Acta Zool. Fennica 190:181–186
Helsinki 21 december 1990

ISBN 951-9481-35-4 ISSN 0001-7299

XI International Congress of Arachnology, Turku, Finland, 7–12 August 1989

The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia

W. F. Humphreys

Department of Biogeography and Ecology, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia

In Cape Range, North West Cape peninsula of Western Australia, there are a number of caves containing large populations of *Schizomus vinei* (Schizomidae) amongst a rich troglobitic fauna containing also a number of other arachnids. *S. vinei* occurs only in caves with high humidities and organic carbon content of the soil; together these account for 50% of the variance in their occurrence in caves. They have high rates of water loss and probably can move only between caves that are physically connected below ground. Major landform features (canyons) separate genetically the populations so that only local panmixis occurs. The troglobitic fauna is probably derived from a wet tropical forest litter fauna, although the area is now semi-arid and separated by >1000 km of desert from the closest potential source area.

1. Introduction

Until recently, troglobites were thought to be rare in tropical caves due to the small influence of Pleistocene climatic changes which were considered necessary to eliminate the surface populations of putative troglobites (Vandel 1965, Barr 1968, 1973, Mitchell 1970, Sbordoni 1982). In addition, Australian caves were considered deficient in troglobites (obligate cave dwellers) compared with other continents (Moore 1964, Hamilton-Smith 1967, Barr 1973). Both of these presumptions have proved incorrect and rich troglobitic faunae have been found in many tropical areas (Leleup 1968, Howarth 1983), including both wet tropical (Chillagoe in Queensland, Howarth 1988) and semi-arid tropical (Cape Range) areas in Australia.

This report concerns *Schizomus vinei* Harvey, 1988, which is part of a rich troglobitic fauna in Cape Range on the North West Cape peninsula (22°S) in Western Australia (Vine et al. 1988, Harvey 1988, Humphreys et al. 1989 and unpubl.). The ecosystems depend on allochthonous organic matter carried into caves by runoff; 25 mm of rain should result in minor inflows into some caves on average every 5.4 months and deep flooding every 56 months; however, these inter-

vals have very low predictability as Cape Range is situated in that area of Australia with the least predictable rainfall (Humphreys et al. 1989).

The rich troglobitic fauna in Cape Range includes a minimum of four arachnids, namely two spiders, a pseudoscorpion and *S. vinei*. In addition, there are troglobitic millipedes, several woodlice, cockroaches, carabid beetles and crickets. A large number of other invertebrates are found whose association with the caves is largely unknown but many are clearly relicts from a wetter climate. Most species await formal taxonomic description. 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. It is now separated by the Great Sandy Desert and more than 1000 km from the closest possible source area.

S. vinei has been found in only 11 of the 212 caves known from the North West Cape peninsula; the caves are up to 9.9 km apart and cover 14 km^2 of Cape Range; the troglobitic millipede is more widespread and covers 25 km^2 of the range. A non-troglobitic schizomid has recently been found in vine thickets in the north of Western Australia (B.Y. Main, pers. comm. 1988) and about 12 non-troglobitic species from the Northern Territory and Queensland await description (M. S. Harvey, pers. comm. 1988).

2. Methods

The methods follow Humphreys et al. (1989) with the exception that in addition to *S. vinei*, the numbers of millipedes and isopods were estimated by mark and recapture methods and their allozyme variation determined using cellulose acetate gel electrophoresis.

3. Results and discussion

3.1. Caves

The population census was conducted in caves C-118 and C-162. Cave C-162 (Fig. 1) is broadly open to the outside and contains several large mud banks lying between gulleys draining to a number of drainage holes. In contrast, the larger cave C-118 has only a 1.5 m^2 opening (a map of C-118 is shown in Humphreys et al. 1989: Fig. 1).

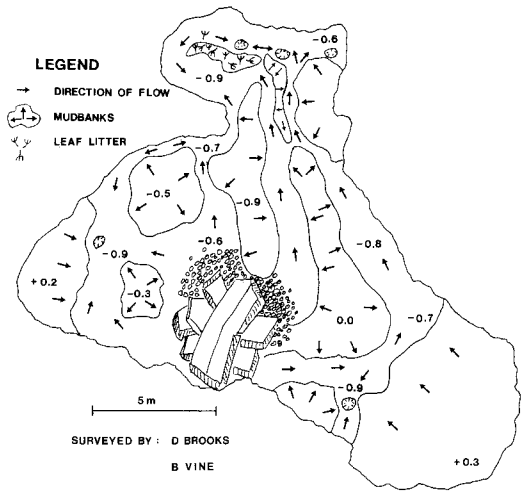

Fig. 1. Plan of C-162 (Rock Bench) showing the location of the mudbanks and other features.

3.2. Cave environment

The caves of Cape Range containing troglobitic fauna have higher relative humidities ($G_{adj} = 79.47$ with 1 *df*; $P<0.001$) than those without fauna, have more water in the mud ($G_{adj} = 18.15$ with 1 *df*; $P<0.001$), but do not differ in temperature (Fig. 2: $G_{adj} = 1.22$ with 1 *df*; $P=0.269$). In addition, caves containing troglobites have higher levels of organic carbon in their soils for both *S. vinei* (Factorial ANOVA; $F_{s1,35} = 21.34$, $P<0.001$) and for millipedes ($F_{s1,35} = 6.744$, $P=0.013$). The troglobitic fauna occurs over the entire and very wide temperature range (11°K) found in the caves of Cape Range. However, they are restricted to areas of soil water >12% 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 troglobitic fauna ($r=0.981$; $P<0.05$), such that between 95–100% R.H. all caves contain troglobites (Fig. 2). The presence of *S.vinei* in caves is closely associated with the

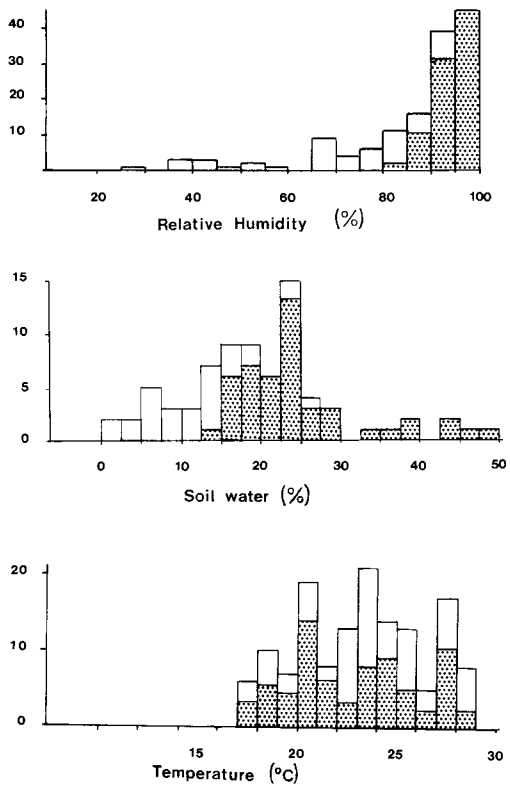

Fig. 2. Distribution of relative humidity (%), soil water content (%) and dry bulb temperature (°C) in the caves of Cape Range. Shaded areas denote the presence of *S. vinei* and f = the number of samples.

amount of organic carbon (C: Fig. 3) and water (H_2O) in the mud-banks, which together account for half the variance in their occurrence

$Y = 0.40\ C + 0.017\ H_2O + 0.084$;
$F_{s2,41} = 22.25$, $P<0.001$, adj. $r^2 = 0.497$.

C-118 was not wetted in the 12 months between the sampling periods in 1987 and 1988, whereas in 1988 C-162 had been flooded within the previous six months, having been previously dry and for the most part devoid of fauna. The troglobites show low resistence to water loss compared with epigean species (Humphreys 1989); the relative water loss for the spiders, *S. vinei*, cave millipedes and cave isopods being 1.0 : 3.1 : 6.8 : 11.1 (Humphreys 1989).

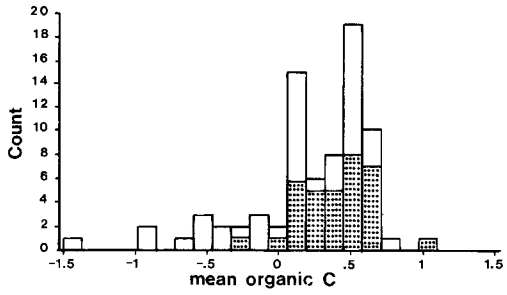

Fig. 3. The frequency distribution of organic carbon (log %) in soils from caves in Cape Range. Shaded areas denote the presence of *S. vinei* and count = the number of samples.

3.3. Population size

The estimated population densities for millipedes, *S. vinei* and isopods are given in Table 1 (isopods were abundant only in C-162). These are large populations for troglobites but are not representative of many of the other troglobitic species in Cape Range, most of which are known from few sightings and specimens; the largest being a blind spider.

3.4. Size class structure

As in 1987 (Humphreys et al. 1989), despite the large reduction in numbers, *S. vinei* in C-118 had a unimodal size class structure (as did the milli-

Table 1. Population size estimates of *S. vinei* from mark-release-recapture experiments from two caves in Cape Range. Also included are the estimates from C-118 made in July 1987 (Humphreys et al. 1989). Estimates were made using Bayes algorithm (Gazey & Staley 1986)

Year	Cave	Population estimates: Mean	Median	Minimum[a]
1987	C-118	1987	3494–3505	1323
1988	C-118	858	990–1010	340
1988	C-162	1029	990–1010	573

[a]This is the minimum population size estimated with 95% confidence.

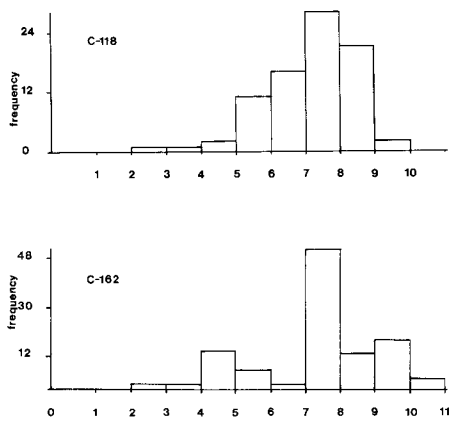

Fig. 4. Size class frequency distribution of *S. vinei* in C-118 and C-162 in 1988.

pedes) with the mode at 7 mm, while in C-162 the size class structure was polymodal (as did the millipedes) with modes at 4, 7 and 9 mm (Fig. 4). The recent flooding of C-162 had reactivated the fauna as is evident from the smaller cohorts in the populations of both millipedes and schizomids and their expansion of range within the cave. C-162 dried rapidly over 44 days in all areas ($P<0.001$), though more rapidly near the entrance. Significant changes in soil water in C-118 could only be detected between years. Wetting and drying of the mud banks in the caves is associated, respectively, with expansion and contraction of the cave fauna populations. The drying of C-162 between 10 August and 22 September 1988 was associated with a contraction of the fauna into about half the cave area — those parts still with the wettest soils. In addition, in cave C-118 between July 1987 and September 1988, there was a four fold reduction in the minimum population size of *S. vinei*, from 1323 to 318 individuals.

3.5. Population pulses

As suggested previously (Humphreys et al. 1989), and shown from the genetics data, the caves must be linked at a level below which cavers can reach. In these levels, relatively devoid of energy, there must be a low population of the cave animals. When caves are wetted and reenergised by the influx of organic matter these populations move upwards into the newly inhabitable areas and breed (see C-162 in Fig. 4). 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.

3.6. Energy flow

The organic carbon content of the soil in C-118 is known from samples in 1987 (Humphreys et al. 1989) and 1988, during which time the cave had no inflow of water or organic matter; the mudbanks occupy *ca* 100 m^2 of the cave. The samples included the top 4 cm of soil, were *ca* 10 m^2 and on the main mud-banks had a mean dry weight of 28.8 g (*SD* 5.1, n=15). From 1987 to 1988 there was a mean reduction of 0.44% in the organic carbon content of the mud-banks containing the fauna (Table 2, a–c); this is ca 12500 g organic carbon, equivalent to ca 140 Mj. I give below a rough energy calculation for the population of the top predator in the cave, *S. vinei*.

The mean population of schizomids was *ca* 3500 in 1987. The respiration rate of *S. vinei* is low, about 0.2 ml/mg/h (Humphreys 1989). Taking an individual weight of 10 mg then the annual respiration rate is ca 61 litres of O_2, equivalent to respiration of ca 1.2 Mj (oxycaloric equivalent ca 20 J/ml O_2). The production efficiency for the animals will be ca 0.3 (Humphreys 1979) so the assimilation of the populations will be ca 1.75 Mj, or ca 1.3% of the estimated loss of organic carbon from the mudbanks. The remaining energy flow

Table 2. The amount of organic carbon (mean %) in the mud of C-118 in 1987 and 1988, during which time the cave had not been flooded.

Area of cave[a]	Organic C 1987	1988	F-test	*df*	*P*
All samples	1.517	1.323	2.381	1,76	0.216
a	1.78	1.29	8.94	1,13	0.010
b	1.85	1.40	11.66	1,7	0.011
c	2.04	1.69	1.39	1,7	0.276
d	1.50	1.27	0.64	1,7	0.450
e	0.42	0.15	27.74	1,7	0.001

[a]These areas are shown in Humphreys et al. 1989.

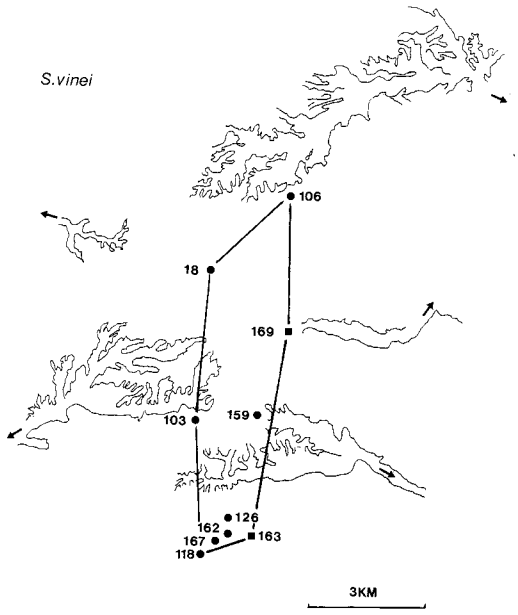

Fig. 5. Distribution of caves containing *S. vinei* in Cape Range. The canyons are shown which cut through the Tulki limestone, in which the caves are formed, and into the Mandu Calcarenite below. The population is not panmictic and divides into southern and northern populations separated by the southern canyon. Points show caves containing *S. vinei*: those denoted by squares were not sampled for genetical analysis.

presumably passes through the microfauna and the much larger biomass of earthworms, millipedes, isopods and other species.

This analysis suggests that during a period without any influx of detritus, such as occurred in C-118 from 1987 to 1988, that a detailed analysis of the organic carbon content of the mud could be used to examine the energetics of the cave ecosystem.

3.7. Genetics

Eight caves were sampled (44 individuals) and 37 enzymes examined and 22 were scored. Of these 19 loci were invariate and three were polymorphic. The eight populations examined (Fig. 5) of *S. vinei* are genetically similar and the data are consistent with the presence of a single biological species. The sample sizes are inadequate to conduct proper statistical comparisons. However, the allele and genotype frequencies suggest that the cave sample sets are not taken from a single panmictic population. The strongest evidence for this suggestion comes from the *Mdh-2* data (malate dehydrogenase [MDH, E.C. 1.1.1.37]), in which the C-159 population exhibits a fixed allelic difference from all other populations. With a null hypothesis that all individuals have come from a single panmictic population, then the chance of not observing an *Mdh-2ab* heterozygote in 44 cases (for a population with allele frequencies a=0.09, b=0.91) is $(1-2\times0.91\times0.09)^{44} = 0.0004$. It is unwise for a number of reasons to use a single marker to form unequivocal genetic conclusions (see Richardson et al. 1986). The data for *Est* (esterase [EST, E.C.3.1.1.1]) and *Pgm* (phosphoglucomutase [PGM, E.C.2.7.5.1]) provide weak support for the idea that the cave samples do not come from a single gene pool. There is strong genetical evidence from the amphipods and millipedes that the canyons which cut through the Tulki Limestone into the Mandu Calcarenite below prevent panmixis of the populations across the canyons (Humhreys & Adams, unpubl.) Assuming that the canyons will affect all troglobites, the data for *S. vinei* were divided into two groups representing the northern and southern areas (Fig. 5). The gene frequencies of two (*Mdh-2* and *Pgm*) of the three polymorphic loci differ significantly between areas (Fishers Exact *P* respectively 0.0071 and 0.0009). While the troglobites clearly are separated genetically by the canyons, the one non-troglobite (isopod) is panmictic throughout its known range. This suggests that the caves were occupied by the troglobites before the formation of the major landform features (canyons) which dominate the area today.

3.8. Origins of cave fauna

The terrestrial component of the Cape Range troglobitic fauna was probably derived in a manner directly analogous to the glacial relict fauna of the northern temperate region, with aridity, rather than low temperature, causing the regional extinction of the original habitat (rainforest) of the ancestors of the troglobites, permitting speciation within the caves.

Acknowledgements. This work would have been impossible without the unstinting cooperation of many individuals and organisations. I thank Charles Blumer, Darren Brooks, Richard Curtiss, Malcolm East, Stefan Eberhard, Michael Gray, Brendon Hart, Eva Hart, Hugh Tomlinson, Gay Turner, Brian Vine, Julianne Waldock, Sue White, Ray Wood, Karl-Heinz Wyrwoll, Rae Young, Brenton Knott, Glen Colless, Helen Miller, as well as those in the support services at the Western Australian Museum. Isozyme electrophoresis was conducted by Mark Adams, South Australian Museum. The organic carbon analysis was conducted by permission of the Director of the Chemistry Centre, W. A. Pigments were provided by Abel, Lemon and Company, Adelaide. The following people offered taxonomic and zoogeographic expertise: Dr H. Dalens, Dr M. Gray, Dr B. Knott and Dr W. A. Shear. Drs W. J. Gazey and V. Palermo (British Columbia) freely provided me with their programs to calculate the sequential Bayes algorithm. The work was funded by the Australian National Parks and Wildlife Service and the Western Australian Museum.

References

Barr, T. C. 1968: Cave ecology and evolution of troglobites. — Evol. Biol. 2:35–102.

— 1973: Refugees of the Ice Age. — Nat. Hist., May 1973:26–35, 72–73.

Gazey, W. J. & Staley, M. J. 1986: Population estimation from mark-recapture experiments using a sequential Bayes algorithm. — Ecology 67:941–951.

Hamilton-Smith, E. 1967: The arthropoda of Australian caves. — J. Austral. Entomol. Soc. 6:103–118.

Harvey, M. S. 1988: A new troglobitic schizomid from Cape Range, Western Australia (Chelicerata: Schizomida). — Rec. West. Austral. Mus. 14:15–20.

Howarth, F. G. 1983: Bioclimatic and geological factors governing the evolution and distribution of Hawaiian cave insects. — Entomol. Generalis 8:17–26.

— 1988: Environmental ecology of north Queensland caves: or why there are so many troglobites in Australia. — In: Pearson, L. (ed.), 17th Biennial Conference, Australian Speleological Federation Tropicon Conference, Lake Tinaroo, Far North Queensland. 27–31 Dec. 1988: 76–84. Australian Speleological Federation, Cairns. 139 pp.

Humphreys, W. F. 1979: Production and respiration in animal populations. — J. Anim. Ecol. 48:427–453.

— 1989: Water loss and respiration of cave arthropods from Cape Range, Western Australia. — Comp. Biochem. Physiol. 95a:101–107.

Humphreys, W. F., Adams, M. & Vine, B. 1989: The biology of Schizomus vinei (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. — J. Zool., Lond. 217:177–201.

Leleup, N. 1968: Introduction. Mission zoologique belge aux îles Galapagos et en Ecuador (N. et J. Leleup, 1964–1965). Resultats scientifiques. — Mus. R. Afriq. Centr. I:9–34. Tervuren.

Mitchell, R. W. 1970: Total number and density estimates of some species of cavernicoles inhabiting Fern Cave, Texas. — Ann. Speleol. 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.

Richardson, B. J., Baverstock, P. R. & Adams, M. 1986: Allozyme electrophoresis: a handbook for animal systematics and population studies. — Academic Press. Sydney. 410 pp.

Sbordoni, V. 1982: Advances in speciation of cave animals. — In: Barrigozzi, C. (ed.), Mechanisms of speciation: 219–240. Liss, New York.

Vandel, A. 1965: Biospeleology: the biology of cavernicolous animals. — Pergamon Press, Oxford. 524 pp.

Vine, B., Knott, B. & Humphreys, W. F. 1988: Observations of Schizomus vinei (Chelicerata: Schizomida) from Cape Range, Western Australia. — Rec. West. Austral. Mus. 14:21–34.