388	414	286	337	326	425	347	279	364	571
256	115	33	406	491	331	395	533	422	413	435	294	346	351	453	365	313	382	578
263	92	102	319	414	240	332	415	352	329	345	222	242	262	375	298	196	301	577
278	-	121	198	325	141	216	278	229	290	210	114	174	230	248	198	202	185	478
312	6	-	369	451	303	391	473	407	391	402	266	312	277	413	345	250	358	621
018	11	17	-	116	22	28	63	25	105	5	23	34	92	82	47	55	24	614
047	11	17	0	-	186	152	203	126	282	175	188	210	263	194	151	251	180	860
056	6	18	0	0	-	19	102	31	77	17	15	19	92	110	47	24	20	577
065	11	22	0	0	0	-	88	5	96	29	13	25	141	130	61	63	46	557
068	12	24	0	6	6	0	-	86	208	59	74	102	183	229	170	192	131	842
079	11	17	0	0	0	0	0	-	111	31	25	39	142	129	69	80	53	602
103	11	17	0	0	0	0	6	0	-	95	96	27	51	189	127	23	100	540
106	11	22	0	0	0	0	0	0	0	-	18	28	79	114	69	45	28	603
107	0	12	0	0	0	0	0	0	0	0	-	21	108	131	68	58	44	543
156	6	18	0	0	0	0	0	0	0	0	0	-	42	138	72	31	47	580
159	13	13	6	13	6	6	13	6	0	6	0	0	-	215	130	44	116	725
215	22	22	0	6	12	11	18	6	11	11	12	12	19	-	54	190	64	602
260	11	22	0	0	0	0	6	0	0	0	0	0	0	0	-	78	19	557
261	8	8	0	0	0	0	8	0	0	0	0	0	0	17	0	-	45	644
281	11	22	0	0	0	0	6	0	0	0	0	0	6	0	0	0	-	536
111b	33	39	39	39	41	39	47	39	33	39	35	41	50	44	39	42	39	-

Table 4: Regressions for single caves which are consistent with the isolation by distance model.

Group	Cave	Nei	Km	D.F.	F	P	slope	intercept
South	154	log	log	1, 6	7.07	0.038	0.704	1.179
South	163	log	log	1, 6	8.158	0.061	1.408	0.446
Central	79	log	lin	1, 4	10.644	0.031	0.334	0.808
Central	47	log	lin	1, 4	9.108	0.039	0.091	1.866
North	254	log	log	1, 3	8.428	0.06	1.375	1.132
North	278	log	log	1, 3	18.48	0.023	1.332	1.142

Appendix B

Genetics of *Schizomus vinei,* a troglobitic schizomid (Chelicerata: Schizomida: Hubbardiidae) from Cape Range, Western Australia.

Summary

Schizomus vinei, a troglobitic Schizomida (Chelicerata) occurs throughout Cape Range wherever caves occur in the Tulki Limestone. They occur only in caves of high relative humidity and with damp soil. Schizomids were collected from 18 of the 36 caves known to contain schizomids. The samples were examined for allozymes at the only four detectable polymorphic loci using gel electrophoresis.

Overall the genetic variation in the schizomids is much lower than that seen in the millipedes (Appendix A) and the amphipods (Appendix C). The allozymes indicate that although there is only one species of schizomid while the fixed genetic differences (4-7%) mean that the populations do not interbreed between some of the cave areas. However, the detailed pattern of genetic variation in the schizomids, unlike the millipedes, is not interpretable by geographical area or from geomorphological features. Nonetheless, the major genetic variation is, for the most part, also associated with the major geomorphological features, the deep gorges which cut through the cavernous Tulki Limestone into the Mandu Calcarenite below. Within extensive areas there is scarcely any genetic distance between the schizomid populations from different caves and yet these caves represent all three millipede genetic provinces; this includes C-15, C-103, C-107, C-126, C-156 , C-162, C-167 and C-278.

The degree of genetic variation between even closely adjacent caves means that individuals should not be transported between caves, even within the genetic provinces defined from the millipede data.

Introduction

At the start of the study in Cape Range no members of the chelicerate Order Schizomida had been described from Australia. The first record of the Order in Australia is of a specimen from south-eastern Queensland exhibited by Dr T.E. Woodward in 1952 (Anon. 1963). A schizomid was collected from a cave in Cape Range in 1962 (Main 1980) and this species was the first Australian member of the Order to be described (*Schizomus vinei* Harvey 1988) by which time it was known to occur sparsly in two caves in Cape Range (Vine, Knott & Humphreys 1988). A recent revision of Australian Schizomida recognizes five new genera and 24 new species, none of which are from caves (Harvey, in press) all in the family Hubbardiidae (Reddell & Cokendolpher 1991). However, schizomids are known to occur in caves in North East Queensland (M. S. Harvey, pers. comm. 1991). The schizomids were the focus of the initial research conducted on the troglobite fauna of the North West Cape peninsula (Humphreys 1989, 1990 1991, in press; Humphreys, Adams & Vine 1989; Humphreys & Collis 1990; Vine, Knott & Humphreys 1988).

Methods

Samples collected from throughout the karst area in 1990 were preserved in liquid nitrogen with replicate material preserved in alcohol.

Electrophoresis: cellulose acetate gel electrophoresis was conducted using standard methods (Richardson, Baverstock & Adams 1986). Homogenates were made from whole individuals and used to examine the allozyme variation between the populations in Cape Range. Samples were available from 18 caves. For systematic purposes, the null hypothesis under test was that all populations were sampled from the gene pool of a single species. A pilot study examined 37 enzymes and non-enzymic proteins of which 22 were scorable and only three were polymorphic (Table 1; Humphreys 1989). Wide screening was conducted also in this study to try and detect further polymorphic loci.

Table 1: Summary of the genetical information (Humphreys 1989).

Attribute	*S. vinei* [1]
# caves sampled	8
# individuals	44
# enzymes examined	37
# enzymes scored	22
# loci invariate (%)	19[2] (86)
# polymorphic loci (%)	3 (14)
H-W Equilibrium	Yes
Panmictic population	No
? more than one species [3]	No
Geographic explanation [4]	Yes[5]
Troglobite	Yes

[1] Two loci dropped from previous study (Humphreys, Adams & Vine 1989). [2] Ten of which were not active in all samples. [3] Genetic differences indicate the possibility of sibling species. [4] The genetic differences are in accord with major geomorphological features. [5] 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; Fisher's Exact test). In addition the population from C-159, for the Mdh-2 data, has fixed allelic differences from the other populations.

The enzymes used are as follows:- Aconitate hydratase (ACON, E.C. 4.2.1.3), Adenosine deaminase (ADA, E.C. 3.5.4.4), Aldolase (ALD, E.C. 4.1.2.13), Enolase (ENOL, E.C.4.2.1.11), Esterase (EST, E.C. 3.1.1.1), Glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.2), Aspartate aminotransferase (GOT, E.C. 2.6.1.1), General protein (GP), Glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), Hexosaminidase (HEX, E.C. 3.2.1.30), Hexokinase (HK, E.C. 2.7.1.1), Isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), Lactate dehydrogenase (LDH, E.C. 1.1.1.27), Malate dehydrogenase (MDH, E.C. 1.1.1.37), Peptidases (PEP, E.C. 3.4.11 or 13.*), Phosphoglycerate mutase (PGAM, E.C. 2.7.5.3), Phosphoglycerate kinase (PGK, E.C. 2.7.2.3), Phosphoglucomutase (PGM, E.C. 2.7.5.1), Pyruvate kinase (PK, E.C. 2.7.1.40) and Triose-phosphate isomerase (TPI, E.C. 5.3.1.1). The nomenclature and conventions for referring to alleles and loci follow Richardson, Baverstock & Adams (1986).

The species meets the criteria for adequate genetic work at the within-species level (Richardson, Baverstock & Adams 1986) in that there were at least six polymorphic loci; the samples could be drawn from the smallest and homogeneous population units (caves) and they were sampled over some geographical distance including the extremities and intermediate locations.

Results

The data represent populations from 18 caves out of 36 caves known to contain schizomid populations. The samples for electrophoresis provide a good regional coverage of the distribution of schizomids in Cape Range (Fig. 1).

Figure 1: The distribution of all caves in Cape Range known to contain schizomids and those from which genetic samples were taken.

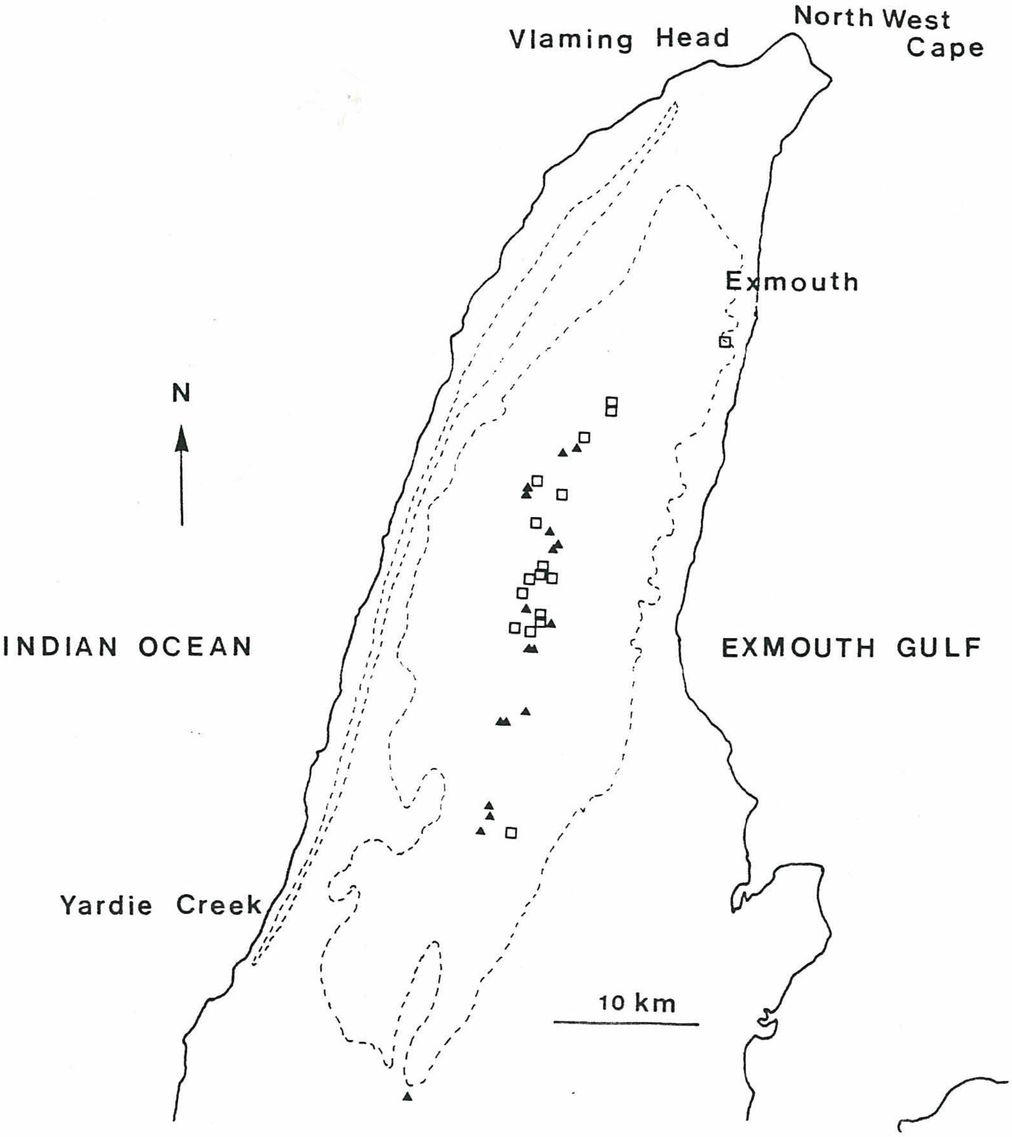
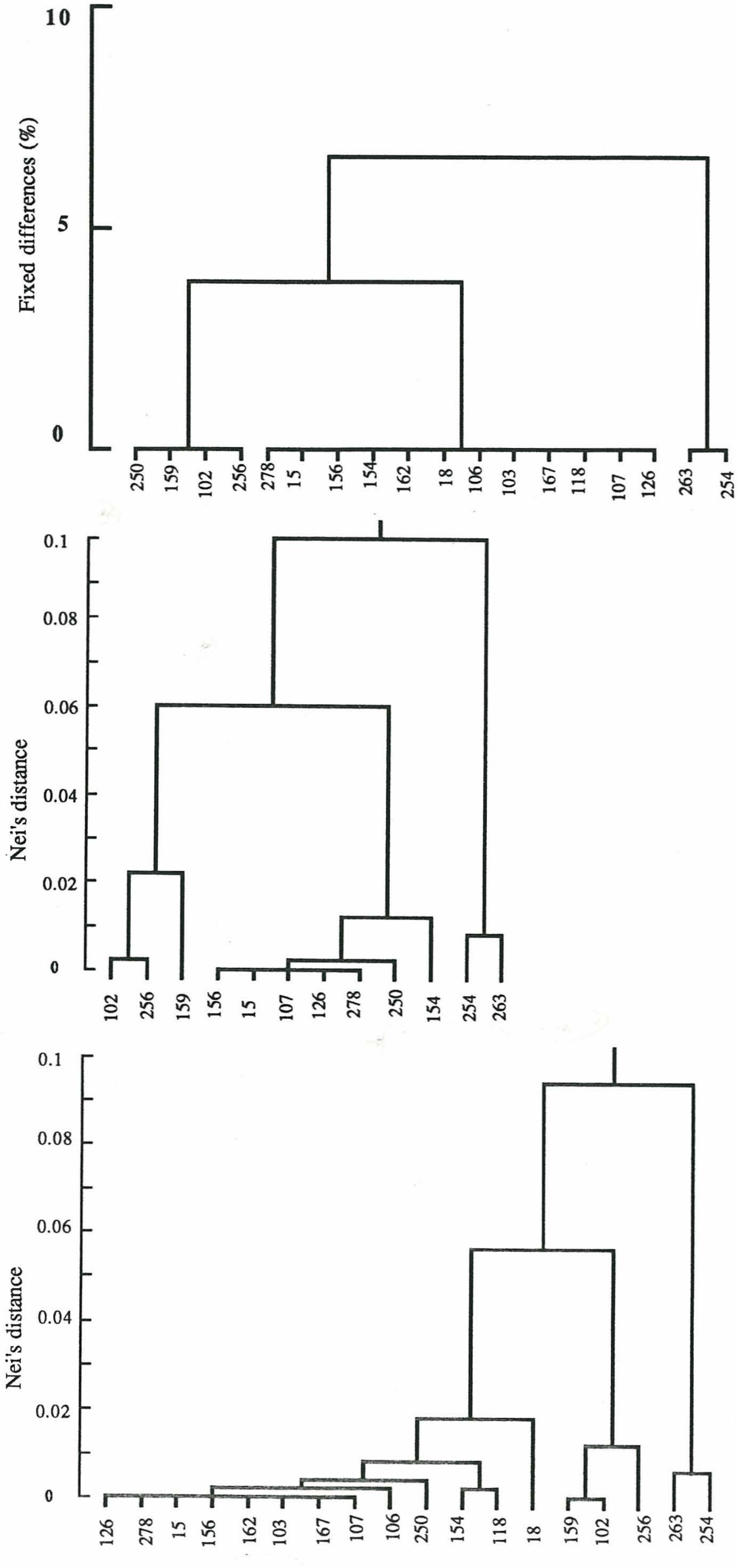


Figure 2: UPGMA phenograms showing the genetic relationships between populations of *S. vinei* from 18 caves in Cape Range. a) Fixed differences for the combined 1989-89 data; b) Nei's distance for 1989 (corrected for small sample size); c) Nei's distance (corrected for small sample size) for the combined data for 1988 (Humphreys 1989) and 1989.



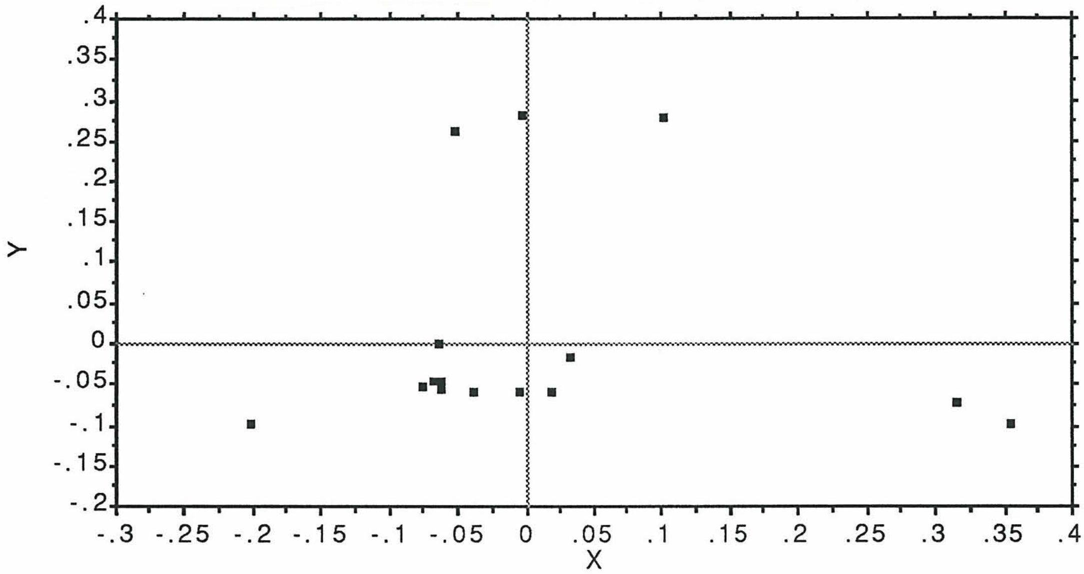
Fixed differences:- The data for 1989 and 1989 have been pooled for some analyses. There is unequivocal evidence that the populations have not been taken from a single gene pool (Appendix 1 a-c). This is supported by the fixed differences between some populations as any fixed differences imply that the populations are not interbreeding. Three major genetic groupings emerge within which there are no fixed differences (FD%; Table 2):- a group of twelve caves (C-15, C-18, C-103, C-106, C-107, C-118, C-126, C-154, C-156 , C-162, C-167 and C-278) which is separated by 4% fixed difference from a group of four caves (C-102, C-159, C-250 and C-256):- both these groups are separated by 7% fixed differences from a group of two caves (C-254 and C-263).

The three genetic provinces indicated by the fixed differences clearly do not follow the genetic provinces defined by the millipede genetics. The pair of caves (C-254 and C-263) are both in the northern millipede genetic province. The group of four caves (C-102, C-159, C-250 and C-256) includes the extreme northern (C-256) and southern population analysed (C-250), the remaining two populations are from the central millipede genetic province. The largest group showing no fixed differences includes populations from caves in the southern (C-15, C-154, C-162, C-167 and C-118 and C-126), central (C-156, C-18, C-106, C-103 and C-107) and northern (C-278) millipede genetic provinces.

Populations from caves C-263 and C-256 are genetically very different but are adjacent to each other (< 0.5 km apart) but separated by a deep gorge. However, C-254 and C-263 are further apart (c. 3 km) and separated by the same gorge but are genetically much closer (Fig. 2). The group of four caves includes two caves from the centre of the range of *S. vinei* , just north of Mt. Hollister, as well as one each from the extreme north (C-256) and south (C-250) of the distribution. The large group shows no fixed differences for 26 km to the south of Shothole Canyon (Figure 2a).

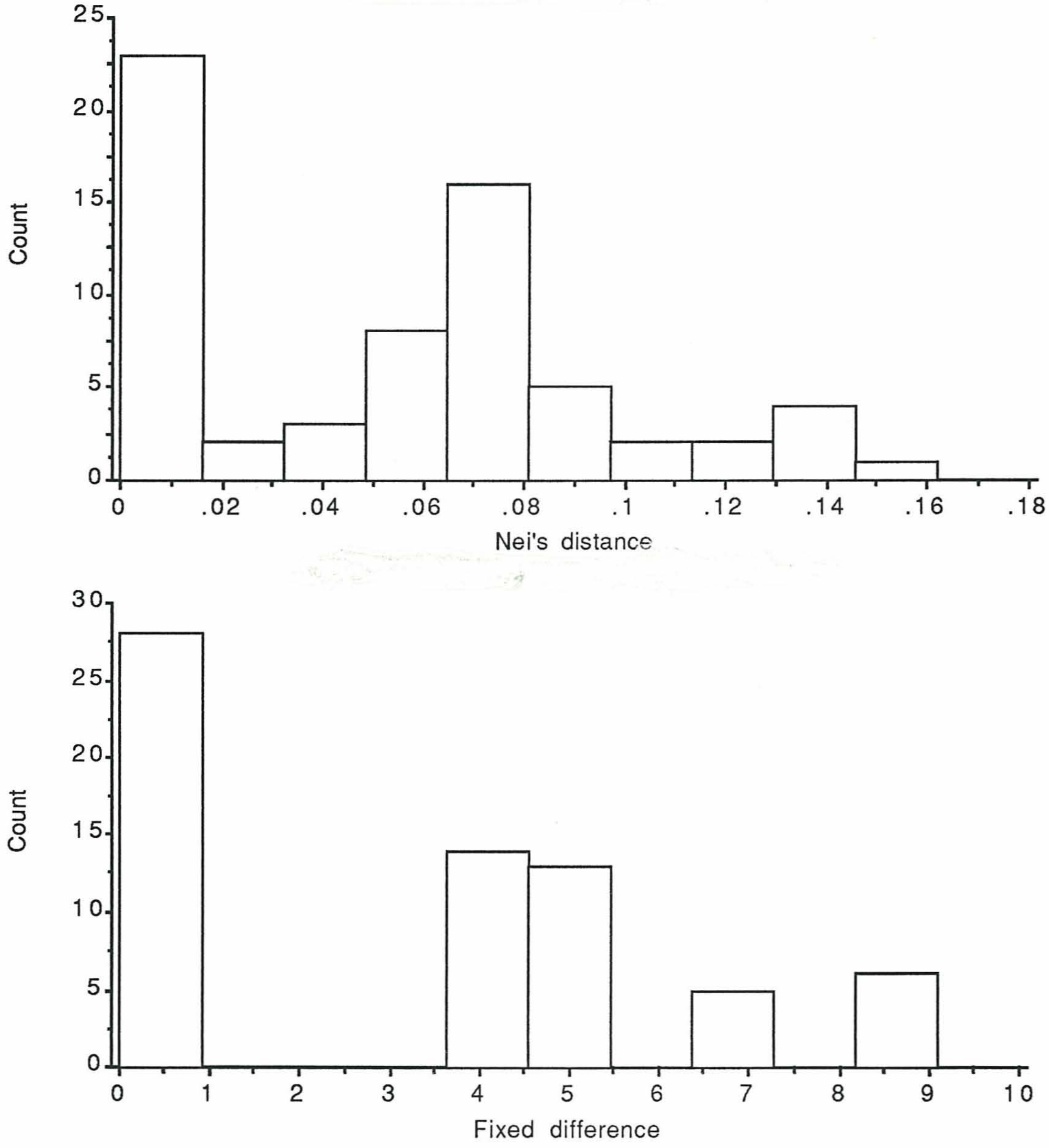
Clearly the pattern of fixed genetic differences shows no simple geographical pattern and no boundaries between genetic areas can be defined which separate genetical provinces as could be done for the millipedes.

Figure 3: Scatter plot of the first and second principal coordinates of the genetical data from *S. vinei* based on the Rogers' distance matrix.



Nei's distance:- A phenogram based on Nei's distance reveals more details in the structure of the populations within Cape Range. The populations in common between the 1988 and 1989 data are joined by a dendrogram with the same topology as the combined data (Figures 2b & 2c). Examination of the pooled data for the 1988 and 1989 samples reveals three distinct groups differing by >0.05 units (Figure 2c). The most disparate group (C-263 and C-254) represents the northern millipede area (north of Shot Hole Canyon) however, the next small group which represents the central millipede genetic province (C-102 and C-159) includes also a population from the northern province (C-256). Most of the remaining populations are included in a group of eight populations separated by zero Nei's distance; this group includes representatives from the northern (C-278), central (C-103 and C-107) and southern (C-126, C-15, C-156, C-162 and C-167) millipede genetic provinces.

Figure 4: Nei's distance (a) and fixed differences (b) between all pairs of caves from which *S. vinei* genetical samples were taken.



Less contorted representation of the data is shown in a plot of the principal coordinates based on Rogers' distance (Fig. 3). This is believed to give a better representation of the phylogenetic relationships than those based on Nei's distance. Rotating the three principal coordinates in all direction reveals a number of separate groups similar to those outlined above except that the population from C-15 become a lone outlier.

These representations are internally consistent and demonstrate that the schizomid data show no equivalent of the millipede genetic provinces. While there are clearly major genetic breaks associated with Shothole Canyon and Mount Hollister as is the case with the millipedes, there are a number of genetic sub-groups which have populations in caves in all millipede genetic areas. There are no clear geographical definition of the genetic areas.

Discussion

The schizomid genetical data support the contention that there are two major genetic discontinuities in Cape Range in that the major genetic divisions are associated with the same geomorphological features as seen in the millipede data (Fig. 3). Namely, the largest genetic differences are associated with the deep gorges around Shot Hole Canyon and Mt Hollister. This is further supported by the data for the amphipods, the only aquatic troglobite from Cape Range (Appendix C). The only non-troglobite examined, a terrestrial isopod, is panmictic throughout the area examined (Humphreys 1989). Owing to this consistency it is likely that troglobite populations derived from the same isolating mechanism will show the same genetic provinces. The period of isolation of the fauna is presumed to be associated with the drying of past climates and the loss of local tropical rainforest from Cape Range.

However, the schizomid data are more complex than those for the millipedes in that there are certain genetic grouping which have populations in all of the millipede genetic provinces. Three possible solutions are given below.

1. A millipede like pattern is being disrupted by dispersal within the superficial underground compartment (milieu souterrain superficiel: Juberthie 1983) or by epigean dispersal. *S. vinei* is much more resistent to water loss than other troglobites tested (Humphreys & Collis 1990) and may possibly survive long enough to move between genetic provinces. However, there is no evidence that schizomids occur outside caves and other components of the fauna are quite distinct inside and outside the caves on Cape Range. For example, 18 specimens of pseudoscorpions collected represented six undescribed species and an undescribed genus with up to three species per cave, but there are no genera or families in common between the epigean fauna and that of the caves (M.S. Harvey, pers. comm. 1991). If migration between caves was a significant factor the effect should be most intense locally and adjacent caves with fixed differences would be unlikely.

2. The groupings obtained may be artefacts resulting from the statistics of small samples. Unlike the millipede analysis, that for the schizomids is based on very few polymorphic loci. Examination of a larger set of polymorphic loci could yield data consistent with the millipede data. However, this is not possible for the schizomids as the polymorphic loci have not been found. I consider that this is the more likely explanation of the observed pattern.

3. The schizomids are very conservative (almost all extant schizomids have been placed in one world wide genus, it is currently being split) and there has been little change in their genetics since they were isolated in the caves; the differences now observed have resulted from founder effects or stochastic events acting within the constraints of small and variable populations (Humphreys in press), or from mutations.

Acknowledgments

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Appendices

Appendix 1a: Genetic profiles of individual *Schizomus vinei* (assuming autosomal loci in a diploid organism). Allozymes are designated alphabetically in order of increasing electrophoretic mobility. - denotes not scorable. The genotypes are arranged according to cave number with the years pooled.

EBU#	Cav-Yr	Acon1	Acon2	Ada	Ald	Enol	Est	Gapd	Got	Gp	Gpi	Hex	Hk	Idh	Ldh
C15a	015-89	--	aa	--	aa	aa	cc	aa	--	--	--	aa	--	aa	aa
C15b	015-89	--	--	--	--	aa	cc	aa	--	--	--	aa	--	--	aa
102a	102-89	aa	aa	--	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
102b	102-89	--	aa	--	aa	aa	--	aa	--	--	--	aa	--	--	aa
107a	107-89	--	aa	aa	--	aa	cc	aa	aa	--	--	aa	--	aa	aa
107b	107-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	--	aa	aa
156a	156-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
156b	156-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
156c	156-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	--	aa	--	aa	aa
156d	156-89	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S19	159-88	aa	--	aa	aa	aa	ac	aa	--	aa	--	aa	aa	aa	aa
S20	159-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
S21	159-88	aa	--	aa	aa	aa	aa	aa	--	aa	--	aa	aa	--	aa
S22	159-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
159a	159-89	--	--	aa	--	aa	bc	aa	--	--	aa	aa	aa	aa	aa
159b	159-89	aa	aa	aa	aa	aa	bb	aa	aa	aa	aa	aa	aa	aa	aa
159c	159-89	--	aa	aa	aa	aa	bc	aa	--	aa	--	aa	aa	aa	aa
154	154-89	aa	--	aa	aa	aa	ac	aa	aa	aa	aa	aa	aa	aa	aa
7	126-88	--	--	--	--	--	cc	aa	--	--	--	aa	aa	--	--
8	126-88	--	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S15	126-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
S16	126-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
S17	126-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S18	126-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
126a	126-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	--	aa	aa	aa
126b	126-89	aa	aa	aa	aa	aa	ac	aa	aa	aa	aa	aa	aa	aa	aa
126c	126-89	--	--	aa	aa	aa	cc	aa	aa	--	--	aa	aa	aa	aa
126d	126-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
126e	126-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
126f	126-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
250a	250-89	aa	aa	aa	--	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
250b	250-89	aa	aa	aa	--	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
250c	250-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
254a	254-89	aa	aa	aa	aa	aa	dd	aa	aa	aa	aa	aa	aa	aa	aa
254b	254-89	aa	bb	aa	aa	aa	dd	aa	aa	aa	--	aa	aa	aa	aa
254c	254-89	aa	aa	aa	aa	aa	dd	aa	aa	aa	--	aa	aa	aa	aa
254d	254-89	aa	--	aa	aa	aa	dd	aa	aa	aa	--	aa	--	aa	aa
254f	254-89	aa	ab	aa	aa	aa	dd	aa	aa	--	--	aa	aa	aa	aa
254g	254-89	aa	aa	aa	aa	aa	dd	aa	aa	--	--	aa	aa	aa	aa

Appendix 1a continued.

EBU#	Cav-Yr	Acon1	Acon2	Ada	Ald	Enol	Est	Gapd	Got	Gp	Gpi	Hex	Hk	Idh	Ldh
256a	256-89	aa	aa	bb	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
256b	256-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
256c	256-89	aa	aa	aa	aa	aa	--	aa	aa	--	aa	aa	--	aa	aa
263a	263-89	aa	aa	aa	aa	aa	dd	aa	aa	aa	--	aa	aa	aa	aa
263b	263-89	aa	aa	aa	aa	aa	dd	aa	aa	aa	aa	aa	aa	aa	aa
263c	263-89	aa	aa	aa	aa	aa	cd	aa	aa	aa	aa	aa	aa	aa	aa
278	278-89	aa	aa	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
15	018-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
16	018-88	--	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
17	018-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
18	018-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S1	018-88	aa	--	--	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S2	018-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S3	018-88	aa	--	--	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S4	018-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	--	aa
S5	103-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S6	103-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S7	103-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S8	103-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
23	106-88	--	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
24	106-88	--	--	aa	aa	aa	cc	aa	--	--	--	aa	aa	aa	aa
26	106-88	--	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
31	106-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S9	106-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S10	106-88	aa	--	aa	aa	aa	ac	aa	aa	aa	aa	aa	aa	aa	aa
S11	106-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S12	106-88	aa	--	aa	aa	aa	ac	aa	aa	aa	aa	aa	aa	aa	aa
1	118-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
2	118-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
6	118-88	aa	--	aa	aa	aa	ac	aa	aa	aa	--	aa	aa	aa	aa
10	118-88	aa	--	aa	aa	aa	aa	aa	aa	aa	aa	aa	aa	aa	aa
S13	118-88	--	--	aa	aa	aa	ac	aa	--	aa	--	aa	aa	--	aa
S14	118-88	--	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
S23	162-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa
S24	162-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S25	162-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S26	162-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S27	167-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S28	167-88	aa	--	aa	aa	aa	cc	aa	aa	aa	--	aa	aa	aa	aa
S29	167-88	aa	--	aa	aa	aa	cc	aa	aa	aa	aa	aa	aa	aa	aa
S30	167-88	aa	--	aa	aa	aa	cc	aa	--	aa	--	aa	aa	aa	aa

Appendix 1a continued.

EBU#	Cav-Yr	Mdh1	Mdh2	Pep1	Pep2	Pgam	Pgk	Pgm	Pk	Tpi
C15a	015-89	aa	bb	--	aa	--	--	aa	aa	aa
C15b	015-89	aa	bb	--	aa	--	--	aa	aa	aa
102a	102-89	aa	aa	aa	aa	aa	aa	ab	aa	aa
102b	102-89	aa	aa	aa	aa	aa	--	aa	aa	aa
107a	107-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
107b	107-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
156a	156-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
156b	156-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
156c	156-89	aa	bb	--	--	aa	aa	aa	aa	aa
156d	156-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
S19	159-88	aa	aa	aa	--	aa	--	aa	aa	aa
S20	159-88	aa	aa	aa	aa	aa	--	aa	aa	aa
S21	159-88	--	aa	aa	aa	--	--	bb	aa	aa
S22	159-88	aa	aa	aa	aa	--	--	ab	aa	aa
159a	159-89	aa	aa	--	aa	--	--	aa	aa	aa
159b	159-89	aa	aa	aa	aa	aa	aa	ab	aa	aa
159c	159-89	aa	aa	aa	aa	aa	aa	ab	aa	aa
154	154-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
7	126-88	aa	bb	--	--	--	--	--	--	aa
8	126-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S15	126-88	aa	bb	aa	--	--	--	aa	aa	aa
S16	126-88	aa	bb	aa	--	--	--	aa	aa	aa
S17	126-88	aa	bb	aa	--	aa	--	aa	aa	aa
S18	126-88	aa	bb	aa	aa	aa	--	aa	aa	aa
126a	126-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
126b	126-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
126c	126-89	--	bb	aa	aa	--	--	aa	aa	aa
126d	126-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
126e	126-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
126f	126-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
250a	250-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
250b	250-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
250c	250-89	aa	ab	--	aa	aa	aa	aa	aa	aa
254a	254-89	aa	bb	aa	aa	aa	aa	ac	aa	aa
254b	254-89	aa	bb	--	aa	aa	aa	cc	aa	aa
254c	254-89	aa	bb	--	aa	aa	--	cc	aa	aa
254d	254-89	aa	bb	--	aa	aa	aa	cc	aa	aa
254f	254-89	aa	bb	--	aa	--	--	cc	aa	aa
254g	254-89	aa	bb	--	aa	aa	aa	cc	aa	aa
256a	256-89	aa	aa	aa	aa	aa	aa	aa	aa	aa
256b	256-89	aa	aa	aa	aa	aa	aa	aa	aa	aa
256c	256-89	aa	aa	aa	aa	aa	aa	aa	aa	aa

Appendix 1a continued.

EBU#	Cav-Yr	Mdh1	Mdh2	Pep1	Pep2	Pgam	Pgk	Pgm	Pk	Tpi
263a	263-89	aa	bb	--	aa	aa	aa	cc	aa	aa
263b	263-89	aa	bb	aa	aa	aa	aa	cc	aa	aa
263c	263-89	aa	bb	aa	aa	aa	aa	cc	aa	aa
278	278-89	aa	bb	aa	aa	aa	aa	aa	aa	aa
15	018-88	aa	bb	aa	aa	aa	aa	ab	aa	aa
16	018-88	aa	bb	aa	--	--	--	aa	aa	aa
17	018-88	aa	bb	aa	aa	aa	aa	ab	aa	aa
18	018-88	aa	bb	aa	aa	aa	aa	bb	aa	aa
S1	018-88	aa	bb	aa	aa	aa	--	ab	aa	aa
S2	018-88	aa	bb	aa	aa	aa	--	ab	aa	aa
S3	018-88	aa	bb	aa	aa	aa	--	ab	aa	aa
S4	018-88	aa	bb	aa	aa	aa	--	bb	aa	aa
S5	103-88	aa	bb	aa	aa	--	--	aa	aa	aa
S6	103-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S7	103-88	aa	bb	aa	aa	aa	--	aa	aa	aa
S8	103-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
23	106-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
24	106-88	aa	bb	aa	--	--	--	aa	aa	aa
26	106-88	aa	bb	aa	aa	--	aa	aa	aa	aa
31	106-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S9	106-88	aa	bb	aa	aa	--	--	aa	aa	aa
S10	106-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S11	106-88	aa	bb	aa	aa	aa	--	aa	aa	aa
S12	106-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
1	118-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
2	118-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
6	118-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
10	118-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S13	118-88	aa	bb	--	aa	aa	--	aa	aa	aa
S14	118-88	aa	bb	aa	aa	aa	--	aa	aa	aa
S23	162-88	aa	bb	aa	--	aa	--	aa	aa	aa
S24	162-88	aa	bb	aa	aa	aa	--	aa	aa	aa
S25	162-88	aa	bb	aa	aa	aa	--	aa	aa	aa
S26	162-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S27	167-88	aa	bb	aa	aa	aa	aa	aa	aa	aa
S28	167-88	aa	bb	aa	--	aa	--	aa	aa	aa
S29	167-88	aa	bb	aa	aa	--	aa	aa	aa	aa
S30	167-88	aa	bb	aa	aa	aa	--	aa	aa	aa

Appendix 1b: Allele frequencies for polymorphic loci of the 18 populations of *Schizoums vinei.*

		Cave																	
allele		15	102	107	156	159	154	126	250	254	256	263	278	18	103	106	118	162	167
Acon-2	b									30									
	a	100	100	100	100	100	**	100	100	70	100	100	100	**	**	**	**	**	**
	N=	1	2	2	3	2		5	3	5	3	3	1						
Ada	b										33								
	a	**	**	100	100	100	100	100	100	100	67	100	100	100	100	100	100	100	100
	N=			2	4	7	1	11	3	6	3	3	1	6	4	8	6	4	4
Est	d									100		83							
	c	100	100	100	100	50	50	96	100		100	17	100	100	100	87	67	100	100
	b					29													
	a					21	50	4								13	33		
	N=	2	1	2	4	7	1	12	3	6	2	3	1	8	4	8	6	4	4
Mdh-2	b	100		100	100		100	100	83	100		100	100	100	100	100	100	100	100
	a		100			100			17		100								
	N=	2	2	2	4	7	1	12	3	6	3	3	1	8	4	8	6	4	4
Pgm	c								92		100								
	b		25			36								56					
	a	100	75	100	100	64	100	100	100	8	100		100	44	100	100	100	100	100
	N=	2	2	2	4	7	1	11	3	6	3	3	1	8	4	8	6	4	4

Invariant loci (not all samples active): Acon-1, Ald, Enol, Gapd, Got, Gp, Gpi, Hex, Hk, Idh, Ldh, Mdh-1, Pep-1, Pep-2, Pgam, Pgk, Pk and Tpi.

Appendix 1c: Matrix of genetic distances for *Schizomus vinei.* Lower matrix - % fixed differences; Upper matrix - Nei's distances (x1000) (corrected; Nei 1989).

Cave	15	102	107	156	159	154	126	250	254	256	263	278	18	103	106	118	162	167
15	-	75	0	0	88	20	0	2	152	74	130	0	25	0	1	8	0	0
102	7	-	49	47	0	66	50	35	138	3	123	50	55	52	54	59	52	52
107	0	5	-	0	54	12	0	1	93	52	80	0	15	0	1	5	0	0
156	0	5	0	-	52	11	0	1	89	50	77	0	14	0	1	5	0	0
159	7	0	5	4	-	59	59	46	116	19	105	60	60	63	60	58	63	63
154	0	5	0	0	5	-	10	13	76	65	73	11	27	11	6	1	11	11
126	0	5	0	0	4	0	-	1	87	50	75	0	15	0	0	4	0	0
250	0	0	0	0	0	0	0	-	91	36	79	1	16	1	2	6	1	1
254	7	9	5	4	9	5	4	4	-	145	6	89	79	88	83	78	88	88
256	7	0	5	4	0	5	4	0	9	-	132	50	68	52	53	58	52	52
263	7	9	5	4	9	5	4	4	0	9	-	77	69	80	76	73	80	80
278	0	5	0	0	4	0	0	0	4	4	4	-	14	0	1	5	0	0
18	0	5	0	0	5	0	0	0	5	5	5	0	-	14	15	20	14	14
103	0	5	0	0	5	0	0	0	5	5	5	0	0	-	1	5	0	0
106	0	5	0	0	5	0	0	0	5	5	5	0	0	0	-	2	1	1
118	0	5	0	0	5	0	0	0	5	5	5	0	0	0	0	-	5	5
162	0	5	0	0	5	0	0	0	5	5	5	0	0	0	0	0	-	0
167	0	5	0	0	5	0	0	0	5	5	5	0	0	0	0	0	0	-

Appendix 1 d: Matrix of Rogers' genetic distance values.

Cave	15	102	107	156	159	154	126	250	254	256	263	278	18	103	106	118	162	167
15	-																	
102	0.08	-																
107	0	0.05	-															
156	0	0.05	0	-														
159	0.12	0.02	0.08	0.07	-													
154	0.03	0.08	0.02	0.02	0.07	-												
126	0	0.05	0	0	0.07	0.02	-											
250	0.01	0.04	0	0	0.07	0.03	0	-										
254	0.15	0.14	0.10	0.09	0.12	0.08	0.09	0.10	-									
256	0.07	0.01	0.06	0.05	0.04	0.08	0.05	0.05	0.15	-								
263	0.13	0.12	0.08	0.07	0.11	0.07	0.07	0.08	0.02	0.13	-							
278	0	0.05	0	0	0.07	0.02	0	0	0.09	0.05	0.07	-						
18	0.04	0.06	0.02	0.02	0.07	0.04	0.02	0.03	0.08	0.08	0.07	0.02	-					
103	0	0.05	0	0	0.08	0.02	0	0	0.08	0.06	0.08	0	0.02	-				
106	0.01	0.06	0	0	0.07	0.01	0	0.01	0.08	0.06	0.08	0	0.03	0	-			
118	0.02	0.07	0.01	0.01	0.07	0	0.01	0.02	0.08	0.07	0.07	0.01	0.04	0.01	0	-		
162	0	0.05	0	0	0.08	0.02	0	0	0.08	0.06	0.08	0	0.02	0	0	0.01	-	
167	0	0.05	0	0	0.08	0.02	0	0	0.08	0.06	0.08	0	0.02	0	0	0.01	0	-

Appendix C

Subterranean aquatic fauna of the North West Cape peninsula

This is the basis for Humphreys and Adams (in press).

The subterranean aquatic fauna of the North West Cape peninsula, Western Australia.

W.F. Humphreys[1] and M. Adams[2].

Abstract

The current status of the subterranean aquatic fauna on the semi-arid tropical North West Cape peninsula of Western Australia is discussed and placed in the context of the rich troglobitic fauna of Cape Range. The range of all four subterranean species has been considerably extended and an amphipod added to the known fauna. The fauna includes the only vertebrate troglobites known from Australia.

The Blind Cave Eel, *Ophisternon candidum* , has been seen for the first time in more than a decade and from the east coast of the peninsula where it was previously unkown. Allozyme electrophoretic data show that the Blind Gudgeon, *Milyeringa veritas*, is not panmictic within its known range. The overt geological discontinuities along the coast of the North West Cape peninsula do not constitute genetic barriers between the gudgeon populations.

Allozyme electrophoretic data confirm that two species of atyid shrimps occur but the species were found on opposite sides of the peninsula. Analysis suggests that the species composition on the east coast is different from that on the west coast.

The relationship between genetic and metric distance between the populations suggests that the coastal fauna is essentially linear along the coast and does not spread beneath Cape Range.

Within Cape Range all four caves with water contain an undescribed amphipod. Allozyme electrophoretic data suggest the presence of a single species showing genetic discontinuities through its range.

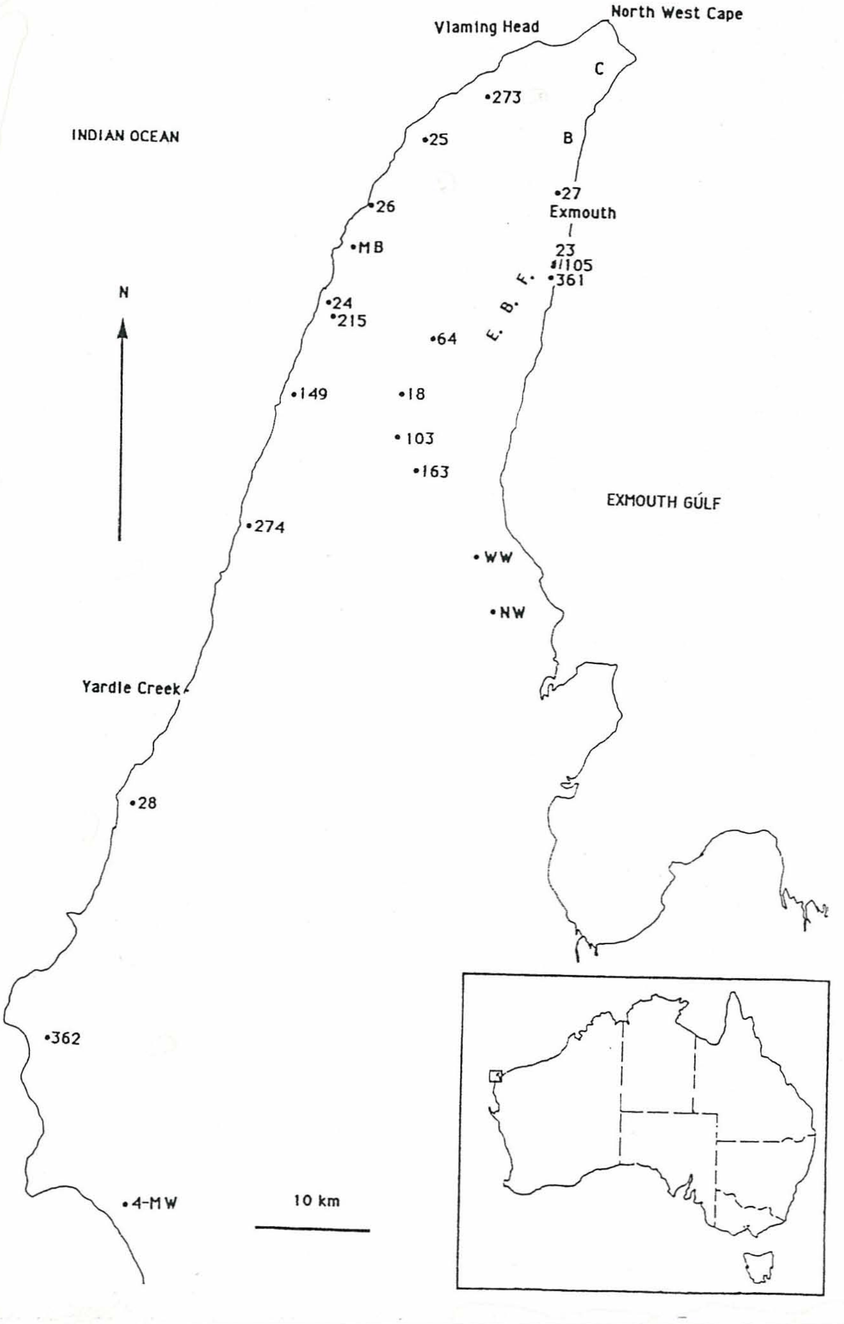
There is a cline in the water chemistry, with most parameters increasing from the mid-east coast, round the north coast and south along the west coast of the peninsula. All coastal species seem to occupy the full range of water chemistries sampled. There is a lack of effective monitoring of the quantity and quality of the water. Examination of diverse evidence from a number of sources suggests that the water table is declining and becoming more saline. Potential disruption of the habitat is discussed and a model presented which indicates that the critical areas for conservation may be close to the scarp where, owing to the absence of wells, the fauna has not been sampled.

INTRODUCTION

The troglobitic fauna of the North West Cape peninsula of Western Australia was first mentioned in the context of the subterranean freshwater fauna of the coastal plain (Whitley 1945) and later by Cawthorn (1953). This fauna was the focus of a paper by Mees (1962) who described the composition and known range of the fauna. Since then the known range of the fauna has expanded considerably but the species composition has remained unchanged. In addition, a rich troglobite fauna has been found within Cape Range, which forms the spine of the peninsula (Vine, Knott & Humphreys 1988; Humphreys 1989, 1990; Humphreys, Adams & Vine 1989).

Nearly three decades after Mees's (1962) publication it is pertinent to review what is known of the four troglobitic species of the coastal plain and relate it to the troglobitic fauna of the peninsula as a whole (Fig. 1). Since that time the peninsula has started to be developed rapidly as an international tourist region and two major national parks have been established (Cape Range National Park and the contiguous Ningaloo Marine Park). This trend represents both quantitative and qualitative changes to the human impact on the region. For this unique troglobite fauna to survive the development must be sensitive to its needs.

Figure 1:- Map showing the North West Cape peninsula of Western Australia and the localities of wells, caves and other geographical features mentioned in the text. E.B.F. denotes the Exmouth bore field from which the town draws its water supply. The military facilities (B and C) have a separate water supply drawn from area B. The stippled line denotes the position of Cape Range. NW, Nabalgee Well; WW, Woolcott Well; 4-MW, 4-Mile Well.



More than 300 caves and wells are known from Cape Range, many containing a rich troglobitic fauna of terrestrial arthropods, while an undescribed amphipod inhabits the four caves containing water (Vine, Knott & Humphreys 1988; Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). This fauna is distinct from that inhabiting the subterranean waters on the *ca* 2 km wide coastal plain fringing Cape Range which contains a unique subterranean fauna, comprising two species of fish and two species of atyid shrimps. Although these taxa were described between 1945 and 1962, almost nothing is known of their biology. Some coastal caves, which were major water sources for aboriginal people (Carter 1902), and recent bores, have been heavily utilized for water by pasturalists, Exmouth Town and military facilities.

This paper reviews the status of the subterranean aquatic fauna of the North West Cape peninsula and shows the lack of information on the biology and dynamics of species involved.

The fauna

Four species are known to occur in the subterranean freshwater on the coastal plain. The Blind or Cave Gudgeon, *Milyeringa veritas* Whitley 1945 (Perciformes: Eleotridae) (Whitley 1960) was described from Milyering Well (cave number **C-24**). It is classified as rare and total protection has been recommended (Michaelis 1985). The Blind Cave Eel, *Ophisternon candidum* (Mees 1962)(Synbranchiformes: Synbranchidae) was described from Tantabiddi Well (**C-26**). It is classified as vulnerable (Michaelis 1985). These two species of fish comprise the entire troglobitic vertebrate fauna of Australia. The Atydid shrimps *Stygiocaris lancifera* Holthuis 1960 and of *S. stylifera* Holthuis 1960 (Decapoda: Natantia) were both described from Kudumurra Well (**C-25**). The Indo-West Pacific area seems to be deficient in troglobitic Decapoda compared with e. g. the Mediterranean and the West Indies (Holthuis 1960). The four species known from the coastal limestone are endemic to the peninsula and co-occur in the same water bodies (Mees 1962, Hamilton-Smith 1967).

Within Cape Range itself amphipods occur in each of the four caves known to contain standing water *viz.* **C-18, C-64, C-103** and **C-163** (Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). The amphipoda are of marine origin and part of the *Victoriapisa* complex (Gammaridae; B. Knott; pers. comm. 1988).

Methods

Numbers with a **C-** prefix refer to caves or karst features described in the karst Index of Cape Range (M. East and B. Vine; pers. comm.). They will eventually be included in the Australian Speleological Federation's catalogue of karst features.

Distribution: Distributions of the taxa have been ascertained incidentally from a series of expeditions examining the troglobitic fauna of Cape Range, by records in the literature and from discussion with people who have examined the caves over a long period. Collections of shrimps and fish were made in September 1989 as detailed in Table 1.

A total of 24 sites, including all known locations for the subterranean coastal fauna were visited with the aim of collecting a minimum of six specimens each of shrimps and gudgeons to be divided between alcohol-preserved material and liquid nitrogen material for genetic analysis. The small number of specimens and few sites of collection (Table 1) attest to the sparsity of the fauna. The following sites were visited:- 4-mile Well, 5-mile Well (**C-273**), Bundera Rockhole (**C-28**), **C-215**, Cape Well, Dozer Cave (**C-23**), Javis Well (**C-362**), Kuburu Well (**C-27**), Kudumurra Cave, Kudumurra Well (**C-25**), Milyering Cave (**C-172**), Milyering Well (**C-24**), Mowbowra Well (**C-361**), Nabalgee Well, Ned's Well, Pilgramunna Well (**C-274**), South Yardie Well (**C-275**), Tantabiddy Well, Trealla Well, Tulki Well (**C-149**), unnamed small rockhole near south ranger's camp, unnamed small rockhole south of Bundera Rockhole, unnamed well (old water supply for NorWest Seafoods) and Woolcott Well.

Table 1: Location and distribution of samples collected for genetic analysis in 1989. The gudgeons are *Milyeringa veritas* , while the shrimps are *Stygiocaris lancifera* except for those from Mowbowra Well and Kubura Well which are *S. stylifera* .

No.	Name	Location	Numbers Shrimps	 Gudgeons	 Amphipods
C-18	Dry Swallett	22° 05' S; 114° 00' E.	-	-	4
C-24	Milyering Well	22° 01' S; 113° 56' E	4	-	-
C-25	Kudamurra Well	21° 53' S; 114° 01' E	4	5	-
C-27	Kubura Well	21° 56' S; 114° 08' E	8	3	-
C-64	Shot Hole Tunnel	22° 03' S; 114° 01' E.	-	-	9
C-103	Trionomo	22° 07' S; 113° 59' E.	-	-	4
C-149	Tulki Well	22° 06' S; 113° 54' E	4	5	-
C-163	Wanderer's Delight	22° 09' S; 114° 00' E.	-	-	9
C-273	5 Mile Well	21° 51' S; 114° 04' E	4	7	-
C-274	Pilgramunna Well	22° 12' S; 113° 52' E	-	5	-
C-361	Mowbowra Well	22° 00' S; 114° 07' E	3	3	-
C-362	Javis Well	22° 36' S; 113° 41' E	-	2	-

Water analysis was conducted using standard methods (American Public Health Association 1965) except for pH which was determined at the time of collection using narrow range pH papers (Merck).

Electrophoresis: Cellulose acetate gel electrophoresis was conducted using standard methods (Richardson, Baverstock & Adams 1986). Homogenates were made from whole individuals of four taxa (*Milyeringa veritas* , *Stygiocaris lancifera* , *S. stylifera* and the amphipods) and used to examine the allozyme variation between the populations around the peninsula. Samples were available from between two and six natural or artificial wells or caves depending on the taxon under study. For systematic purposes, the null hypothesis under test was that all populations were sampled from the gene pool of a single species. A large number of enzymes and non-enzymic proteins were examined (Table 4), of which 37 displayed electrophoretic patterns suitable for reliable genetic interpretation in at least one of the four taxa. The enzymes used are as follows:- aconitate hydratase (ACON, E.C. 4.2.1.3), Aminoacylase (ACYC, E.C. 3.5.1.14), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), aldolase (ALD, E.C. 4.1.2.13), alkaline phosphatase (AP, E.C. 3.1.3.1), arginine kinase (ARGK, E.C. 2.7.3.3), carbonate dehydratase (CA, E.C. 4.2.1.1), creatine kinase (CK, E.C. 2.7.3.2), diaphorase (DIA, E.C. 1.6.99.?), enolase (ENOL, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fructose-1, 6-diphosphatase (FDP, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.12), guanine deaminase (GDA, E.C. 3.5.4.3), lactoyl-glutathione lyase (GLO, E.C. 4.4.1.5), aspartate aminotransferase (GOT, E.C. 2.6.1.1), general protein (GP), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), alanine aminotransferase (GPT, E.C. 2.6.1.2), glutathione reductase (GSR, E.C. 1.6.4.2), hexosaminidase (HEX, E.C. 3.2.1.30), hexokinase (HK, E.C. 2.7.1.1), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), leucine amino peptidase (LAP, E.C. 3.4.11.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), malic enzyme (ME, E.C. 1.1.1.40), mannose-phosphate isomerase (MPI, E.C.5.3.1.8), peptidases (PEP, E.C. 3.4.11.? or 3.4.13.?), phosphoglycerate mutase (PGAM, E.C. 5.4.2.1), 6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 5.4.2.2), pyruvate kinase (PK, E.C. 2.7.1.40), L-iditol dehydrogenase (SORDH, E.C. 1.1.1.14) and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). The nomenclature and conventions for referring to alleles and loci follow Richardson, Baverstock & Adams (1986).

Table 4: Summary of the genetic information.

Attribute	*Milyeringa veritas*	*Stygiocaris lancifera*	*Stygiocaris stylifera*	Amphipoda
# caves/wells sampled	7	4	2	4
# individuals	24	16	11	25
# loci scored	43	28	28	28
# loci invariate (%)	12 (28)	21 (75)	22 (79)	13 (46)
# polymorphic loci (%)	31 (72)	7 (25)	7 (21)	15 (54)
More than one species?[1]	No	No	No	No
Panmictic population[2]	No	-	Yes	No
Geographic explanation	Yes	No	No	Yes
Troglobite	Yes	Yes	Yes	Yes

[1] Null hypothesis of all populations from the gene pool of a single species.

[2] Null hypothesis of panmixia not refuted using genetic data.

All species met the criteria for adequate genetic work at the within-species level (Richardson, Baverstock & Adams 1986) in that they had at least six polymorphic loci; the samples could be drawn from the smallest and homogeneous population units (wells or caves) and they were sampled over some geographical distance including the extremities and intermediate locations.

RESULTS AND DISCUSSION

Distribution of the fauna

Table 2: The current status of the subterranean fauna on the North West Cape peninsula. Mees refers to Mees (1962). √ = reported to occur. - = not found and never reported.

Cave #	Name	Shrimp	Gudgeon	Eel	Salinity (‰) 1983	1988	pH 1988
-	Unnamed	√	-	-	-	-	-
-	Woolcott Well	-	-	-	-	-	7.0
-	Nabalgee Well	-	-	-	-	-	7.3
-	4-Mile Well	none	none	-	-	-	7.6
C-23	Dozer Cave	none	few	-	-	-	-
C-24	Milyering Well	Mees[1]	1989	Mees	5	4	7.4
C-25	Kudamurra Well	1989	Mees[1]	Mees	-	2	7.3
C-26	Tantabiddy	none	none	Mees		3	-
C-27	Kubura Well	1989	1989	1973	-	-	6.8
C-28	Bundera Sinkhole	-	1988	-	-	16	-
C-105	The Gnamma Hole	none	none	1988	1	-	-
C-149	Tulki Well	1989	1989	-	5	5	7.5
C-215	Unnamed	none	1989	-	-	-	7.3
C-273	5 Mile Well	1989	1989	-	-	-	-
C-274	Pilgramunna Well	1989	1989	-	-	-	7.5
C-332	-	1977	-	-	-	-	-
C-361	Mowbowra Well	1989	1989	1989	-	-	7.3
C-362	Javis Well	1989	1989	-	-	-	7.3

[1] Also collected in 1989.

The distribution of the subterranean aquatic fauna of the North West Cape peninsula is outlined in Fig. 1 and Table 2, together with salinity and pH readings from 1983 and 1988. The distributional range of each species has been considerably extended by this study over that detailed by Mees (1962). There are clearly inadequate data on the time course of the water chemistry as will be discussed more fully below.

The gudgeon, *Milyeringa veritas*, was known in 1962 from only two locations on the north-west coast of the peninsula, namely Milyering Well (**C-24**) and Kudamurra Well (**C-25**). It is now fairly widely known from south of Yardie Creek at Javis Well (**C-362**), round North West Cape and down the east coast as far as Mowbowra Well (**C-361**: Fig. 1). The latter locality is south of the proposed Exmouth marina. The range extension since 1962 is *ca* 740%. The gut contents of four specimens contained detrital matter and the remains of diptera; it is not known whether the latter are taken live.

The eel, *O. candidum* , was known also in Mees's time (1962) only from Milyering and Kudamurra Wells on the north-west coast of the peninsula. In 1973 it was seen in Kubura Well (**C-27**) on the north east coast in Exmouth town site (Fig. 1). The only known sightings in more than a decade have been south of the proposed Exmouth marina:- in the Gnamma Hole (**C-105**: 29 May 1988 - M. East; pers. comm.) and in Mowbowra Well (**C-361**: 10 September 1989 - B. Vine; pers. comm.). In 1977 one was seen for several days in a recently excavated 4 m deep well south of Yardie Creek (Allen 1982). The range extension since 1962 is *ca* 340%.

The shrimps, *Stygiocaris lancifera* and *S. stylifera* are here treated together as field observers have not been able to distinguish the two species; this point will be discussed further below. Holthuis (1960) described the species sympatrically from both Milyering and Kudamurra Wells and unspecified water holes near Milyering. They are now known to occur from Tulki Well on the west coast, round North West Cape and down the east coast as far as Mowbowra Well (Fig. 1). The latter locality is south of the proposed Exmouth marina. The range extension since 1962 is *ca* 530% for *Stygiocaris lancifera* and 340% for *S. stylifera.* All range extensions were calculated assuming the fauna occupies only the coastal plain (see below).

The Cape Range amphipods (*Victoriapisa* complex) were not known in Mees' time and occur in a band about 12 km long in the central part of the range (Fig. 1). Alcohol preserved material from each cave is held at the Western Australian Museum; Cape Range 1989 -3212, -3225, -3236, -3241; and WAM 954/88 to 987/88).

There are reports of 'shrimps' pumped from a bore further south on the east coast (M. East; pers. comm.), the west coast and from the bore field supplying Exmouth, but no specimens are known. Their identity cannot be assumed because the Exmouth bore field enters Tulki Limestone from which only the Cape Range amphipods have been confirmed.

Only 1.1 km from Milyering Well is a cave (**C-215**) within the same Tulki Limestone formation that contains the typical Cape Range troglobitic fauna (Humphreys 1989 and unpublished). The coastal water table is reached at a depth of 23.8 m (*ca* +1.2 m MSL; *cf* +0.42 to +0.98 m MSL in Exmouth bores 1 to 6; Bestow 1966). This is the only locality known from the North West Cape peninsula where elements of both the Cape Range and the coastal fauna co-occur, namely the gudgeon and a troglobitic millipede (an undescribed genus of the Paradoxosomatidae [Craspedosomida]; W. A. Shear, pers. comm. 1989). Clearly the potential exists for the subterranean fauna to extend from close to the coast into the foothills of Cape Range proper (see below).

Numbers

No estimates of the continuity or abundance of this subterranean fauna has been made and so assessment of its status relative to the time of its discovery is impossible; detailed biological work is required to set this base line. The impression of those who have examined the wells over many years is that numbers are considerably lower than they once were. We present below the little information about numbers that can be deduced.

Mees (1962: 29) describes removing the *ca* six visible specimens of the gudgeon from Milyering Well several times during one day as they were replaced by individuals from the subterranean channels. Several days later only one or two individuals were found on subsequent visits. The next year about six were seen again.

The collections made from which Holthuis (1960) described the shrimps are well documented as to the number of specimens; Snell's samples were collected mainly in May 1959 (a few in April 1957), and Mees and Douglas's samples were collected in August that year (Table 3). The proportion of the two species of shrimps, *Stygiocaris lancifera* and *S. stylifera*, did not differ between collectors (Table 3: $c^{2}1 = 2.635$, $P=0.105$) or the two major collections (Table 3: $c^{2}1 = 3.166$, $P=0.075$). Note the large number of specimens collected in the wells at that time where it is now difficult to find several specimens.

Table 3: The numbers of shrimps (*Stygiocaris* spp.) collected by various people and their locations. Data for Mees & Douglas and Snell are from Holthuis (1960).

Well	**Collector**	***S. lancifera***	***S. stylifera***
Kuddamurra	Snell	75	12
Kuddamurra	Mees & Douglas	56	2
Milyering	Snell	7	0
near Milyering	Snell	9	1
		147	15
West coast	Humphreys	20	0
East coast	Humphreys	0	24
		20	24
		167	39

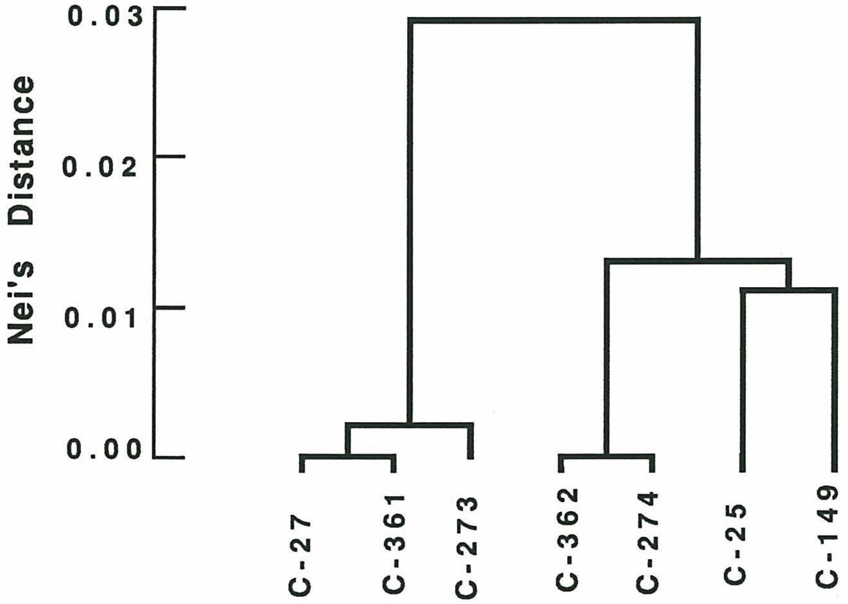
In the samples collected for genetic analysis (below) all specimens from the west coast were of one genetic species while all those from the east coast were of another genetic species. Some specimens collected at the same time as the samples used for genetic analysis were fixed in formalin and preserved in alcohol. Comparison of these specimens with paratypes held at the Western Australian Museum shows all specimens from the west coast to be *Stygiocaris lancifera* Holthuis, while all those from the east coast were *S. stylifera* Holthuis (Table 3). The proportion of the two species of shrimps collected on the west coast in the 1950's (Mees 1962) and in 1989 did not differ (Table 3: $c^{2}1 = 0.980$, $P = 0.322$), despite the total absence of *S. stylifera* in 1989. Hence, it is unclear whether there has been a change in the composition of the shrimp populations on the west coast as we may be considering a sampling artifact. However, there is a significant difference in the proportion of the two species collected on the east coast in 1989 and the earlier samples (Table 3: c21 = 106.05, P = <0.001); hence, it seems that a real difference may exist between the shrimp communities on the east and west coasts.

Genetics of the subterranean fauna.

On the coastal plain of the North West Cape peninsula, within the known range of the subterranean aquatic fauna, there are two geological discontinuities which potentially could isolate water bodies. The first is at Vlaming Head (Fig. 1), where a band of Vlaming Sandstone and the Pilgramunna Formation abut the coast. The second is the bisection of the coastal plain by Yardie Creek which exposes to the coast the Tulki Limestone in which the caves of Cape Range are formed (see surface geology maps in Condon, Johnstone & Perry 1955). The genetic analyses were conducted to test the null hypothesis that species are panmictic throughout their range, and secondly, that the potential geological barriers do not constitute a barrier to gene flow around the coastline. A summary of the genetic analyses is given in Table 4 and the data are in Appendices 1-4.

Gudgeon: Forty-three loci were scored of which 12 were found to be polymorphic. Examination of the genetic distances (Fig. 2 and Appendix 1) shows that there are four populations separated by a Nei's Distance of > 0.01:- the north and east coast, on either side of Yardie Creek, and two partly isolated populations on the mid-west coast. The populations on either side (**C-362** and **C-274**) of Yardie Creek, 35 km apart, are very similar genetically (Fig. 2, Appendix 1). Similarly, the geological discontinuity at Vlaming Head straddles populations 10 km apart (**C-27** and **C-273**) which are also of close genetic similarity. Clearly, the two geological discontinuities do not constitute genetic barriers to the gudgeons.

Figure 2: Dendrogram of the relationships between the populations of the The Blind Gudgeon, *Milyeringa veritas* from six localities on the North West Cape peninsula, based on Nei's Distance (see Appendix 1).

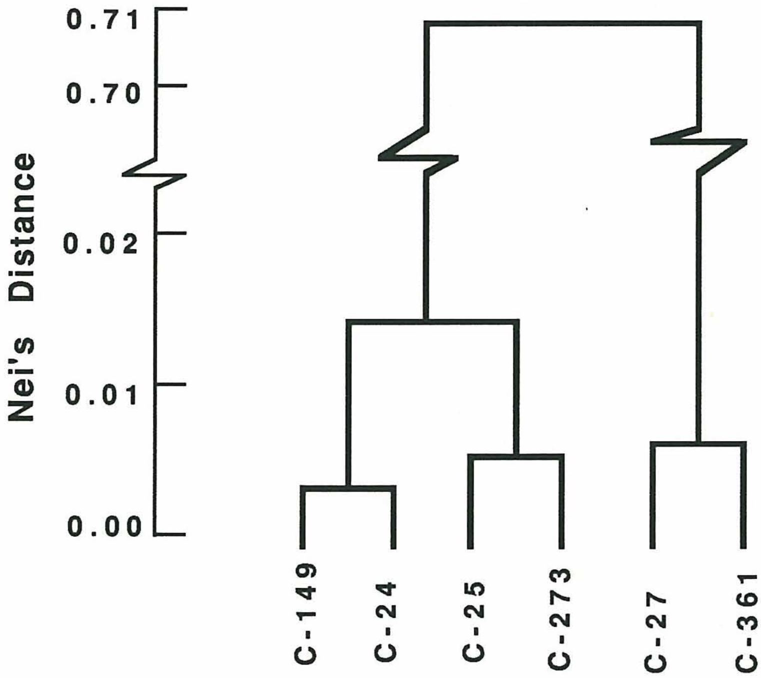


Nevertheless, the gudgeon populations are not sampled from one panmictic gene pool. This was tested by pooling the data within the four groups identified in Fig. 2. Four loci show significant departure from the distribution of allele frequencies expected in sample sets taken from a panmictic population, namely Gpi-1 ($c^{2}2 = 8.89$, P= 0.012), Enol-2 ($c^{2}2 = 17.55$, P< 0.001), Mdh-3 ($c^{2}2 = 15.86$, P< 0.001) and Idh-2 ($c^{2}2 = 17.12$, P= 0.002).

Shrimps: Twenty-eight loci were scored of which 9 were found to be invariant (Appendix 2). The electrophoretic data clearly demonstrate the presence of two species as the two genetic groups identified have 50% fixed differences, differing at 14/28 loci (Appendix 2), and they conform with the taxonomy of Holthuis (1960).

Examination of the genetic distances (Fig. 3 and Appendix 2) shows two groups in the data for the west coast (*S. lancifera*), one from the extreme north-west of the peninsula and the other from the mid-west coast. The distribution of the species and the lack of common species between the east and the west coasts prevent testing the geological discontinuity hypothesis using the shrimp genetical data.

Figure 3: Dendrogram of the relationships between the populations of the Atydid shrimps *Stygiocaris spp.* from six localities on the North West Cape peninsula, based on Nei's Distance (corrected: see Appendix 2). The four localities on the left represent *Stygiocaris lancifera* , while the two to the right represent *S. stylifera.* Note the break in the scale.



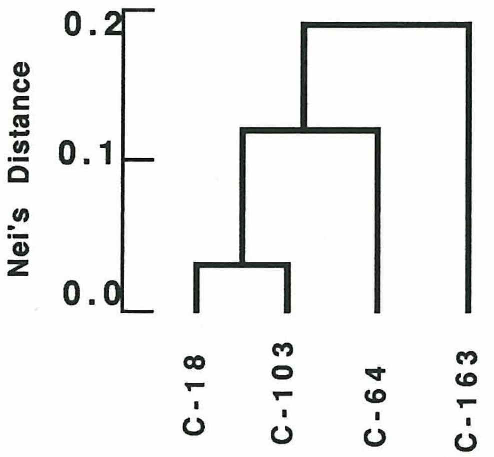
However, the data suggest that the populations on the west coast (***S. lancifera***) are not panmictic. This was tested by pooling the data within the two groups identified in Fig. 3.

The locus Got-1 showed significant departure from the distribution expected in a panmictic population ($c^2_1 = 18.31$, $P < 0.001$), while the locus Got-2 was significant if Yates correction is not applied ($c^2_1 = 4.57$, $P = 0.033$, or $c^2_1 = 2.93$, $P = 0.087$ with Yates correction), a matter of statistical debate. No significant departure from panmixia was detected for ***S. stylifera*** on the east coast.

Given the small size of the shrimps compared with the gudgeons, the genetic continuity of the latter between the east and west coasts suggests that there are no obvious barriers to the continuity of distribution in the shrimps. The data presented here do not demonstrate this. It is clear that suitable habitat for the gudgeons does not imply that the area is also suitable for the shrimps. In **C-215,** where the Cape Range troglobites and the coastal subterranean fauna co-occur, the gudgeons were common but shrimps were absent, despite once being present in Milyering Well, only 1.1 km away.

Amphipods: Twenty-eight loci were scored of which 13 were found to be invariant (Appendix 3). In contrast to the other taxa, there is evidence of considerable genetic divergence between the four cave populations (Appendix 3, Fig. 4). Populations **C-18** and **C-103**, in the centre of the distribution, are genetically similar, displaying minor differences in allele frequency (not significant because of small sample sizes) at several loci. Population **C-64** at the northern edge of distribution shows more divergence, although only one locus, Tpi, reveals the presence of a fixed difference involving a unique allele. The most divergent population is **C-163**, located at the southern end of the distribution. This population displays a number of fixed differences when compared with the other three populations (range 14-23%), although only three loci (Gpi, Pgm-1, and Tpi) involve alleles unique to **C-163**.

Figure 4: Dendrogram of the relationships between the populations of the amphipods from the four caves in Cape Range known to contain standing water. It is based on Nei's Distance (corrected: see Appendix 3).



Clearly the null hypothesis of panmixia is refuted on the evidence of the allozyme data. The levels of genetic divergence are quite high, and by themselves might indicate the presence of more than one species. However, the data are not able to resolve this situation because of the allopatric nature of the distribution of the genetic types. The high levels of polymorphism, coupled with the fact that only a small component of the genetic distance estimates is due to the fixation of unique alleles, suggests that the concept of a single, highly variable species, consisting of discrete sub-populations is the more appropriate model.

The caves in Cape Range are formed in Tulki Limestone which is highly dissected by gorges, some of which cut into the Mandu Calcarenite below. **C-18** and **C-103** are 4 km apart and are not separated by deep gorges cutting into the Mandu Calcarenite. **C-18** and **C-64** are 5.5 km apart and are separated by deep gorges cutting into the Mandu Calcarenite and exhibit 4% fixed differences. **C-103** and **C-163** are only 3.4 km apart but the latter is separated from the other caves by a major gorge which, however, does not appear to cut into the Mandu Calcarenite as far as can be ascertained from surface geology maps. These major gorges are associated also with genetic discontinuities in terrestrial troglobites, but not in cave dwelling but non-troglobitic species (Humphreys 1990).

Continuity of the fauna

The possibility exists that the coastal aquatic fauna is continuous beneath Cape Range, where it cannot be sampled. The four caves in Cape Range which contain amphipods have all been surveyed. The water in the caves is at an altitude of from 110 m (**C-64**) to 240 m (**C-103**), whereas the freshwater lens beneath Cape Range has an expected elevation of < 5 m (Hocking, Moors & van de Graaff 1987), perhaps as low as 0.7 m (calculated from the hydraulic gradient of 6 cm km^{-1}; Bestow 1966). No cave known from Cape Range approaches a depth where a continuation of the coastal fauna beneath Cape Range would have been sampled. If the coastal fauna extends beneath the range then the genetic distances between the populations would be expected to be correlated with the direct metric distance between the populations. If the populations are restricted to the coastal limestone then the genetic distances between the populations, would be expected to be correlated with their metric distance apart along the coastal plain, namely around the northern end of the peninsula. This analysis is appropriate as panmixia has already been rejected, hence this relationship will not be a straight line with a slope of zero (see Richardson, Baverstock & Adams 1986: 287). The two measures of genetic distance for the gudgeons were regressed on both these measures of metric distance (Appendix 4; this cannot be done for the shrimps because the samples for each species are restricted to either the east or the west coast).

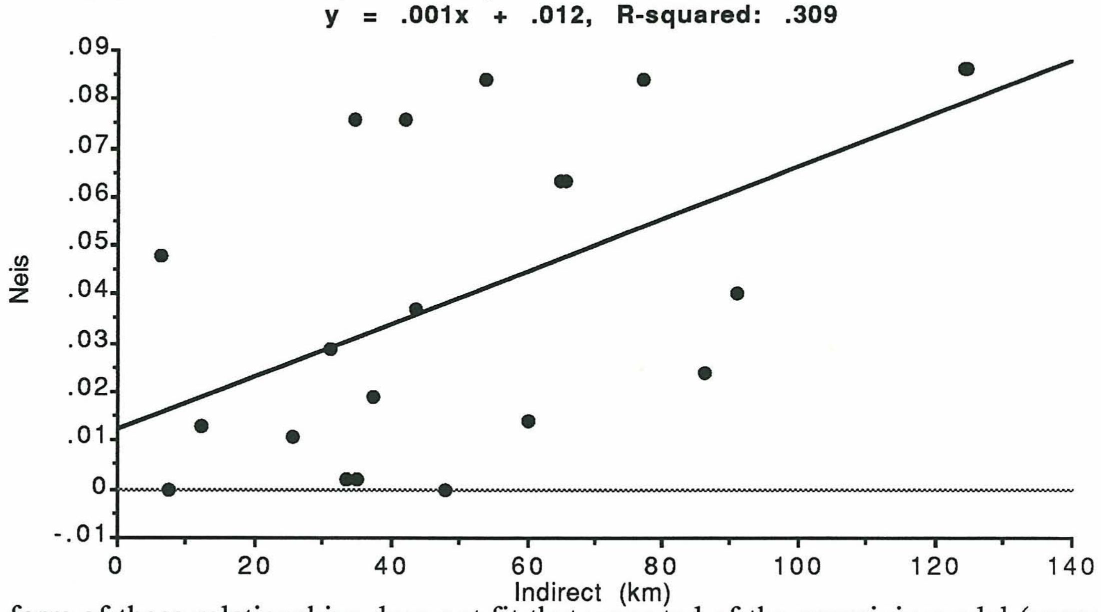
Table 5: Summary of the statistics relating genetic distance between the gudgeon populations to two measures of metric distance between the sampling locations (see text), and the direct measure between shrimp (*S. lancifera*) populations.

Genetic Distance	Metric Distance	D.f.	Fs	P	r^2 adj.	Intercept	Slope
			Gudgeon				
Nei's	**Direct**	1,5*	1.062	>0.25	-	-	-
Nei's	**Indirect**	1,5	8.497	<0.05	0.273	0.012	0.00014
Fixed	**Direct**	1,5	0.313	>0.10	-	-	-
Fixed	**Indirect**	1,5	7.651	<0.05	0.250	-0.158	0.012
			Shrimp				
Nei's	**Direct**	1,2	72.241	<0.03	0.934	-0.008	0.00036

* In Figs 5 and 6 each point represents a comparison between two of n populations and there are n(n-1)/2 points. As these are not statistically independent the degrees of freedom in the above analyses are based on n rather than n(n-1)/2 comparisons.

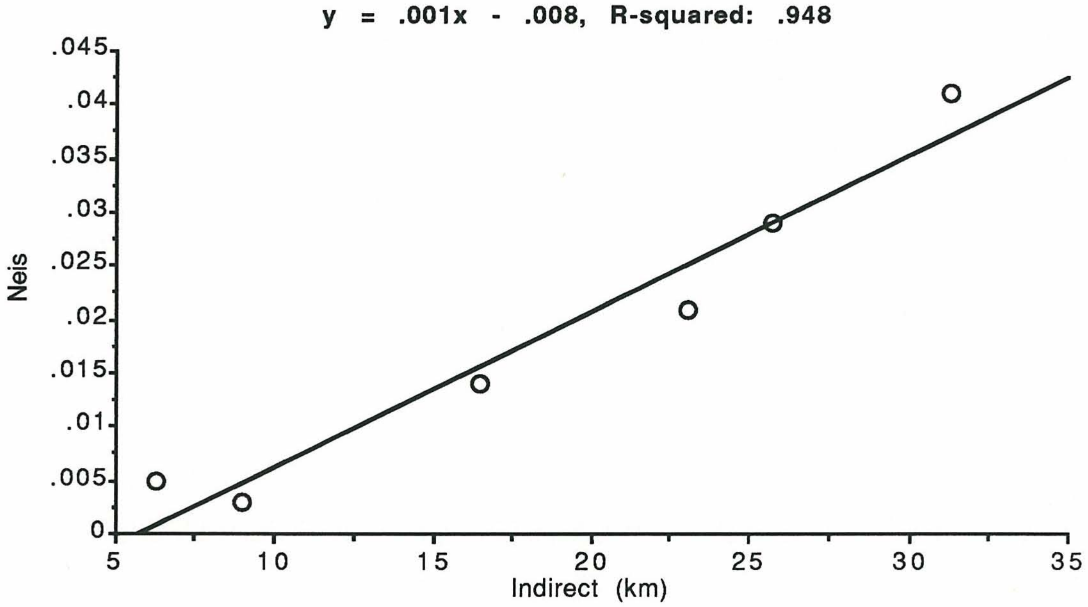
No significant relationship was found between genetic separation of the gudgeon populations and the direct metric distance between the wells (Table 5). However, both measures of genetic distance were significantly regressed on indirect metric distance (assuming contact only along the coastal plain; Table 5, Fig. 5). In addition there is a close relationship between metric and genetic distance for the shrimps, *S. lancifera* (Table 5, Fig. 6). Together these analyses suggest that the coastal fauna on the North West Cape peninsula inhabits a linear system (corridor), and does not occupy the available water lens beneath Cape Range.

Figure 5: The relationship between Nei's Distance for the gudgeons and the indirect metric distance (km) which assumes the populations inhabit only the coastal plain.



The form of these relationships does not fit that expected of the panmixia model (panmixia has already been rejected), nor the isolation by distance model in which the curve should be steep initially and gradually flatten out with increasing distance (see Richardson, Baverstock & Adams 1986: 287). This suggests that the discrete sub-population model may be appropriate but more detailed sampling would be required to verify this hypothesis as the sample sizes used here are too low for detailed analysis of population sub-structuring. Morton's Kinship Coefficient (not shown) is zero at a distance apart of 44 km; individuals at this distance can be considered independent of one another.

Figure 6: The relationship between Nei's Distance for the shrimp (*S. lancifera*) populations and the direct metric distance (km). No indirect measure of distance is available because all samples were from the west coast.



The consequences of non-panmictic cave populations have been discussed extensively elsewhere (Humphreys 1989). It is suffice to say that uncertainty about the extent of the interconnection of the fauna in the coastal system(s) complicates considerably potential management of the region. A more detailed analysis of the interconnections is required.

Groundwater

Nature of the water bodies: Water occurs in four of the caves in Cape Range for which the only evidence of continuity are the contained amphipods; one (**C-64**) is an outflow cave and always contains water, two caves contain accessible pools (**C-18** and **C-103**; the former can silt up; Humphreys 1989) , while the fourth (**C-163**) contains long water filled passages (R. Wood; pers. comm. 1988). The estimated height of the water in the caves is >100 m above the freshwater lens beneath Cape Range (see above). The latter is recharged after exceptional rain, and that the coastal areas are recharged by run off from the range (Hocking, Moors & van de Graaff 1987). The coastal fauna probably occurs at the periphery of this freshwater lens barely above sea level (up to *ca* 1.2 m; see above).

From the mouths of the gorges in Cape Range alluvial gravel deposits fan across the coastal plain (Sofoulis 1951a). In the foothills and on the coastal plain a wedge of freshwater overlies sea water so the water is more saline closer to the coast. Dissolved solids in the water increase from 430 mg L^{-1} near the scarp to more than 2850 mg L^{-1} near the coast. The successful bores are on these drainage lines, while between them water is absent or saline (Sofoulis 1951b). This could result in interfluvial salinity barriers to the dispersal of the coastal fauna, indeed all the known faunal sites are on these drainage lines.

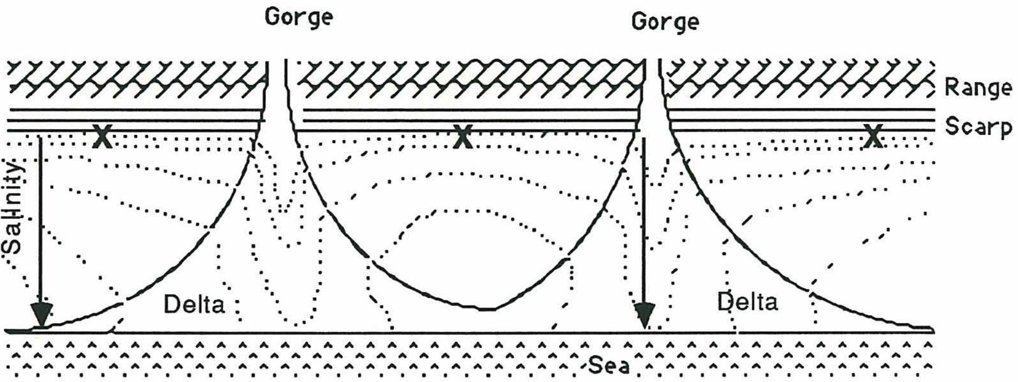
The lateral hydraulic conductivity in the Exmouth bore field varies by three orders of magnitude (10 to 1000 m d^{-1}; Forth 1973) and is indicative of the varied cavernous nature of the Mandu, Tulki and Trealla Limestones where the bores occur; cavernous flow can be seen at some coastal locations (*ibid.*). In such cavernous karst areas the sea water/freshwater interface is rarely found as a line of demarcation, as in a uniformly porous and permeable medium, but will occur as a broad irregular zone of diffusion which is broadest at the coast due to tidal influence and is reduced away from the sea (Forth 1973).

The influence of marine tides on the water level is not known in detail. There are daily tidal movements of 15 cm in Kudamurra, Tantabiddy and Milyering Wells on the west coast (Mees 1962). Bundera Sinkhole, a cenote, to the south of Yardie Creek clearly is also tidal. On the east coast, south of Exmouth, tidal effects on the groundwater level are evident up to *ca* 3.5 km inland (Forth 1973) and this probably affects the draw capacity of the bores.

A model for population interaction

From the foregoing discussion it is evident that there is a band of decreasing salinity away from the coast. This is superimposed on fan-shaped channels of freshwater drainage broadning towards the coast and on the gradient in the thickness of the zone of mixing of fresh and saltwater. This information permits the development of a general model, with direction but not magnitude, of the likely form of the isohalines along the coast near the drainage lines from Cape Range. It can be seen (Fig. 8) that any connections between populations along the coast, and hence gene flow, will likely be close to or in the foothills of Cape Range. These areas, away from productive wells and from known subterranean fauna, are likely to be the critical areas for conservation. While this model is contraindicated by the distributional data, it needs to be explored or else any management may be both misdirected and sidetracked. The gudgeons do indeed occur in at least one area of Tulki Limestone, well into the foothills of Cape Range (**C-215**; see above).

Figure 8: Schematic diagram of the scarp and coastal plain of the peninsula. The general form of the isohalines (.........) was determined from the evidence discussed in the text. The wells, hence the coastal fauna, are known mainly from the fan shaped drainage areas below the gorges in Cape Range. **X** marks the narrow corridor of lower salinity hypothesised to be close to or in the foothills of Cape Range and through which the populations may connect.



Water quality: The fauna inhabits water from which samples vary in salinity from 0 (**C-23**) to 16‰ (Bundera Sinkhole; Tables 2 and 6). Excluding the latter the salinity range is from 0 to 5‰ and a more detailed analysis of Bundera Sinkhole should be made to confirm this anomalous reading. Such coastal freshwater usually floats on a saltwater wedge but no salinity profiles have been conducted in these wells. The pH range of 6.8-7.6 (mean 7.3 [S.D. 0.29, N=11]) is characteristic of limestone areas with fast flowing water (Culver 1982).

The results of water chemistry analysis from some of the wells on the coastal plain and from caves in Cape Range are presented in Table 6. A factor analysis by sample location shows that there is a cline in the quality of the water, with a gradual increase in ionic content anti-clockwise around the coast, from the caves in Cape Range, down onto the east coastal plain, around the north coast and on down the west coast to the south of Yardie Creek (Fig. 7). Linear regression analysis (Table 7) shows that most of the parameters exhibit a significant cline in this direction. If the anomalous data from Bundera Sinkhole (**C-28**) are excluded, salinity (log) is still significantly regressed on distance (log) ($\mathbf{Fs1,10} = 5.367$, $P=0.043$: $\mathbf{r^2adj.} = 0.284$).

Table 6:- The results of water analysis from caves within Cape Range and from wells and bores on the coastal plain. The locations are shown in Figure 1.

Cave Number	**Cave name**	**Salinity** %o	Na^+ mM/L	K^+ mM/L	Ca^{++} mM/L	Mg^+ mM/L	Cl^- mM/L	**Total P** ug/L	**Total N** ug/L
C-23	Dozer Cave	0.0	3.60	0.04	0.21	0.19	2.04	9	193
C-24	Milyering Well	4.0	55.80	1.12	2.90	4.80	58.70	9	68
C-25	Kudamurra Well	2.0	21.20	0.45	1.67	2.87	23.20	4	114
C-26	Tantabiddy Well	5.0	41.10	0.81	2.47	4.54	39.60	32	207
C-28	Bundera Sinkhole	16.0	248.70	5.44	5.72	23.40	253.70	21	167
C-64	Shot Hole Tunnel*	0.0	1.59	0.03	0.74	0.46	2.10	4	187
C-103	Trionomo*	0.0	0.88	0.01	1.18	0.09	1.48	14	286
C-105	The Gnamma Hole	1.0	7.34	0.15	0.75	1.10	7.73	3	134
C-149	Tulki Well	3.0	66.70	1.36	3.31	7.00	70.50	7	141
C-163	Wanderer's Delight*	0.5	1.59	0.02	1.33	0.19	2.35	4	174
C-273	5 Mile Well	4.0	57.80	1.18	3.03	5.94	59.50	23	259
-	Mangrove Bore	1.5	13.90	0.31	1.53	2.30	15.54	3	101

* Denotes caves in Cape Range rather than wells on the coastal plain; the two areas have no fauna at the level of Order in common.

Table 7: Results of regression analysis of various water chemistry parameters (log [Y+1]) on distance around the coast (log [X+1]) of the North West Cape peninsula. The distance is measured from the most southerly cave on the east coast, around the north coast and down the west coast, hence it is assumed that the water body is coastal and does not continue beneath Cape Range. It illustrates the significant cline in most water chemistry parameters.

Parameter	F_s	P
Salinity (%o)	7.80	0.018
Na^+ (mM/L)	10.30	0.008
K^+ (mM/L)	9.94	0.009
Ca^{++} (mM/L)	13.72	0.004
Mg^+ (mM/L)	12.91	0.004
Cl^- (mM/L)	10.61	0.008
Total P (ug/L)	2.44	0.147
Total N (ug/L)	2.26	0.161

Groundwater salinities in the Carnarvon Basin, of which the peninsula is a part, show a systematic increase in the direction of the groundwater flow (Hocking, Moors & van de Graaff 1987: 239), with the exception of areas of very saline groundwater such as occur on the coastal plain to the east of Exmouth Gulf (*ibid.*). This appears to be the case around Cape Range. groundwater flow should radiate from the range but the only long reach is south of the range; it is in this downstream area that the ionic content of the groundwater is greatest. Elsewhere on the peninsula the sampling resolution is too low to detect this.

Examination of the known range of the parameters reveals that the coastal fauna inhabits a wide range of water chemistries (Table 8). The amphipods from the caves in Cape Range inhabit a narrower range of these parameters but, as a wider range of parameters does not occur within Cape Range, the data are not informative as to the tolerance of the amphipod species involved. The most notable feature is the high level of total nitrogen in the caves in Cape Range compared with the water bodies on the coastal plain.

Figure 7: Unrotated orthagonal plot from a factor analysis on the parameters in Table 6 arranged by well number (C-) or name. Note that there is a trend in the data from the east coast, round the north coast and south down the west coast.

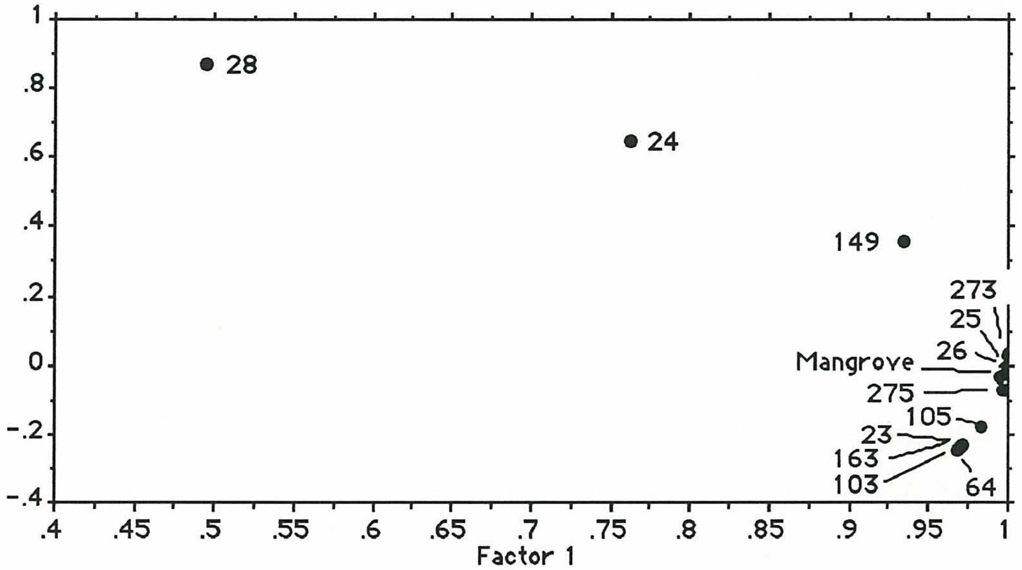


Table 8: The known range of various of water chemistry parameters within which the various taxa of subterranean species have been found.

Parameter	Shrimps[1]	Eel[1]	Gudgeon[1]	Amphipods[2]
pH 1988	6.8- 7.5	6.8 -7.3	6.8- 7.5	6.8
Salinity (%o)	2- 5	1- 5	0-16[1]	0-0.5
Na^+ (mM/L)	21.2-66.7	7.34-55.80	3.60-248.70	0.88-1.59
K^+ (mM/L)	0.45-1.36	0.45-1.12	0.04-5.44	0.01-0.03
Ca^{++} (mM/L)	1.67-3.31	0.75-2.90	0.21-5.72	0.74-1.33
Mg^+ (mM/L)	2.87-7.00	1.10-4.80	0.19-23.4	0.09-0.46
Cl^- (mM/L)	23.2-70.5	7.73-58.70	2.04-253.7	1.48-2.35
Total P (ug/L)	4-9	3-32	4-21	4-14
Total N (ug/L)	68-141	68-207	68-193	174-286

[1] These species occur exclusively as subterranean fauna of the coastal plain; the Blind Cave Eel, *(O. candidum)*, being too rare, is the only member of the fauna not represented in the analysis. [2] Amphipods occur exclusively in caves in Cape Range, where they are the only aquatic fauna.

Together, Tables 4 and 8 suggest that within the known range of the coastal subterranean fauna all sampled sites have a water chemistry suitable for habitation. Hence, the absence of fauna from any water body within this range is likely to be explained by the isolation of that water body from adjacent inhabited water. Such absence may result from lack of continuity of adequately sized cavities within the coastal limestone, or from a temporary drop in the water table which would prevent recolonisation following local extinction due to the stochastic processes operating on small populations.

Status of the water table:- The Water Authority of Western Australia consider that the water being drawn from the Exmouth bore field is connate water, namely recharge not 'fossil water (pers. comm. 1989), and that there is plenty of space left to expand the bore fields (pers. comm. 1988). While this water is heavily drawn upon there appears to have been no consistent monitoring of the level, depth of the saline layer or the quality of the water in the areas known to be inhabited by the subterranean fauna; monitoring bores have recently been added to the Exmouth bore field. There is consistent evidence, of diverse types and sources, that the water table and water quality are falling, but it is not known whether this has resulted from fluctuations in the rainfall or from the extraction of the water for human use. That the latter is the cause, at least within the Exmouth bore field, is indicated by the rising salinity of this water supply (Water Authority of Western Australia; pers. comm. 3 February 1988).

The North West Cape peninsula of Western Australia lies just within the tropics. This semi-arid region is in that part of Australia with the least predictable rainfall, with both the constancy and contingency (*sensu* Colwell 1974) being low (Humphreys, Adams & Vine 1989). In consequence there is low probability of rainfalls sufficient to flood deeply the caves within the range (see full discussion in Humphreys, Adams & Vine 1989), and the recharge pattern of the coastal groundwater will be similarly influenced.

The evidence:- several bores have dried up or gone saline in both the military Area B and Area C of the Joint Naval Communications Facility, to the north of the Exmouth bore field (L. Banfield; pers. comm. and **Exmouth Expression**, February 1989: 6). Town Well has become more saline and a number of other wells have dried up (Cape Well, Trealla Well and South Yardie Well), or the water level has been substantially lowered (Neds Well, **C-119**, Milyering Cave, Tantabiddy Well; B. Vine, pers. comm. 1989). The presence of recent bores alongside many of the wells is an indication of lowering water table. In addition a number of natural seepages from the scarp slopes have dried up e.g. Maduradura gorge (flow greatly diminished; 'used to be able to swim but can now hardly get wet feet'), a spring in Shot Hole Canyon (dried up mid to late 1970's; 'used to flow continuously but is now not even damp') and Padjari Manu (formerly Bunbury cave) in which there used to be a permanent soak into a gour pool but since the mid 1970's has been dry except after heavy rain (B. Vine, pers. comm. 1989); this was a traditional occupation site for aboriginal people (Site Reference **P0267**).

The trend in water use in Exmouth was described as 'alarming' (Water Authority of Western Australia; pers. comm. 3 February 1988), even before the major development of the area was mooted. The salinity of the water extracted from the Exmouth bore field is constantly rising (*ibid.*) but it is not known whether this results from saltwater coning below the bore or from a general rise in the level of the saltwater. Clearly this is not a sustainable usage and if it continues lasting damage may be done to both the water supply and the habitat of the subterranean fauna. Extension of the bore field, the current method of management (*ibid.*), will extend the area over which this damage occurs. Considerable accuracy (±5 mm) is required to monitor changes in water level and salinity because changes need to be distinguished from the tidal influence reported in these bores and because a mere 75 mm lowering of the water table would reduce freshwater storage by 20% (Forth 1973)

Age

The age of isolation of troglobitic species remains controversial. Some authors claim a general trend/pattern for cave fauna. In general 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). Of the species examined from North West Cape peninsula the aquatic amphipods genetically show the most genetic divergence between caves (Humphreys 1990), while within the coastal fauna speciation has occurred in the shrimps. However, some other aquatic groups are considered to have been isolated more recently; <10 k yr BP in the Mexican characin *Astyanax mexicanus* (Mitchell, Russell & Elliott 1977) and between 20 and 0.09 k yr BP for the diverse Hawaiian larva tube fauna, but the latter may be complicated by the ability of the species to move between caves (Howarth 1972). Peck (1981a, 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.

The coastal plain limestones on the North West Cape peninsula originate from fringing coral reefs during periods of higher sea level. There are three higher terraces along the west coast scarp of Cape Range, to a height of *ca* 57 m above the present sea level, which are thought to represent stadia in the Quaternary sea levels changes (Graaff, Denman & Hocking 1976). The high degree of troglobitic adaptation in the species suggests that the coastal subterranean fauna is of an age such that it did not evolve *in situ* in the current limestones (Mees 1962). They could not have occupied the current coastal limestone during the high sea levels, at which time Cape Range (together with Rough Range) would have been an island, separated from Giralia Range, and large areas of the hinterland of Cape Range would have been inundated by the sea.

With the changing sea levels following the uplift of the Miocene limestones into the Cape Range anticline, there has been ample opportunity for the present coastal fauna to have colonised water within Cape Range itself or to have evolved there and subsequently moved down to their present location. However, the lack of common fauna (no common Orders) between Cape Range and the coastal plain (Humphreys 1989), despite the suitability of the water and probable opportunity for its invasion (superficial speleothem material from **C-163** has been dated by Th/Ur method at 123014 y BP [+50886, -34814]; D. Smith, pers. comm. 1990).

the cave systems within the range being >200,000 years (unpublished data from Ur/Th analysis of speleothems) suggests neither to be the case.

Alternatively the coastal fauna may have arrived in the area by migration along the coast in similar limestones with connecting water channels. Current conditions (not considering sea level changes) preclude migration along the coast owing to the highly saline groundwater to the east (along the shore of Exmouth Gulf) and to the south (salinity is high [Hocking, Moors & van de Graaff 1987] and traditional water sources were lacking [Carter 1902]). Indeed, there is currently a barrier of high salinity (> 6000 mg L^{-1} total dissolved solids) in the unconfined groundwater across the neck of the peninsula (Hocking, Moors & van de Graaff 1987: 240).

Milyeringa' s closest affinity is possibly with the eleotridid genus *Butis*. *Butis* is a mangrove dwelling genus of brackish and fresh waters of the Indo-Australian Archipelago (i.e. Malay Peninsula to northern Australia including Indonesia, Philippines and most of Melanesia) (G.R. Allen; pers. comm. 1990). At the height of the Pleistocene glaciation, when sea level was 150 m lower than the present level (Chappell & Thom 1977), the western shore would have been no more than 12 km from the current shoreline (Morse 1988). Such slow lateral migration of the shoreline, over what are presumably coastal limestone deposits, offer an alternative route for immigration onto the North West Cape peninsula along a broad coastal plain.

Hence, it may be worth searching wider afield for this fauna or for related faunae. However, the cline in salinity, increasing to the south-west, suggests that isolation may have resulted from increasing salinity in the groundwater as the climate dried. Adjacent to Cape Range the groundwater is recharged from water captured in the limestone of the range. The water supply here is probably more consistent and less saline than in adjacent coastal areas without an elevated hinterland, thus permitting the fauna to survive.

Concluding remarks

The karst area on North West Cape is of international significance (Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). Some of the caves and wells lie within Cape Range National Park where legislation provides for the 'protection of indiginous .... fauna and .... any feature of scientific interest` and management objectives aim to 'protect and conserve indiginous .... animals and their habitats`, to 'maintain scientific reference areas` and to 'conserve and protect groundwater resources' (CALM 1987). However, informed management of the coastal subterranean aquatic fauna is hampered by its main distribution being outside Cape Range National Park and by the lack of information on the biology of the fauna and the characteristics of the subterranean water. Recent sightings of the eel lie in the area of greatest development and the other species occur as isolated populations on the north-west and east coasts are outside the area of protection, as are two of the four amphipod localities, all lying in a temporary limestone reserve (TR5980H), under the authority of the Minister for Mines.

The fauna is presumably dependent upon allochthonous energy sources washed into the system during heavy rain (Humphreys, Adams & Vine 1989), although in **C-215** it may receive substantial energy inputs from the dense root mats, and their exudates (Culver 1982) which penetrate the cave system; the extent of these is unknown as the coastal subterranean caverns are rarely accessible to people, but a characteristic fauna associated with such root mats seems absent. The total nitrogen levels in the coastal waters is much lower than found in Cape Range.

Alteration to the quantity or quality of the water in the caves and wells of the North West Cape peninsula will affect the populations of aquatic troglobites, as changes affecting the Tulki Limestone will influence the humid adapted terrestrial troglobites of Cape Range (Humphreys 1989; Humphreys, Adams & Vine 1989; Humphreys & Collis 1990).

At this stage little is known of the water bodies within Cape Range other than, as there is no common fauna, they are isolated from those of the coastal plains. The genetical evidence from the amphipods within Cape Range suggests that the major canyons separate not only the populations, but also the water bodies they inhabit (Humphreys, Adams & Vine 1989). In addition the genetical evidence from the coastal plain suggests that there may be partially separate water bodies also along the coastal plain. A faunal survey would have the advantage of determining the extent of the Cape Range fauna and the continuity of the water bodies.

Cave faunae generally, even terrestrial components, are vulnerable to change in the water table. *Schizomus wessoni* (Chamberlin) was eliminated from its type locality due to long term drying of the Santa Cruz River due to agricultural activities, and oases were rendered unsuitable for *S. joshuensis* by draining (Rowland & Reddell 1981). *Schizomus vinei* inhabits many caves within Cape Range, and with its associated fauna is highly dependent on the status of hydration of the caves, being derived from a tropical wet forest community (Humphreys 1989; Humphreys, Adams & Vine 1989).

Dewatering during the construction of the proposed Exmouth marina could be expected to affect the area within a 1000 m radius (Morgan and Associates 1990: 16). This will cause the saltwater wedge to move further inland and potentially bisect the known distribution of all species of the subterranean aquatic fauna. While this paper shows that knowledge of the distribution of this coastal fauna is sparse and fragmentary, the information available has led to a testable model. This suggests that the critical areas for conservation are not, as would seem obvious, those areas from which the fauna has been recorded, but the likely narrow corridors of freshwater close to the scarp between the areas from which the fauna has been recorded. Any future management strategy should consider this model.

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APPENDICES

Appendix 1: Genetic data for the Blind Gudgeon, *Milyeringa veritas*.

Appendix 1a: Allele frequencies for the seven populations of gudgeon. Alleles are designated alphabetically with a being the most cathodal. Where present, multiple loci are designated numerically according to increasing electrophoretic mobility.

LOCUS	allele	Well C-25 Kudamurra	C-149 Tulki	C-273 5 Mile	C-274 Pilgramunna	C-362 Javis	C-361 Mowbowra	C-27 Kubura
Enol-2	b			75			100	100
	a	100	100	25	100	100		
Fum	b	90	100	100	100	100	100	100
	a	10						
Acon-2	c					25		
	b	90	90	100	100	75	100	100
	a	10	10					
PepB	b	90	100	100	100	100	100	100
	a	10						
Ldh-1	b	50	80	67			100	100
	a	50	20	33	100	100		
Idh-1	b	90	100	100	100	100	100	100
	a	10						
Idh-2	c	20	60	93	75	100	100	100
	b	80	40		25			
	a			7				
Pgm-2	b				12			
	a	100	100	100	88	100	100	100
Mdh-3	b		40	100	37	25	100	100
	a	100	60		63	75		
Ca	b	100	100	100	87	100	100	100
	a				13			
Gpi-1	b	50	100	42	100	100		
	a	50		58			100	100
Sordh	b	80	62	100	87	75	100	100
	a	20	38		13	25		
Maximum N		5	5	7	5	2	3	3

Invariant loci: **Acon-1**, **Ada**, **Adh**, **Ak**, **Ald-1**, **Ald-2**, **Ck**, **Enol**, **Est**, **Fdp-1**, **Fdp-2**, **Gapd**, **Glo**, **Got-1**, **Got-2**, **Gp-1**, **Gp-2**, **Gpi-2**, **Gpt**, **Ldh-2**, **Mdh-1**, **Mdh-2**, **Me**, **Mpi**, **PepD**, **Pgam**, **6Pgd**, **Pgk**, **Pgm-1**, **Pk** **and** **Tpi**.

Appendix 1b: Genetic distance matrix. Upper = Nei' Distance (corrected for small sample size, Nei 1978); lower = Fixed Differences (%).

Well	C-25	C-149	C-273	C-274	C-362	C-361	C-27	
C-25		_	0.011	0.048	0.019	0.024	0.076	0.076
C-149		0	_	0.029	0.013	0.014	0.063	0.063
C-273		2	0	_	0.037	0.040	0.002	0.002
C-274		0	0	0	_	0.000	0.084	0.084
C-362		0	0	0	0	_	0.086	0.086
C-361		5	5	0	7	7	_	0.000
C-27		5	5	0	7	7	0	_

Appendix 2: Genetical data for the Atydid shrimps *Stygiocaris spp.*

Appendix 2a: Allele frequencies for the six shrimp populations. Data from C-361 and C-27 are for *S. stylifera* while the remaining four localities are from *Stygiocaris lancifera*.

LOCUS	allele	WELL C-273 5 Mile	C-24 Milyering	C-25 Kudamurra	C-149 Tulki	C-361 Mowbowra	C-27 Kubura
Acon	d				25		
	c	100	100	100	75		
	b					83	100
	a					17	
Acyc-2	b	25					
	a	75	100	100	100	100	100
Argk-1	b						6
	a	100	100	100	100	100	94
Argk-2	b				12	100	100
	a	100	100	100	88		
Est-1	b	100	100	100	100		
	a					100	100
Est-2	c	100	100	100	100		
	b					100	87
	a						13
Gapd	b					100	100
	a	100	100	100	100		
Got-1	d			12			
	c					17	
	b	75	12	75		83	100
	a	25	88	13	100		
Got-2	c					100	100
	b	37	87	87	100		
	a	63	13	13			
Gpi	c	12				50	31
	b						6
	a	88	100	100	10	50	83
Gpt	c	37	25	37			
	b	63	75	63	100		
	a					100	100
Hk	b	100	100	100	100		
	a					100	100
Mpi	b					100	100
	a	100	100	100	100		
PepA	b	100	100	100	100		
	a					100	100
PepB-1	b	100	100	100	100		
	a					100	100

PepB-2	b	100	100	100	100		
	a					100	100
PepD-1	b	100	100	100	100	50	100
	a					50	
Sordh	b	100	100	100	100		
	a					100	100
Tp1	b	100	100	100	100		
	a					100	100
Maximum N 4		4	4	4	3	8	

Invariant loci: **Acyc-1**, **Ald**, **Enol**, **Fdp**, **Fum**, **Gda**, **Gp**, **Ldh** and **PepD-2**.

Appendix 2b: Genetic distance matrix. Upper = Nei' Distance (corrected); lower = Fixed Differences (%).

LOCUS	allele	C-273	C-24	C-25	C-149	C-361	C-27
C-273		_	0.021	0.005	0.041	0.742	0.708
C-24		0	_	0.014	0.003	0.787	0.758
C-25		0	0	_	0.029	0.739	0.704
C-149		0	0	0	_	0.791	0.783
C-361		50	50	50	50	_	0.006
C-27		50	50	50	50	0	_

Appendix 3a: Allele frequencies of Amphipoda.

LOCUS	allele	C-18	C-64	C-103	C-163
Acon-1	b				17
	a	100	100	100	83
Acyc	b	100	50		100
	a		50	-	
Adh	b	12	100		
	a	88		-	100
Fdpase	b	50		100	100
	a	50	100		
Gapd	b		28		100
	a	100	72	100	
Got-1	b	62	78		100
	a	38	22	100	
Got-2	b				6
	a	100	100	100	94
Gpi	e				5
	d				89
	c				6
	b	75	100	100	
	a	25			
Idh	b	100	100	100	39
	a				61
Lap	b	100	50		100
	a		50	-	
Mpi	b	12			
	a	88	100	100	100
PepB-1	b		17		
	a	100	83	-	100
PepB-2	a	100	100	-	100
PepD	c				56
	b	75	100	37	44
	a	25		63	
6Pgd	a	100	100	-	100
Pgm-1	c				100
	b	100	83	100	
	a		17		
Tpi	c		100		
	b	100		100	
	a				100
Maximum N		4	9	4	9

Invaraint loci:- Acon2, Enol, Gp-1, Gp-2, Gpt, Ldh, Mdh-1, Mdh-2, PepA, Pgm-2 and Pk.

Appendix 3b: Genetic distance matrix. Upper = Nei's Distance (corrected); lower = Fixed Differences (%).

Cave	C-18	C-64	C-103	C-163
N	4	9	4	9
C -18	-	0.108	0.033	0.194
C-64	4	-	0.155	0.286
C-103	0	9	-	0.310
C-163	14	18	23	-

Appendix 4: Distances between caves and wells.

Appendix 4a: Matrix of the distance between the wells on the North West Cape peninsula. Upper right: - shortest distance (km) between all pairs of wells. Lower left:- distance (km) around the north of the peninsula under the assumption that the subterranean aquatic fauna does not live beneath Cape Range.

	C-24	C-25	C-27	C-149	C-273	C-274	C-361	C-362
C-24	-	17	22	9	23	21	20	69
C-25	17	-	13	26	6	38	16	86
C-27	50	35	-	29	10	40	8	87
C-149	9	26	65	-	31	12	25	60
C-273	23	6	34	31	-	44	17	91
C-274	69	38	54	12	44	-	35	48
C-361	58	42	8	66	35	77	-	80
C-362	69	86	124	60	91	48	125	-

Appendix 4b: Matrix of the distance (km) between all pairs of caves in Cape Range containing amphipods.

	C-18	C-64	C-103	C-163
C-18	-	5.8	3.8	7.5
C-64		-	9.0	11.5
C-103			-	3.3
C-163				-

Appendix D

Dating of the cave system

Appendix D 2

Appendix D 3

Counting statistics for Uranium series dating of speleothem material from caves in Cape Range.

Determined by Dr D. Smith, Department of Inorganic Chemistry, University of Melbourne.

Table 1: Counting statistics for U-series dating of speleothem from C-163

Sample # 2 - Wanderer's Delight floor material; round water warn stalactite. 8/12/89

U counting time = 77728 s
Th counting time = 78519 s
^{238}U counts =65 Background =0
^{232}U counts =366 Background =0
^{230}Th counts =52 Background =0
Sample mass = 11 g

U background counttime = 1 s
Th background counttime = 1 s
^{234}U counts =71 Background =0
^{228}Th counts =386 Background =0
^{232}Th counts =8 Background =0
Spike weight = 0.0787 g

U chemical yield = 40.5%
Th chemical yield = 42.7%
^{238}U concentration = 0.076 ± 0.0102 ppm
^{230}Th concentration = 9.22E-07 ± 1.36E-07 ppm
Present ^{234}U / ^{238}U = 1.09 ± 0.188
Present ^{230}Th / ^{234}Th = 0.69 ± 0.125
Present ^{230}Th / ^{232}Th = 6.50 ± 2.47
^{230}Th activity in sample = 0.0423 ± 0.00587 dpm g^{-1}
^{234}Th activity in sample = 0.0616 ± 0.00731 dpm g^{-1}
Initial ^{234}U / ^{238}U = 1.13 ± 0.28

Sample age = 123014 + 50886 years
- 34814 years

Table 2: Counting statistics for U-series dating of speleothem from C-125

Sample # 3(ii) C-125
Mid-section of small stalagmite

20/12/89

U counting time = 328467 s
Th counting time = 328467 s

U background count time = 1 s
Th background count time = 1 s

^{238}U counts =303 Background =0
^{232}U counts =1267 Background =0
^{230}Th counts =74 Background =0
Sample mass = 11.75 g

^{234}U counts =497 Background =0
^{228}Th counts =1696 Background =0
^{232}Th counts =14 Background =0
Spike weight = 0.0736 g

U chemical yield = 35.4%
Th chemical yield = 47.9%
^{238}U concentration = 0.089 ± 0.00527 ppm
^{230}Th concentration = 2.61E-07 ± 3.10E-08 ppm
Present ^{234}U / ^{238}U = 1.64 ± 0.120
Present ^{230}Th / ^{234}Th = 0.11 ± 0.014
Present ^{230}Th / ^{232}Th = 5.29 ± 1.54
^{230}Th activity in sample = 0.0120 ± 0.00140 dpm g^{-1}
^{234}Th activity in sample = 0.109 ± 0.00489 dpm g^{-1}
Initial ^{234}U / ^{238}U = 1.66 ± 0.24

Sample age = 12555 + 1745 years
- 1555 years

Appendix E

Age of the sedimentary sequence in C-118

Appendix E 2

Counting statistics for carbon dating of material from C-118.

Table 1: Counting statistics for carbon dating of charcoal from C-118 sediment banks.

Accelerator Mass Spectromtery Dating at DSIR, Institute of Nuclear Sciences, New Zealand.

INS Code	R 11911-5	NZA 1032
Description	Charcoal	
Sample ID	114-1	
Graphite yield	1.19 mg	
Date run	10 May 1990	
$\partial^{13}C$	-18 per mille	
$\partial^{14}C$	-29.0 ± 8.0 per mille	
Age	**236 ± 66 years BP**	
Per cent modern	96.6 ± 0.8	

Appendix F

Biology of the millipedes

Troglobitic millipedes (Diplopoda: Craspedosomatidae) from semi-arid Cape Range, Western Australia - biology.

SUMMARY

1. A new genus of Craspedosomatid millipedes occurs in caves in the semi-arid tropical Cape Range, Western Australia.

2. The millipedes are found in at least 55 of the 282 caves known from Cape Range.

3. As determined by allozyme electrophoresis the caves form three major genetic subregions separated by deeper gorges which cut through the cavernous limestone into the next, non-cavernous, strata.

4. The millipedes occur in dense populations but only in areas of high relative humidity and organic carbon content.

5. Evidence is presented which suggests that the millipedes are opportunistic and are able to grow and breed rapidly on the intermittantly available patches of organic matter washed into the caves by unpredictable rainfall.

6. The millipedes are part of a rich troglobitic community whose affinites lie with the wet tropical forest of N.E. Queensland, rather than with the current semi-arid fauna.

INTRODUCTION

Craspedosomatid millipedes are an important component of a rich troglobitic fauna (obligate cave dwelling species) in Cape Range on the North West Cape peninsula (22° S) of Western Australia (Humphreys, 1989, 1990, 1991, in press; Humphreys & Adams, in press; Humphreys, Adams & Vine, 1989; Humphreys & Collis 1990; Vine, Knott & Humphreys, 1988).

The regional, climatic and biological setting of the fauna has been described elsewhere (Humphreys, 1989b; 1990; in press; Humphreys & Adams, in press; Humphreys, Adams & Vine, 1989a; Humphreys & Collis, 1990; Vine, Knott & Humphreys, 1988) and information is given here only to describe broadly the system.

Cape Range lies just within the semi-arid tropics of Western Australia (Fig. 1) and the rainfall is highly unpredictable - both in terms of its seasonality and between year variation (Humphreys, Adams & Vine 1989). The caves occur in the deeply dissected Cape Range and contain a rich troglobitic fauna that relies on organic matter and water entering the caves from intermittent flooding. This reactivates the cave fauna following which the populations widely occupy the cave and breed (Humphreys in press).

The frequency of water influx into a given cave depends on the occurrence of significant rainfall and on the nature and size of the catchment area of the cave. The rate of drying of a given cave depends on the relative size of the cave and its opening to the outside. Cave C-162 receives an inflow after relatively low rainfall (every few months) but then dries rapidly (in a few months). In contrast, cave C-118 receives an inflow after only heavy rainfall (every few years) but thereafter dries very slowly (over several years: Humphreys, Adams & Vine 1989; Humphreys 1989).

The caves must be linked at a level below which cavers can reach (Humphreys, Adams & Vine 1989). 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 C-162). 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.

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, Adams & Vine 1989). Hence, the caves in Cape Range have highly dynamic troglobite communities (Humphreys in press) which belie the stability normally associated with such systems (Poulston and White 1969).

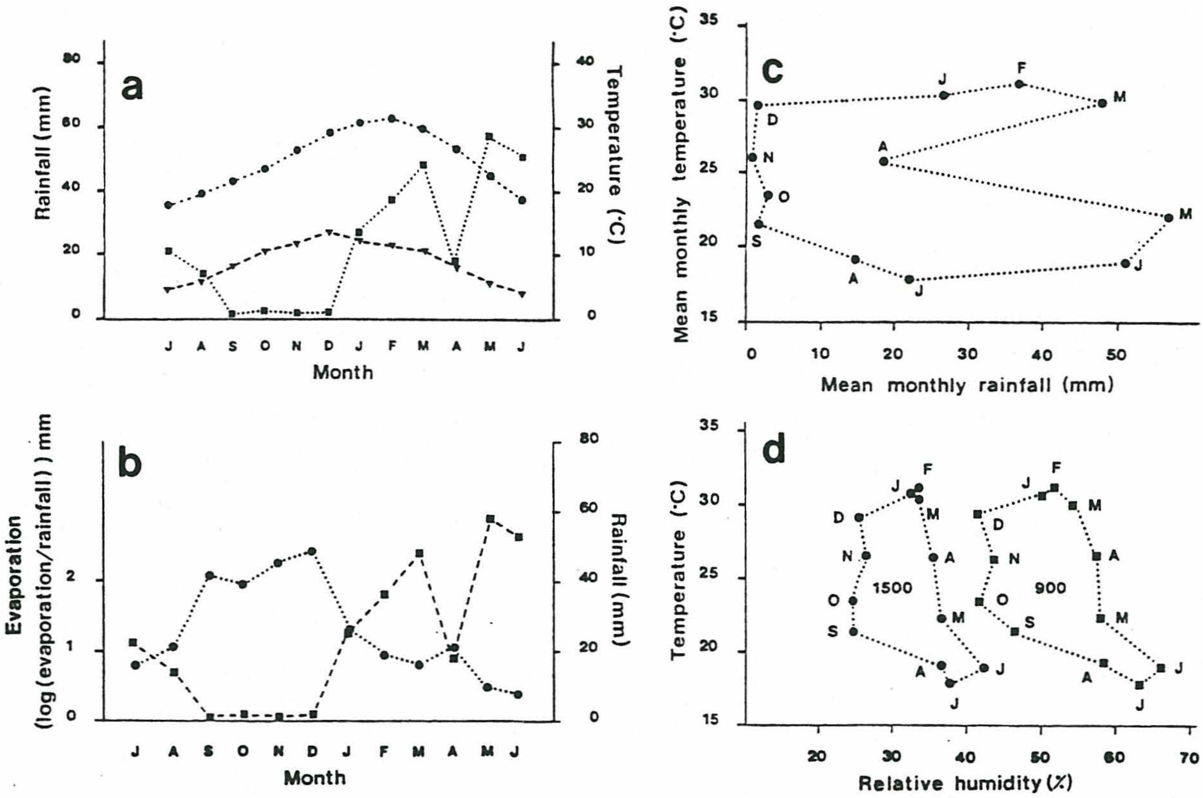
A synopsis of the climate of the area is given in Fig. 1.

METHODS

Field: Temperature and relative humidity were spot measured by whirling hygrometer (Brannan, England) and continuously by thermohydrographs (Okawa Seiki Company Ltd., Tokyo). Soil water content was determined gravimetrically and soil organic carbon was determined by the Walkley-Black dichromate oxidation method with glucose as a standard (Allison 1965).

Millipedes were enumerated by mark and recapture methods. Individuals were marked with fluorescent powders (Daylight Pigments; Abel Lemon Company, Adelaide). Previous marks were detected using an ultraviolet lamp (Model MS-47: Ultra-violet Products Inc. San Gabriel, California). Millipedes were coerced into a narrow glass tube to keep them straight and the total length measured using a x10 Lupe (Peak).

Figure 1: Climatographic synthesis for the North West Cape peninsula. a) Mean monthly temperature (°C) and rainfall (mm). b) Log (mean monthly evapotranspiration)/ (mean rainfall (mm)). c) Hythergraph of mean monthly rainfall (mm) and temperature (°C). d) Hythergraph of mean monthly temperature (°C) and 09⁰⁰h and 15⁰⁰h 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).



The population size was estimated from the mark and recapture data using the sequential Bayes algorithm (Gazey and Staley 1986) as was used previously (Humphreys, Adams & Vine 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, Baverstock & Adams 1986) on samples from 36 caves. For systematic purposes, the null hypothesis under test was that all populations were sampled from the gene pool of a single species. A pilot study examined 46 enzymes and non-enzymic proteins of which 27 were scorable and 18 were polymorphic (Table 1). Only these latter loci were examined in subsequent work.

The following loci were polymorphic:- aconitate hydratase (ACON, E.C. 4.2.1.3), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), diaphorase (DIA, E.C. 1.6.99.?), enolase (ENOL, E.C. 4.2.1.11), fructose-1, 6-diphosphatase (FDP, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), hexokinase (HK, E.C. 2.7.1.1), malate dehydrogenase (MDH, E.C. 1.1.1.37), peptidases (PEP, E.C. 3.4.11.? or 3.4.13.?), and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). The following loci were invariate:- Aldolase (ALD, E.C.4.1.2.13), Alkaline phosphatase (AP, E.C. 3.1.3.1), General protein (GP), Glutathione reductase (GSR, E.C.1.6.4.2), Isocitrate dehydrogenase (IDH, E.C.1.1.1.42), Leucine amino peptidase (LAP,E.C. 3.4.11 or 13), Lactate dehydrogenase (LDH, E.C.1.1.1.27), Mannose-phosphate isomerase (MPI, E.C.5.3.1.8), Phosphoglycerate mutase (PGAM, E.C.2.7.5.3) and Pyruvate kinase (PK, E.C.2.7.1.40). The nomenclature and conventions for referring to alleles and loci follow Richardson, Baverstock & Adams (1986).

The species meets the criteria for adequate genetic work at the within-species level (Richardson, Baverstock & Adams 1986) in that there were at least six polymorphic loci; the samples could be drawn from the smallest and homogeneous population units (caves) and they were sampled over some geographical distance including the extremities and intermediate locations.

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. They were 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.

RESULTS

The millipedes have been found 55 of the 282 caves known from the North West Cape peninsula; the caves are up to 61 km apart and cover >500 km^2 of Cape Range (Fig. 2). These caves are:- C-15, C-18, C-21, C-45, C-47, C-56, C-60, C-63, C-64, C-65, C-68, C-79, C-102, C-103, C-104, C-106, C-107, C-111, C-118, C-119, C-126, C-152, C-154, C-156, C-159, C-161, C-162, C-163, C-167, C-169, C-171, C-177, C-190, C-198, C-201, C-203, C-207, C-215, C-222, C-225, C-227, C-250, C-252, C-254, C-256, C-260, C-261, C-262, C-263, C-277, C-278, C-281, C-291, C-300 and C-312 (Fig. 2). Thirty-one of these caves also contain *Schizomus vinei* Harvey (Chelicerata: Schizomida). Samples collected for allozyme analysis came from 36 of these caves (Fig. 2).

Cave morphology

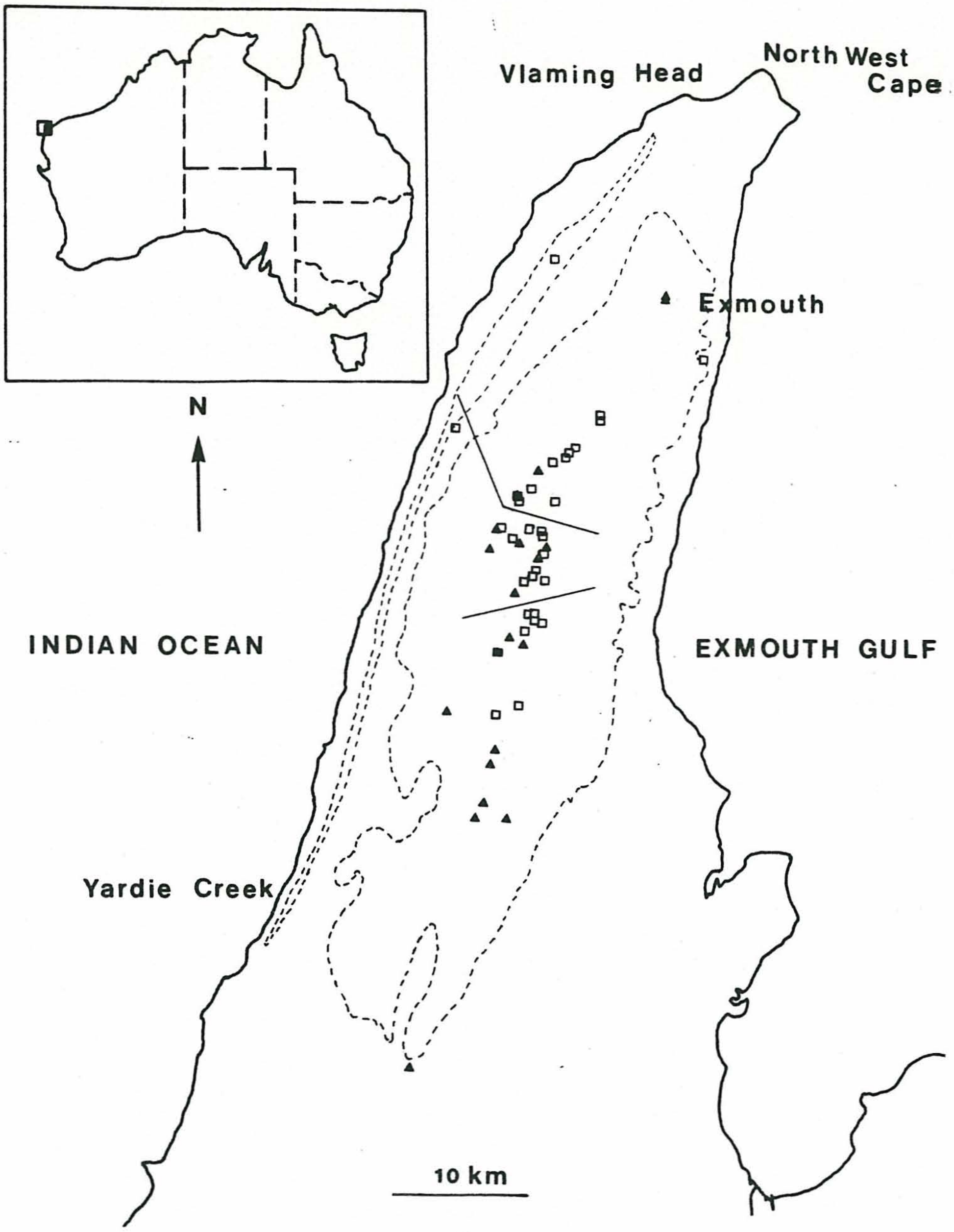
The population census was conducted in two caves:- C-162 (illustrated in Humphreys 1990) is broadly open to the outside and thus has variable temperature and humidity. The cave receives inflows of water and its contained organic matter after modest rainfall and dries rapidly (Humphreys 1989, 1990, in press). In contrast the larger C-118 (illustrated in Humphreys, Adams & Vine 1989) opens to the surface through a narrow tunnel and in consequence dries very slowly but receives water only once every five years . Both caves contain extensive banks of soil separated by pebble filled gullies which lead to a number of drainage holes (Humphreys 1989, 1990, in press).

Cave environment

The typical troglobitic fauna (*S. vinei* and millipedes) is known from *ca* 20% of caves in Cape Range. Compared with caves lacking troglobitic fauna, those caves with such fauna have higher relative humidities, greater soil water and soil organic carbon content, but do not differ in temperature (Humphreys 1990). Hence, the troglobitic fauna occurs throughout the temperature range (11^{o}K) found in the caves of Cape Range but is restricted to areas of soil water >12% and relative humidity >80%. 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 (Humphreys 1990).

The millipedes may be found in the daylight part of caves (e.g. C-162) and even outside entrances in daylight if the humidity is sufficiently high as a result of outflow (e.g. C-222) or condensation

Figure 2: The location of Cape Range on the North West Cape peninsula and the distribution of caves and caves with millipedes. Cape Range encompasses all the outcropping Tulk Limestone (dashed lines) in which the caves containing troglobites are found; the one cave outside this area is also in Tulki Limestone but it is superficially covered by other deposits. The points denote caves from which millipedes have been recorded; the open points being the locations of samples used for the allozyme study. The solid lines across the range denote the boundaries between the three major subregions as indicated by the electrophoretic work. The sympatric populations occur in cave C-111 at the extreme north- west of the distribution.



of water from outflowing air (e.g. C-15). However, they have never been trapped even 5 m from cave entrances as part of the epigean fauna. In the caves they are mostly found wondering on bare mud-banks, piles of organic detritus or, in large numbers, on algae supported by the condensation of water from outflowing air (e.g. C-15).

Population size

The estimated population densities for millipedes are given in Table 1 and the pertinent posterior distributions and the cumulative posterior distributions (probabilities) against population size are given in Figure 3.

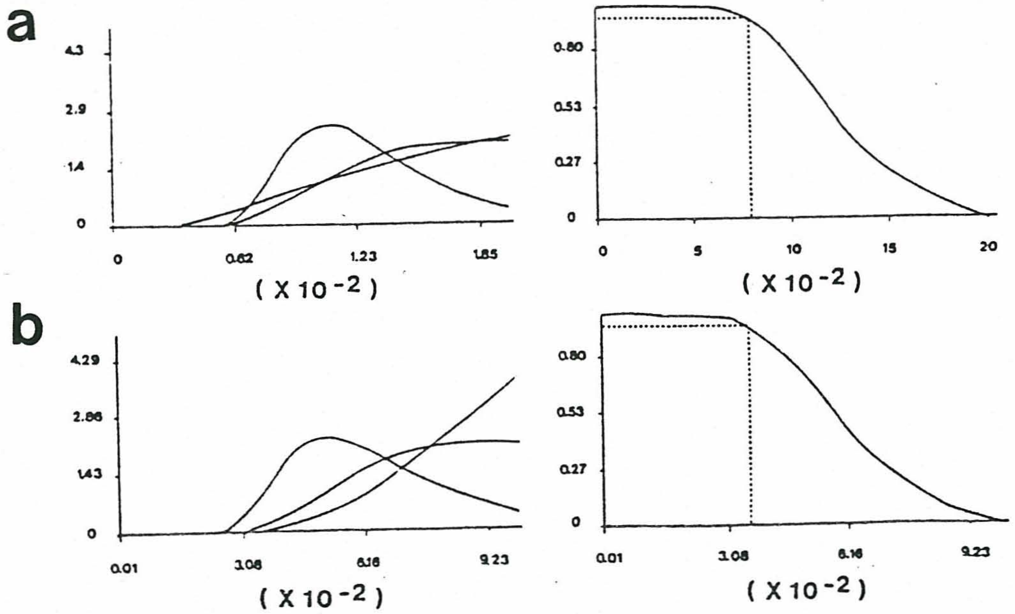
Table 1: Population size estimates from mark release recapture experiments on millipedes > 9 mm total length from two caves in Cape Range.

Cave	Population estimates:-		
	Mean	Median	Minimum[1]
C-118	123	990-1011	767
C-162	184	496-506	136

[1] This is the minimum population size estimated with 95% confidence using Bayes algorithm.

There were visually fewer millipedes in C-162 than in C-118 during 1988 and this is reflected in the population estimates. From the view point of conservation the statistic of most interest is the minimum population size with 95% confidence (Fig. 3).

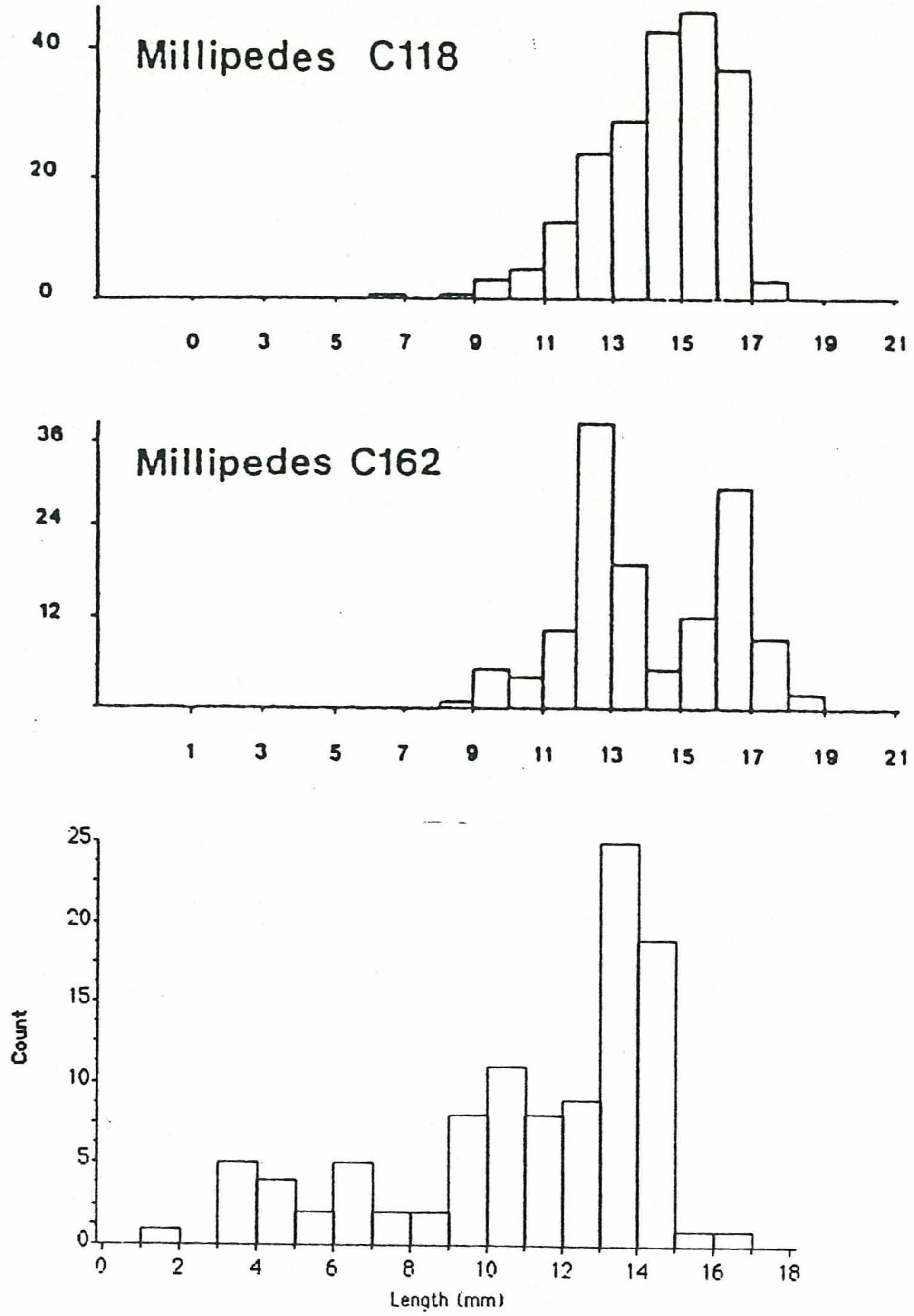
Figure 3: Statistical distributions of the millipede populations derived from the capture-mark-release and recapture data using the Bayes algorithm (see Gazey and Staley 1986). In each row the left figure shows the posterior distribution plotted against population size, while the right figure shows the cumulative posterior distribution (probability) against population size. In the latter figure the dotted line shows the minimum population size estimated with 95% confidence. a) Cave C-118; b)Cave C-162.



Size class structure

As is the case with *S. vinei* (Humphreys 1989, 1990), the millipedes in long unflooded caves are dominated by the larger size classes and thus have a unimodal population structure (C-118: Fig. 4). In caves recently reactivated by flooding the millipedes start to breed and cohorts of smaller (assumed to be younger) individuals pass through the population (C-162: Figs. 4 & 5) It has been demonstrated experimentally that water and surface organic matter are the prime factors in the establishment of the millipede populations (Humphreys in press).

Figure 4: Size class frequency distribution (total length, mm) of millipedes in mid-1988:- a) in cave C-118 (n=205); b) in cave C-162 (n= 134); c) in C-118 at the end of the experiment to re-establish troglobite populations within the cave (Humphreys in press).



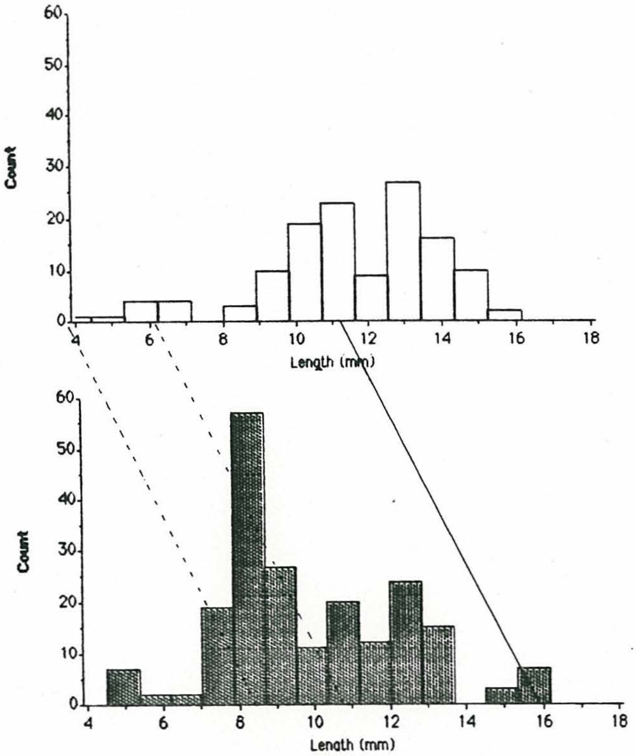
Growth rate

There is no direct evidence of the growth rate of the millipedes but several lines of evidence suggest that they grow rapidly in reponse to favourable conditions.

Of millipedes bred in the laboratory the smallest individual seen on the surface was 4 mm in length, compared with the smallest seen in a cave of 3.5 mm. Hence, as with the schizomids (Humphreys, Adams & Vine 1989), it would appear that the entire size range of surface active millipedes was sampled in the caves. Laboratory observations show that the young millipedes remain grouped in a cell within the soil for some time while they grow.

Examination of the population structure in C-15 in mid July 1989 following 107 mm of rain in May and June of that year (the heaviest rainfall for 38 months). The population was examined again in early September (Fig. 5). Three cohorts present in the initial sample are tentatively identifiable in the later sample. Joining the cohorts parsimoniously indicates growth rates between 0.03 and 0.05 mm d^{-1}.

Figure 5: Changes in the size class frequency distributions of millipedes in C-15 over a period of seven weeks (upper = 16th July, n= 129; lower = 3rd September 1989, n=206). The diagonal lines between the histograms are the forward (__) and backward (......) extrapolations of the maxima by the mean growth rate in the laboratory (Table 2) to show the expected outcome and origin respectively of the cohorts.

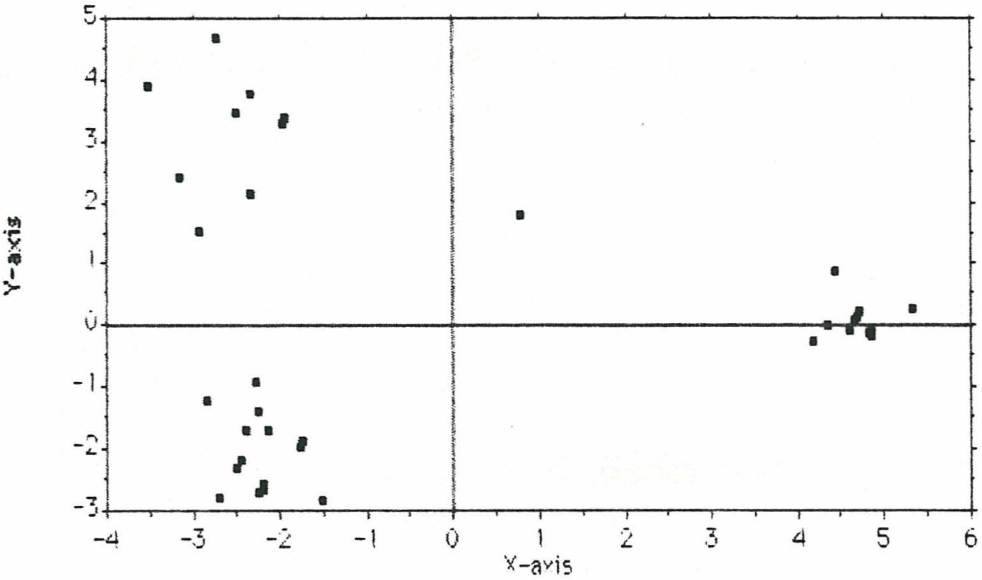


However, data from the laboratory suggest that growth rates may be twice this value (Table 2) in which case the cohorts in Fig. 5 have moved across much further in the time interval between measurements. This faster growth rate is supported by the dominant 8 mm cohort in the September sample, a large cohort absent in the July sample and presumably representing emergence of young from the soil cells at about 3.5 mm length.

Table 2: Mean growth rate of millipedes in the laboratory over 67 days. The determinations were done in batches owing to the difficulty of maintaining millipedes in the laboratory.

Initial length mm	S.D.	N	Final length mm	S.D.	N	Growth rate mm d^{-1}
3.72	0.55	16	10.67	2.02	3	0.10
7.33	0.97	9	13.17	0.29	3	0.09

Figure 6: Plot of the Principal coordinates based on % fixed differences matrix.



Hence several lines of evidence from both the field and the laboratory are consistent with the faster growth. Thus, the evidence indicates that the cohorts should be connected in the manner shown of Fig. 5. These growth rates are very high and quite unlike the highly **k**-selected fauna expected in caves. It would appear that the millipedes are opportunistic (' **r**-strategists'), holding on in deeper refugia until conditions become more widely suitable for them, and then undergoing rapid growth and breeding in the newly but temporarily favourable sites.

Genetics

In this paper we only present the results appropriate to the systematics of the millipedes; a detailed analysis of the millipede genetics will be presented elsewhere. It is not appropriate to infer phylogenetic relationships from the measures of genetic distance used (Carpenter 1990).

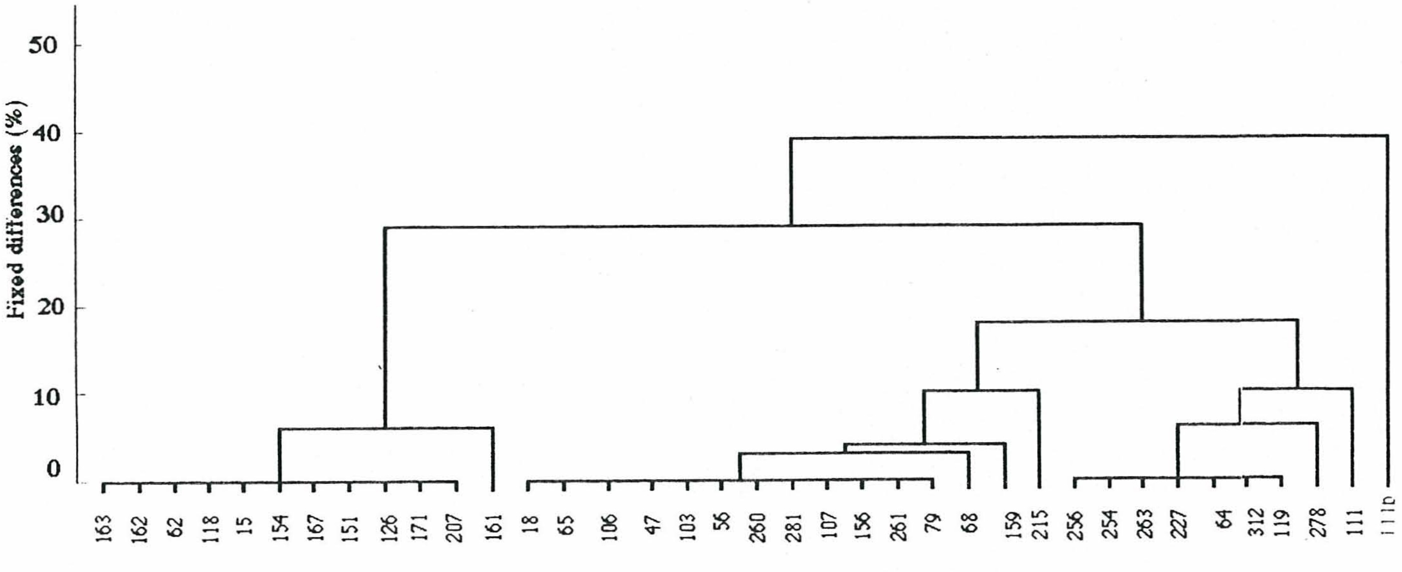
A plot of the pricipal coordinates shows 36 populations from the 35 caves. Two sympatric species occur in cave C-111, one of them having >39% fixed differences from all other populations (Figure 6; Table 3). Three major populations groups occur throughout Cape Range. A moderately variable northern group which includes the other species from C-111. An homogeneous southern group and a very heterogenous central group (Figure 6; Table 3).

Table 3: The fixed differences between the four groups of millipedes in Cape Range

Compare Group:-	Fixed differences > %	Nei's Distance >
South v's central	29	0.42
South v's north	29	0.42
Central v's north	17	0.32
All v's C-111b	39	0.60

As with the amphipods from Cape Range (Humphreys & Adams in press), there is evidence that sibling species may be involved. Each of the three populations is genetically isolated from the other two. Ignoring allele frequency differences, there are at least 17% fixed genetic differences between the three sub-regions Table 3). Such multiple fixed differences indicate that there is no gene flow between any of the sub-regions. The genetic differences observed between sub-regional 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 populations represent sibling species.

Figure 7: UPGMA dendrogram based on Nei's genetic distance between populations of millipedes in caves.



DISCUSSION

For troglobites the population densities of the millipedes is high but, from visual assessment, they 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 and, thus, are more typical of troglobite populations. The most conspicuous of these is the blind Ctenid spider (nr *Janusia*) which seemed most abundant in C-126 and the highly adapted cockroach *Nocticola flabella* Roth 1991 which has been seen in only 14 caves.

Significance of the Cape Range fauna

Despite the very limited amount of work which has been conducted there Cape Range already is known to be very rich in troglobitic species having at least 17 species. In contrast *c.* 12 species of troglobites are known from the entire and relatively well worked Nullarbor karst region of southern Australia, 24 species in larva tubes in wet tropical Australia (Bayliss Cave) and 24 species on the well worked and species rich Hawaii I. where many of the species have close epigean relatives (Howarth 1987).

The following 17 taxa are definite troglobites:- *Schizomus vinei* Harvey 1988 (Chelicerata: Schizomida), Ctenidae (Araneae), Mysmenidae (Araneae), Anapidae (Araneae), Linyphiidae (Araneae: M.R. Gray, pers. comm.), Nemobiinae (Orthoptera: > 1 spp.), *Nocticola flabella* Roth 1991 (Blattodea), Amphipods (1+ spp.), *Mecyclothorax* sp. (Coleoptera: Psydritae), *Beddelundia* sp. (Isopoda: Armadillidae), *Australophiloscia* sp. (Isopoda: Philosciidae: H. Dalens, pers. comm.), Pseudoscorpionida (6 species: Harvey, in ms a).

A large number of other invertebrates are found whose association with the caves is largely unknown but many are clearly relicts of a wetter climate; these include siphonophorid millipedes, many isopod species and carab beetles. Most species await formal taxonomic description.

As shown below a section of the troglobitic fauna is clearly derived from a humid tropical forest litter fauna and provides the only evidence of such vegetation in Cape Range since the Miocene. The region is now separated by the Great Sandy Desert and more than 1600 km from the closest possible source area.

The cave fauna of Cape Range has mixed affinities but clearly has a large wet tropical forest element. *Pseudopeas interioris* Tate 1894 (Mollusca: Subulinidae) is normally found in rainforest litter (A. Solem, pers. comm. 1989). Several species of Diplopoda all have clear wet tropical forest affinities (W.A. Shear, pers. comm.). The genus *Ideoblothrus* (Chelicerata: Pseudoscorpionida) is found in rainforests while *Tyrannochthonius* spp. (Chelicerata: Pseudoscorpionida) have tropical and sub-tropical affinities; a new hyid genus (Chelicerata: Pseudoscorpionida) belongs to a family found only in rainforest patches (Kimberley, India and Madagascar) (M.S. Harvey; in ms b). Schizomida are primarily confined to the tropical and sub-tropical regions of the world. *Nesticella* (Araneae: Nesticidae) and the Ctenidae (Araneae) are clear indications of tropical faunal relationships and both have close relatives in North Queensland (Undarra Caves; M. R. Gray, pers. comm.). *Nocticola flabella* Roth 1991 (Blattodea) has affinities with species in north-east Queensland (Roth 1991). *Lecanomerus* sp. (Coleoptera: Carabidae: Harpalitae), *Mecyclothorax* sp. and *Craspedophorus* sp. (Coleoptera: Carabidae: Panagaeitae) clearly have affinities with wet forest faunae, though not necessarily tropical ones (B.P. Moore; pers. comm. 1989).

Origins of cave faunae

It has been argued that the effects of Pleistocene glaciation, considered to have played an important role in the evolution of north temperate troglobite populations (Barr 1973; Peck 1981; Culver 1982; Delay *et al.* 1980), are not applicable to lowland tropical areas (Howarth 1987), such as Cape Range. However, the parsimonious explanation for the rich troglobitic fauna of Cape Range is that the caves are refugia from the now semi-arid conditions on Cape Range. Hence the model for isolation is similar to the north temperate model, with aridity rather than glaciation being the isolating mechanism.

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Appendix G

Conservation and Management

The status of the fauna and of the caves

Cave exploration in the area is quite recent and, except for the two expeditions (1988 and 1989), has never been intense. As a result most of the caves are in pristine condition and most are likely to remain so because few have spectacular decoration, many are small and many are remote. Few caves are used as tourist caves (C-4) although this usage could expand rapidly.

Only one of the caves is protected physically (C-163) and it was gated at the base of the doline by private initiative (Appendix A 12). Nonetheless, this cave has received an unacceptable level of rubbish (Appendix A 19), partly through inadvertent loss of items in this difficult cave. The remaining caves in Cape Range are unprotected other than by virtue of many being within Cape Range National Park. However, the caves are remote from the sphere of operation of management personnel and are effectively unprotected. In the past several caves were filled in as dangerous or as refuse sites.

Whilst the caves are not physically spectacular by comparison, for example, with those of Tasmania, Cape Range does contain the only predominantly vertical caving area in Western Australia. In consequence use of the area by cavers of all persuasions will gradually expand. Intense caving will focus on the most spectacular deep caves of easy access.

Should pressure on the area increase substantially some direct management may be required, mainly restricting easy access to the area. This can be readily achieved for much of the area by controlling access to the few tracks (other than Charles Knife Road and Shothole Canyon road) giving access to the cave area. Such restriction of vehicular access will dissuade all but the most determined cavers thus relieving pressure on the caves.

Management implications

The information presented here represents the early stages in understanding the Cape Range karst and the adjacent, but unrelated, coastal plains. It is the first major karst area in Australia, and perhaps the world, where the majority of caves have been found and explored as an integrated program of assessment and scientific exploration. In addition, it is the first area for which a considerable body of background information has been assembled prior to the area becoming generally utilized. Indeed, so little caving had been done in the area that the only mention of caves in the Management Plan for Cape Range National Park is in reference to vertebrate fossils (CALM 1987).

For reasons discussed fully elsewhere (Humphreys 1989), general management of the area should follow the sensible practices normally conducted in conservation areas:- prevent degradation of the vegetation, limit sediment transport and do not change the surface drainage patterns as even modest changes may seriously affect caves. Ideally caves should not be physically obliterated by infilling (refuse tip) or by removal (quarrying).

However, management of karst areas has special requirements which lie beyond the scope of this work (Ford & Williams 1989). The connectance of the caves and the general permeability of the landscape means that water flows on the surface only after exceptional rainfall, the remainder percolating through the limestone. Hence, the effects of siltation or pollution can spread widely and rapidly through the karst area; this process is both directed and facilitated by any major connections between caves owing to the mass flow they permit.

In Cape Range the genetic evidence suggests that there are three independent areas for both the terrestrial and aquatic components of the fauna, that areas can and should be managed independently, and that all three areas need to be maintained to sustain the very great genetic diversity of the area.

Nonetheless, the three areas may require different management philosophies. The southern area is much more genetically homogeneous than the other areas and the greatest genetic diversity is in the central area where the caves, despite their close proximity, are well isolated from each other. One can predict that extinction of the populations in one cave in the southern region would be followed by relatively rapid repopulation, whereas the elimination of a local population in the central region may be permanent.

The troglobitic fauna alone warrants the enactment of the proposed extensions (CALM 1987) to Cape Range National Park. However, the proposed extensions do not encompass some of the most important caves in Cape Range (e.g. C-111 and C-222). Extensions should be implemented to the north to encompass the entire outcropping Tulki Limestone (see Front Cover). This report provides the evidence required to justify a rare opportunity to include an entire natural unit within a national park.

The alignment of the proposed road across Cape Range (CALM 1987) between Shot Hole Canyon and Milyering should be reconsidered as it traverses the boundary between the northern and central genetic areas. Hence, any adverse effects will impinge on two distinct faunistic areas.

All works projects within the outcropping Tulki Limestone (as defined in Condon, Johnstone, Perry & Crespin, 1955) or which penetrate the Tulki Limestone, should be undertaken only following a biospeleological survey and, if excavation works or drilling are included, this consultation should continue during the progress of the work.

Every effort should be made to maintain the integrity of the genetical provinces, both as a means of maintaining the genetic diversity of the area and for its scientific value in understanding cave adaptation, speciation and population biology. To this end no animals should be transferred between caves. The chance of cavers accidentally transferring animals between caves is remote as rarely do they work within two fauna areas during one day owing to their physical separation. However, should the ease of access to the range be improved, such as the proposed cross-range road, then such incidents would markedly increase even if the intensity of caving were to stay constant.

Conservation value of the area

Caves of special significance or requiring special consideration.

Of a series of unspectacular small caves and rock shelters close to the Exmouth town site (C-218 to C-225), Loop Cave (C-222) is of special significance. This was clearly a stream passage now cut through by the valley. The cave is nowhere totally dark yet it has populations of troglobites right to the entrance on small wet patches of soil. These include millipedes and a pseudoscorpion (*Austrochthonius* sp.). In addition a number of non-troglobitic animals have been found in the drier areas of the cave:- *Gastrotheus* sp. (Thysanura: Nicoletiidae: Atelurinae), *Metistete* sp. (Coleoptera: Tenebrionidae), Isopoda, Heteroptera, epigean millipedes, ant lions (Neuroptera: Myrmeleontidae), Araneae, Collembola, Isoptera and Diptera.

This cave is a good example of the unspectacular cave that barely warrants the title of 'cave' and yet is one of the more important caves in Cape Range. It contains species that are considerable outliers from their main distribution and which show morphological differences. It is very vulnerable owing to its location close to Exmouth Townsite, ease of access (it is a walk-in cave) and small size. In addition it is likely to be biologically active (*sensu* Humphreys in press) only after sustained heavy rainfall.

Hence, it is imperative that all caves should be properly surveyed and tagged by a biospeleologist prior to any development work in this or any other karst area. Although they may not at the time contain fauna, a wetter period may reveal a significant troglobitic fauna as was the case in C-222. For this reason two shallow caves (C-346 and C-347) were tagged adjacent to a proposed quarry (Appendix A 4); the quarry site was subsequently relocated for aesthetic reasons (Environmental Protection Authority 1991).

Breakdown Maze (C-111), an unspectacular cave near the western coastal plain, is the only cave in Cape Range known to contain two sympatric species of troglobitic millipedes. In addition it contains an undescribed species of troglobitic pseudoscorpion (*Tyrannochthonius* sp.), Isopoda, Pholcidae (Araneae), epigean millipedes, Blattodea, Orthoptera, Oligochaeta and Heteroptera.

Cave C-215 is the only cave that contains elements of the Cape Range fauna (millipedes) and the coastal subterranean fauna (the Blind Gudgeon, *Milyeringa veritas*). The millipedes can be found feeding on mud-banks within a few cm of the gudgeons. To date there is no evidence that the millipedes have generally invaded the coastal habitat although there seems to be no *a priori* reason why they should not do so.

Locations of special significance

Areas

1. Cape Range contains two troglobitic communities, one terrestrial and one aquatic. The former is very rich and contains the only evidence that the area was once occupied by wet tropical forest.

2. The coastal plain of the North West Cape peninsula is inhabited by a subterranean aquatic fauna (troglobitic) which contains the entire known vertebrate troglobite fauna of Australia.

3. Most of the caves in Cape Range, and many of those known to contain troglobites, lie within Cape Range National Park or in the proposed southern and eastern extension.

4. Many of the caves in Cape Range, including those known to contain troglobites, lie within the temporary limestone reserve (TR5980H), under the control of the Minister for Mines. The Mines Act is senior to the CALM Act.

5. Most of the range of the coastal subterranean aquatic fauna lies outside the current or proposed boundaries of Cape Range National Park, on pastural property, defence establishment land and the Exmouth town site. A marina is proposed which will bisect the known range of this fauna. None of the species in this system is specifically or generally protected by legislation.

6. Cape Range National Park is on the Register of the National Estate, together with the adjoining Ningaloo Marine Park.

7. Some caves, especially C-118 and C-162 are sites of special scientific importance owing to the work that has been conducted in them (Humphreys, 1989, 1990, 1991a, 1991c; Humphreys, Adams & Vine. 1989; Humphreys & Collis. 1990; Vine , Knott & Humphreys . 1988).

Biological Type Localities

1. C-24 (Milyering Well): 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).

2. C-26 (Tantabiddi Well): 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 (C-27) in 1973. Since then it has been seen only twice, both time south of the proposed Exmouth Marine:- in C-105 on 29 May 1988 (M. East; pers. comm.) and in Mowbowra Well (C-361) on 10 September 1989 (B. Vine; pers. comm.).

3. C-25 (Kudumurra Well): type locality of *Stygiocaris lancifera* Holthuis (Crustacea: Decapoda) (Holthuis 1960).

4. C-25 (Kudumurra Well): type locality of *Stygiocaris stylifera* Holthius (Crustacea: Decapoda) (Holthuis 1960).

5. C-106 (Shot Pot): type locality of *Schizomus vinei* Harvey 1988 (Chelicerata: Schizomida).

6. C-6: type locality of *Austropholochaetella kendricki* Jamieson 1971 (Oligochaeta)(see also Humphreys *et al.* 1989).

7. C-118: type locality of *Nocticola flabella* Roth. (Blattodea), a very highly cave adapted species..

8. C-18: type locality of *Austrochthonius* sp. (Pseudoscorpionida: Chthoniidae) WAM 91/272 (M.S. Harvey, pers. comm.).

9. C-21: type locality of *Tyrannochthonius* sp. (Pseudoscorpionida: Chthoniidae) WAM 91/280 (M.S. Harvey, pers. comm.).

10. C-167: type locality of *Tyrannochthonius* sp. (Pseudoscorpionida: Chthoniidae) WAM 91/275 (M.S. Harvey, pers. comm.).

11. C-15: type locality of *Ideoblothrus* sp. (Pseudoscorpionida: Syarinidae) WAM 91/288 (M.S. Harvey, pers. comm.).

12. C-167: type locality of *Ideoblothrus* sp. (Pseudoscorpionida: Syarinidae) WAM 91/286 (M.S. Harvey, pers. comm.).

13. C-15: type locality of undescribed genus (Pseudoscorpionida: Hyidae) WAM 90/726 (M.S. Harvey, pers. comm.).

14. C-161:type locality of *Trinemura* sp. (Thysanura: Nicoletiidae: Nicoletiinae) (G. Smith, pers. comm.).

15. C-18, C-64, C-103 and C-163 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.

16. An number (>20) of undescribed genera and species, both epigean 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, India and the Americas.

Geological Type Sections

1. Mandu Calcarenite (Cape Range Group): Badjirrajirra Creek - 22° 06S., 114° 02' E).
2. Tulki Limestone (Cape Range Group): Badjirrajirra Creek - 22° 06'S., 114° 03' E).
3. Trealla Limestone (Cape Range Group): Trealla Hill (Mount Lefroy) - 22° 13' S., 114° 00' E).
4. Pilgramunna Formation (Yardie Group): Yardie Creek - 22° 20' S., 113° 49' 30" E.

5. Vlaming Sandstone (Yardie Group): 1 mile SSE of Tulki Well - 22^{o} 06S., 113^{o} 54' E.

Other significant sites

1. C-21 (Monajee):- thylacine bones (*Thylacinus cynocephalus*, Marsupialia: Dasyuridae: Kendrick and Porter 1973).

2. There are significant sites of human occupation in the caves 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).

3. 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 (C-21, Monajee; Kendrick and Porter 1973). Similar shells have been found in C-163 (clearly washed in to where it was found) and there is a number of broken baler shells in the area of C-203, suggesting the doline, now very dry, was once a source of water. A rock shelter at C-193 has a blackened roof and was possibly utilized by aboriginal people.

4. Bats (Chiroptera) do not commonly enter vertical caves such as those found in Cape Range. Bats have been seen but not collected in C-192, C-194, C-200. Webb (1981) saw two species in C-64. Several species have been identified from bone material in caves, namely *Chalinolobus gouldii, Eptesicus finlaysoni, Tadarida australis, Taphozous georgianus* and *Pteropus scapulatus.*

5. 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 C-144). The cave deposits have led to significant extensions of the known range of some species of recent mammals (see above).

6. 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 C-18, C-103, C-106 and C-118, and in the speleothems.

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

8. Those caves containing standing water (C-18, C-64, C-103 and C-163) are significant sites for the sampling of deep water bodies within Cape Range for assessment of the nature of the water bodies.

9. 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).

Appendix H

The cave fauna

This report represents the state of knowledge at the start of 1991 and is much as reported in Humphreys (1991b). Many taxa currently are being described or examined by systematists.

The 1988 field work was funded under the Australian National Parks and Wildlife Service Consultancy Program. The 1989 field work was funded by the Australian Heritage Commission and the Western Australian Heritage Committee.

Appendix H 2

The 1989 field season resulted in a massive increase in the number of caves in Cape Range known to contain troglobites and other cave inhabiting fauna, and in their geographical extent. I present here an annotated list of specimens on which some taxonomic progress has been made. The remaining material is recorded in the data base and much of the material is with specialists world wide.

Annelida

Austropholochaetella kendricki Jamieson 1971 is widely distributed in cave soils.

Mollusca

The identifications of the non-Camaeinidae are tentative; most species are endemic to the Cape Range peninsula (S.M. Slack-Smith, pers. comm. 1988). *Pupoides* sp. (Pupillidae) may prove to be an endemic species to the North West Cape peninsula (S.M. Slack-Smith, pers. comm. 1988). *Pseudopeas interioris* Tate 1894 (Subulinidae) is normally found in rainforest litter. The Camaeinidae are all restricted endemics to Cape Range (A. Solem, pers. comm. 1989).

Biogeographically the Sinumeloninae occur from the North West Cape peninsula, 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.). *Rhagada* sp. nov. is restricted to North West Cape. Biogeographically *Rhagada* extends from Mitchell Plateau in the Kimberley District (monsoonal tropics) to Shark Bay, south of Cape Range; *ca* 25 species are known (A. Solem, pers. comm. 1989.). *Quistrachia* sp.nov. is restricted to the North West Cape peninsula; *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

The two species of *Stygiocaris* have been confirmed using allozyme electrophoresis and they conform with the taxonomy of Holthuis (1960); their distribution has been extended considerably and may have changed (Appendix C).

Amphipoda

Undescribed species of marine origin and part of the *Victoriapisa* complex (Gammaridae; B. Knott; pers.comm. 1988). Allozyme electrophoresis indicates that there is no gene flow between the four 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 (Appendix C).

Isopoda

One of four undescribed species in the genus *Beddelundia* (Armadillidae) collected from caves has clear adaptations to cave life (H. Dalens, pers. comm. 1989) and one other *Beddelundia* sp. is found also outside caves.

One of two undescribed species of Philosciidae collected in caves is troglobitic while the second species (*Australophiloscia* sp.) has a wide distribution outside caves.

Diplopoda

The widespread cave millipede 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). Craspedosomida is a family found in rainforest of eastern Australia and is probably a relict rainforest species.

Chelicerata

Pseudoscorpionida

Two undescribed species of *Ideoblothrus* (Syarinidae) are known from Cape Range. The family Syarinidae have not previously been described from Australia although two genera including *Ideoblothrus* are found in rainforests of eastern Queensland and there is an undescribed genus in Tasmanian temperate rainforest (M.S. Harvey; pers. comm. 1991). All members of the genus lack eyes.

Two undescribed species of troglobitic *Tyrannochthonius* (Chthoniidae) are known from Cape Range. *Tyrannochthonius* is a common genus in tropical and sub-tropical areas and two cave dwelling species previously described from Australia (M.S. Harvey; pers. comm. 1991).

One undescribed species of *Austrochthonius* (Chthoniidae) has some modification for cave existence; it has lost the posterior eyes and has reduced anterior eyes. *Austrochthonius* have been collected throughout Australia and members of the genus not commonly troglobitic.

The undescribed genus of the family Hyidae required a complete revision of the family (M.S. Harvey; pers. comm. 1991).

The affinities of the Cape Range pseudoscorpions are diverse and are discussed elsewhere (M.S. Harvey, pers. comm. 1991). The new hyid genus found only in rainforest patches (Kimberley, India and Madagascar). *Ideoblothrus* found on tropical rainforests of Africa, Asia, the Americas and eastern Australia but not in the Kimberley.

The affinities of *Austrochthonius* are uncertain other than that they are a Gondwanan element. *Tyrannochthonius* species are widespread in the temperate and tropical zones of the world.

Surface fauna: five epigean pseudoscorpions species are known from Cape Range, none of which have been found in the caves. They include four species of Olpiidae (*Xenolpium* sp,, *Austrohorus* sp., Genus A, Genus B) and *Tyrannochthonius* sp. (Chthoniidae).

Schizomida

At the start of the study in Cape Range the only described species in Australia belonging to the Order Schizomida (Chelicerata) was *Schizomus vinei* Harvey 1988 then known from tiny populations in two caves in Cape Range (Vine, Knott & Humphreys 1988). A recent revision of Australian Schizomida recognises four new genera and 24 new species although none are from caves (M.S. Harvey, pers. comm. 1991). A species of schizomid is known to occur in caves in North East Queensland (M. S. Harvey, pers. comm. 1991).

Araneae

The Desidae (gen. nov.) may prove to be a dictynid near *Callevopthalmus.*

The *Mysmenopsis* sp. (Mysmenidae) is troglobitic. This is the first record of the genus in Australia; previously known only from the Americas. Another genus (*Troglonata*) previously known only from the northern hemisphere has been found in caves from eastern Australia (M. Gray; pers. comm. 1990). Mysmenidae (Araneae): C-141 under overhang in entrance. A family of tiny spiders (*c.* 1 mm long) typical of wet forest; this is the first definite record of the family in W.A.

Nesticella and the Ctenidae are clear indications of tropical faunal relationships; both have close relatives in North Queensland (Undarra Caves). The filistatid is unusual in its large size and relatively long legs (probably not related to cave living).There is a somewhat similar looking species from the Diamantina R., Queensland. *Fosterina* and *Badumna* are widely distributed in Australia and have northern Indo-melanesian relatives, though *Fosterina* also has a New Zealand element. The ?Linyphiid has femoral thorns that suggested *Cyphognatha* but then they are confined to males; the females have them here. The females also lack palpi, perhaps an indication of 'lungless spiders' relationships (M.R. Gray, pers. comms 1989-90).

Theridiidae: Phoroncidinae (tiny): epigean

Liocranidae, *Orthobula* sp. nr entrance of C-171 under *Ficus*.

Insecta
Thysanura

Ateluriins (*Gastrotheus* sp.) are usually associated with ant or termite nests so possibly washed in as happens iat Bungonia in NSW - the family is always eyeless (G. Smith, pers. comm. 14/8/1990). In Cape Range they have not been found outside caves. The genus is found in Australia, Africa, South America and Asia. The whole genus needs to be reworked before descriptions are made (G. Smith, pers. comm. 20/11/1990).

The nicoletins are an undescribed species closely related to *Trinemura novae-hollandiae* Silvestri (described from Perth in 1906). - the family is always eyeless. The species from Cape Range has more spindly legs suggesting slight cave adaptation (G. Smith, pers. comm. 14/8/1990). The species is being described by G. Smith.

Acrotelsella spp. are also found in litter on the surface. An undescribed genus of Lepismatidae has been found in litter on the surface but not in any cave. The Nicoletiidae have not been found outside caves. *Heterolepisma* spp. has been found only in litter on the surface and not in caves.

Blattodea

Nocticola flabella Roth 1991 is the only described member of the genus that is troglobitic. There are three species of *Nocticola* in north-east Queensland including one undescribed epigean species.

Type locality C-118. Known from :- C-15, C-64, C-78, C-103, C-104, C-118, C-126, C-154, C-160, C-167, C-169, C-179, C-256 and C-263.

Orthoptera

The unknown cricket (Nemobiinae) is troglobitic, being eyeless.

Hemiptera
Heteroptera

Centrogonus sp. (Reduviidae: Reduviinae) appears to be the same species collected in Chillagoe Caves, Queensland. *Ploiaria* sp. (Reduviidae: Emersinae) is similar to species from Chillagoe Caves, Queensland. *Poecilosphodrus* sp. nov. (Reduviidae: Harpactorinae) is to be described (M. Malipatil; pers. comm. 1988-89).

Coleoptera

Lecanomerus sp. (Harpalitae) has fully developed hindwings and is 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).

Mecyclothorax sp. (Psydritae) 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).

Species in the genus *Craspedophorus* sp. (Panagaeitae) 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 King Sound, north-west of Western Australia (B.P. Moore; pers. comm. 1989).

The affinities of *Lecanomerus* sp., *Mecyclothorax* sp. and *Craspedophorus* sp. 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).

Tenebrionidae: a new genus of the tribe Ectychini which is largely endemic to Western Australia; it contains two other genera and *c.* ten species, none of which are from caves (E. Matthews, pers. comm. 1990).

Brises sp. nov. closer to *B. katherinae* of the Northern Territory than to *B. occidentalis* which occurs in nearby caves in the Murchison District (Matthews 1986). Since 1986 three more species of *Brises* have been found; none of the known species are from caves in non-arid areas (E. Matthews, pers. comm. 1991).

Tenebrionidae from Cape Range caves, Western Australia.

Eric G. Matthews (South Australian Museum)

The 11 specimens collected in June, July and August 1989 comprise five specimens of the genus *Brises* Pascoe, four of an undescribed genus of Ectychini, one *Mesomorphus* sp. and one *Metistete* sp. The last two are probably adventitious, as they belong to widespread genera not known to live in caves, and they will not be further discussed here.

The *Brises* represent two undescribed species. One, which will be designated species C, is represented by two males, field ID 3127 and 3130, both from cave 200 (22° 13' 26"S 114° 00' 37"E), and one designated species D, represented by three females, ID 3062, 3073, and 3201 from two caves, 161 (22° 12' 33"S 113° 58' 14"E) and 96 (22° 15' 05"S 113° 57' 24"E).

The two forms differ in the surface sculpture of the pronotum and it is unlikely that this difference is sexual, since dimorphism of this sort is unknown in the group. The known species to which C and D bear the closest resemblance is *B. katherinae* Matthews from caves in the Katherine area, N.T.

The most striking difference is seen in the structure of the ovipositor of D (unknown in C), which has terminal coxite lobes drawn out into long points. Such a structure is otherwise unknown in the genus.

Geographically C and D are fairly close to *B. occidentalis* Matthews, known from the Weld Range, Mileura H.S. and Wilgie Mia, but there are no points of resemblance between the Cape Range species and *occidentalis*.

The conclusion is that C and D are closely-related but distinct species showing more resemblance to *katherinae* than to other species of the genus, without being very close to it.

Brises is a genus of 12 species (four undescribed) of the very large autocthonous Australian tribe Heleini, which is very diverse especially in southern and Western Australia. *Brises* is largely confined to the arid zone (see map in Matthews 1986) and in the north and west of its range it is known only from caves. In the south and east it occurs in both caves and mammal burrows, sometimes foraging on the surface.

There are no morphological features of *Brises* which indicate adaptation to cave life. Most species, including the present two, are fully winged, pigmentation is well developed, eyes are only a little smaller than normal, and appendages are not markedly elongate.

A preliminary phylogenetic analysis of the tribe Heleini indicates that *Brises* is the most plesiomorphic genus. This is in contrast to the remaining arid-zone genera, which are the most apomorphic in the tribe. The conclusion is that *Brises* represents an almost unmodified remnant of an original heleine fauna which predates the onset of aridity in the mid-Tertiary, and which has been able to survive *in situ* by taking refuge in caves and burrows. The other arid -zone heleines have had to reinvade secondarily from peripheral areas by evolving extreme adaptations to arid surface conditions.

The known fauna of *Brises* suggests that practically every cave complex in the arid zone has its own species, and that more species remain to be discovered. The genus does not occur in caves substantially outside the arid zone.

The Ectychini are an autocthonous Australian tribe of uncertain affinities not clearly assignable to any sub-family (Doyen *et. al.* 1989). There are 10 species mostly in Western Australia with two of them extending to the Northern Territory and South Australia respectively.

The new genus differs from all other species of the tribe in not showing two characteristic apomorphies of the latter: fossorial forelegs and an excision of the hind angle of the prothorax. Its placement is based mainly on the unique female genital apparatus of the Ectychini, described in Doyen *et. al.* (1989). It is therefore an exceptionally plesiomorphic member of the tribe which, like *Brises*, does not show any notable adaptations to cave life apart from a somewhat reduced level of pigmentation compared to the other species. It is flightless but this is true of all Ectychini. No other members of the tribe are known to occur in caves or burrows.

Chordata
Vertebrata
Pisces

The Blind or Cave Gudgeon, *Milyeringa veritas* Whitley 1945 (Perciformes: Eleotridae) (Whitley 1960) ranges from south of Yardie Creek around North West Cape to the east coast. Allozyme electrophoresis shows that the geological discontinuities at Yardie Creek and Vlaming Head do not constitute genetical barriers to the gudgeons. However, the populations are not panmictic and the crucial areas may lie close to the scarp of Cape Range between the alluvial fans at the mouths of the gorges (Appendix C).

The Blind Cave Eel, *Ophisternon candidum* (Mees 1962)(Synbranchiformes: Synbranchidae) is classified as vulnerable (Michaelis 1985).

These two species of fish comprise the entire troglobitic vertebrate fauna of Australia.

Mammalia

Thirty-two species of modern mammals have been recorded from bones and sub-fossil deposits in caves, namely *Dasyurus hallucatus, Dasycercus cristicauda, Phascogale calura, Antechinus rosamondae, Pseudantechinus macdonnellensis, Planigale maculata, Sminthopsis longicaudata, Sminthopsis macroura, Thylacinus cynocephalus, Isoodon 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* and *Pteropus scapulatus* (A. Baynes and B. Jones; pers. comm.).

6. To undertake assessment of the population characteristics (including genetic isolation) of selected caves faunae.

Genetical work on selected species, both troglobitic and epigean, has shown that the deeper gorges, those that cut through the Tulki Limestone into the Mandu Calcarenite below, form barriers to the movement between caves and cave regions (Humphreys 1989 and unpublished). Epigean species are panmictic throughout the area as they are not restricted to the cave and subterranean systems. Troglobitic species are not panmictic throughout Cape Range and there are considerable restrictions in gene flow, much of which is associated with the deep gorges. In essence, there are three genetic areas, one northern, one central and one southern. The boundaries between the sub-regions are respectively Shot Hole Canyon and the gorges around Mount Hollister (Humphreys 1989).

Materials were collected in 1989 and 1990 to examine more fully the genetical boundaries between the sub-regions in Cape Range. In addition collections of the coastal fauna were made to establish a minimum base of information required to plan further work. Only the necessary outline of the results is given here and more detail is presented in Appendices E and F.

Coastal subterranean fauna

The fauna is not panmictic around the peninsula. However, there are no genetical discontinuities associated with the major geological and geomorphological features. There is evidence that the populations do not extend beneath Cape Range. Hence, the coastal fauna is an essentially linear system, the bisection of which will permanently disrupt gene flow within the populations (see full discussion in Appendix C). There is evidence that the water table is changing but there is no effective monitoring of the level and quality of the water bodies either as they impinge on the fauna or on the availability of water for human use. A monitoring protocol should be established pertinent to both the requirements of human usage and the fauna.

Most of the range of this coastal fauna lies outside Cape Range National Park and part of the area is subject to development projects (Environmental Protection Authority 1991). Water is drawn from the system for pastural and town use, both by the Water Authority and from private bores. Hence, the whole system is potentially threatened with fragmentation, by draw down or increased salinity of the water table, and by pollution from sewage and garbage dumps. The quality of the groundwater should be monitored to detect long term trends.

Until the system is better understood the exploitation of the resource, both as a source of water and as an inadvertent repository for waste, should be treated conservatively, as has been the approach of the Environmental Protection Authority (1991) when considering a single development project potentially impinging on this fauna.

Cape Range aquatic fauna

Only four caves in Cape Range are known to have standing fresh water and all contain an amphipod of marine origin (see above). The populations are clearly isolated from each other (Appendix C). The amphipods are the only known aquatic fauna from these caves although other species are likely to be present. Two of the populations are in small pools, one of which (C-18) was eliminated by sedimentation in 1988 but was reformed in 1989, while the other seems stable, if inaccessible, at the end of the long low crawl in C-103 . A third population is in the only known outflow cave (C-64) while the fourth is in the canal system in the longest cave (C-163). The quality of these water bodies is discussed in Appendix C.

Cape Range terrestrial fauna

The millipedes and the Schizomida are the best studied species in Cape Range and details of their biology and genetics are presented elsewhere (Millipedes: Appendix A)(Schizomida: Appendix B; Humphreys,1989, 1990, 1991; Humphreys, Adams & Vine, 1989; Humphreys & Collis, 1990; Vine, Knott & Humphreys, 1988).

The essential characteristics of these populations are as follows. The cave fauna depends on organic matter for its energy source and this is carried into the caves by the run-off after heavy rainfall. In Cape Range, long unflooded caves contain troglobites with old age populations (Humphreys, Adams & Vine 1989; Humphreys 1989, in press) which start to breed after flooding and to more widely occupy the cave *(ibid.)*. Flooding both wets a cave and deposits organic matter within the cave. In Cape Range the troglobitic fauna is associated with both the organic carbon and water contents of the mud-banks within the caves (Humphreys, Adams & Vine 1989). Experimental evidence (Humphreys 1991c) has demonstrated the importance of water and organic matter in the colonisation of uninhabited areas.

There is genetical (see below) and circumstantial evidence that neighbouring caves, most of which are probably entrance less (Curl 1966), are linked at a level below which cavers can reach (Humphreys 1989, 1990). At these levels, relatively devoid of energy, there must occur low populations of the cave animals. When caves are wetted and re-energised by the influx of organic matter, these population move upwards into the newly inhabitable areas and breed (*ibid.*). Until the next influx of water the caves slowly dry and the populations retract and then leave entirely those parts of the cave accessible to cavers.