

The cavernicolous Arachnida and Myriapoda of Cape Range, Western Australia

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Abstract

The terrestrial cavernicolous fauna of Cape Range is dominated by a wide array of arachnids and myriapods, of which 64 species have been collected from the caves or their entrances. Sixteen species are fully troglobitic (two schizomids, two pseudoscorpions, one harvestman, seven spiders, four millipedes), while others show either partial modification for cave existence, or are unmodified representatives of the surface fauna that opportunistically occur in the caves. The biogeographic affinities of at least five of these species is found to be tropical Australia, with at least one maintaining links with an ancient Gondwanan fauna presently found in northwestern Australia, India, and southern Africa (including Madagascar). Another distinct component of the cavernicolous fauna is derived from southern Australia. The significance of the Cape Range troglobitic arachnid and myriapod fauna is highlighted by comparisons between the faunae in three other Australian karst systems (Nullarbor Plain, Chillagoe, and Tasmania) in which the richness of the Cape Range fauna is exceeded only by the Tasmanian region, which contains twice as many troglobites but which includes over 60 karst regions. Complete knowledge of the cavernicolous fauna is hampered by lack of taxonomic expertise and, in some cases, lack of sufficient specimens.

Introduction

Australia has the dubious honour of being the second driest continent (after Antarctica) on Earth, with an annual average rainfall of 451 mm (Bridgewater 1987), with much of this concentrated on the eastern seaboard, the northern tropics, and the extreme southwest of Western Australia. Much of the flora and fauna of the country shows marked adjustments to aridity, with peculiar life-cycles to exploit irregular rainfall patterns, or with unusual morphological traits to cope with a parched land. In desert regions, few clues remain of a bygone era when wetter climatic regimes were prevalent. Fossils provide some clues, but are generally poorly represented due to subsequent erosion and inadequate quality. Relictual habitats may provide other clues, with gorges often supporting relictual suites of organisms. Another relictual habitat is cave environments. The weathering and erosion of suitable substrates allow smaller animals, particularly arthropods, to move into fissures and caverns where moisture and humidity are maintained at higher levels than on the dry surface. These cavernicolous environments allow a glimpse into the past that partially reflects the environment prior to the time of ecological stress, such as glaciation or aridity.

Arachnids and myriapods have been recorded from a variety of Australian cave systems (Hamilton-Smith 1967), such as the Nullarbor Plain (South Australia/Western Australia), Margaret River (Western Australia), Jenolan (New South Wales), Chillagoe (Queensland), Naracoorte (South Australia), Buchan (Victoria) and various regions of Tasmania. The recent

discovery of a rich, previously uncollected cavernicolous fauna in Cape Range, Western Australia, heralds a significant expansion in the troglobitic arthropod fauna of Australia.

The Cape Range arachnid and myriapod fauna is an exciting blend of taxa that suggests an ancient and diverse past. This paper presents a summary of those species collected from the caves. The other arthropods groups that have been encountered in the caves are either treated in this volume (aquatic Crustacea: Knott 1993) or are excluded due to the lack of sufficient identifications (Insecta).

Materials

All specimens mentioned in this paper are lodged in the Western Australian Museum, Perth, or the Australian Museum, Sydney, and were collected on a variety of expeditions to the region, mostly under the leadership of Dr W.F. Humphreys. Caves were searched by hand, and specimens collected from the walls and floor of the caves, under rocks or amongst litter. Some specimens were extracted from litter with the aid of Tullgren funnels.

Results and discussion

Of the fauna considered in this paper, 54 species of arachnids and 10 species of myriapods were found either in the caves or their entrances (Tables 1, 2), with 16 species considered to be fully troglobitic. These are discussed in detail below.

The definitions utilised here for troglobite (Tb), troglophile second level (Tp2), and troglophile first level (Tp1) follow Hamilton-Smith (1967).

Class Arachnida

Schizomida

The most abundant is *Draculoides vinei* (Harvey) which occurs in many caves in the Tulki Limestone region. Specimens of *D. vinei* feed upon other cavernicolous small arthropods such as isopods, other schizomids, millipedes, cockroaches and earthworms (Vine *et al.* 1988; Humphreys *et al.* 1989). The limited electrophoretic data available indicate that a single species is represented (Humphreys *et al.* 1989), although the small sample size and lack of polymorphic loci restricts the interpretation (Adams and Humphreys 1993). A second, smaller species of *Draculoides* has recently been collected from cave C-452 on the coastal plain which appears to be conspecific with an undescribed cavernicolous species from Barrow Island, Western Australia. These two species are the only known species of the genus *Draculoides*, whose affinities lie with the tropical northern Australian fauna (Harvey 1992).

Pseudoscorpionida

Six species have been recorded to date (Harvey 1991, 1993). The three chthoniids (*Austrochthonius easti* Harvey, *Tyrannochthonius butleri* Harvey and *T. brooksi* Harvey) are small pseudoscorpions which display varying degrees of morphological modifications that can be attributed to cave life, and varying biogeographic affinities. *A. easti* has only two small eyes, and other members of the genus are known from northwestern and southwestern Australia (as well as eastern Australia, New Zealand, South America and South Africa). *T. brooksi* retains a full complement of four eyes, while *T. butleri* is completely blind and possesses long, slender appendages which are commensurate with its status as a troglobite. A single undescribed species of *Tyrannochthonius* has been collected from surface regions of

Table 1. List of Arachnida collected from Cape Range caves. Tb, troglobite, obligate cave inhabitant; Tp2, troglophile, always in caves; Tp1, troglophile, not always in caves. * = Australian Museum specimens.

Taxon	Status	Caves	Authority	Relatives
Schizomida				
Hubbardiidae				
<i>Draculoides vinei</i> (Harvey)	Tb	15 18 56 62 63 64 65 102 103 106 107 113 118 126 142 154 156 159 160 161 162 167 203 207 227 247 250 254 256 260 263 277 291 300 402 [163 169 278 -sightings, but no specimens]	Harvey (1988, 1992)	N. Australia/Cape Range
<i>Draculoides</i> sp.	Tb	452	Harvey (unpublished data)	Barrow I./N. Australia
Pseudoscorpionida				
Chthoniidae				
<i>Astrochthonius easti</i> Harvey	Tp2	18 222 103	Harvey (1991)	N. & S. Australia
<i>Tyrannochthonius butleri</i> Harvey	Tb	167 291 15	Harvey (1991)	N. & S. Australia?
<i>Tyrannochthonius brooksi</i> Harvey	Tp2	21 107 111	Harvey (1991)	N. & S. Australia?
Syarinidae				
<i>Ideoblothrus woodi</i> Harvey	Tp2	167	Harvey (1991)	N. Australia
<i>Ideoblothrus papillon</i> Harvey	Tp2	15	Harvey (1991)	N. Australia
Hyidae				
<i>Hyella humphreysi</i> Harvey	Tb	15 103	Harvey (1993)	N. Australia, India, Madagascar
Opiliona				
Assamiidae				
? <i>Anjulus</i> sp. (undescribed)	Tb?	65 103 167 179 345	Hunt (unpublished data)	N. Australia
Araneae				
Barychelidae				
Genus? sp.	Tp1	15 63 167		Australia
Filistatidae				
Undescribed genus and species	Tp2	18 64 94 141 199 256 294*	Gray (1994)	India
Pholcidae				
<i>Trichocyclus septentrionalis</i> Deeleman-Reinhold	Tp1	4 18 60 64 65 68 91 96 102 106 107 111 119 144 147 156 16 162 177 198 200 215 221 224 227 230 291 295 Bunbury 402	Deeleman-Reinhold (1993)	Western Australia
Segestriidae				
<i>Ariadna</i> sp.	Tp1	4 18 27		World-wide

Table 1 (cont).

Taxon	Status	Caves	Authority	Relatives
Desidae				
Genus? sp.	Tb	18 103 106 107 188		?
<i>Forsterina</i> sp.	Tp1	18 21 47 91 94* 96 107 118 142 156 161 162 167* 199 200 215 221 222 263 278 300 328 345		Australia, New Caledonia
Lycosidae				
<i>Lycosa</i> sp.	Tp1	324		Australia
Ctenidae				
Undescribed genus and species 1	Tb	15 18 21 65 103 104 106 118 126 159 162 163 167 169 227 254 256 278	Gray (unpublished data)	N.W. Cape, Barrow I., N. Qld
Undescribed genus and species 2	Tp1	161 203	Gray (unpublished data) N.Qld	N.W. Cape, Barrow I., N.Qld
Selenopidae				
<i>Selenops</i> sp.	Tp1	94		World-wide
Corinnidae				
<i>Supunna</i> sp.	Tp1	6		Australia
Gallieniellidae				
Genus? sp.	Tp1	15 63 64 68 91 107 111 118 119 156 162 203 215 300 + surface	Platnick (unpublished data)	E. Australia, Madagascar, Comoro
Gnaphosidae				
Genus A sp.	Tp1	203		?
Genus B sp.	Tp1	15 47		?
Genus C sp.	Tp1	15		?
Genus D sp.	Tp1	64 119 222 224		?
Trochanteriidae				
Genus? sp.	Tp1	15		?
Uloboridae				
<i>Philoponella</i> sp.	Tp1	15 107 215 222 Bunbury		World-wide
<i>Uloborus</i> sp.	Tp1	4		World-wide
Cyatholipidae				
<i>Matilda</i> sp.	Tp1	106		Australia
Symphytognathidae				
<i>Anapistula</i> sp.	Tb	15 126 167		Northern Australia/Tropics
Mysmenidae				
Genus? sp.	Tp2	15 91 141 260 291		?
Theridiidae				
<i>Steatoda</i> sp. 1	Tb	18 107 161		World-wide

Taxon	Status	Caves	Authority	Relatives
<i>Steatoda</i> sp. 2	Tp1	162		World-wide
<i>Pholcomna</i> sp.	Tb	47		World-wide
Linyphiidae				
<i>Dunedinia occidentalis</i> Millidge	Tb	106	Millidge (1993)	Southern Australia/New Zealand
<i>Chthiononetes tenuis</i> Millidge	Tb	18 106 162 188 324	Millidge (1993)	Southern Australia/New Zealand
Acarina: Prostigmata				
Penthaleidae sp.	Tp1?	106 167		?
Acarina: Mesostigmata				
Ascidae				
? <i>Cheiroseius</i> sp.	Tp1?	167		World-wide
Ascinae sp.	Tp1?	167		?
Laelapidae: Laelapinae sp. 1	Tp1?	18		?
Laelapidae: Laelapinae sp. 2	Tp1?	167		?
Acarina: Astigmata				
Acaridae				
? <i>Tyrophagus</i> sp.	Tp1?	167		?
Family? sp.	Tp1?	167		?
Acarina: Cryptostigmata				
Brachychthoniidae				
<i>Brachychthonius</i> sp.	Tp1?	167		?
Eremobelbidae				
<i>Eremobelba</i> sp.	Tp1?	167		?
Galumnidae sp.	Tp1?	167		?
Haplozetidae sp.	Tp1?	167		?
Hypochthoniidae				
<i>Eohypochthonius</i> sp.	Tp1?	167		?
Lohmanniidae sp. 1	Tp1?	167		?
Lohmanniidae sp. 2	Tp1?	167		?
Oppiidae sp.	Tp1?	18		?
"Phthiracaroid" sp.	Tp1?	167		?
Xylobatidae sp.	Tp1?	18		?
"Plateremaeoid" sp.	Tp1?	167		?

Cape Range that appears to be closely related to the two troglobites. They all possess homodontate chelal teeth and a small, rounded epistome which are relatively uncommon character states within the genus (Harvey 1991).

The two syarinids, *Ideoblothrus woodi* Harvey and *I. papillon* Harvey, are extremely similar to each other and appear to represent sister-species. *Ideoblothrus* is a common tropical genus (Muchmore 1982), with several known troglaphiles.

Hyella humphreysi Harvey, which represents a new genus and species of Hyidae, is the most extremely cave-adapted pseudoscorpion in Australia, with large body size, very long, slender appendages, and complete absence of eyes. Despite careful searching for this species, it remains one of the most elusive troglobites of Cape Range. Its affinities lie with Gondwana, as it is placed with *Indohya* in a subfamily that is known only from southern India, northwestern Australia and Madagascar (Harvey 1993).

Opilionida

Only one definite species has been recorded and belongs to the largely tropical family Assamiidae. Compared to surface species, it is relatively pale, has a low eyemound, attenuated legs, and its elongate pedipalps are armed with long spines. These characters are possible adaptations to life in caves. The eyes appear slightly reduced but are nevertheless conspicuous.

Despite being collected from several caves, most specimens were taken from the "northern electrophoretic province". A single juvenile has been taken from a cave in the "southern electrophoretic province". It will be interesting to see whether the distribution of harvestmen species or electrophoretic variants correlates with the "electrophoretic provinces" established for other taxa (Adams and Humphreys 1993).

A closely related species has been taken from a lava tube cave in northern Queensland, but is much more pigmented and has a larger eyemound and eyes than the apparently troglitic Cape Range species. The Cape Range and northern Queensland species are clearly congeneric with three undescribed species from the Kimberley region, and with a species from the King River area, Northern Territory, which was recorded and described by Forster (1955) but incorrectly identified as *Euwintonius continentalis* Roewer (Hunt, unpublished data).

The three Kimberley species were identified as *Dampetrus* spp. and *Dampetrellus* sp. (Hunt 1991) but closer study reveals that they belong to a single genus distributed across northern Australia. All of these species may belong to a new genus, or may possibly be referable to the monotypic *Anjulus* which occurs in the Kimberley. Data from a male of *A. malkini* Goodnight and Goodnight will be necessary before a decision can be made.

The Assamiidae of Australia probably originated in tropical southeast Asia and New Guinea (Hunt 1993).

Araneae

The spider fauna is clearly a dominant portion of the Cape Range cavernicolous fauna, with several species occurring at moderately high densities in many of the caves. A preliminary list was provided by Gray (1989), based solely on the Australian Museum collections; some of these identifications now require modification (see below).

Five juvenile barychelids were taken from three caves. These specimens exhibit no troglomorphic tendencies and are presumed to represent epigeal species.

The filistatid represents a new species in a genus whose closest relatives occur in eastern India (Gray 1994). Its large size and reduced anterior median eyes are atypical for the family.

Table 2. List of Myriapoda collected from Cape Range caves. Tb, troglobite, obligate cave inhabitant; Tp2, troglophile, always in caves; Tp1, troglophile, not always in caves.

Taxon	Status	Caves	Authority	Relatives
DIPLOPODA				
Polyxenida				
Polyxenidae	Tp1	65		Semi-arid Australia?
Polyzoniida				
Siphonotidae	Tb?	18		Southern Australia
Polydesmida				
Paradoxosomatidae				
<i>Boreoesperus capensis</i> Shear	Tp1	18 21 68 107 111 162 177 203 222 225 232 324 328	Shear (1992)	Southern Australia?
<i>Antichiropus humphreysi</i> Shear	Tp1?	225	Shear (1992)	Southern Australia?
<i>Stygiochiropus communis</i>	Tb	15 18 47 56 64 65 68 79 102 103 104 106 107 111 118 119 126 152 154 156 159 161 162 163 167 171 201 203 207 215 227 254 256 260 261 263 277 278 281 291 300 312	Humphreys and Shear (1993)	Southern Australia?
<i>Stygiochiropus sympatricus</i> Humphreys and Shear	Tb	111	Humphreys and Shear (1993)	Southern Australia?
<i>Stygiochiropus isolatus</i> Humphreys and Shear	Tb	222	Humphreys and Shear (1993)	Southern Australia?
Chilopoda				
SCUTIGERIDA				
Scutigeridae				
<i>Allothereua maculata</i> (Newport)	Tp1	291		Semi-arid Australia
SCOLOPENDRIDA				
Cryptopidae	Tp1	18 107		?
GEPHILIDA	Tp1?	18 103 106 126 162 225		?

Individuals builds webs associated with bat guano, where they presumably feed upon other arthropods such as mites.

Trichocycclus septentrionalis Deeleman-Reinhold (Pholcidae: ?*Pholcus* in Gray 1989) commonly occurs in large flimsy webs in the entrances of caves and overhangs in Cape Range. It is only the second species of the genus (Deeleman-Reinhold 1993); the other was originally recorded from Yalgoo, Western Australia, and is common in the mideastern wheatbelt (B.Y. Main, personal communication).

Four specimens of *Ariadna* sp. (Segestriidae) have been taken in two caves. Specimens of this genus occur in silken tubes amongst rocks in many parts of arid Australia, and the cave habitat is not obligatory.

Of the two species of Desidae, one is represented by a small weakly pigmented female provisionally placed in this family. The other is a species of *Forsterina*, an Australian and New Caledonian genus with a continental distribution (Gray 1992b, and unpublished data). This species is not obviously cave-adapted but seems to be confined to the cave biotope (especially entrance chambers). A different species occurs on the surface.

Several juvenile lycosids were taken from C-324 that are clearly an epigeal species.

The large, completely blind ctenid (undescribed genus and species), represents a species restricted to the Cape Range caves. They are very pale and roam freely over the floors and lower walls of the caves. A similar epigeal species has been collected from Cape Range which differs from the cave form by the presence of eyes and the form of the female genitalia. These spiders are related to other cavernicolous and epigeal species from southern and northeastern Australia, including *Janusia muiri* Gray. They are closely allied to the southern African ctenoid genera *Phanotea* and *Machadonia* (Gray, unpublished data). *Phanotea* also contains several cavernicolous species (Lawrence 1952, 1964).

A single immature *Selenops* sp. was found in C-94, which undoubtedly represents a surface form.

The gallieniellid is found in the twilight zone of several caves, and is clearly troglophilic; the family is only known from Australia, Madagascar, the Comoro Islands and southern Africa (Platnick 1990).

Four species of Gnaphosidae were taken within Cape Range caves, although all appear to be surface species only occasionally found in cave twilight zones. A single female gnaphosid (Genus A) was found in C-203; its pale colouration may indicate a preference for cave habitation, but no further specimens have been encountered, and it may simply represent a surface species. Genus B and Genus C are clearly surface species. Genus D was found in four caves and in pitfall traps in surface environments.

A single trochanteriid was found dead in C-15, and appears to be identical to a male collected in surface pitfall traps.

Two uloborids have been collected from their orbwebs in cave entrances: *Philoponella* sp. and *Uloborus* sp. It seems likely that these are widespread species occurring in rock overhangs, cave entrances and other protected places in the region.

A single female *Matilda* sp. (Cyatholipidae) was taken from C-106 deep within the cave. It does not appear to possess any troglomorphic tendencies and is considered a first level troglophile.

Anapistula sp. is an undescribed species of Symphytognathidae (Mysmenidae: *Mysmenopsis* in Gray 1989) that is the only known cavernicolous representative of the family. It is extremely pale, has elongate appendages, and possesses two indistinct eyespots. Other species of the

genus are known from central America, central Africa, and northern Australia (Forster and Platnick 1977; Harvey, unpublished data).

The Mysmenidae are represented by a single species which may represent an undescribed genus (Harvey, unpublished data). Mysmenids can be found in the entrances of caves in several regions of Western Australia.

Three theridiid species have been found in the caves, and all retain their eyes. A small, pale species tentatively assigned to *Steatoda* is known from three caves. A solitary female from cave C-162 of a second species is also assigned to *Steatoda*; it appears to be a surface species fortuitously taken in the cave. A single female of another species tentatively assigned to *Pholcomma* (Anapidae in Gray 1989) is also small and pale; it resembles other undescribed species of this genus from Nullarbor and Margaret River caves.

The Linyphiidae are represented by two species which possess slightly elongate legs, but which appear to lack any other cavernicolous traits. *Chthiononetes tenuis* Millidge (Nesticidae: *Nesticella* in Gray 1989) is common in several of the caves, whilst *Dunedinia occidentalis* Millidge is currently represented by a single male (Millidge 1993). The affinities of both species lie amongst the southern regions of Australasia (Millidge 1993).

Acarina

Numerous mites were encountered in the caves, and 23 species have been identified (Table 1). At present, it is difficult to determine the level of cave adaptations due to insufficient knowledge of soil and surface mites in the region. Norton *et al.* (1983) report *Paralycus* sp. (Pediculocheilidae) from leaf litter and soil at the base of a large fig at Goat Cave (C-17).

Class Diplopoda

Polyxenida

A single polyxenid was collected from C-65, which seems to represent an epigeal incursion.

Polyzoniida

A single sucking millipede of the family Siphonotidae was collected from C-18. It is difficult to determine the affinities of this species, but the family tends to possess a Gondwanan distribution, although some genera are known from the tropical regions of southeast Asia (Hoffman 1979).

Polydesmida

Five polydesmids of the family Paradoxosomatidae have been recorded from the caves of Cape Range, with varying levels of cave adaptations. *Boreoesperus capensis* Shear and *Antichiropus humphreysi* Shear are apparently unmodified for existence in caves (Shear 1992). *B. capensis* belongs to an endemic Cape Range genus which is known from several caves, as well as cave entrances and surface habitats near caves. *A. humphreysi* is known only from cave C-225 (Shear 1992). The recently described genus *Stygiochiropus* and its three new species is known from the peninsula (Humphreys and Shear 1993), which are all highly modified for cave existence. They are extremely pale, and possess elongate appendages and body segments. *S. communis* is widespread in the Range and occurs in numerous caves. Three distinct populations are discernible by allozyme electrophoresis, but distinguishing

morphological characters cannot be found (Humphreys and Shear 1993). The other two species are known from single caves.

Class Chilopoda

Several species of centipedes are known to inhabit the caves, and none appear to be restricted to the caves, although further study may reveal that the geophilids possess cavernicolous traits.

Scutigera

Allothereua maculata (Newport) was collected from one cave, and the larger *A. lesueurii* (Lucas) was occasionally observed in entrances where they sit on the walls of caves or on rocks. *Allothereua maculata* was also collected from epigeal habitats, most often in pitfall traps. Hamilton-Smith (1967) reports an unidentified scutigera from Cape Range.

Scolopendrida

Two caves were found to contain cryptopid centipedes, which presumably represent incursions from surface or interstitial habitats.

Geophilida

Several unidentified geophilids have been found in the Cape Range caves, and on the surface. It is not known how many species are involved.

The surface fauna

Knowledge of the surface fauna of Cape Range is crucial to our understanding of the cave systems, even if it shows that the faunas are completely different, and do not overlap. Limited pitfall trap collections have yielded significant numbers of arachnids and myriapods that seem to be typical inhabitants of the semi-arid zones of Western Australia, mostly unrelated to the cave fauna. Only two genera of troglotic (or Tp2) arachnids and myriapods possess representatives on both the surface and in the caves: the ctenid and *Tyrannochthonius*. Further collections and study of the presently unknown male of the ctenid are needed to ascertain the significance of the surface species to their cavernicolous congeners.

Biogeography

The affinities of the Cape Range cavernicolous arachnids and myriapods are diverse. Several groups (*Draculoides*, Syarinidae, Hyidae, Assamiidae, Ctenidae, etc.) have their closest relatives in northern Australia. Others have affinities with western Gondwana: the filistatid appears to be most similar to an Indian species, while the hyid belongs to a genus that is the sistergroup of *Indohya* known from the relictual rainforests of India, Madagascar and the Kimberley region of Western Australia.

Others, such as the millipedes, and the spiders *Pholcomma* and the linyphiids, are clearly representatives of a southern fauna.

The remaining have obscure or widespread affinities, often due to uncertain knowledge of relationships within major taxonomic groups. For example, congeners of the pseudoscorpion *Austrochthonius easti* occur in southern and northern Western Australia, southeastern and northeastern Australia (Harvey 1991, unpublished data), South Africa, New Zealand and

southern South America. A wide ranging revision of the genus may reveal distinct clades within the Australian radiation that could give clear indications of the affinities of *A. easti*. However, due to the large number of undescribed species (Harvey, unpublished data), such a study is not possible in the short term, despite the potentially powerful information that this may provide concerning the origins of the Cape Range fauna.

These diverse origins of the fauna may indicate disparate temporal invasions into the caves from periods when the Cape was blanketed by northern tropical rainforests and, later, southern temperate rainforests (Truswell 1990).

Few Cape Range cavernicoles are represented by epigeal congeners on the peninsula. Three arachnid groups have representatives found in both ecosystems which may lend themselves to future research on relationships between surface and cave species. The first is the blind ctenid which has an eyed and partially pigmented representative on the surface. An intriguing possibility is the prospect that the eyed species may have evolved from a blind, cave ancestor once epigeal conditions alleviated. The second is the two species of *Steatoda*, but this relationship is very weak, and depends on the correct placement of the cave species in this genus (see above). The third case is *Tyrannochthonius* in which the three species display an array of modification, from fully troglobitic to fully epigeal. Firm evidence that these groups of species are each others closest relatives is currently lacking, mostly due to unresolved taxonomic problems within the genera.

Comparisons with other karst regions

Few karst regions of Australia are as well collected and documented as that of Cape Range, but broad comparisons can be made with at least three zones (Table 3). Comparisons are here made only with troglobites (Tb).

Nullarbor, South Australia/Western Australia

The Nullarbor caves contain a small number of troglobitic arachnid and myriapod species (Main 1969; Richards 1971; Gray 1973, 1992a) (the family names have since changed in two cases). The three spiders listed by Richards (1971) (*Troglodiplura lowryi* Main, *Tartarus mullamullangensis* Gray and *Janusia muiri* Gray) can now be augmented with *Icona* sp., *Tartarus nurinensis* Gray, *T. murdochensis* Gray and *T. thampannensis* Gray (Gray 1992a).

A new genus of Scolopendrida is known from N37.

Chillagoe, Queensland

The Chillagoe cave region (including the lava caves in the McBride Formation, 100 km SW. of the Chillagoe limestone), situated in tropical Queensland, contains a rich troglobitic fauna, over half of which come from Bayliss Cave (Howarth 1988). Numerous arachnids and myriapods have been recorded (Table 3), including one schizomid, one pseudoscorpion, two opilionids, six spiders, four millipedes and one centipede.

Tasmania

The invertebrate cavernicolous fauna of Tasmania's 60 or more karst regions was recently reviewed by Eberhard *et al.* (1991), who list numerous troglobitic arachnids and myriapods, including at least four pseudoscorpion species (all of the genus *Pseudotyrannochthonius*), five opilionid genera, numerous spiders, and two species of millipedes. The age of the fauna is not known with certainty, but the diversity seems to indicate a lengthy period of isolation.

Table 3. Comparisons between arachnid and myriapod troglobites (Tb) of four karst regions in Australia, with approximate comparative data on the systems.

	Cape Range	Nullarbor	Chillagoe	Tasmania
Maximum age of karsts (y)	<12 million	15 million	10 million	Not known with certainty
Area (km ²)	1700	ca. 195,000 (entire Nullarbor Plain)	not known with certainty	21,000
Cave temperature (°C)	17°-29°	13°-19°	19°-30°	4°-12° (mostly 9°-10°)
Order				
Family				
Schizomida				
Hubbardiidae	<i>Draculoides vinei</i> Harvey <i>Draculoides</i> sp. (undescribed)		Genus, sp. indet	
Pseudoscorpionida				
Chthoniidae	<i>Tyrannochthonius butleri</i> Harvey		<i>Tyrannochthonius rex</i> Harvey	<i>Pseudotyranochthonius typhlus</i> Dartnall <i>Pseudotyranochthonius</i> (>3 spp.)
Hyidae	<i>Hyella humphreysi</i> Harvey			
Opilioniida				
Assamiidae	? <i>Anjulus</i> sp. (undescribed)			
Triaenonychidae				<i>Hickmanoxyomna</i> (6 spp.) <i>Lomanella troglodytes</i> Hunt(1 sp.) <i>Nuncioides</i> (1 sp.) <i>Mestonia</i> (1 sp.) <i>Notonuncia</i> (1 sp.)
Phalangodidae			<i>Zalmoxis lavacaverna</i> Hunt <i>Zalmoxis</i> sp.	
Araneae				
Nemesiidae		<i>Troglodiplura lowryi</i> Main		
Pholcidae			<i>Spermophora</i> sp. (undescribed)	
Oonopidae			Gen., sp. indet	
Stiphidiidae		<i>Tartarus mullamullangensis</i> Gray <i>Tartarus murdochensis</i> Gray <i>Tartarus nurinensis</i> Gray <i>Tartarus thampannensis</i> Gray		Undescribed genus and species
Desidae	Gen., sp. indet.			
Ctenidae	Undescribed genus 1	<i>Janusia muiri</i> Gray	Undescribed genus 2	

	Cape Range	Nullarbor	Chillagoe	Tasmania
Zodariidae			" <i>Storena</i> " sp. (undescribed)	
Symphytognathidae	<i>Anapistula</i> sp. (undescribed)			
Micropholcommatidae				<i>Olgania</i> (several spp.)
Anapidae				<i>Chasmocephalon</i> sp.
Gen. indet.				
Mysmenidae				Undescribed genus and species
Theridiidae	<i>Steatoda</i> sp. 1 <i>Pholcomma</i> sp.	" <i>Icona</i> " sp.		" <i>Icona</i> " (several spp.)
Nesticidae			<i>Nesticella</i> sp. (undescribed)	
Synotaxidae				<i>Tupua troglodytes</i> Platnick <i>Tupua cavernicola</i> Platnick
Linyphiidae	<i>Dunedinia occidentalis</i> Millidge <i>Chthiononetes tenuis</i> Millidge		Gen., sp. indet.	
Polyxenida				
Family?			Gen., sp. indet.	
Polyzoniida				
Siphonotidae	Gen., sp. indet.			
Polydesmida				
Paradoxosomatidae	<i>Stygiochiropus communis</i> Humphreys and Shear <i>Stygiochiropus sympatricus</i> Humphreys and Shear <i>Stygiochiropus isolatus</i> Humphreys and Shear			
Dalodesmidae				Gen. indet. (2 spp.)
Family?			Gen., sp. 1 Gen., sp. 2	
Spirostreptida				
Family?			Gen., sp. indet. (as Cambalida)	
Scutigera				
Scutigera			Gen., sp. indet.	
Scolopendrida				
Family?		Undescribed genus		
Total	16	8	14	> 29

Conclusions

Despite the small karst area of Cape Range, the region contains a significant number of troglobites (Table 3). Compared with other cave systems in Australia, Cape Range contains a diverse and biogeographically interesting arachnid and myriapod fauna, with more species known than from either the entire Nullarbor Plain or Chillagoe/McBride regions. The maximum age of the Cape Range, Nullarbor and Chillagoe systems is middle to late Miocene, when each area was uplifted above the marine zone and weathering of the limestone into karst features could begin (Wyrwoll *et al.* 1993).

The troglobitic arachnids and myriapods of Cape Range comprise approximately half of the known terrestrial troglobitic fauna of Australia, and are clearly significant components of the cave ecosystems present in the region.

One of the greatest limiting factors in understanding the origins of the Cape Range cavernicolous fauna is the lack of taxonomic descriptions and comparable descriptions of the epigeal fauna to place the cavernicolous fauna in perspective. This requires a huge amount of work, as it is generally acknowledged that the terrestrial arthropod fauna is the least studied and most poorly known of any animal group (Wilson 1988), with a diminishing number of taxonomists to conduct the research (e.g. Coddington *et al.* 1990; Wheeler 1990). Although 63% of the Cape Range arachnid and myriapod troglobites are described or in press, the lack of specialists for several families or the lack of sufficient specimens for other taxa limits the speed at which the fauna can be described and placed in a regional or global biogeographic context.

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References

- Adams, M. and Humphreys, W.F. (1993). Patterns of genetic diversity within selected subterranean fauna of the Cape Range peninsula, Western Australia: systematic and biogeographic implications. *Records of the Western Australian Museum, Supplement* 45: 145-164.
- Bridgewater, P.B. (1987). The present Australian environment terrestrial and freshwater. Pp. 69-100 in G.R. Dyne and D.W. Walton (eds). *Fauna of Australia, vol. 1A. General articles*. Australian Government Publishing Service, Canberra.
- Coddington, J.A., Larcher, S.F. and Cokendolpher, J.C. (1990). The systematic status of Arachnida, exclusive of Acari, in North America north of Mexico. Pp. 5-20 in M. Kosztarab and C.W. Schaefer (eds). *Systematics of the North American insects and arachnids: status and needs*. Virginia Agricultural Experiment Station Information Series 90-1. Virginia Polytechnic Institute and State University, Blacksburg.
- Deeleman-Reinhold, C.L. (1993). *Trichocyclus septentrionalis* n. sp. a new cave dwelling pholcid spider from northwestern Australia (Araneae: Pholcidae). *Records of the Western Australian Museum* 16: 323-329.
- Eberhard, S.M., Richardson, A.M.M. and Swain, R. (1991). *The invertebrate cave fauna of Tasmania*. University of Tasmania, Zoology Department: Hobart.

- Forster, R.R. (1955). Further Australian Opiliones. *Australian Journal of Zoology* 3: 354-411.
- Forster, R.R. and Platnick, N.I. (1977). A review of the spider family Symphytognathidae (Arachnida, Araneae). *American Museum Novitates* 2619: 1-29.
- Gray, M.R. (1973). Cavernicolous spiders from the Nullarbor Plain and southwest Australia. *Journal of the Australian Entomological Society* 12: 207-221.
- Gray, M.R. (1989). Cavernicolous spiders (Araneae) [sic] from Undara, Queensland and Cape Range, Western Australia. *Helictite* 27: 87-89.
- Gray, M.R. (1992a). The troglobitic spider genus *Tartarus* Gray with a cladistic analysis of *Tartarus* and *Baiami* Lehtinen (Araneae: Stiphidiidae). *Proceedings of the Linnean Society of New South Wales* 113: 165-173.
- Gray, M.R. (1992b). New desid spiders (Araneae: Desidae) from New Caledonia and eastern Australia. *Records of the Australian Museum* 44: 253-262.
- Gray, M.R. (1994). A review of filistatid spiders (Araneae: Filistatidae: Prithinae) from Australia with notes on subfamily classification. *Records of the Australian Museum* 46 (in press).
- Hamilton-Smith, E. (1967). The Arthropoda of Australian caves. *Journal of the Australian Entomological Society* 6: 103-118.
- Harvey, M.S. (1988). A new troglobitic schizomid from Cape Range, Western Australia (Chelicerata: Schizomida). *Records of the Western Australian Museum* 14: 15-20.
- Harvey, M.S. (1991). The cavernicolous pseudoscorpions (Chelicerata: Pseudoscorpionida) of Cape Range, Western Australia. *Records of the Western Australian Museum* 15: 487-502.
- Harvey, M.S. (1992). The Schizomida (Chelicerata) of Australia. *Invertebrate Taxonomy* 6: 77-129.
- Harvey, M.S. (1993). The systematics of the Hyidae (Pseudoscorpionida: Neobisioidea). *Invertebrate Taxonomy* 7: 1-32.
- Hoffman, R.L. (1979). *Classification of the Diplopoda*. Muséum d'Histoire Naturelle, Genève.
- Howarth, F.G. (1988). Environmental ecology of north Queensland caves: or why are there so many troglobites in Australia. Pp. 76-84 in L. Pearson (ed.). *Australian Speleological Federation Tropicon Conference, Lake Tinaroo, Far North Queensland*. Australian Speleological Federation, Cairns.
- Humphreys, W.F., Adams, M. and 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. and Shear, W.A. (1993). Troglobitic millipedes (Diplopoda: Paradoxosomatidae) from semi-arid Cape Range, Western Australia: systematics and biology. *Invertebrate Taxonomy* 7: 173-195.
- Hunt, G.S. (1991). Opiliones (Arachnida) of the Kimberley rainforests, Western Australia. Pp. 295-297 in N.L. McKenzie, R.B. Johnston and P.G. Kendrick (eds). *Kimberley Rainforests*. Surrey Beatty, Chipping Norton.
- Hunt, G.S. (1993). A new cavernicolous harvestman from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum* 33: 217-219.
- Knott, B. (1993). Stygofauna from Cape Range peninsula, Western Australia: tethyan relicts. *Records of the Western Australian Museum, Supplement* 45: 109-127.
- Lawrence, R.F. (1952). The cave-living spiders of the South African genus *Phanotea* Simon (Agelenidae). *Revue de Zoologie et de Botanique Africaines* 45: 49-54.
- Lawrence, R.F. (1964). New cavernicolous spiders from South Africa. *Annals of the South African Museum* 48: 57-75.
- Main, B.Y. (1969). A blind mygalomorph spider from a Nullarbor Plain cave. *Journal and Proceedings of the Royal Society of Western Australia* 52: 9-11.
- Millidge, A.F. (1993). Three new species of the spider family Linyphiidae from Australia (Araneae). *Records of the Western Australian Museum*. 16: 211-219.
- Muchmore, W.B. (1982). The genera *Ideobisium* and *Ideoblothrus*, with remarks on the family Syarinidae (Pseudoscorpionida). *Journal of Arachnology* 10: 193-221.
- Norton, R.A., O'Connor, B.M. and Johnston, D.E. (1983). Systematic relationships of the Pediculocheilidae (Acari: Acariformes). *Proceedings of the Entomological Society of Washington* 85: 493-512.
- Platnick, N.I. (1990). Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosoidea). *American Museum Novitates* 2978: 1-42.
- Richards, A.M. (1971). An ecological study of the cavernicolous fauna of the Nullarbor Plain, southern Australia. *Journal of Zoology, London* 164: 1-60.
- Shear, W.A. (1992). A new genus and two new species of millipedes from the Cape Range, Western Australia (Diplopoda, Polydesmida, Paradoxosomatidae). *Records of the Western Australian Museum* 15: 777-784.

- Truswell, E.M. (1990). Australian Rainforest: the 100 million year record. Pp. 7-22 in L.J. Webb and J. Kikkawa (eds). *Australian Tropical Rainforest, Science - Values - Meaning*. CSIRO, East Melbourne.
- Vine, B., Knott, B. and Humphreys, W.F. (1988). Observations on the environment and biology of *Schizomus vinei* (Chelicerata: Schizomida) from Cape Range, Western Australia. *Records of the Western Australian Museum* 14: 21-34.
- Wheeler, Q.D. (1990). Insect diversity and cladistic constraints. *Annals of the Entomological Society of America* 83: 1031-1047.
- Wilson, E.O. (1988). The current state of biological diversity. Pp. 3-18 in E.O. Wilson and F.M. Peter (eds). *Biodiversity*. National Academy Press, Washington, D.C.
- Wyrwoll, K-H., Kendrick, G. and Long, J. (1993). The geomorphology and Late Cenozoic geomorphological evolution of the Cape Range - Exmouth Gulf region. *Records of the Western Australian Museum, Supplement* 45: 1-23.