

BIOLOGICAL RESEARCH INTO THE CAPE RANGE KARST AREA, NORTH WEST CAPE PENINSULA, WESTERN AUSTRALIA.

W.F. Humphreys
Department of Biogeography and Ecology,
Western Australian Museum,
Francis Street, Perth,
Western Australia 6000

Abstract; Over the last three years the Cape Range karst area has emerged as one of the more significant troglobitic areas in Australia. A brief history of speleological research in the area is given together with the geographical setting. A synopsis of the fauna is presented as epitomised by C-118. The geographical range of two of the most abundant troglobitic species, a schizomid and a millipede, was increased from 7 to 10 fold between 1988 and 1989 and are now known from 35 and 52 caves respectively. Speciation between the caves appears to be limited but clear genetical discontinuities occur associated with deep gorges. Some detail is presented about the cave environments especially pertaining to the energy source and the association of the fauna with high humidity caves and soil moisture. The caves vary widely in temperature (11⁰K) and this has profound implications to the drying cycles of the caves. Many caves are dry and/or have high levels of carbon dioxide.

Historical background

Speleological work in Cape Range can be conveniently divided into a number of periods. An Ad Hoc Period (1962 to 1980) when caves were found but often inadequately described or located, the Vine Period (1980 to 1986) when systematic recording of caves commenced, the East Period (1986 -) when intensive exploration began with a number of well equipped and organised workers and the Research Period (1987-), when scientific research started in earnest.

Early expeditions by the Western Australian Museum (1965) and the Western Australian Speleological Group (1968) recorded caves but they were poorly located and not tagged; this is true of many of the early caves. In 1980 Brian Vine, then resident in Exmouth, started to conduct cave exploration in the area, mostly alone, and systematically worked through the old records, authenticated the early records and tagged the caves, in addition he found many new caves in the area and by the time he left Exmouth the index was up to C-119.

Malcolm East inherited the knowledge from Brian Vine in 1986, recruited and trained a number of other local residents, especially Ray Wood and Tom Tomlinson, and set about a major expansion of the knowledge of the caves in Cape Range. By mid-1988 the cave numbers reached C-186.

At this stage two major expeditions undertook a scientific study of the troglobites in the caves. In 1988 funding from the Australian National Parks and Wildlife Service to Bill Humphreys of the Western Australian Museum, permitted Brian Vine and Darren Brooks to spend two months in Cape Range, helping the scientific work and conducting further exploration. By the end of this trip the cave numbers had reached C-210.

In 1989 further funding to Bill Humphreys from the Western Australian Heritage Committee permitted Darren Brooks, Malcolm East, Brian Vine and Ray Wood to spend three months in Cape Range, again helping the scientific work and conducting further exploration. By the end of this trip the cave numbers had reached C-362. As of April 1990 the karst index for Cape Range, Western Australia, included 282 caves, 60 karst features and 11 wells.

During the years a number of publications have dealt with aspects of the cave fauna of the North West Cape peninsula and many more are in preparation (Holthuis 1960; Humphreys 1989, in press a; Humphreys, Adams & Vine 1989; Humphreys, Brooks & Vine 1990; Humphreys & Collis in press; Mees 1962; Knott 1985; Vine, Knott & Humphreys 1988; Whitley 1945).

Regional location and geomorphology.

Cape Range forms the 300 m high spine of North West Cape of Western Australia (Fig. 1) and lies just within the tropics (22° S) in a semi-arid climate. The range is an anticline formed in marine limestones of Miocene age. The caves are formed in Tulki Limestone which overlays Mandu Calcarene and is overlain by Trealla Limestone (details in Vine, Knott & Humphreys 1988, Humphreys, Adams & Vine 1989).

Cook (1962) believed that caves extending to sea level (300 m deep) could occur on Cape Range, with solution pipes in the hard Tulki Limestone connecting below to caverns in the friable Mandu Calcarene, none has yet been found. The change with depth in many caves from vertical solution pipes to horizontal development has

been interpreted as reflecting this transition (Kendrick & Porter 1973) epitomised by C-163 (Wanderer's Delight), the only cave with considerable lateral extent (ca 4 km of passages to date). However, a fossil found there is *Echinolampas westralensis* (Echinoidea: Echinolampadidae) which occurs only in Tulki Limestone. It is a good marker species as different species occur in the Mandu Calcarene below and the Trealla Limestone above (K. J. McNamara; pers. comm. 1989). Hence it seems that all of the known deep caves are in the Tulki Limestone and do not extend into the Mandu Calcarene beneath. Similarly some caves which open into a surface geology of Trealla Limestone are, according to the fossils, developed in the Tulki Limestone below (e.g. C-203 and C-246).

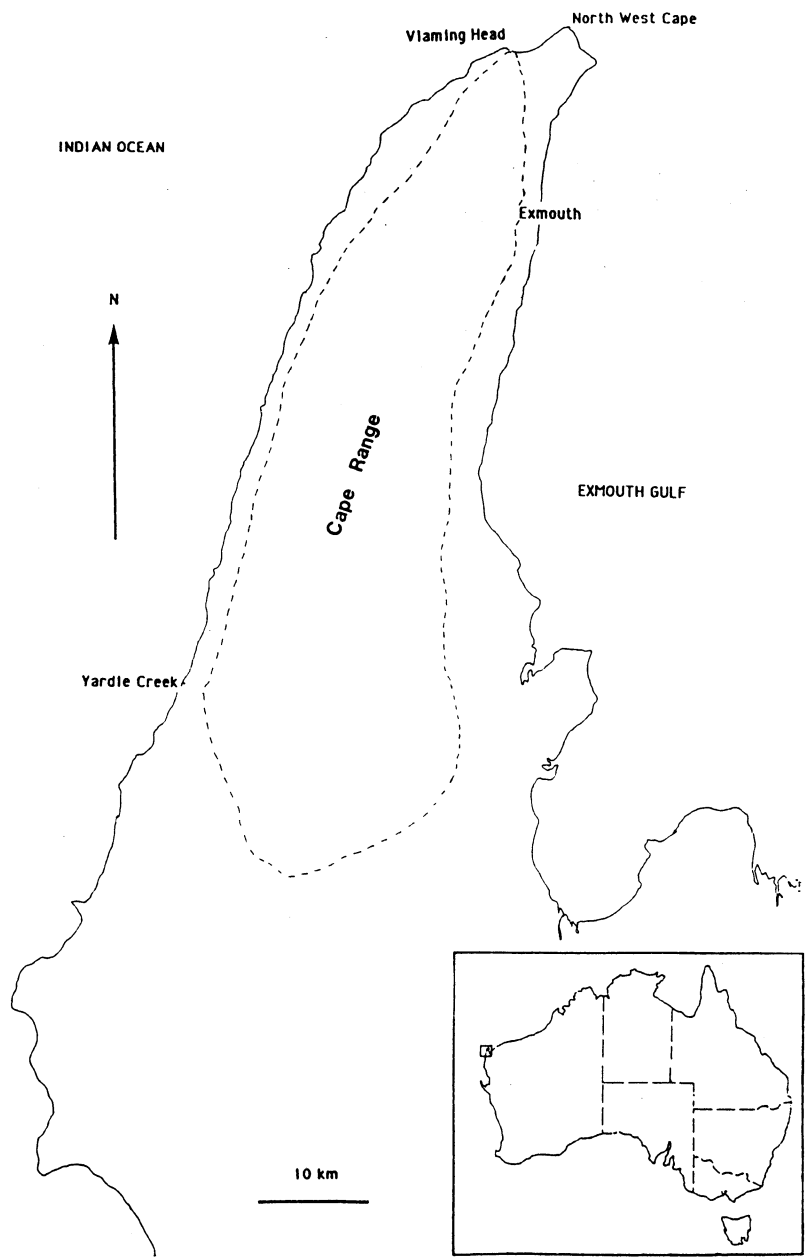


Figure 1: Regional location of Cape Range on North West Cape, Western Australia and the main geomorphological features.

Definitions

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

The categories are based on the level of dependence on the cave system (Hamilton-Smith 1971) deduced from their distribution within and without caves and the degree of morphological adaptation presumed to be adaptive to cave life. Second level troglaphiles may turn out to have clear adaptations to caves in non-morphological characters, e.g. physiological (Barr 1963) or reproductive effort (H. Dalens; Pers. comm. 1989).

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

Cave fauna

Despite the long standing conviction that troglobites were rare both in Australia (Moore 1964; Hamilton-Smith 1967; Barr 1973) and in tropical caves in general (Vandel 1965; Barr 1968, 1973; Mitchell 1970; Sbordoni 1982), rich troglobitic faunae have been found in many tropical areas (Leleup 1968; Howarth 1983), including both wet tropical (Chillagoe in Queensland; Howarth 1988) and semi-arid tropical (Cape Range) Australia (Vine, Knott & Humphreys 1988; Humphreys 1989, in press; Humphreys, Adams & Vine 1989).

The troglobitic fauna of the North West Cape peninsula of Western Australia was initially mentioned in the context of a subterranean freshwater fauna of the coastal plain (Whitley 1945) and later by Cawthorn (1953). 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 *et al.*, 1988; Humphreys, 1989, in press a; Humphreys *et al.*, 1989). The faunae have no taxa in common at the level of Order.

The coastal plain fringing Cape Range which contains a unique subterranean fauna, comprising two species each of fish and of atyid shrimps. These are the Blind or Cave Gudgeon, *Milyeringa veritas* Whitley (Perciformes: Eleotridae) 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, *Anommatophasma candidum* (Mees) (Synbranchiformes: Synbranchidae) described from Tantabiddi Well (C-26). It is classified as vulnerable (Michaelis 1985). The Atydid shrimps *Stygiocaris lancifera* Holthuis and of *S. stylifera* Holthuis (Decapoda: Natantia) were both described from Kudumurra Well (C-25).

The only other aquatic taxa on the peninsula are Amphipoda of marine origin and part of the *Victoriopisa-Eriopisa* complex (Gammaridae; Knott 1985). They occur in each of the four caves known to contain standing water within Cape Range itself, viz. C-18, C-64, C-103 and C-163 (Humphreys 1989, in press; Humphreys, Adams & Vine 1989).

The caves in Cape Range contain a rich, mostly undescribed, troglobitic fauna, in the main representing a relict of a tropical rainforest litter fauna (Humphreys, Adams & Vine 1989; Humphreys 1989, in press), now separated by the Great Sandy Desert and more than 1000 km from the closest possible source area. Much is endemic at the generic level. In addition there are many non-troglobitic species whose association with the caves is unknown due to lack of information on the surface fauna; however, many would probably be unable to survive the present surface climate. This cave fauna has a wide distribution in Cape Range and occurs wherever the Tulki Limestone, in which the caves develop, outcrops.

The fauna includes few as yet described species but the richness of the fauna is evidenced by the known inhabitants of one of the smaller caves. C-118 is small and shallow (23 m; illustrated in Humphreys, Adams & Vine 1989) and is not itself particularly species rich fauna. It includes *Schizomus vinei* Harvey (Chelicerata: Schizomida). A new genus of highly adapted troglobitic millipedes (Diplopoda: Craspedosomida: Paradoxosomatidae). Earthworms (Annelida: Lumbricidae). Mollusca:- n. gen. (Camæinidae: Sinumeloninae); *Strepsitaurus rugus* (Cotton 1953) (Camæinidae: Sinumeloninae); *Quistrachia* n. sp. (Pleurodontidae). Crustacea:- *Buddelundia* n. sp. 1 (Isopoda: Armadillidae), not cave adapted; Philosciidae n. sp. A (Isopoda: Philosciidae), troglobite and several other undescribed species and genera. Chilopoda:- *Allothereuea leseurii* (Scutigermorpha), not cave adapted. Chelicerata:- n. gen. (Araneae: Desidae), depigmented; n. gen. near *Janusia* (Araneae: Ctenidae), troglobite; *Nesticella* n. sp. (Araneae: Nesticidae), depigmented; *Pholcus* sp. (Araneae: Pholcidae), some pigment loss. Collembola:- *Lepidosira* sp. (Entomobryidae). Blattodea:- *Nocticola*

n. sp., highly cave adapted troglobite. Orthoptera:- Nemobiinae: unknown cricket. Hemiptera:- Reduviinae sp. (Heteroptera: Reduviidae); *Stenolemoides* sp. (Emersinae). Coleoptera:- *Clivina* sp. (Carabidae: Clivinini); *Myllocerus* n. sp. (Curculionidae: Polydrosinae); *Mecyclothorax* sp. (Carabidae: Psydritae).

An indication of the early stage of the research in Cape Range can be gained from the fact that between 1988 to 1989 the geographic range extension for the paradoxosomatid millipedes was 7.7 times and for *S. vinei* was 10.6 times and they are now known from 52 and 35 caves respectively.

There are major genetic discontinuities in the fauna associated with the deep gorges which cut through the Tulki Limestone in which the caves have formed, into the Mandu Calcarenite below. Of the species examined in Cape Range the only non-troglobite, an isopod, is panmictic throughout the area, that it interbreeds freely throughout the geographic range examined. The three non-troglobitic species show area of interbreeding separated by geological discontinuities from other areas in which interbreeding occurs. These include the amphipod, the only aquatic species, *S. vinei* and the paradoxosomatid millipedes. While the former two species are considered to represent isolated populations of the same species (Humphreys & Adams, in press), the millipedes show clear genetic and morphological separation and speciation clearly has occurred since isolation.

There is genetical 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, in press). 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.

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). However, it is not clear whether the reactivation of the fauna results from increases in partial pressure of water in the air, from increased soil water, from increase organic matter or from changes in the structural complexity of the substrate.

The cave environments

Cave faunae are generally considered dependent upon allochthonous organic matter carried into caves by streams, surface run-off or by animals, mainly bats (Harris 1970, 1973) and crickets (Norton, Kane & Poulson 1975; Kane, Norton & Poulson 1975; Kane & Poulson 1976).

The caves of Cape Range are mostly dry and have neither substantial cave cricket populations (of great significance in many North American caves :- Norton, Kane & Poulson 1975; Kane, Norton & Poulson 1975; Kane & Poulson 1976), nor bats to import energy into the caves to support troglobitic populations. As such they are dependent for their energy primarily by the influx of organic matter washed into the cave by intermittent run-off associated with heavy rain.

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

Whether a cave floods after a given rainfall depends on the size and nature of its catchment. Some caves flood after little rain (e.g. C-162), while others flood rarely and may not flood for several years and only after >150 mm of rain (e.g. C-118); 25 mm of rain should result in minor inflows into some caves on average every 5.4 months and deep flooding every 56 months (Humphreys, Adams & Vine 1989).

Caves also dry at varying rates according to the characteristics of the cave. Caves with wide openings and/or small size dry rapidly (e.g. C-162), while those with large size and/or narrow openings dry slowly (e.g. C-118). The populations of troglobites are dependent on the influx of organic matter and on the cave humidity and soil water. Hence the presence of fauna in the accessible parts of the caves is a dynamic balance between the probability of inflow into the cave (weather dependent:- low predictability in Cape Range) and the rate of drying of that cave (predictable:- dependent on the physical characteristics of the cave). Hence the caves in Cape Range contain a complex series of troglobite populations expanding and contracting at different rates and on different time scales. The system is quite unlike the classic stable and/or predictable models of caves systems normally encountered in the literature.

In addition the populations of some of the troglobitic species are large. While on the Nullarbor populations are measured in weeks searching per specimen, in Cape Range populations can be measured in number of individuals per hour. In the small caves C-162 and C-118, detailed population work has indicated the presence of thousands of individuals of the species examined (Humphreys, Adams & Vine 1989; Humphreys 1989).

The limited genetic evidence to date suggests that, unlike Chillagoe, there has been little speciation within the karst area, that local caves are connected in areas inaccessible to cavers and that the karst area is separated into genetically distinct population the boundaries of which are related to major geomorphological features. In addition the genetic and geomorphological evidence (bisection of caves by gorges) suggest that the caves were formed and occupied by the troglobites before the major present day landform features (gorges) were formed.

The typical troglotic fauna (*S. vinei* and millipedes) occurs in about 20% of the 282 caves currently known from Cape Range. The caves containing troglotic fauna have higher relative humidities ($G_{adj} = 79.47$ with 1 d.f; $P < 0.001$) than those without the fauna, have more water in the mud ($G_{adj} = 18.15$ with 1 d.f; $P < 0.001$), but do not differ in temperature (Fig. 2: $G_{adj} = 1.22$ with 1 d.f; $P = 0.269$). The troglotic fauna occurs over the entire and very wide temperature range (11°K) found in the caves of Cape Range. However, they are restricted to areas of soil water $>12\%$ (Fig. 2) and relative humidity $>80\%$ (Fig. 2). Above 80% R.H. there is a strong positive correlation between R.H. and the proportion of caves containing troglotic fauna ($r=0.981$; $P<0.05$), such that between 95-100% R.H. all caves contain troglotes (Fig. 2).

Caves temperatures generally are close to the mean annual surface temperature (MAST), which at Learmonth is 27.3°C . However, the temperature in winter of different caves is between 17 and 28°C (Fig. 2). Only three of the caves recorded have temperatures within 2°K of MAST (C-159, C-167 and C-169) and the remainder group into warm caves (C-103, C-96, C-64, C-118, C-157 and C-207) ranging between 23.0°C (C-103) and 24.7°C (C-207) and cool caves (C-107, C-18, C-106, C-126, C-163 and C-162) with temperatures between 18.1°C (C-107) and 21.5°C (C-162).

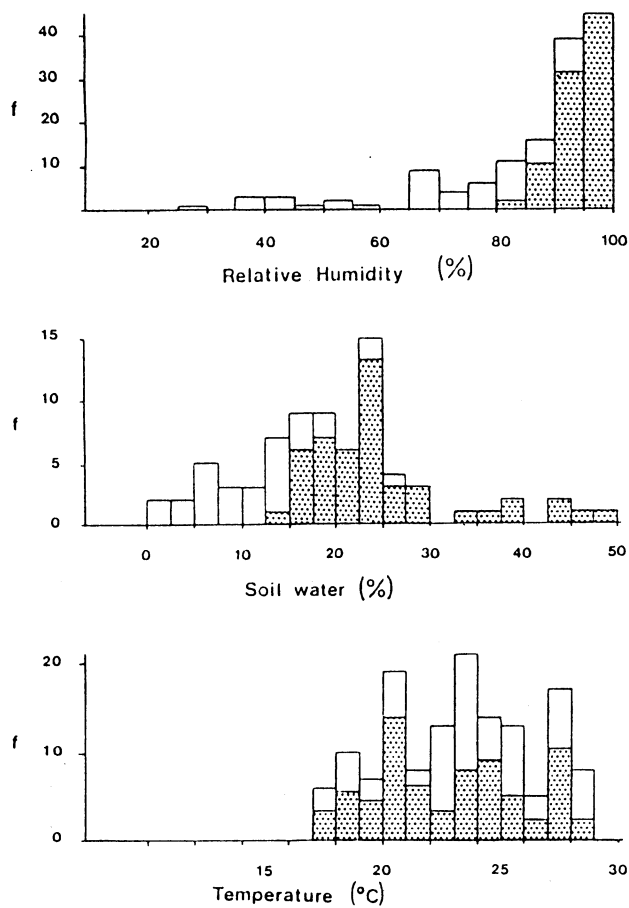


Figure 2: Distribution of relative humidity (upper), soil water content (middle) and dry bulb temperature (lower) in the caves of Cape Range. Shaded area denote the occurrence of troglotes. For relative humidity and temperature ($^{\circ}\text{C}$) $n = 141$. For soil water (% dry weight) the values are the mean of from two to five samples (299 samples); mean sample number = 3.93, s.d. = 0.98; $N=76$.

In Cape Range there is no clear reason why cave temperatures differ; caves with similar characteristics vary widely in temperature:- deep, open caves with long leads (C-18, C-207, C-106 and C-163) vary from 18.4°C (C-18) to 24.7°C (C-207); while deep caves with tight entrances cover the range 20.3°C (C-126) to 25.7°C (C-159). The two caves with considerable lateral extension range from 20.7°C (C-163) to 23.3°C (C-64). Conversely the shallow caves often have temperatures clearly related to the relative size of the opening; wide open caves vary in temperature with outside air temperature (C-162 - 21.5°C), while those with tight entrances are closer to MAST (C-118 - 24.5°C). Geographical location also seems unimportant as caves C-167 and C-163 are only 0.9 km apart but differ in temperature by 6.9 °K.

Examining the two caves (C-118 and C-162) in which the population work was conducted shows that the range of temperatures and humidities in C-162, as expected from its low volume to entrance size ratio (VESR), was much greater in C-162 (see plan in Fig. 2) than in C-118 (Table 1) which has a high VESR. The greater range at the back of C-118 is due to this location being a blind collapse close to the surface (survey point 15 Fig. 1 of Humphreys, Adams & Vine 1989); it is an area of dry soil devoid of fauna.

The range of relative humidity is much greater than previously appreciated (Humphreys, Adams & Vine 1989) in the more open caves due to the minima occurring in the early morning (Fig. 3). The humidities are sufficiently low at night to restrict the movement of the cave fauna and one would expect, therefore, to find diurnal changes in the activity patterns of the fauna. It also means that the animals would most likely be driven deeper into the cave at night, rather than potentially moving to the humid surface; this would further restrict the possibility of above ground dispersion (see discussion in Humphreys, Adams & Vine 1989).

Water vapour movement into and from caves.

While temperature *per se* is unimportant to the distribution of the troglobites in Cape Range (Fig. 3), temperature indirectly can have a major influence on the water vapour pressure in the caves and hence the rate of drying of caves.

The net movement of water between caves and the outside is determined by the gradient in partial pressure of water vapour (Edney 1977). Cape Range is just within the world climatic area in which the average daily range in temperature exceeds the average monthly range (Petterssen 1958). Hence in Cape Range, as in many tropical areas (Howarth 1980), the night time temperatures often fall below the cave temperatures; this results in a net movement of water vapour out of the cave at night (tropical caves containing troglobites usually have R.H. close

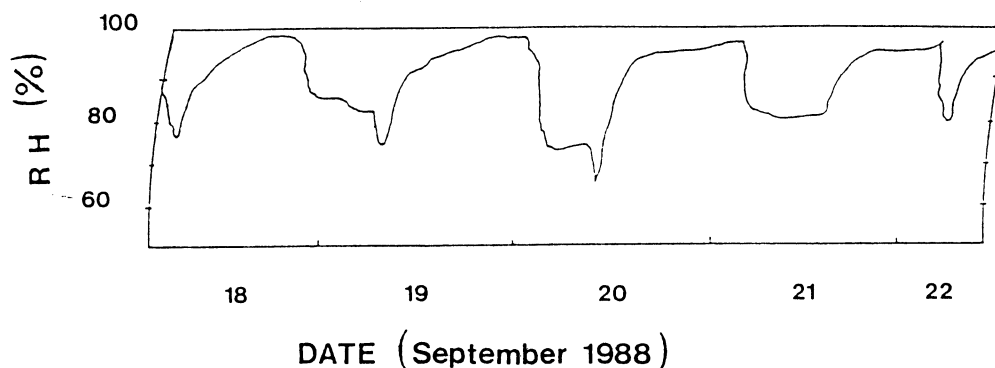


Figure 3: Tracing of the chart from the front thermohydrograph in C-162 for the period 16-20 September 1988. This was the period of most extreme and diurnally synchronised changes in relative humidity. The maximum diurnal change in temperature at this location was ca 3°C.

to 100%). This has been termed the 'tropical winter effect' (Howarth 1980, 1983) by analogy with the excessive drying of caves in colder climates in winter. Hence, all else being equal, warm caves will dry more rapidly and have shorter periods when they are suitable for troglobites. The relevance of this effect will become apparent in the discussion below in relation to the pulses in both the population sizes and the local range of the species in the caves of Cape Range.

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

The mean minimum temperature is below most cave temperatures from April through September in Cape Range and a net loss of water from the caves would be expected at night during these months. The data for August and September support this conjecture (Table 1 and Fig. 4). No data are available for diurnal changes in cave humidities for Cape Range in summer. However, despite cave temperatures being below outside temperatures throughout the day, the low surface humidities would be expected to prevent an influx of water vapour for much of the summer. The expected vapour pressure gradients, determined from meteorological data from the coastal areas of North West Cape, suggest that only the cooler caves would gain water during the height of summer (Fig. 4). However, these mean monthly values are misleading as there was clearly a diurnal change in the direction of the vapour pressure gradient in the caves in September 1988 (Fig. 4; Table 1).

Figure 4: Annual changes in the partial vapour pressure (mbars) of water on North West Cape and the water vapour pressure of caves at various temperatures and humidities. The surface data are for Learmonth and are calculated for the 0900h (solid line and circles) and 1500h (solid line and squares) meteorological readings of temperature and humidity, as well as for the mean monthly maximum

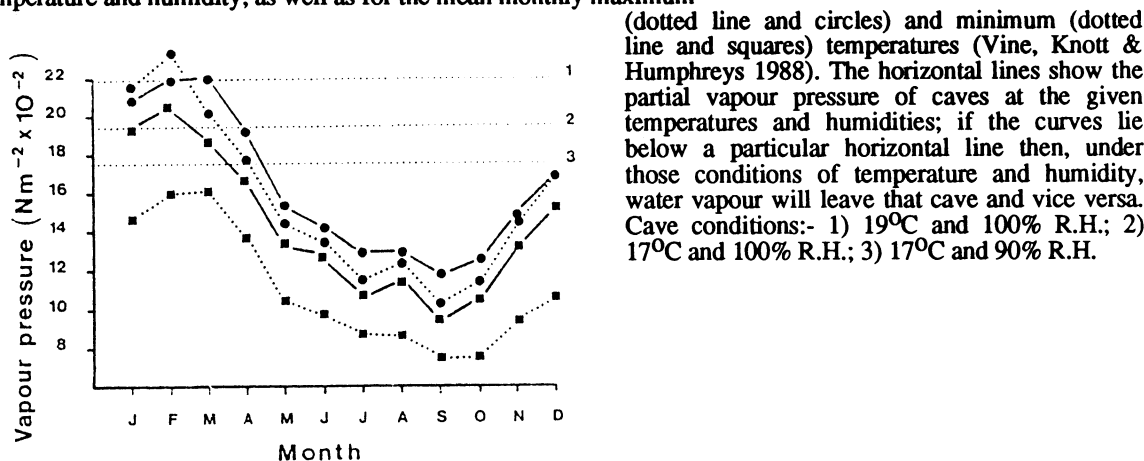


Table 1: The range of temperature and relative humidity recorded in the faunal area closest to the entrance and that in the location furthest from the entrance between 10.8.88 to 22.9.88.

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

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

Carbon dioxide

Many caves in Cape Range contain high levels of CO₂ as indicated by human physiological response (e.g. C-66 and C-69). This is particularly the case after rain, even in shallow caves such as C-118 (M. East; pers. comm. 1988). Sections of caves containing troglobites have levels of CO₂ ranging from 0.06% (C-126) to 0.5% (C-167) with a mean of 0.18% CO₂ (s.d.=0.16, n=7) in cave areas containing troglobites. Because cavers could not sustain entry into some areas of high CO₂ levels (>>8% CO₂; off scale of indicator tube in a vertical lead in C-207), it is not known whether troglobites inhabited such areas as has been reported for a few caves elsewhere. Troglobites survive high CO₂ levels (5.4%; Vandel 1965) and in Bayliss Cave, at Chillagoe in north Queensland, 75% of the 24 species of troglobites occur only in the foul air zone where CO₂ concentrations ranged from 0.6 to 6.0% (Howarth 1988).

Other cave contents

The caves contain significant deposits of fossil and sub-fossil material and much of the knowledge of the

original fauna of the range has come from these deposits (Kendrick & Porter 1973; Humphreys 1988; A. Baynes and B. Jones, pers. comm. 1989).

The only location in Australia of a Pleistocene habitation site representing a maritime economy is located in rock shelters at the foot of Cape Range (Morse 1988). Evidence of aboriginal occupation of Cape Range is widespread through the range itself in the form of baler shells which are sometimes found in caves. However, owing to the vertical nature of most of the caves few overt signs of cave usage by aboriginal people have been found in Cape Range itself.

Conclusions

Despite the little research conducted into the caves of Cape Range it has emerged as one of the most significant karst areas in Australia in terms of fauna. There is a lack of palaeoclimatic information from this region of Australia and the cave fauna is the only evidence that wet forest has covered the area since the Miocene when the limestones in which the caves have formed were deposited. The high degree of cave adaptation of some of the troglobites suggests that the fauna has been isolated in the caves for a long time but there is no reliable dating for a significantly wetter period. Dates (Th/Ur method) from superficial speleothems range from 12500 to 123000 years BP but with wide errors owing to the very low uranium content (D. Smith, pers. comm. 1990).

ACKNOWLEDGMENTS

This work would not have been possible without the unstinting help of a large number of people in a professional and voluntary capacity. In particular I would like to thank the generosity of Dr S. Baseden, Dr A. Baynes, Darren Brooks, Dr H. Dalens, Malcolm East, Dr M. Gray, Dr M. Harvey, Angus Humphreys, Barbara Jones, Ms D. Jones, Dr B. Knott, Dr J. Lawrence, Dr M.B. Malipatil, Dr B. P. Moore, Dr D.C.F. Rentz, Dr L.M. Roth, Dr W.A. Shear, Mrs S.M. Slack-Smith, the late Dr A. Solem, Brian Vine, Julianne Waldock, Ray Wood and Rae Young. Numerous other people have been acknowledged in separate publications.

The Department of Conservation and Land Management permitted work in Cape Range National Park and access to Exmouth Gulf Station is acknowledged from the Lessees. Financial support for various aspects of this work is acknowledged from the Western Australian Museum, the National Heritage Committee and the Australian National Parks and Wildlife Service.

REFERENCES

- Barr, T.C. 1963. Ecological classification of cavernicoles. *Cave Notes* 5: 9-12.
- Barr, T.C. (1968). Cave ecology and evolution of troglobites. *Evolutionary Biology* 2: 35-102.
- Barr, T.C. (1973). Refugees of the Ice Age. *Natural History*, May 1973: 26-35, 72.
- Cawthorn, P. 1953. Discovery of subterranean freshwater fauna on the eastern side of North West Cape. *Western Australian Naturalist* 8: 129-132.
- Colwell, R.K. (1974). Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55: 1148-1153.
- Cook, D. 1962. Caves of the Cape Range, North West Cape, Western Australia. *J. West. Aust. Speleological Group of the West. Aust. Naturalists Club* 1962: 4-11.
- Culver, D.C. (1982). *Cave life: evolution and ecology*. Harvard University Press.
- Curl, R. (1966). Caves as a measure of karst. *Journal of Geology* 74: 798-830.
- Edney, E.B. (1977). *Water balance in land arthropods*. Springer Verlag, Berlin.
- Hamilton-Smith, E. (1967). The arthropoda of Australian caves. *Journal of the Australian Entomological Society* 6: 103-118.
- Hamilton-Smith, E. 1971. The classification of cavernicoles. *National Speleological Society (US) Bull.* 33: 63-66.
- Harris, J.A. (1970). Bat-guano cave environment. *Science, New York*. 169: 1342-1343.
- Harris, J.A. (1973). Structure and dynamics of a cave population of the guano mite *Uroobovella coprophila* (Womersley). *Australian Journal of Zoology* 21: 239-275.
- Holthuis L.B. 1960. Two new species of Atydid shrimps from subterranean waters of N.W. Australia (Decapoda Natantia). *Crustaceana* 1: 47-57.

- Howarth, F.G. (1980). The zoogeography of specialized cave animals: a bioclimatic model. *Evolution* 34: 394-406.
- Howarth, F.G. (1983). Bioclimatic and geological factors governing the evolution and distribution of Hawaiian cave insects. *Entomologia Generalis* 8: 17-26
- Howarth, F.G. (1988). Environmental ecology of north Queensland caves: or why are there so many troglobites in Australia. pp. 76- 84 In Pearson, L (Ed.) 17th biennial conference, Australian Speleological Federation Tropicon Conference, Lake Tinaroo, Far North Queensland. 27-31 Dec. 1988. Australian Speleological Federation, Cairns. 139 pp.
- Humphreys, W.F. (1989). The status of relict cave fauna of Cape Range, Western Australia, especially the Schizomida. Report to the Australian National Parks and Wildlife Service, Canberra. 104 pp.
- Humphreys, W.F. in press. The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. *Acta Zoologica Fennica*.
- Humphreys, W.F., Adams, M. & Vine, B. (1989). The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. *Journal of Zoology, London* 217:177-201.
- Humphreys, W.F., Brooks, R. D. and Vine, B. in press. Rediscovery of the palm *Livistona alfredii* on the North West Cape Peninsula. *Records of the Western Australian Museum*
- Humphreys, W.F. and Collis, G. 1990. Water loss and respiration of cave arthropods from Cape Range, Western Australia. *Comparative Biochemistry and Physiology* 95A: 101-107.
- Kane, T.C., Norton, R.M., & Poulson, T.L. (1975). The ecology of a predaceous troglobitic beetle, *Neaphaenops tellkampffii* (Coleoptera: Carabidae, Trechinae). I. Seasonality of food input and early life history stages. *International Journal of Speleology* 7: 45-54.
- Kane, T.C. & Poulson, T.L. (1976). Foraging by cave beetles: spatial and temporal heterogeneity of prey. *Ecology* 57: 793-800.
- Kendrick, G.W. and Porter, J.K. 1973. Remains of a thylacine (Marsupialia: Dasyuridae) and other fauna from caves in Cape Range, Western Australia. *Journal of the Royal Society of Western Australia* 56: 116-122.
- Knott, B. 1985. Australian aquatic cavernicolous amphipods. *Helictite* 23: 51-55.
- Leleup, N.(1968). Introduction. Mission zoologique belge aux îles Galapagos et en Ecuador(N.et J.Leleup, 1964-1965). Resultats scientifiques. Musee Royal de l'Afrique Centrale. Premier Partie: 9-34. Tervuren, Belgium.
- Mees, G.F. 1962. The subterranean fauna of Yardie Creek station, North West Cape, Western Australia. *Journal of the Royal Society of Western Australia* 45: 24-32.
- Michaelis, F. 1985. Threatened fish. A report on the threatened fish of inland waters of Australia. Report Series No. 3. 45 pp. Australian National Parks and Wildlife Service Canberra.
- Mitchell, R.W. 1970. Total number and density estimates of some species of cavernicoles inhabiting Fern Cave, Texas. *Annales de Speleologie* 25: 73-90. Moore, B.P. (1964). Present-day cave beetle fauna in Australia, a pointer to past climatic change. *Helictite* Oct. 1964, 3-9.
- Morse, K. 1988. Mandu Creek rockshelter: Pleistocene human coastal occupation of North West Cape, Western Australia. *Archaeol. Oceania* 23: 31-88.
- Norton, R.M., Kane, T.C. & Poulson, T.L. (1975). The ecology of a predaceous troglobitic beetle, *Neaphaenops tellkampffii* (Coleoptera: Carabidae, Trechinae). II. Adult seasonality, feeding and recruitment. *International Journal of Speleology* 7: 55-64.
- Petterssen, S. (1958). Introduction to meteorology. McGraw-Hill Book Company, New York.
- Sbordoni, V. (1982). Advances in speciation of cave animals. pp 219-240. In Barrigozzi, C. (Ed.). *Mechanisms of Speciation*. Liss, New York.
- Vandel, A. (1965). *Biospeleology: the biology of cavernicolous animals*. Translated by B. E. Freeman. Pergamon Press, Oxford. Vine, B., Knott, B. & Humphreys, W.F. (1988). Observations on the biology of the cave dwelling *Schizomus vinei* (Chelicerata: Schizomida) in Cape Range, Western Australia. *Records of the Western Australian Museum* 14: 21-34.
- Whitley, G. P. 1945. New sharks and fishes from Western Australia. Part 2. *Australian Zoologist* 11: 35-37.