Troglobitic Millipedes (Diplopoda : Paradoxosomatidae) from Semi-arid Cape Range, Western Australia: Systematics and Biology

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Abstract

Paradoxosomatid millipedes are an important component of the rich troglobitic fauna of the semi-arid tropical Cape Range, Western Australia. They are found in at least 55 of the 282 caves known from Cape Range covering >500 km^2. The millipedes occur in dense populations only in areas of high relative humidity and organic carbon content. They appear to be opportunistic and are able to grow and breed rapidly on the intermittently available patches of organic matter washed into the caves by unpredictable rainfall. A new genus of paradoxosomatid millipedes (*Stygiochiropus*, gen. nov.), comprising three species (*S. communis*, sp. nov., *S. sympatricus*, sp. nov., and *S. isolatus*, sp. nov.) is described from the caves. A key is provided for males, but females cannot be identified. The only widespread species (*S. communis*) separates into three provinces between which there are many fixed allelic differences, as determined by allozyme electrophoresis. Although these genetic provinces are separated by deep gorges that cut through the cavernous limestone into the underlying non-cavernous strata, the millipede populations cannot be separated using morphological criteria. The affinities of the millipedes are unknown, but they are part of a rich community of troglobites (>26 species) of which many species have affinities with the northern wet tropical forest fauna, rather than with the current semi-arid fauna.

Introduction

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 (Vine *et al.* 1988; Humphreys 1989, 1990, 1991*a*, 1991*b*; Humphreys *et al.* 1989; Humphreys and Collis 1990; Humphreys and Adams 1991). Paradoxosomatid millipedes comprise one of the most conspicuous, abundant and genetically diverse components of this fauna. As such they provide a convenient focus for ecological and genetic work aimed at under-standing the working of the cave ecosystems, the population processes involved and the nature of the genetic isolation occurring within the karst region. The research is designed to provide the basis for the conservation management of the karst region as a whole.

Here we consider aspects of the biology and genetics of the millipedes and describe a new genus, comprising three new species, of highly cave-adapted paradoxosomatid millipedes.

Materials and 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 with 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 with a ×10 Lupe (Peak).

The population size was estimated from the mark–recapture data by means of the sequential Bayes algorithm (Gazey and Staley 1986), as used previously (Humphreys et al. 1989), and where the rationale is explained in more detail. The algorithm estimates the minimum population size with 95% confidence and the mean and median population size.

Husbandry

Animals were maintained in the laboratory in either 50-mL vials or small vivaria; in either case, the floor comprised 1 cm 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 sterilised to prevent contamination by other species of invertebrates and micro-organisms.

Electrophoresis

Cellulose acetate gel electrophoresis was conducted according to standard methods (Richardson et al. 1986) on samples of frozen millipedes 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.

Table 1. **Genetic information on the millipedes obtained from the pilot study**

Attribute	Millipedes[A]	Attribute	Millipedes[A]
No. of caves sampled	10	H-W equilibrium	Yes
No. of individuals	40	Panmictic population	No
No. of enzymes examined	46	? More than one species[B]	Yes
No. of enzymes scored	27	Geographic explanation[C]	Yes
No. of loci invariate (%)	9 (33)	Troglobite	Yes
No. of polymorphic loci (%)	18 (67)		

[A] There are two major genetic groupings differing at an average of 19% of loci. Group I: C-118, C-203, C-126 and C-127; 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.
[B] Genetic differences indicate the possibility of sibling species.
[C] The genetic differences are in accord with major geomorphological features.

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 et al. (1986). The fixed-allelic difference matrix was examined by principal coordinate analysis to determine whether distinct genetic provinces occur associated with geomorphological diversity or other criteria.

Institutions

AMNH: American Museum of Natural History, New York; WAM: Western Australian Museum, Perth; ZMA: Zoölogisch Museum, Universiteit van Amsterdam, Netherlands.

The Ecosystem

The regional, climatic and biological setting of the fauna have been described previously (Vine *et al.* 1988; Humphreys 1989, 1990, 1991*a*; Humphreys *et al.* 1989; Humphreys and Collis 1990; Humphreys and Adams 1991), and so only sufficient information is given here 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 *et al.* 1989). The caves, occurring in the Tulki Limestone of the deeply dissected Cape Range, contain a rich troglobitic fauna. This community is dependent on organic matter and water entering the caves from intermittent flooding (Humphreys 1991*b*). 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. Major water inflow brings with it the energy source (leaves, twigs, etc.) for the cave ecosystem and water to maintain the humidity of the air required by the troglobites (Humphreys 1989; Humphreys *et al.* 1989).

Some caves must be linked at depth by minor cavities (Humphreys *et al.* 1989) and in these depths, relatively devoid of energy, low populations of the cave animals persist (Humphreys 1991*b*). When caves are wetted and re-energised by the influx of organic matter, these populations move upwards into the newly inhabitable areas and breed there. Until the next influx of water the caves slowly dry, the organic matter is consumed, 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 are inaccessible areas of the cave in which the community is maintained and from which the populations extend upwards at intervals, like
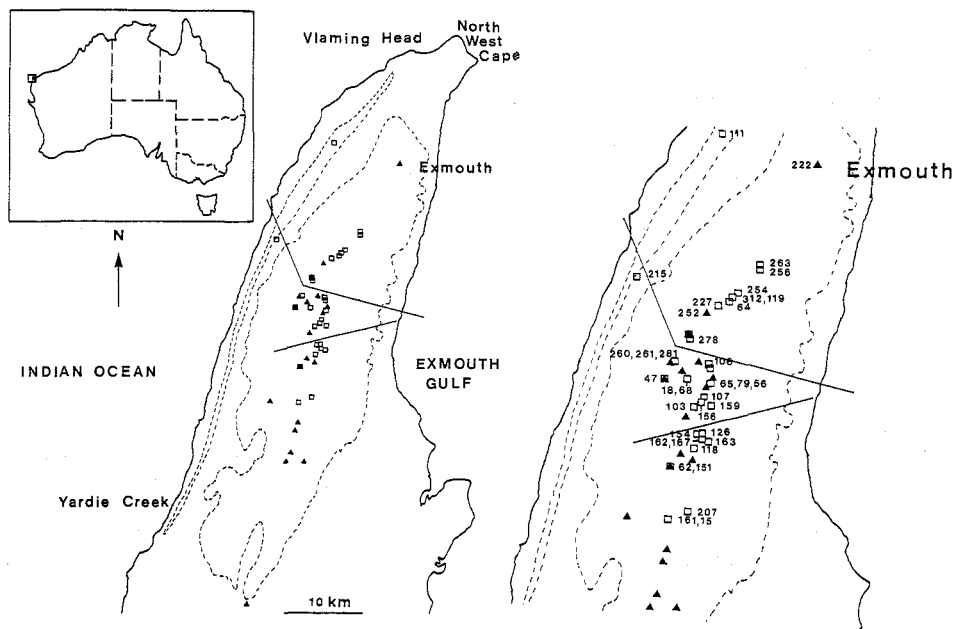
Fig. 1. The location of Cape Range on the North West Cape peninsula and the distribution of caves (▲) with millipedes. Cape Range encompasses all the outcropping Tulki Limestone (dashed lines) in which the caves containing troglobites are found; the cave outside this area is also in Tulki Limestone but is covered by other deposits. □, the locations of samples used in the allozyme study. The solid lines across the range denote the boundaries between the three major genetic subregions as indicated by the electrophoretic work. The sympatric populations occur in cave C-111 at the extreme NW. of the distribution and *S. isolatus* in C-222 to the extreme NE.

pseudopodia, into the accessible areas of caves. Depending on the characteristics of a cave, its catchment size and the weather, these pulses of the community extend into the accessible areas of the caves with different frequencies and have different rates of decay. The habitable areas are dynamic, continually expanding and contracting, and are fed by unpredictable pulses of organic matter washed into the cave (see Humphreys et al. 1989). Hence, the caves in Cape Range contain highly dynamic troglobite communities (Humphreys 1991b) which belie the stability normally associated with such systems (Poulson and White 1969).

A synopsis of the climate of the area is given in Fig. 2.

Results

The Caves

By the end of 1989, millipedes were known from 55 of the 282 caves then known from the North West Cape peninsula; the caves are up to 61 km apart and occur in an area over 500 km^2 of Cape Range (Fig. 1). *Draculoides vinei* (Harvey) (Chelicerata:Schizomida) also occurs in 31 of the caves. Samples collected for allozyme analysis came from 36 of these caves (Fig. 1). Except where specifically mentioned, the biological data refer to the one widespread species, *Stygiochiropus communis*.

Cave morphology

The population census was conducted in two caves. Cave C-162 (22°09'S.,114°00'E.) (see Humphreys 1990, fig. 1) 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, 1991b). In contrast, the larger cave C-118 (22°09'S.,113°59'E.) (see Humphreys et al. 1989, fig. 1) opens to the surface
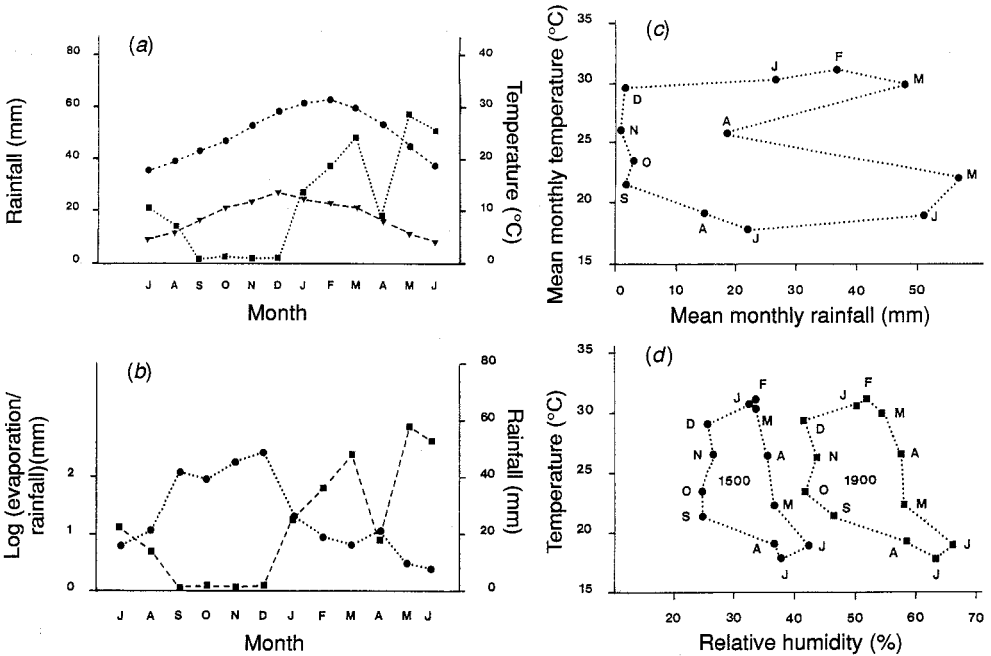
Fig. 2. Climatographic synthesis for the North West Cape peninsula. (*a*) Mean monthly maximum (●) and minimum (▼) temperatures and rainfall (■); (*b*) log (mean monthly evapotranspiration/mean rainfall) (●) and rainfall (■); (*c*) hythergraph of mean monthly rainfall (mm) and temperature (°C); (*d*) hythergraph of mean monthly temperature (°C) and relative humidity at 0900 and 1500 hours. The data are composite and were extracted from the available data for Exmouth, Learmouth and Exmouth (Navy) (Microfiche Climatic Averages, Australia and TABS Elements May 1986: Bureau of Meteorology, Canberra).

through a narrow tunnel and in consequence dries very slowly, but receives water on average only once every five years. Both caves contain extensive banks of soil separated by pebble-filled gullies leading to a number of drainage holes (Humphreys 1989, 1990, 1991a, 1991b).

Cave environment

The typical troglobitic fauna (*D. vinei* and millipedes) is known from c. 15% of caves in Cape Range. Compared with caves lacking troglobitic fauna, caves with such fauna have higher relative humidities, greater soil water and soil organic carbon content, but do not differ in temperature (Humphreys 1990). The troglobitic fauna occurs throughout the temperature range (18–29°C) found between the caves of Cape Range, but is restricted to areas of soil water >12% and relative humidity (RH) >80%. Above 80% RH there is a strong positive correlation between RH and the proportion of caves containing troglobitic fauna ($r = 0·981$, $P < 0·05$), such that between 95 and 100% RH all caves contain troglobites (Humphreys 1990).

The millipedes may be found in the daylight part of caves (e.g. C-162) and even on the threshold in daylight if the humidity is sufficiently high as a result of water outflow (e.g. C-222) or condensation from exhalent air (e.g. C-15). However, they have never been trapped outside caves as part of the epigean fauna. In the caves they are mostly found wandering on bare mud-banks, stones, piles of organic detritus or, in large numbers, on algae supported by the condensation of water (e.g. C-15).

The Millipedes

Population size

The estimated population densities for millipedes are given in Table 2 and the pertinent posterior distributions and the cumulative posterior distributions (probabilities) against population size are shown in Fig. 3.

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).

Table 2. Population size estimates from mark–recapture experiments on millipedes more than 9 mm total length from two caves in Cape Range during 1988

| Cave | Population estimates | | |
	Mean	Median	Minimum[A]
C-118	1231	990–1011	767
C-162	184	496–506	136

[A] Minimum population size estimated with 95% confidence using Bayes algorithm.

Size class structure

As is the case with *D. 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 and 5).

Growth rate

There is no direct evidence of the growth rate of the millipedes in the field, but several lines of evidence suggest that they grow rapidly in response to favourable conditions. Eggs are laid in a cell in the mud of the caves or cultures where the young millipedes remain

for some time while they grow and from which they subsequently emerge to feed on the mud surface. Of millipedes bred in the laboratory, the smallest individual seen on the surface of the mud was 4 mm long, compared with the smallest seen in a cave of $3 \cdot 5$ mm. Hence, as with the schizomids (Humphreys *et al.* 1989), it would appear that the entire size range of surface-active millipedes was sampled in the caves.

Additional evidence comes from the millipede population structure in cave C-15 which had been activated by 107 mm of rain in May and June 1989 (the heaviest rainfall for 38 months). In mid-July 1989, three cohorts were present in the population. The population was examined again in early September (Fig. 5) when the three cohorts present in the initial sample are tentatively identifiable in the later sample. Joining the cohorts parsimoniously would indicate growth rates of $0 \cdot 03$–$0 \cdot 05$ mm day^{-1}. However, data from the laboratory suggest that growth rates may be twice this value (Table 3), 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 that was absent in the July sample and that presumably represents emergence of young from the soil cells at about $3 \cdot 5$ mm length. This interpretation is supported by further growth rate data from cohorts in five laboratory cultures which give rates of $0 \cdot 14$ (s.d., $0 \cdot 066$) mm day^{-1}. The high variance seems typical, with individuals in some cultures growing much faster than others; this is consistent with the suggested opportunism. Hence, the field and the laboratory evidence are consistent with the faster growth and indicate that the cohorts should be connected in the manner shown in Fig. 5.

Genetics

In this paper we present only 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).
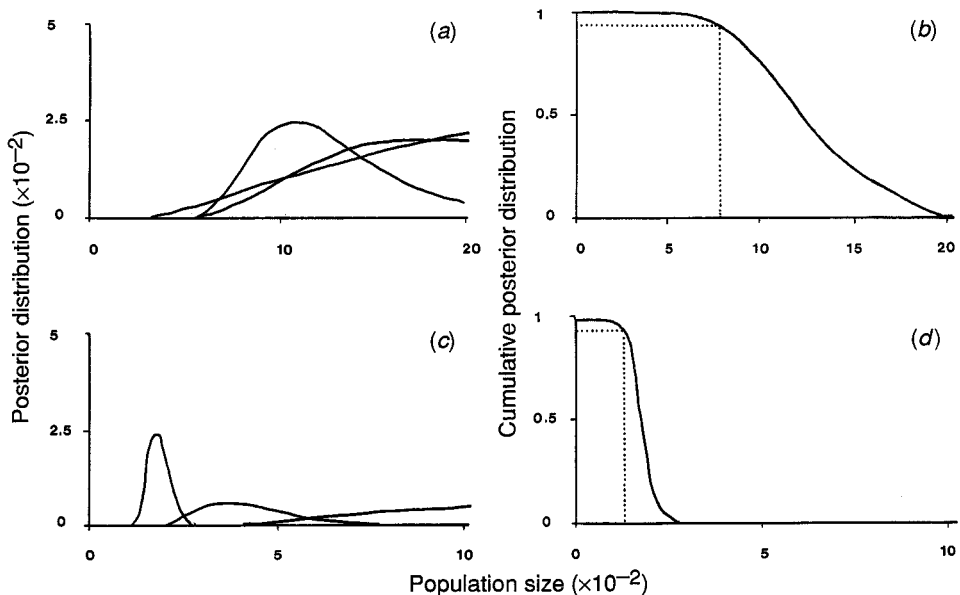

Fig. 3. Statistical distributions of the millipede populations derived from the mark–recapture data using Bayes algorithm (see Gazey and Staley 1986). (*a*) and (*c*) The posterior distribution plotted against population of all millipedes; (*b*) and (*d*), the cumulative posterior distribution (probability) against population size, the dotted lines show the minimum population size estimated with 95% confidence. (*a*) and (*b*) Cave C-118 (minimum population size of 767 at $P=0 \cdot 95$); (*c*) and (*d*), cave C-162 (minimum population size of 136 at $P=0 \cdot 95$).

A plot of the principal coordinates based on the fixed allelic differences (see Appendix) shows 36 populations from the 35 caves (Fig. 6). Two sympatric species of *Stygiochiropus* occur in cave C-111 (*S. communis* and *S. sympatricus*), one of them having >39% fixed allelic differences (Richardson *et al.* 1986) from all other populations (Fig. 6, Table 4). Three major genetic provinces of *S. communis* occur in Cape Range: a moderately variable northern group (sympatric with *S. sympatricus* in cave C-111), a homogeneous southern group, and a very heterogenous central group (Fig. 6, Table 4).

As with the amphipods from Cape Range (Humphreys and Adams 1991), 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 subregions (Table 4), indicating that there is no gene flow between any of the subregions. The genetic differences observed between subregional populations are at the higher end of the range normally observed for allopatric populations of a single species; rearing experiments are required to determine whether these populations represent sibling species.
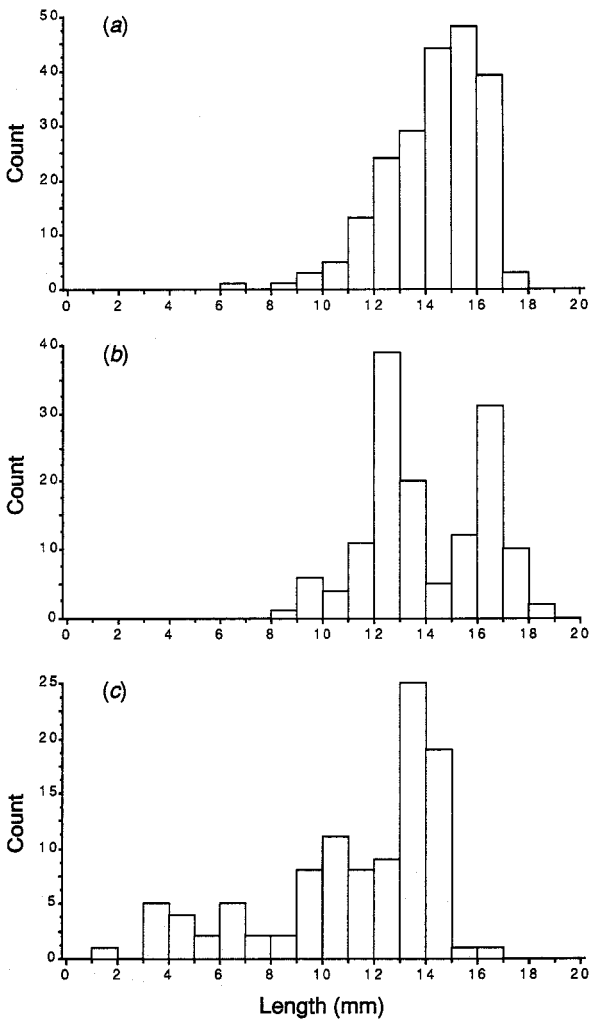
Fig. 4. Size-class frequency distribution (total length, mm) of millipedes in mid-1988. (*a*) Cave C-118 (*n* = 205); (*b*) cave C-162 (*n* = 134); (*c*) C-118 at the end of the experiment to re-establish troglobite populations within the cave (*n* = 103; Humphreys 1991*b*).
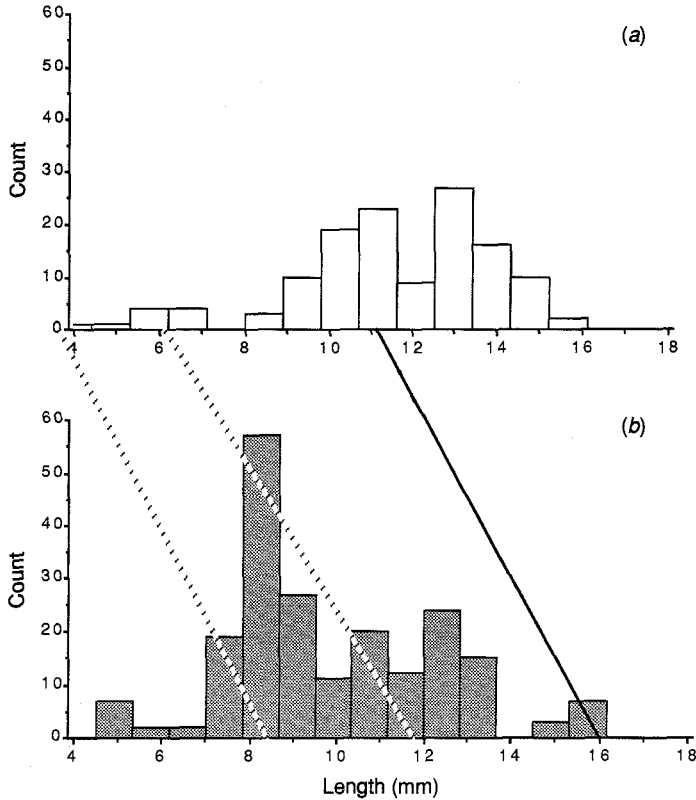
Fig. 5. Changes in the size-class frequency distributions of millipedes in C-15 over a period of seven weeks. (*a*) 16 July, *n* = 129; (*b*) 3 September 1989, *n* = 206. The diagonal lines between the histograms are the forward (solid line) and backward (dashed lines) extrapolations of the maxima by the mean growth rate in the laboratory (Table 3) to show the expected outcome and origin, respectively, of the cohorts.

Table 3. Mean growth rate of millipedes surviving in the laboratory over 67 days

Millipedes were maintained in batches owing to the difficulty of maintaining them 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
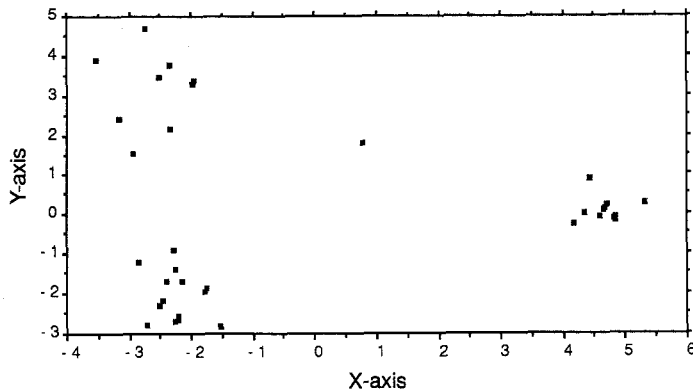
Fig. 6. Plot of the principal coordinates based on the matrix of fixed allelic differences (%). The three clusters represent the variation found in *Stygiochiropus communis*, and the lone point represents *S. sympatricus*. The clusters represent the southern (right), central (lower left) and northern (upper left) genetic provinces. The rationale for this approach is given in chapter 12 of Richardson *et al.* (1986).

Table 4. The fixed differences and genetic distances between the three major genetic provinces of millipedes in Cape Range

C-111b is the distance between *S. communis* and *S. sympatricus*

Groups compared	Fixed differences (%)	Nei's distance
South *v.* Central	29	0·42
South *v.* North	29	0·42
Central *v.* North	17	0·32
All *v.* C-111b	39	0·60

Systematics

Family **PARADOXOSOMATIDAE** Daday

Subfamily **AUSTRALIOSOMATINAE** Brölemann

Tribe **ANTICHIROPODINI** Brölemann

Stygiochiropus, gen. nov.

Type species: *Stygiochiropus communis*, sp. nov.

Diagnosis

Distinct from all other members of the Tribe Antichiropodini (see Jeekel 1968) in being strongly modified for cave life, with greatly enlongated legs and antennae (Fig. 57), total lack of pigment, brittle cuticle, and narrow, elongated segments with short, angular, spine-like paranota (Fig. 58). The male gonopods are distinctive in the comparatively short, broadly expanded, laminate solenomerite with three processes at its base, the proximal (**a**) short and sometimes bifid or toothed, and the distal (**b**) unbranched, evenly curved, and equal to or exceeding the solenomerite (Figs 59–61).

Description

Twenty segments. Pore formula normal. Segments more than twice as long as broad, moderately constricted between prozonite and metazonite, unsculptured, bearing 2 transverse rows of setae, the posterior row of 8–10 setae at the posterior margin of the metazonite (Fig. 58). Pleural keels absent.

Paranota present from segment 2 onward as short, subtriangular extensions as posterio-lateral corners of metazonites, larger on poriferous segments (Figs 57, 58). Sternites sparsely setose; anterior sternites of males not modified.

Legs and antennae strongly attenuate (Fig. 57). First legs of males with strong ventral femoral tubercle; other anterior legs of males unmodified.

Gonopod coxae robust, prefemora short, densely setose, articulation with acropodite indistinct. Acropodite long, curved strongly laterally and slightly ventrally (Fig. 59). Femoral process absent (*S. communis* and *S. sympatricus*) or present only as ledge-like corner at distal end of femur (*S. isolatus*); articulation at end of femur completely suppressed. Solenomerite (Figs 9, 10) with three accompanying processes; the most proximal (**a**) usually simple and acuminate, or significantly thickened and with knob-like teeth, or distally bifid; the most distal (**b**) laminate, broadly curved, equally or exceeding solenomerite; medial process (**c**) highly variable but usually with thickened base and by far the smaller of the three processes. Solenomerite with thickened base, distally flaring and laminate, with many fine marginal teeth.

Distribution

Known only from caves in the Cape Range, Western Australia.

Included Species

Stygiochiropus communis, sp. nov., *S. sympatricus*, sp. nov., and *S. isolatus*, sp. nov.

Remarks

The paradoxosomatid millipede fauna of Western Australia is poorly known. Only two antichiropodine genera, *Antichiropus* Attems (seven species) and *Helicopodosoma* Verhoeff (two species), have been previously recorded, together with the australiosomatine *Akamptogonus novarae* (Humbert and de Saussure), a synanthropic species that has also reached New Zealand (Johns 1967; Jeekel 1968) and has recently been collected in the San Francisco Bay region of the United States (Hoffman 1980) and in Hawaii (Jeekel 1981). Its original home is probably somewhere in south-eastern Australia.

Stygiochiropus has very clear affinities with *Antichiropus*, including the evident suppression of the femoral process of the gonopod, and at least a basal fusion of the tibiotarsus and solenomerite. However, the gonopods of members of both genera are so highly modified in comparison with australosomatine gonopods that the various processes are very difficult to homologise. Hence we have followed Jeekel (1965) in labelling the gonopod processes with the same letters used by Attems (1911) in describing *Antichiropus*, but we have not tried to distinguish tibiotarsal and parasolenomerite branches. The major difference between the two genera, aside from the troglobitic modifications of *Stygiochiropus*, is in the form of the solenomerite, which is very long and curved in a circle or helix in *Antichiropus*, but is short, broad, and lamellate in *Stygiochiropus*. Also, in the latter genus, there are three terminal processes around the base of the solenomerite, while in all *Antichiropus* species (except *A. fossulifrons* Attems, and a new species to be described later), there are only two.

On one side, relatives of these two genera would appear to be the two species of *Pogonosternum* Jeekel, from Victoria. A femoral process persists in this genus, in addition to three processes near the base of the solenomerite (Jeekel 1965). Following a trend to greater simplification of the gonopods, *Notodesmus scotius* (Chamberlin), from Tasmania, has two remaining processes, both much shortened (Jeekel 1979), and species of *Helicopodosoma* have lost all processes and the gonopod ends only in a coiled solenomerite (Attems 1937).

Obviously, it is premature to do anything more than suggest these relationships. The Australian paradoxosomatid fauna contains numerous undiagnosed genera and species; descriptions of these and discussions of synapomorphies are required in order to treat the phylogeny of the group as a whole. However, the Australian fauna would be a good place to start as it is relatively coherent and of manageable size (Jeekel 1968).

An absence of detailed distributional information prevents any meaningful discussion of the biogeography at the generic level (some taxa were described only as from 'Australia'), but it may be meaningful to note that a new species of *Antichiropus* has been described from Cape Range (Shear 1992). Another useful fact is that *Helicopodosoma* (if it includes *Brochopeltis* Verhoeff) has three species in Queensland in addition to the two in Western Australia; this may fit in with the suggested rainforest affinities of some elements of the Cape Range cave fauna, but Jeekel (1981) has stated that paradoxosomatids occur much more abundantly in open eucalypt forests than in rainforests. Further, it is not clear if the Western Australian species are congeneric with either *Helicopodosoma* or *Brochopeltis*.

More can be said regarding the three species of *Stygiochiropus*. Of the 282 caves so far explored on the North West Cape, 55 host *Stygiochiropus*. We cannot say with complete assurance that no more than the three species described here will be found, because sexually mature males from some caves have not been collected. In cases where mature males were not available but juvenile or female specimens were used for electrophoretic studies, all clustered with *Stygiochiropus communis*. However, there remain some caves for which neither electrophoretic data nor mature males are available, and it is possible that some represent additional species. *Stygiochiropus communis* is clearly the most widespread and abundant species, as the other two occur only in single caves (*Stygiochiropus sympatricus* is so far known only from cave C-111, where it is found together with *S. communis*, and *S. isolatus* has been collected only from cave C-222).

It was possible to assess gonopod variation both within and between cave populations by making careful camera lucida drawings of gonopods and examining them side-by-side. Obviously, this work was done with *Stygiochiropus communis*, and the results will be discussed under that species, but we can say here that it is not possible to differentiate any

populations of this species on the basis of gonopod anatomy. With only single males of the two other species available, no study of variation was possible, but the gonopods and body size of both these species indicate distinctness from *S. communis*. In addition, the electrophoretic analysis showed that *S. sympatricus* has greater than 39% fixed differences from any other populations studied, including the *S. communis* population that occurs with it in the same cave. Unfortunately, *S. isolatus* was not included in the analysis.

Etymology

From stygio-, the infernal regions, and -chiropus ('hand-foot'), as a combining stem indicating a relationship to the genus *Antichiropus* Attems.

Key to Males of *Stygiochiropus*

1*a*. End of gonopod femorite with a distinct angular shelf (Figs 17, 18); length of mature males
       7–8 mm, width 0·6 mm .... *S. isolatus*

1*b*. End of gonopod femorite without a distinct angular shelf (Figs 14–16); length of mature males
       14–15 mm, width 1·0 mm 2

2*a*. Process **a** of gonopod deeply bifid (Figs 14–16) .... *S. sympatricus*

3*a*. Process **a** of gonopod simple (Figs 7–10) .... *S. communis*

Stygiochiropus communis, sp. nov.

(Figs 7–13)

Material Examined

Holotype. ♂, cave C-18 (22°05'S.,113°59'E.), Cape Range, Western Australia, 13.viii.1988, W. F. Humphreys *et al.* (WAM 88/2452).

Paratypes. 1♂, 2♀, same data as holotype (WAM 91/1402–1404); 7♂, 6♀, cave C-126 (22°09'S., 114°00'E.), Cape Range, W.A. 18.viii.1988, W. F. Humphreys *et al.* (WAM 88/2483–95); 2♂, 2♀, same data as last, deposited in AMNH and ZMA.

Diagnosis

Distinct from *S. sympatricus* in the simple process **a** (bifid in *S. sympatricus*) and the less robust base of the solenomerite; from *S. isolatus* in the larger gonopod lacking a projecting angle at the distal end of the femorite.

Description

Male

Length, 14–15 mm; width at seventh metazonite, 1·0 mm; third antennal article 0·6 mm long. Segments in dorsal view as in Fig. 58. Postgonopodal legs (Fig. 12) long and slender, first legs (Fig. 11) typical of tribe, with strong distal femoral tubercle.

Gonopods moderately robust for size of animal, *in situ* with coxae and prefemora in contact, acropodite curving laterally, then mesally so tips of gonopods touch or cross (Figs 7, 59). Coxa about twice as long as broad. Prefemur short, about $\frac{1}{3}$ length of coxa, heavily setose, sharply curved. Prefemur/acropodite articulation obscure, acropodite at obtuse angle to prefemur. Femorite basally narrow, expanding to maximum width in distal $\frac{2}{3}$, evenly curved basally but widened part is nearly straight; transition to apical division smooth, marked by narrow neck; femoral process absent. Process **a** (probably tibiotarsus) a little shorter than solenomerite, cylindrical-acuminate. Process **b** (probably parasolenomerite) exceeding solenomerite, sickle-like. Process **c** shortest of three processes, base somewhat bulbous, distally bifid. Solenomerite laminate, broadly expanded distally, longitudinally striate, with many marginal teeth or fimbriae.

Cuticle extremely brittle, colourless; gut clearly visible dorsally.

Female

Length, 15–17 mm; width at seventh metazonite, 1·15 mm; nonsexual structures otherwise as in male.

Distribution

Mature males of this species have been taken from the following Cape Range caves: C-15, 18, 47, 56, 64, 68, 79, 102, 103, 104, 106, 107, 111, 118, 119, 126, 152, 154, 156, 159, 161, 162, 163, 167, 171, 201, 203, 207, 254, 256, 260, 277, 291, 300 and 312. Of these, the following were not included in the genetic analysis: C-102, 104, 152, 201, 203, 250, 277, 291 and 300. Included in the genetic analysis, but lacking mature males, are the following: C-65, 119, 215, 227, 261, 263, 278 and 281; the analysis showed all of these specimens to belong to *S. communis*. *Stygiochiropus* females and/or juveniles, not genetically analysed, have been taken in the following: C-21, 45, 63, 169, 250, 252 and 262; we cannot be sure that all these represent *S. communis*. The relative locations of the caves in which any *Stygiochiropus* specimens have been collected are shown in Fig. 1.
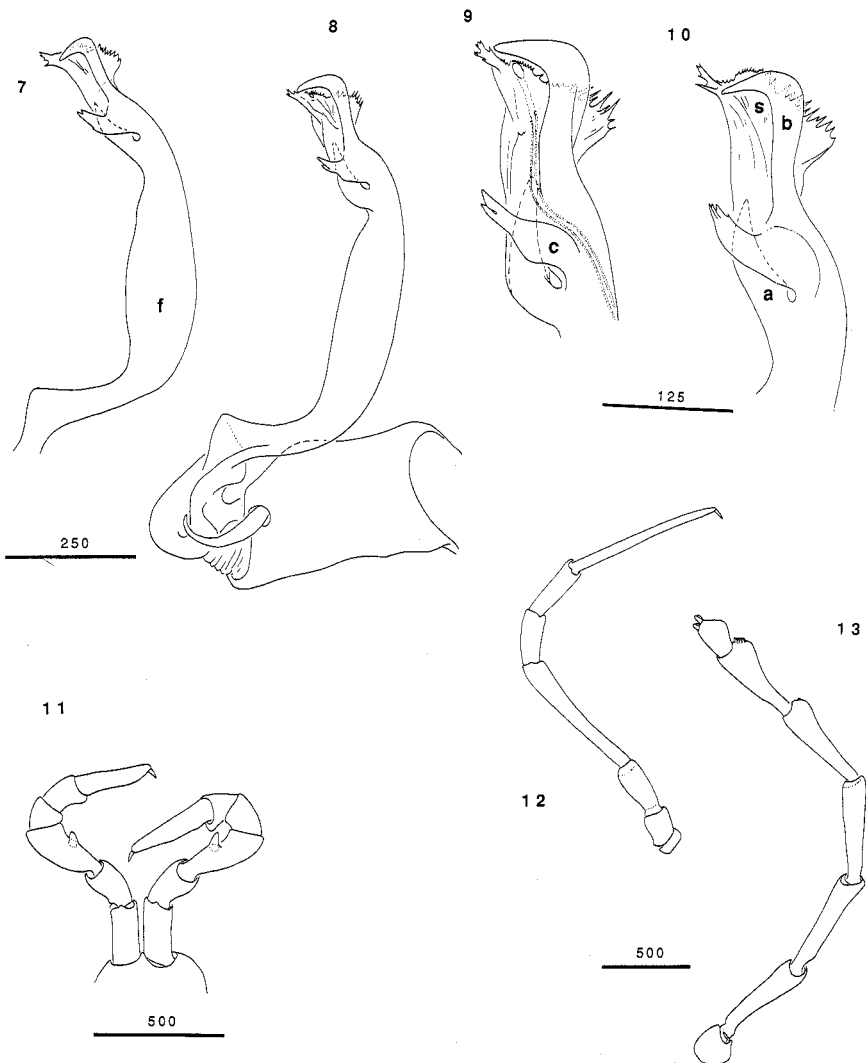
Figs 7–13. *Stygiochiropus communis*: *7–10*, gonopods, mesal view; *8*, *9*, holotype; *7*, *11*, paratype; *11*, leg 1, holotype; *12*, legs from segment 12, holotype; *13*, antenna, holotype. Processes a, b and c are labelled (see text) together with the solenomerite (s) and the femorite (f).   Scale bars in μm.

Remarks

The genetic analysis already described shows that the populations assigned here to *S. communis* readily divide into three clusters which, by ordinary criteria, are genetically isolated. The southern cluster appears to be the most divergent, with the central and northern clusters more similar to one another. The genetic analysis and traditional systematics based on morphology were carried out independently, and the populations used for the two methods do not entirely overlap, as indicated in the section above.

Gonopod variation in this species was assessed by making careful camera lucida drawings of the gonopods and comparing them side-by-side. Usually only one or a few males were available from a single cave, but in several instances more than three were examined. As a preliminary conclusion, we found that variation between all caves, regardless of grouping in the electrophoretic experiments, was not significant and that variation within single cave populations was comparable to between-cave variation. Variation in the form of the several gonopod processes showed no coherent pattern within this species; in other words, a particular form of process **a** did not correlate with a particular form of process **b** or **c**. The three geographically coherent population clusters revealed in the genetic analysis, despite levels of fixed differences indicative of complete isolation, are not recognisable on the basis of gonopod anatomy. Because of the complex nature of the gonopods, this represents a subjective judgement. The range of variation is illustrated in Figs 21–56 and briefly discussed below.

As all figures are drawn to the same scale, it can be seen that there is no meaningful variation in size, but that the width of the femorite does show some differences. It is not possible to say whether this is real or that it results from the angle of view (the gonopods were temporarily mounted in glycerine on microscope slides for illustration).

The form of the solenomerite was essentially invariable.

Process **a** showed almost no variation, though in a few cases a small subterminal swelling or knob may suggest that the ancestral form was bifid, as in *S. sympatricus*. A male from C-260 had this process unusually strengthened (Fig. 36), and a possibly abnormal male from C-300 had process **a** of a form approaching that in *S. isolatus* (Figs 22, 23).

Process **b** varied mostly in its curvature. A simple 'C' curve was found in males from C-18 (Fig. 32), 107 (Fig. 30), 18 (Figs 9, 10), 126 (Fig. 27), 154 (Fig. 26), 159 (Fig. 29), 201 (Fig. 24) and 203 (Fig. 21). A sigmoid, or 'S' curve of varying degree occurred in males from C-64 (Fig. 38), 106 (Fig. 34), 162 (Fig. 25) and 260 (Fig. 36); an extreme version of the sigmoid curve occurred in one male from C-260 (Fig. 35). In males from C-68 (Fig. 31) and 103 (Fig. 28), both 'C' and 'S' curves were found.

Process **c** showed the greatest degree of variation. A simple form appeared in a male from C-106 (Fig. 34). A bifid form occurred in males from C-103 (Fig. 28), 106 (Fig. 33), 107 (Fig. 30), 159 (Fig. 29), 201 (Fig. 24) and 203 (Fig. 21); in males from C-103, the two prongs diverged widely (Fig. 28), and the base was noticeably thickened in examples from C-159 (Fig. 29) and 106 (Fig. 34). A thicker shape with several to many small acute projections occurred in males from C-64 (Fig. 38), 111, 126 (Fig. 27), 154 (Fig. 26), 162 (Fig. 25) and 260 (Fig. 36). This process was evidently absent entirely in males from C-68 (Fig. 31) and in one male from C-260 (Fig. 36). Finally, males from C-18 showed either simple, bifid, or many-toothed processes (Figs 9, 10).

Thus, while the electrophoretic work revealed three clusters of populations that meet the criterion for genetic isolation, it would not be possible for a systematist working with museum specimens to place males in one cluster or another, or to guess from which cave a male was taken if such data were not available. This poses a practical problem: should the three population clusters, regardless of one's inability to separate them morphologically, each be named to indicate their possible status as sibling species? To do so would be to adopt that hypothesis. We have decided not to name these forms separately but to simply draw attention by this discussion to their relationships. It may be entirely possible that while genetic exchange does not in fact take place between these populations because of geographical isolation, such exchange would be possible if the populations came into contact again (because surely they represent the descendents of a once panmictic ancestor). If in fact gonopod morphology is an isolating factor in millipede speciation [see Eberhard (1985,

1990) for an exhaustive discussion of this subject in animals in general], then all known populations of *S. communis* showing no gonopod variation taken by analogy to be indicative of speciation may be potentially interfertile. By including all these populations under one species name, that is the hypothesis we wish to put forward.

In cave C-111, *S. communis* is sympatric with *S. sympatricus*, and with a predominantly surface-dwelling paradoxosomatid, *Boreohesperus capensis* Shear, 1992. The latter species is also found with *S. communis* in caves C-18, 68, 106, 107, 162 and 203.

Stygiochiropus sympatricus, sp. nov.
(Figs 14–16)

Material Examined

Holotype. ♂, cave C-111, Cape Range, Western Australia, 5.vii.1989, E. R. Wood (WAM 91/1405).

Diagnosis

Distinct from *S. isolatus* in the larger size of the gonopod, and from *S. communis* in the bifid nature of gonopod process **a**.

Description

Length, about 14 mm; width at seventh metazonite, 1·0 mm; third antennal article 0·65 mm long. Structure closely similar to above description of *S. communis*.

Gonopod (Figs 14–16) similar to that of *S. communis*, with the following differences. Width of femorite more even throughout length, maximum width of femorite somewhat less, constriction between femorite and apical division less pronounced. Process **a** more robust, deeply bifid, ectal branch with a small subapical tooth. Process **b** relatively shorter, thicker, more cylindrical, especially at base, hardly curved except near apex, not exceeding solenomerite. Process **c** with distinct bulbous base, shorter, complex, fundamentally bifid but with 3–5 teeth on each branch. Solenomerite with much heavier, bulbous base, thickened portion extending from base nearly to apex, lamina somewhat less expanded.

Remarks

This species is known only from the holotype, though others were sacrificed for the electrophoretic work. The holotype was a deviating male in a collection from cave C-111, so presumably represents the genetically divergent population, but this could only be confirmed by first examining the gonopods of males that would then be used for electrophoresis. However, W.A.S. was immediately able to pick out this male as different from *S. communis* at low magnification under a dissecting microscope. The only available collection contained one male of *S. communis*, one male of *S. sympatricus*, a single female, and six immature individuals. It is not possible to determine which species the female represents. Obviously, additional material of both species from cave C-111 is needed to clarify the status of the two sympatric species.

Cave C-111, the only cave known with sympatric *Stygiochiropus* species populations, is at the extreme north-west of Cape Range and separated from other caves containing *Stygiochiropus* populations by c. 8 km both to the east (C-222) and to the south (C-215; Fig. 1). Another species of paradoxosomatid, *Boreohesperus capensis*, is also found in this cave, but is an obvious accidental or at most a troglophile (Shear 1992). The cave (Breakdown Maze) is a large breakdown structure, mostly dry. The millipedes were collected from a single, small patch of damp mud in the twilight zone. The cave was completely dry in July 1991, and no millipedes were found.

Stygiochiropus isolatus, sp. nov.
(Figs 17–20)

Material Examined

Holotype. ♂, cave C-222, Cape Range, Western Australia, A. J. Humphreys, 30.vi.1989 (WAM 91/1406).

Paratype. ♀, same data (WAM 91/1407).

Diagnosis

Much smaller (7–8 mm long, 0·6 mm wide) than the other species; gonopods (Figs 17–20) with a unique acute shelf-like projection (arrow in Fig. 19) at the end of the femorite, which is absent in the others.

Description

Male

Length, 7–8 mm; width at seventh metazonite, 0·6 mm; third antennal article 0·25 mm long. Structure typical of genus but differing in the much longer segmental setae, producing distinctive setose appearance.
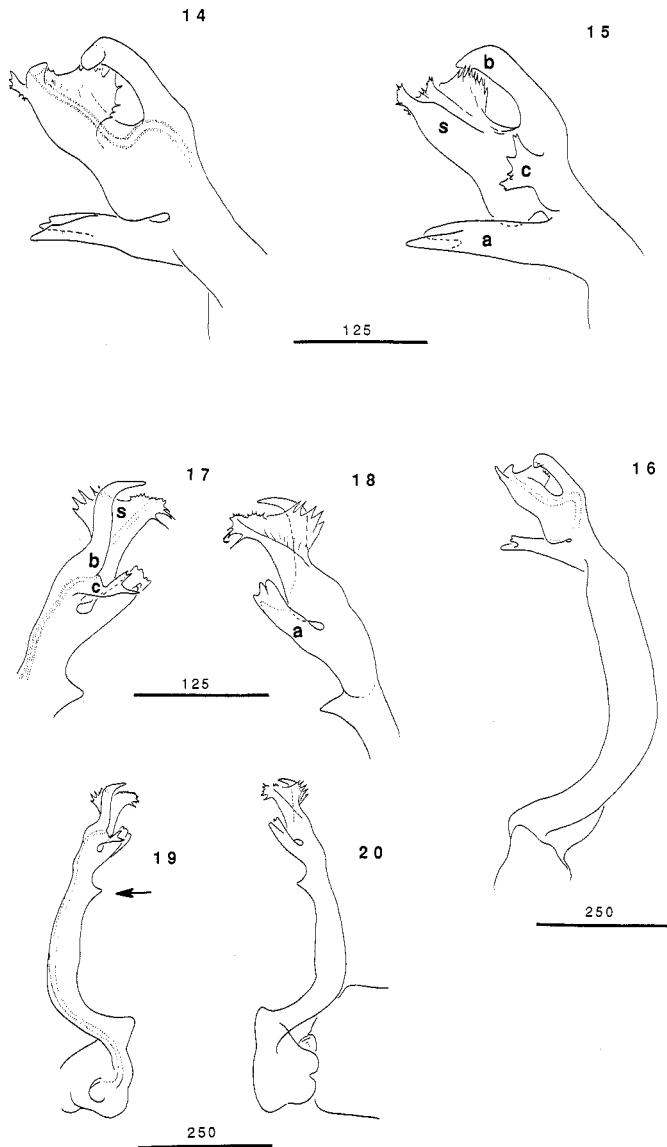
Figs 14–16. *Stygiochiropus sympatricus* gonopods. *14*, lateral view left gonopod; *15*, mesal view right gonopod; *16*, lateral view of left gonopod.   **Figs 17–20.** *Stygiochiropus isolatus* left gonopod. *17, 19*, mesal views; *18, 20*, lateral views. Processes a, b, c and arrow (see text) and the solenomerite (s) are labelled. Scale bars in μm.

Gonopod (Figs 17–20) differs from the other species in the following. Femorite narrowed basally, abruptly widened at about $\frac{1}{3}$ its length, curve less pronounced; femorite ending in pronounced shelf-like or subtriangular projection perhaps representing femoral process, neck separating apical division from femorite less pronounced, but in lateral view entire apical division with distinct bulbous base. Process **a** very heavy, seen in posteroventral view nearly half as wide as long, blunt, ending in 5–7 rounded teeth. Process **b** evenly and shallowly curved, proportionally less robust, about equal to solenomerite. Process **c** relatively gracile, base not pronouncedly bulbous, bifid, ectal branch with 2 apical teeth. Solenomerite with moderately expanded base, otherwise similar to *S. communis*.

Female

Length, 9–10 mm; width at seventh metazonite, 0·7 mm; third antennal segment 0·25 mm long. Nonsexual characters as in male.
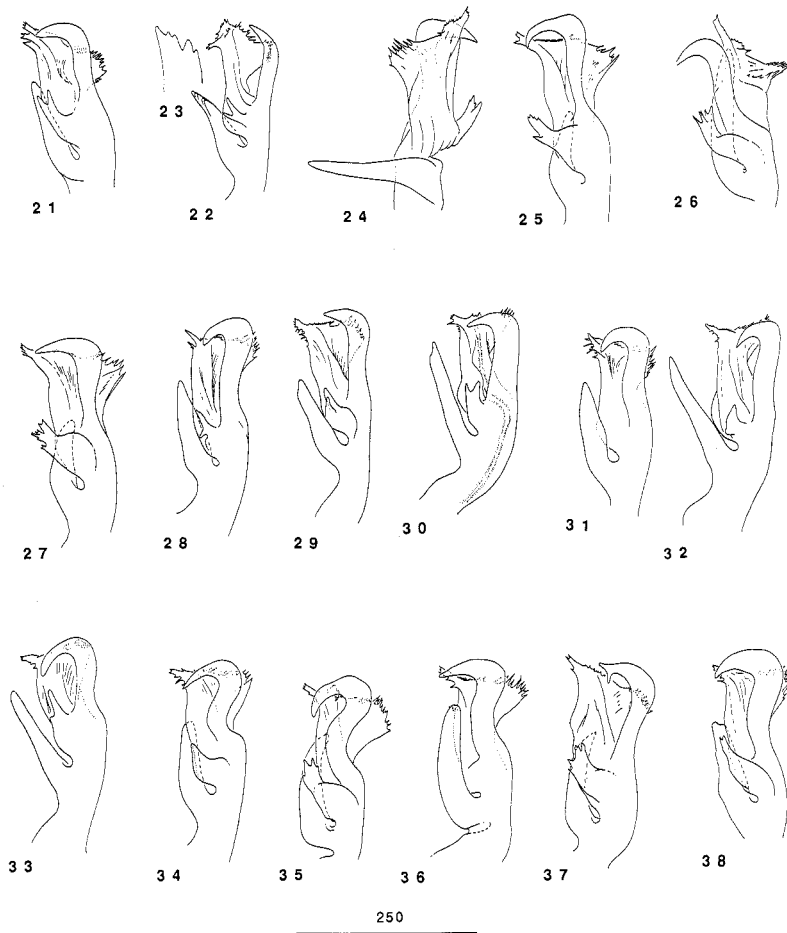
Figs 21–38. *Stygiochiropus communis*, variation in gonopods. The figures are arranged so they represent a schematic latitudinal gradient from south to north across the rows from upper left to bottom right. All represent the mesal view of the right gonopod unless stated otherwise. Cave numbers are denoted with a C- prefix. *21*, C-203; *22*, C-300; *23*, C-300 detail; *24*, C-201 posterio-mesal view; *25*, C-162; *26*, C-154; *27*, C-126; *28*, C-103; *29*, C-159; *30*, C-107; *31*, C-68; *32*, C-18; *33*, C-106; *34*, C-106; *35*, C-260; *36*, C-260; *37*, C-277; *38*, C-64.   Scale bars in μm.

Remarks

Clearly distinct from the other two species, *S. isolatus* is known only from two specimens, but the differences are so strong that its status cannot be in doubt. The overall impression from this species is that of less extreme troglobitic adaptation. The body seems more compact, the antennae and legs less attenuate.

Cave C-222 is at the extreme north-east of Cape Range and separated from other known *Stygiochiropus* populations by *c.* 8 km to the west (C-111) and to the south (C-263; Fig. 1). The cave is a small horizontal tunnel in the side of a gorge. *Stygiochiropus isolatus* was found on a small, isolated, wet patch on a mud-bank just inside the entrance, and in the
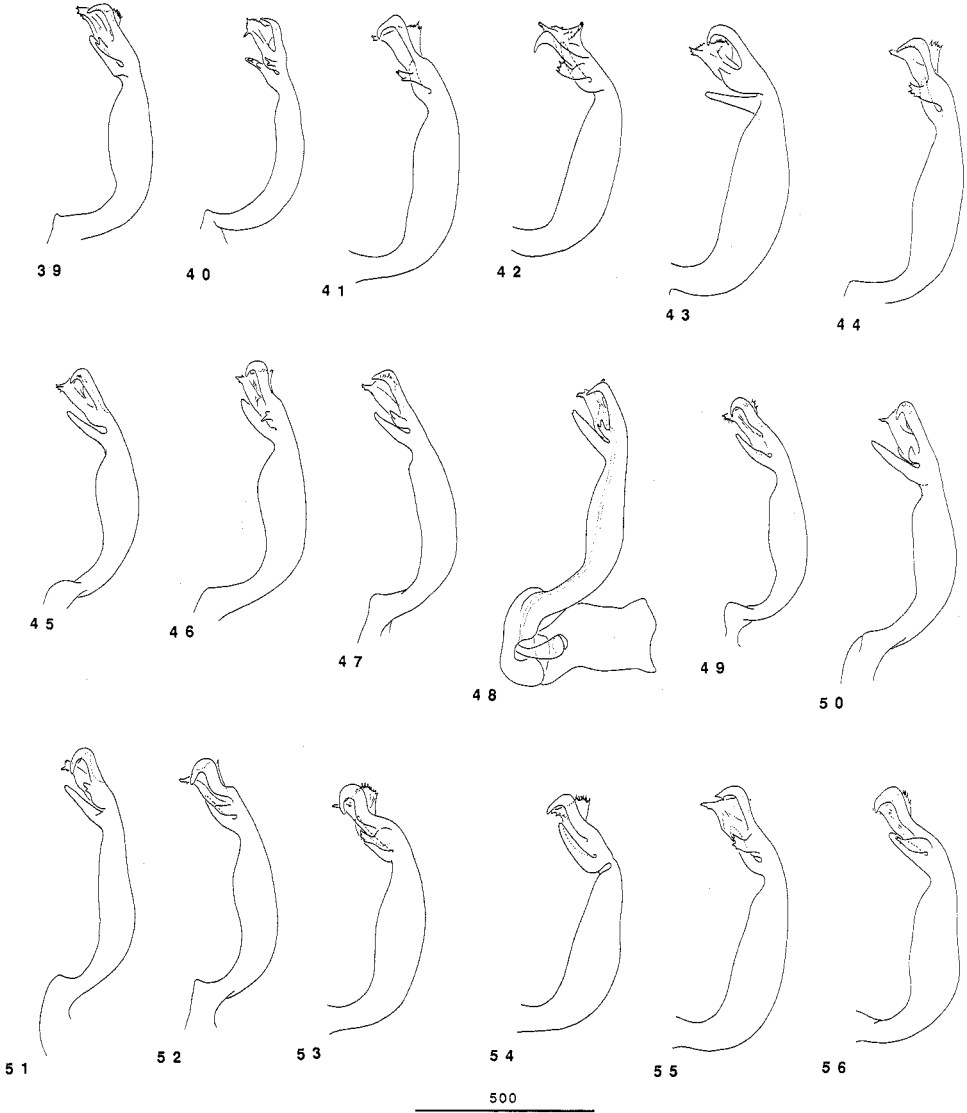

Figs 39–56. *Stygiochiropus communis*, variation in gonopods. The figures are arranged so they represent a schematic latitudinal gradient from south to north across the rows from upper left to bottom right. All represent the mesal view of the right gonopod unless stated otherwise. Cave numbers are denoted with a C- prefix. *39*, C-203; *40*, C-300; *41*, C-162; *42*, C-154; *43*, C-126; *44*, C-126; *45*, C-103; *46*, C-103; *47*, C-159; *48*, C-107; *49*, C-68; *50*, C-18; *51*, C-106; *52*, C-106; *53*, C-260; *54*, C-260; *55*, C-277; *56*, C-64.   Scale bars in μm.

drip zone at the entrance, both in daylight. *Boreohesperus capensis*, a predominantly surface-dweller, has also been taken in this cave (Shear 1992). The cave was completely dry in July 1991, and no millipedes were found.

Discussion

It has been demonstrated experimentally that water and surface organic matter are the prime factors in the re-establishment of millipede populations in caves depleted of
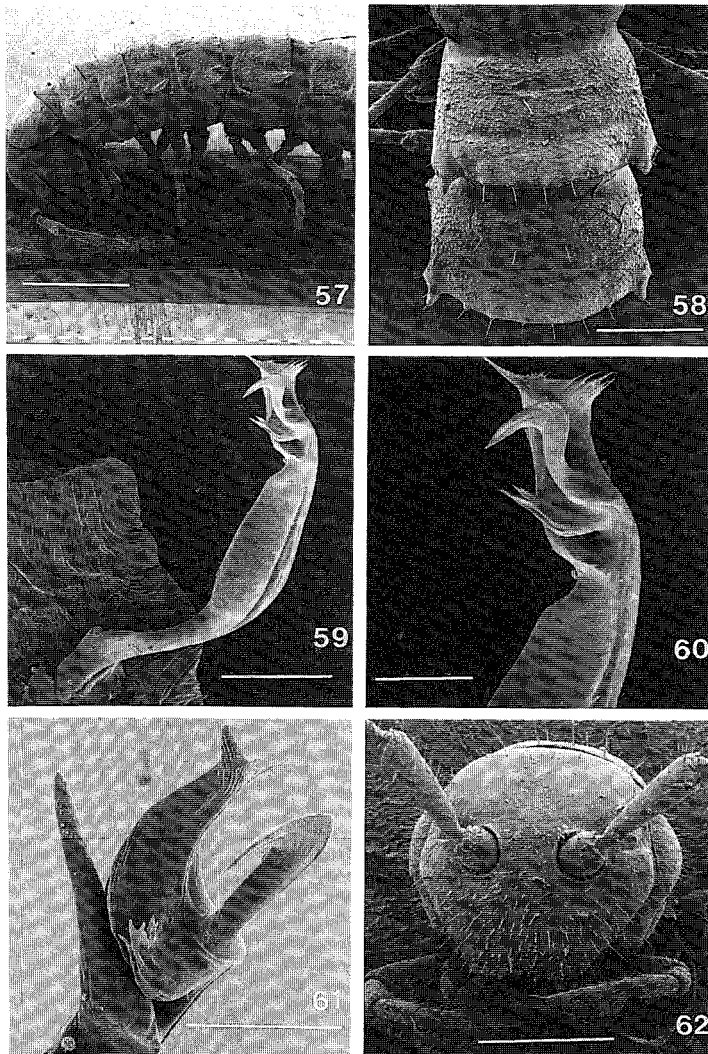
Figs 57–62. Scanning electron micrographs of *Stygiochiropus communis* from cave C-118, a cave in the southern genetic province (Humphreys 1991*b*). *57*, lateral view of male, pores open at the tip of the paranota, scale bar 1000 μm; *58*, dorsal view of two tergites showing the paranota and setae at the posterior margin of the metazonite, scale bar 500 μm; *59*, mesal view of the right gonopod, scale bar 200 μm; *60*, mesal view of the right gonopod, scale bar 100 μm; *61*, anterio-ventral view of the right gonopod; scale bar 100 μm; *62*, anterior view of the head, scale bar 500 μm.

water and energy (Humphreys 1991*b*). While there is no direct evidence of growth rates of *S. communis* in the caves, both field and laboratory evidence are consistent with high growth rates. Hence, it would appear that the millipedes may be opportunistic ('*r*-strategists'), holding on in deeper refugia until conditions become more suitable for them, and then undergoing rapid growth and breeding in the newly but temporarily favourable sites.

We suspect that *Stygiochiropus* millipedes are relictual forest forms that were isolated in caves in the North West Cape when the region became too dry to support forests some time after the Miocene. While some elements of the Cape Range cave fauna have clear rainforest affinities, Jeekel (1980, 1981, 1984, 1985), in the only systematic effort ever mounted to collect millipedes in Australia, found paradoxosomatids more common in open eucalypt forests. However, Jeekel's work was done during an abnormally hot and dry year. It is possible that eucalypt forests, with a richer paradoxosomatid fauna, succeeded rainforest in the North West Cape region as it dried out.

The allozyme analysis is robust in that the samples meet the criteria for adequate genetic work at the within-species level (Richardson *et al.* 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. The only widespread species (*S. communis*) separates into three genetic provinces between which there are substantial fixed allelic differences. These provinces are bounded by clear geomorphological divides, but the millipede populations cannot be separated using morphological criteria.

It is not possible to say whether the three species now known represent separate colonisations or are descended from a single colonising ancestor. The major populations of the millipedes probably exist in a vast maze of underground spaces inaccessible to man, and which may indeed connect with one another over very wide areas. Thus, prior to the erosional barriers that now exist separating the three clusters, *Stygiochiropus communis* could have spread underground from an originally limited area.

This leads to the following historical scenario.

1. Invasion of caves by one or more species of *Stygiochiropus* or its ancestors as the region became more arid after the Miocene.

2. Subsequent extinction of many cave populations, perhaps during dry intervals in the Pleistocene. At this time the three extant species (and perhaps others) were isolated geographically (probably by distance) and in all likelihood 'bottlenecked', leading to strong genetic differences.
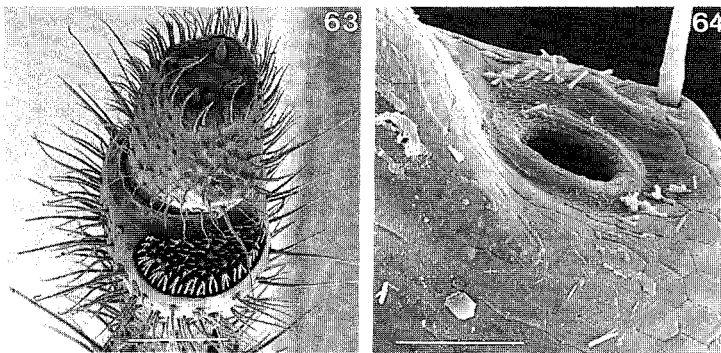
Figs 63, 64.   Scanning electron micrographs of *Stygiochiropus communis* from cave C-118. *63*, two distal segments of the right antenna, note the conical sensilla on the terminal segment and the sensory organ on the penultimate segment (cf. Fig. 13), scale bar 100 μm; *64*, pore opening at the tip of the paranota of segment V; note the hexagonal cuticular pattern, scale bar 20 μm.

3. One of the surviving species (*Stygiochiropus communis*) developed the ability to disperse rather rapidly through the deeper underground connections between caves and, as conditions improved (more moisture), spread out from one or more restricted foci.

4. Subsequently, contact between the three population clusters was cut off by erosion and they began to differentiate, but not enough to produce differences in the gonopods. Part of the population reached cave C-111, already occupied by *Stygiochiropus sympatricus*, which probably evolved there in isolation; the two have coexisted since. *Stygiochiropus communis* probably did not reach cave C-222.

Acknowledgments

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Appendix. Genetic distance matrix

Upper right: corrected Nei's D (×1000). Lower left: % 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	3	–	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	1	–	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	27	27	17	17	22	11
068	35	35	40	31	35	29	35	35	35	35	31	35	24	25	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	25	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	36	29	29	31	31	29	29	29	31	29	18	13	27	18	18	18	6
159	31	31	40	31	25	29	33	25	25	31	29	31	19	27	21	13	13	19	13
215	33	33	33	28	33	24	33	28	28	33	24	33	29	25	40	28	22	33	22
260	28	28	27	25	28	25	25	28	28	28	25	25	18	19	27	17	17	22	11
261	25	25	33	28	28	24	25	25	25	25	24	28	8	18	17	8	8	8	8
281	28	28	33	28	28	24	28	28	28	28	25	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 (*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	6	13	6	6	13	0	0	6	0	–	42	138	72	31	47	580
159	13	13	0	6	12	11	18	6	0	6	0	0	–	215	130	44	116	725
215	22	22	0	0	0	0	6	6	11	11	12	12	19	–	54	190	64	602
260	11	22	0	0	0	0	8	0	0	0	0	0	0	0	–	78	19	557
261	8	8	0	0	0	0	6	0	0	0	0	0	0	17	0	–	45	644
281	11	22	0	0	0	0		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	–