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Subterranean Fauna of Christmas Island, Indian Ocean

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Abstract

The subterranean environment of Christmas Island is diverse and includes freshwater, marine, anchialine, and terrestrial habitats. The cave fauna comprises swiftlets, and a diverse assemblage of invertebrates, both terrestrial and aquatic, which includes a number of rare and endemic species of high conservation significance. At least twelve species are probably restricted to subterranean habitats and are endemic to Christmas Island. Previously poorly known, the cave fauna of Christmas Island is a significant component of the island's biodiversity, and a significant cave fauna province in an international context. The cave fauna and habitats are sensitive to disturbance from a number of threatening processes, including pollution, deforestation, mining, feral species and human visitors.

Keywords: Island karst, biospeleology, stygofauna, troglobites, anchialine, scorpion, Procarididae

INTRODUCTION

As recently as 1995 Christmas Island (Indian Ocean) was considered to have no specialized subterranean fauna (Gray, 1995: 68), despite biological collections having been made since 1887 (especially Andrews et al., 1900). However, in 1996 a specimen of blind scorpion was recovered, collected by a speleologist in 1987. Subsequently in April 1998 we spent three weeks on Christmas Island, on behalf of Parks Australia North, to determine the affinities and significance of any subterranean fauna and the ensuing management implications. We sampled terrestrial, freshwater, and near-coastal salt water (anchialine) subterranean habitats which were accessed at boreholes, springs and 23 of the 42 caves recorded on Christmas Island, including all the major caves which are popular with visitors. This paper summarizes our findings which are reported fully elsewhere (Humphreys and Eberhard, 1998).

METHODS

Fauna was sampled by a variety of methods traditionally employed in caves and groundwater sites (Camacho, 1992; Pospisil, 1992). Terrestrial cave fauna was collected by means of visual searching, but guano samples were collected and examined for fauna in the laboratory.

Aquatic fauna was sampled by handnet following visual sighting, or by plankton nets of appropriate dimensions hauled through the water column with or without pre-baiting, and by the use of baited traps left in place overnight and working on the principle of cray pots. The entire stream flow was filtered through nets in cave streams and on spring outlets for 24 hours or more.

DEFINITIONS

It has been found useful to classify cave-dwelling animals according to their presumed degree of ecological/evolutionary dependence on the cave environment. Many surface-dwelling forms enter caves by chance and while such ‘accidentals’ may survive for some time they do not reproduce underground. Trogloxenes spend part of their life cycle in caves, as for example, Glossy Cave Swiftlets roost and nest in caves but emerge to seek food outside. Swiftlet excreta may form the basis of distinct guano dwelling invertebrate communities, comprising guanophiles. Troglophiles are species found outside caves as well as inside caves, but they are able to complete their entire life cycle within caves. First level troglophiles are species known to occur in above ground (epigean) habitats, and second level troglophiles are species that have never been found outside caves but which display no obvious adaptations to cave life (Hamilton-Smith, 1971).

Troglobites are species which obligatorily spend their entire lives within caves (troglodytes are people inhabiting caves). Troglobites are highly specialized to life underground and they cannot survive on the surface for any length of time. They are of considerable interest to scientists because of their degree of specialization, and because they are frequently found to be relicts that have survived in underground refugia long after their surface dwelling ancestors have become extinct. However, this does not preclude active colonization of caves by their epigean ancestors (Rouch and Danielopol, 1987; Hoch and Howarth, 1999).

Troglobites display a number of characteristic convergent morphological traits. Amongst them, the reduction or loss of characters (regressive evolution), such as the loss of eyes, pigment, sclerotization and wings. This is complimented by the enhancement of other characters—elongate legs and antennae and other non-optic senses in arthropods and lateral line organs in fish—to compensate for the lack of visual sensory information. Collectively, these traits are referred to as troglomorphies.

It is convenient to distinguish those subterranean fauna restricted to water by the prefix stygo-, leading to the comparable terms stygoxene, stygophile, stygobite and stygofauna (following Gibert et al., 1994: 13), in contradistinction to troglobites, which are essentially terrestrial animals restricted to subterranean air-filled voids. The term troglobites is sometimes used in the broadest sense to encompass the obligate inhabitants of all hypogean environments.

RESULTS

The climate is tropical monsoonal (latitude c. 10°30'S) with a high rainfall (mean annual rainfall of 2109 mm) that supports rainforest throughout the 360 m high island. Further information is given in Grimes (2001).

Cave development

The basaltic core of Christmas Island is encased in a series of limestones dating from the Eocene to the Recent and eustatic changes have produced a series of marine terraces (see Grimes, 2001). Cave development is largely associated with the interface between the basalt and limestone, and between freshwater and seawater. Access to these caves is, respectively, from the plateau, and from the sea or the lower coastal terraces. Near the coast seawater intrudes beneath the freshwater within the karstic limestone, possibly penetrating to the basalt core, and so forming an anchialine collar around the island. The saltwater interface caves are strongly tidal. Owing to the mode of development of these caves (Grimes, 2001; for examples from the Bahamas see Mylroie et al., 1991; Vogel et al., 1990), and the predominantly lower sealevel stands during the Pleistocene (Chappell and Thom, 1977), these saltwater interface caves are likely to extend to at least 80 m below the present sea level, notwithstanding an uplift of the island of 12–30 m in the last 124 ka (Woodroffe, 1988; Veeh, 1985). Evidence of lower sea level is seen in speleothems originally formed subaerially but now drowned to a depth of 3 m in Thunder Dome Cave, and at least -6 and -5 m in Lost Lake Cave and Bishops Cave respectively. Scuba divers have reported caves and freshwater outflows up to 55 m depth off shore, whilst submarine springs (vruljas) have been reported at 200 m depth in Flying Fish Cove (Pettifer and Polak, 1979). Grimes (2001) addresses speleogenesis on Christmas Island.

Eight caves (CI- 1, 4, 7, 20, 53, 70, 73/74, 83: for names of caves see Table 1) have entrance openings directly into the sea. A further six caves (CI- 87, 88, 89, 91, 92, 93) are fully submerged, or almost entirely submerged, and can only be explored with SCUBA. At least 14 caves (CI- 1, 2, 3, 7, 8, 9, 10, 16, 19, 20, 53, 70, 89, 90) contain tidally influenced freshwater/anchialine habitats. The three plateau caves (CI- 5, 6, 11) contain non-tidal freshwater streams. Grimes (2001) discusses the karst drainage on Christmas Island in some depth.

Cave environment

The subterranean environments of Christmas Island are diverse and include both terrestrial and aquatic ecosystems, the latter comprising freshwater, marine, and anchialine habitats.

Cave temperatures on Christmas Island did not differ over the island (25.9±0.19°C, N=12) and were close to the mean annual surface temperature of 25.1°C , as expected. The cave humidities were nearly saturated (RH = 97.5±0.88%, N=14) and were similar in both coastal and plateau caves. Such warm and humid caves are a most suitable habitat for troglobitic fauna if the soils are moist. It has been found elsewhere in tropical caves that terrestrial cave fauna requires high humidity and/or moist cave soils (Queensland: Howarth, 1988; Cape Range: Humphreys, 1991; Kimberley: Humphreys, 1995). The north-west monsoon, that usually brings rain between December and April, had not commenced prior to our visit in April 1998 owing to the effect of the El Niño/Southern Oscillation; rainfall in the 14 months preceding sampling was only 55% of the annual average of 2109 mm. As a result cave soils were largely dry and cracked, a sign that the soil was too dry to support troglobitic fauna, at least in the voids large enough to be accessible by people: the macrocavernous spaces.

Carbon dioxide concentrations of 3% were recorded in Jedda Cave and Jane-up Cave on the plateau and were associated with a concomitant reduction in oxygen concentration, consistent with biogenic production of carbon dioxide. It is uncertain whether this reflects a flush of microbial activity following the onset of the rain, or is a normal, even a lower than normal, concentration of carbon dioxide in these caves. Cave fauna is commonly encountered in caves with much greater concentrations of carbon dioxide, and while Howarth and Stone (1990) claim that highly troglomorphic species are restricted to such areas in Far North Queensland, this association is not corroborated by observations elsewhere in Australia (W.F. Humphreys and S. Eberhard, unpublished).

The cave waters were all well oxygenated (dissolved oxygen >73% saturated) and the pH (7.65±0.41, N=13) did not differ either between plateau and coastal caves or between fresh and anchialine systems, no doubt reflecting the dominant influence of the limestone on the water chemistry. The conductivity of caves streams was in the range 0.51–0.94 mS cm^{-1} (0.66 ±0.154 mS cm^{-1}, N=6), whereas those caves affected by marine tides had a range of 5.54–34.4 mS cm^{-1} (22.8 ±12.17 mS cm^{-1}, N=7). These values are equivalent to salinities of about

Table 1. Summary of biological significance and vulnerability of caves on Christmas Island, including principal habitats and fauna present. This table is a synopsis of Appendix 3 in Humphreys and Eberhard (1998).

Cave number	Name	Type	Biology	Biological significance	Vulnerability to caver impacts
CI-1	The Grotto	Sea cave	Marine	?hydrological connection	Medium
		-	-	with CI-54 and CI-2.	-
CI-2	Runaway	Anchialine	Stygofauna	High	Low
CI-3	Daniel Roux (main)	Anchialine	Swiftlets, guano	Low/Medium	Low
CI-5	Jedda	Streamway	Troglobites	High	Medium
CI-6	Jane-up	Streamway	Troglobites	Medium (?high if wetter)	Medium
CI-7	Lost Lake	Anchialine	Marine & other?	Medium	Low
CI-8	Bishops	Aquatic	Troglobites	Medium	Low
CI-9	Smiths	Aquatic	Swiftlets, guano	Medium	Med/High
CI-10	Freshwater	Aquatic	Troglobites	Medium	Low
CI-11	Grants Well	Streamway	Aquatic fauna	Medium	Low
CI-16	Strangler	Roots, aquatic	Fauna	Medium	Low
CI-20	Full Frontal	Anchialine	Fauna	Medium	Low
CI-30	Swiftlet	-	Swiftlets, guano	? High	?
CI-31	Indian	Small cave	?	? Low	Low
CI-45	-	Alcove[1]	Guano	?	?
CI-50	Managers Alcove	-	Swiftlets, guano	? High	? High
CI-53	Grimes	Anchialine	Swiftlets	Medium: ?hydrological connection with CI-3	Low/Med
CI-54	-	Anchialine, roots	Stygofauna	High	Medium
CI-56	Daniel Roux (upper)	Terrestrial	Swiftlets, guano	High	High
CI-68	Wobble	Small cave	?	? Low	? Low
CI-70	Boat	Sea cave	Marine, ?anchialine	Medium	Low
CI-73	The Tunnel	Sea cave	Marine	Low	Low
CI-90	Thunder Cliff	Anchialine	Marine & other?	Medium	Low
CI-91	Thunder Dome	Sea cave	Marine	Medium	Low
CI-92	Councillor	Sea cave	Marine	Medium	Low

[1] R. Webb, pers. comm., 1998.

0.39 and 16.5 g L^{-1} TDS respectively (sea water c. 36 g L^{-1} TDS).

Major ion analyses of water from underground streams on the plateau are given in Polak (1976: 28, and plates 21–24). The water typically has total dissolved solids (TDS) of 195–280 mg L^{-1}—the analysis for Grants Well (mg L^{-1}) was TDS=195, Ca= 64, Mg= 2, Na= 9, K=<1, HCO_3 =212, SO_4= 4, Cl =12, NO_3 =<1, pH= 8.0. No major ion analysis is available for the anchialine systems, but experience elsewhere has shown that the composition largely results from the degree of mixing of the fresh and sea water (Humphreys, 1994, 1999; Yager and Humphreys, 1996).

Subterranean fauna

The cave fauna comprises swiftlets, and a diverse assemblage of invertebrates, both terrestrial and aquatic, which includes a number of rare and endemic species of high conservation significance. At least twelve new species are probably restricted to subterranean habitats and are endemic to Christmas Island. The habitual cave-dwelling fauna is summarized in Table 2 whilst a complete systematic listing of all fauna collected is given in Appendix 1. A synopsis of the fauna with significant or unusual biogeographical, evolutionary or conservation attributes is given in Table 3. Undoubtedly, many addition taxa remain to be found.

Troglofauna

The terrestrial fauna comprises six troglobites, plus a number of troglophiles, trogloxenes, guanophiles and accidentals (Table 2). Troglophiles include spiders (Pholcidae and Theridiidae), whip scorpions, millipedes, crabs, isopods, and springtails (Collembola). Despite the island's diverse crab fauna (Gray, 1995), only one species, Jackson's crab *Sesarma jacksoni* Balss was habitually found in the dark zone. Trogloxenic species include the glossy swiftlet *Collocalia esculenta natalis* Lister and the robber crab *Birgus latro* Linnaeus. Guanophiles (generally, species living on bat or bird excreta) include mites (Acarina), moths (Lepidoptera) and fly larvae (Diptera) that are associated with guano piles of the swiftlet. Accidentals included several crab species, plus snails, beetles, millipedes, and isopods.

A number of highly troglomorphic animals was found, such as the cockroach *Metanocticola christmasensis* Roth (Blattodea: Nocticolidae) which represents a genus endemic to Christmas Island and shows advanced troglomorphies (Roth 1999). Other troglobitic nocticolid species occur on mainland Australia, and elsewhere in

Table 2: Synopsis of the habitual cave-dwelling fauna of Christmas Island. The assessed cavernicolous status of the taxa is recorded as: Tx — trogloxene, Tp1 — first level troglophile, Tp2 — second level troglophile, Tb — troglobite, Gp — guanophile, Sb — stygobite including anchialine pool inhabitants, Sp — stygophile.

Terrestrial

Papuaphiloscia undescribed sp. Tp2
Metanocticola christmasensis Roth Tb
Blattellidae, ? undescribed gen. Tb
Cocytocampa undescribed sp. 2 ?Tb
Metrinura Mendes (sensu Smith), undescribed sp. ?Tb
Liocheles polisorum Tb Scorpion (Plate 1)
Charon gervaisi Harvey & West Tp1
Trochanteriidae, undescribed gen. Tb
Pholcidae. indet. Tp2
Theridiidae indet. Tp
Collembola. ?Tb
Acarina Indet. Tb by association.
Acarina, indet. Gp
Lepidoptera, indet. Gp
Diptera, indet. Gp
Myrmecophilidae Tp (?inquilines)
Collocalia esculenta natalis Lister, 1888. Tx

Aquatic

Microturbellaria. ?Sb
Aphanoneura. ?Sb
Nerilla, undescribed sp. Sp
Enchytraeidae. ?Sb
Antecaridina lauensis (Edmondson). Sb
Alpheidae ?Sb several species.
Procaris undescribed sp. Sb (Plate 2)
Macrobrachium microps Holthuis, 1978. Sb
Parahippolyte (?*P. uveae* Borradaile). ?Sb
Ostracoda. Sb
Copepoda. Sb
Amphipoda. Sb
Eleotris fusca (Bloch & Scheider). Sp
Sesarma jacksoni Balss. Sp

southeast Asia. A second troglobitic cockroach of the family Blattellidae also represents an undescribed genus (L.M. Roth, pers. comm. 1998).

The first troglobitic scorpion recorded for Australia, *Liocheles polisorum* Volschenk, Locket and Harvey (Scorpionida: Ischnuridae) (Plate 1) was collected in Bishops Cave (CI-8) in 1987: we also recorded it from the 19th Hole (CI-19), but it is apparently rare. A species of troglobitic scorpion is now recorded from mainland Australia (Barrow Island: W.F. Humphreys, unpublished). Globally, outside Australia, only 14 species of blind scorpions are known, of which only one species occurs outside the New World tropics (11 in Mexico, one each in Equador and Sarawak). An epigean scorpion, *Hormurus australasiae* Fabricius has also been recorded from the island (in Gibson-Hill, 1947).

A new genus of troglobitic spider of the family Trochanteriidae (pers. comm., N. Platnick.) was recorded. An eyed species of the same genus is known from a cave on the Togian Islands, off Sulawesi. A parasitic mite (Acarina) occurs on the troglobitic trochanteriid which may, by association, be troglobitic.

The dipluran *Cocytocampa* sp. nov. 2 (Diplura: Campodeidae) collected has 39 articles in its antenna (maximum number in congeneric species is 30) and this may be a cave adaptation. The only other campodeid known from caves in Australia is not troglomorphic (Condé 1998) but two species of cave-adapted campodeids are known from the Australian region, from New Ireland and from Papua New Guinea.

The silverfish *Metrinura* Mendes (*sensu* Smith, 1998) collected is probably an undescribed species (male required) and represents a range extension for the genus from New Caledonia, the Northern Territory and Queensland (Smith, 1998). Of the six congeneric species, four species are probably soil dwelling and two species are from caves, at Chillagoe and from caves, now flooded, at Texas, Queensland (*M. russendenensis*). Species collected in caves in Australia tend to be longer and thinner or larger bodied on average than surface dwelling species but they do not show the degree of adaptation seen in North American and European troglobitic species (G. Smith, pers. comm., 1998). Members of the family characteristically lack eyes, are thin, often lack scales, and have reduced pigmentation and sclerotization, all of which are preadaptations to cave life.

The most commonly seen large arachnid in Christmas Island caves is the troglophilic whip scorpion, *Charon gervaisi* Harvey & West (Amblypygi: Charontidae). It occurs in the caves near the settlement such as Runaway (CI-2), 19th Hole (CI-19) and CI-54 but it was originally collected on the surface and is likely to have been an anthropogenic introduction from Java, only some 360 km away (Harvey and West, 1998). This opinion is

Plate 1: *Liocheles polisorum* (Scorpionida: Ischnuridae). The first blind scorpion known from Australia. Photo Stefan Eberhard, Western Australian Museum.

Table 3: Synopsis of fauna with significant or notable biogeographical, evolutionary or conservation attributes.

- A second species of *Nerilla* (Archiannelida: Nerillidae) from Australia.
- Subterranean forms of Aphanoneura (Annelida) are only known from Europe, west Africa and USA.
- *Microcystis* sp. (Pulmonata: Helicarionidae); unknown species of previously unrecorded group.
- *Myrmecodillo* n.sp. 1 (Isopoda: Armadillidae).
- *Myrmecodillo* n.sp. 2 (Isopoda: Armadillidae).
- *Papuaphiloscia* n.sp. (Isopoda: Philosciidae); first record of the genus for the Indian Ocean area.
- *Procaris* n. sp. (Decapoda: Caridea: Procarididae). A primitive, highly aberrant, family seemingly restricted to anchialine caves. Family known from four other species in two genera from Hawaii, Ascension Island and Bermuda. (Plate 2)
- Several species of Alpheidae (Decapoda: Caridea) in C-54. Only one species listed in the synopsis of the world's stygofauna, from an anchialine cave in Bermuda.
- *Macrobrachium microps* Holthuis, 1978 (Decapoda: Palaemoninae). Elsewhere known from New Ireland, Samoa and the Loyalty Islands.
- *Antecaridina lauensis* (Edmondson, 1935)(Decapoda: Atyidae). First record from Christmas Island of this widely distributed species.
- A new genus of troglobitic spider of the family Trochanteriidae (pers. comm., N. Platnick.) occurs in Jedda Cave (CI-5). An eyed species of the same genus is known from a cave on the Togian Islands, off Sulawesi!
- *Liocheles polisorum* (Scorpionida: Ischnuridae). The first blind scorpion known from Australia and the second outside the Americas where 12 species occur. (Plate 1)
- *Charon gervaisi* Harvey & West (Amblypygi: Charontidae). This new species will probably be found in Java.
- Diplopoda (Polyzoniida: Family Indet.) belonging to a small order of obscure millipedes known mainly from the western hemisphere.
- *Campodea* (*Indocampa*) sp. nov. (Diplura: Campodeidae). Possibly first troglomorphic campodeid from Australia.
- *Metrinura* (prob. n. sp.)(Thysanura: Nicoletiidae: Nicoletiinae). Range extension of the genus from New Caledonia and eastern Australia.
- *Metanocticola christmasensis* Roth (Blattodea: Nocticolidae). This is a new troglobitic genus.
- *Balta notulata* (Stoll) (Blattodea: Blattellidae). New record for Christmas Island.
- indet (Orthoptera: Grilloidea: Myrmecophilidae). An ancient family that live off the secretions of ants as inquilines in ant nests.
- *Cyphoderopsis* Carpenter 1917 (Collembola: Paronellidae) Springtail not recorded from Australia before.
- *Scleropages formosus* (Müller & Schlegel)(Teleostei: Osteoglossoidei: Osteoglossidae), Asian bony tongue. Almost certainly introduced. Listed on the IUCN Red List of threatened animals as vulnerable being an endemic of very restricted distribution, now threatened by overfishing.
- *Eleotris fusca* (Bloch & Scheider)(Perciformes: Gobioidei: Eleotridae), brown gudgeon. Pale forms seen in dark zone of cave.
- *Oreochromis* sp., tilapia. (Percoidei: Cichlidae). Introduced.
- *Poecilia reticulata* Peters (guppy) and *Xiphophorus maculatus* (Gunther) (swordtail). Introduced.
- (Cyprinodontiformes: Cyprinodontoidei: Poeciliidae). Introduced.
- *Collocalia esculenta natalis* Lister (Aves: Apodiformes: Apodidae), Christmas Island glossy swiftlet, endemic.

reinforced by the lack of sightings, during this survey, of specimens from caves in parts of the island further from the settlement. Two other species of *Charon* are found in tropical mainland Australia (Harvey and West, 1998) but neither is troglomorphic.

We recorded the trogloxenic (Tx) Christmas Island glossy swiftlet, *Collocalia esculenta natalis*, from Upper Daniel Roux Cave (CI-56); Smiths Cave (CI-9); Managers Alcove (CI-50); Grimes Cave (CI-53); Swiftlet Cave (CI-30). It appears to be restricted to nesting in caves. The subspecies is endemic to Christmas Island although many other subspecies and species occur in South-east Asia, Queensland and Pacific islands. The nests of *Collocalia* species in Southeast Asia and India are intensively harvested for the gourmet delicacy 'birds nest soup' (Nguyen Quang and Voisin, 1998), and there is anecdotal evidence which suggests that nests of Christmas Island swiftlets may have been harvested in the past (Brooks, 1990).

Stygofauna

About 12 stygobiontic species were recorded from Christmas Island, comprising more than seven species found in the anchialine systems, and more that six species from freshwater (Table 2).

Freshwater fauna

Flatworms (Platyhelminthes: Turbellaria: 'Microturbellaria' cf Schwank 1986) were recorded from freshwater streams in the plateau caves.

Crustaceans of the order Podocopa (Ostracoda) were widely collected from freshwater at underground streams and springs and from anchialine habitats.

The copepod *Bryocyclops* (*B.*) *muscicola* (Menzel, 1926)(Cyclopinidae: Copepoda) was collected from springs and underground streams. The species was known previously from Java and Sumatra from interstitial, cave and moss habitats. These collections expand the known habitat of the species to groundwater and anchialine systems and its range to Christmas Island. Harpacticoid copepods of the family Ameiridae are primarily marine forms but isolated representatives have secondarily invaded freshwater (Huys and Boxshall, 1991). *Nitocrella*/*Nitokra* complex (Harpacticoida: Ameiridae) was taken from groundwater, anchialine and freshwater spring habitats. A species of Canthocamptidae, the largest family of freshwater Harpacticoida (Huys and Boxshall, 1991), was taken from a gour pool. A species of Phyllognathopodidae was taken from a water bore.

Macrobrachium microps Holthuis, 1978 (Decapoda: Palaemoninae) appears to be restricted to caves, in contrast to the wide ranging *Macrobrachium lar* (Fabricius, 1798), also found on Christmas Island (Short and Meek, 2000).

The brown gudgeon, *Eleotris fusca* (Bloch & Scheider) (Perciformes: Eleotridae), is the only native freshwater fish known to penetrate into the dark zone of the cave systems—cave dwelling specimens display some degree of depigmentation.

A number of human introduced fish occur in freshwater of Christmas Island, including the asian bony tongue, *Scleropages formosus* (Müller & Schlegel), cichlid tilapia (*Oreochromis* sp.), the guppy (*Poecilia reticulata* Peters), mosquito fish (*Gambusia affinis* Baird & Girard), and swordtails (*Xiphophorus maculatus* (Gunther)). Some of these species have the potential to threaten native fauna, including fauna in anchialine systems (Allen, 1991; Ridgley and Chai, 1990).

Anchialine systems

Anchialine habitats are characterized by having fresh groundwater overlying seawater, usually with a restricted exposure to open air and always with more or less extensive subterranean connections to the sea. Many such systems in the tropics are renowned both for their relict faunas and their species richness (Sket, 1981, 1996)—at least ten new families of Crustacea have been described from them in recent years. Anchialine systems are considered to be vulnerable to even slight organic pollution (Iliffe et al., 1984; Notenboom et al., 1994). They are the focus of widespread conservation assessment (Sket, 1981; Maciolek, 1983, 1986; Brock et al., 1987; Ridgley and Chai, 1990; Thomas et al., 1991, 1992; Iliffe, 1992; Bailey-Brock and Brock, 1993) and public interest (*vide* Waikoloa Anchialine Pond Preservation Area Trust Fund in Hawai'i: Brock et al., 1987). Other than Christmas Island, the only other anchialine system reported in Australia is the Cape Range/Barrow Island area, the former being the only continental anchialine habitat reported for the southern hemisphere (Humphreys, 2000).

Access to the anchialine systems on Christmas Island is available in many of the coastal caves but logistical constraints meant that the system was sampled sparsely, predominantly in the settled part of the island. However, a significant anchialine fauna was recorded comprising a variety of Crustacea.

The stygobitic shrimp *Procaris* n. sp. (Decapoda: Procarididae) (Plate 2) occurred in anchialine waters together with alpheid, hippolytid and atyid shrimps. Only two species are described from the genus *Procaris*, *P. hawaiana* Holthuis, 1973, from Hawaii and *P. ascensionis* Chace and Manning, 1972 from Ascension Island in the South Atlantic; two undescibed species are known from Fiji (J. Short, pers. comm. 2000).

Nerilla sp. (Archiannelida: Nerillidae) were taken amongst tree roots in anchialine waters. The genus is free living and is cosmopolitan in marine systems.

Calanoid copepods were also collected from the anchialine system. Members of some of the most primitive families typically inhabit the near bottom hyperbenthic environment from where they have invaded anchialine habitats (Huys and Boxshall, 1991).

Other crustaceans in the anchialine system include podocopodid ostracods, cyclopinid copepods and harpacticoid copepods (Ameiridae).

DISCUSSION

Previously poorly known, the cave fauna has proved to be a significant component of the island's biodiversity and a significant cave fauna province in an international context. The cave fauna comprises swiftlets, and a diverse assemblage of invertebrates, both terrestrial and aquatic, which includes a number of rare and endemic species of high conservation significance. At least twelve species which are endemic to Christmas Island are probably restricted to subterranean habitats which ranks Christmas Island significant in terms of its subterranean fauna.

Christmas Island has, minimally, six stygal and six troglobitic species. The biodiversity of the subterranean fauna is most appropriately compared with that of islands and tropical systems elsewhere. Whilst Christmas Island is not in the most species-rich category of islands with respect to troglomorphic species (Table 4), it is already approaching the richness seen in entire, well researched, karst regions such as Mexico and Central America, Southeast Asia, Virginia and the Central Pyrenees. It was a poor year for collecting terrestrial cave fauna owing to the failure of the north-west monsoon that typically influences the area from December through April. Undoubtedly, further sampling of cave fauna will locate numerous additional cave dependent species, as typically found elsewhere (Humphreys and Eberhard, 1998: figure 2).

It is now appreciated that: 1, most caves do not have surface openings; 2, the vast bulk of subterranean voids comprise air and water filled spaces much too small for people to enter; 3, many species found in caves may be more numerous in the crevicular habitat, both within and without the traditional hypogean matrices; 4, many species found in these alternative habitats are not found in caves, and 5, that there is a continuum of hypogean spaces, both air and water filled, that merge, often imperceptibly, with epigean, lacustrine, riverine and marine systems (Humphreys and Eberhard, 1998). The preferred habitat of many terrestrial troglobites appears to be the smaller, so called, mesocavernous voids (0.1–20 centimetres) where the micro-climatic conditions tend to be more stable (Howarth, 1983).

The existence of extensive terrestrial and aquatic mesocavernous habitat on Christmas Island is likely given the high secondary porosity of the limestone, as evidenced by the characteristic honeycombed appearance of the rock surfaces both above and below ground. This extensive, and possibly continuous, sponge-like network provides a refuge for terrestrial fauna when environmental conditions in the larger cave passages are less suitable due to dryness for example. The extreme rarity of many of the troglobitic species—most are represented by single specimens despite intensive searching—and experience in other tropical karsts such as Cape Range (Humphreys 1991), support the contention that mesocaverns are the principal habitat of Christmas Island troglobites. For both terrestrial and aquatic fauna, the mesocaverns also provide underground dispersal routes between separate cave systems.

A number of factors are pertinent to the origins of the cave fauna. Namely, the period of time that the island has been above the sea level, the size of the island, likely routes of colonization, the proximity and size of other land masses, and the prevailing and intermittent winds and ocean currents, as well as the characteristics of the lineage in question. The main limestones were laid down in shallow water with fossil dates (Adams and Belford, 1974) from the Late Oligocene (26 Ma) to the Late Miocene (10 Ma). The existence of the terraces suggests the island was above sea level for much of the Quaternary. Grimes (2001) is confident that the island has been land for most of the Quaternary (2 Ma—evidence of uplift rates and the presence of the terraces), that it is reasonably likely to have been exposed continuously since the early or mid-Pliocene (3–5 Ma—evidence of volcanics), and there is a possibility that it may have been land since the late Miocene (10 Ma—last shallow water limestones).

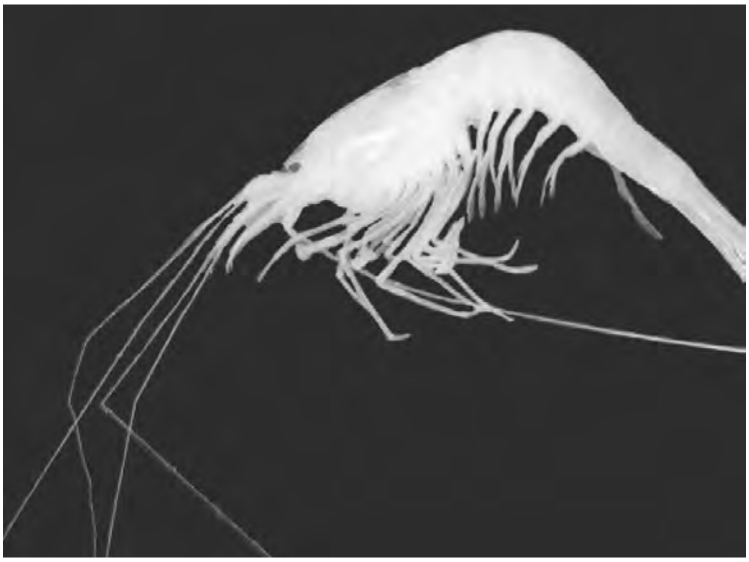

Plate 2: *Procaris* n. sp. (Decapoda: Caridea: Procarididae). A primitive, highly aberrant, family seemingly restricted to anchialine caves. Photo Stefan Eberhard, Western Australian Museum.

Table 4: Approximate numbers of recognized subterranean species from various islands and tropical locations.
Extracted from compilations in Juberthie and Decu (1994), and Deharveng and Bedos (2000). The figures in parentheses denote the percentage of all species that are troglobites. Australian sites are underlined and • denotes tropical locations.

Location	Troglobites	Stygobites	Total troglomorphic
Islands			
•Cuba	29	61	90
Bermuda	0	56	56
•Cape Range/Barrow I.[2]	33	22	55
Tenerife: Canary Islands (lava tubes)	34	11	45
•Galapagos: Ecuador	17	24	41
•Jamaica	25	14	39
Bahamas (numerous islands)	-	35	35
La Palma: Canary Islands[1]	19	2	21
Azores	16	-	16
Lanzarote: Canary Islands (lava tube)[1]	-	15	15
•Christmas Island[3]	6	6	12
Hierro: Canary Islands (lava tubes)[1]	8	1	9
Fuertoventura: Canary Islands[1]	1	5	6
Gomera: Canary Islands[1]	4	2	6
•Virgin Islands: Netherlands Antilles	-	4	4
•Mona Island: Netherlands Antilles	2	1	3
Gran Canaria: Canary Islands[1]	1	2	3
Karst regions			
•Mexico and Central America	0-14	0-10	-
•Southeast Asia	-	-	16-28
Virginia	-	-	14-21
Central Pyrenees	-	-	18-23
Caves	**-**	**-**	**-**
•Panama: Chilibrillo cave	-	-	3 (5)
•Ecuador: Jumandi cave	-	-	1(5)
•Venezuela: Serrania de San Luis	9	2	11(12)

[1] Mainly from lava tubes. [2] Cape Range is included for comparison and because it is isolated on a peninsula. [3] Provisional figure only.

Terrestrial and freshwater lineages are most likely to have been transported from the nearest land masses, the Indonesian archipelago, but freshwater species of marine origin may have invaded from the sea. Cave adapted terrestrial and freshwater invertebrates most likely will have arrived on the island as an epigean progenitor and will have evolved troglobitic adaptations *in situ* on Christmas Island and will thus be endemic to Christmas Island. By contrast only 16 taxa of plants, 3.9% of the total, are endemic to Christmas Island (Du Puy, 1993: 12), and probably none of the marine fauna (Berry, 1988). The vegetation on Christmas Island has predominantly Indo–Malesian affinities, with many species having distributions extending from Southeast Asia through Malaysia to Australia (northeast Queensland), New Guinea and into the Pacific islands. All species are tolerant of limestone and alkaline soils (Du Puy, 1993). However, it should be recognized that the species composition of the vegetation may have been influenced by the predation pressure of the land crabs on seeds and seedlings (Green et al., 1997), and this may bias the use of the flora as a model for colonization by terrestrial invertebrates. The fauna of tropical caves largely comprises lineages characteristic of forest floor leaf litter communities (Harvey et al., 1993; Humphreys, 1993; Deharveng and Bedos, 2000). The leaf litter on Christmas Island is sparse owing to its utilization by dense populations of land crabs of several species (Green, 1997). This intense competition for fallen leaves may be relevant to the colonization of the subterranean environment on Christmas Island and the subsequent onset of troglogenesis.

The marine fauna of Christmas Island largely comprises widespread Indo–west-Pacific taxa with representations of some western Indian Ocean species not typical of Australian waters. The species diversity of the marine fauna is not high, probably owing to the restricted habitat diversity (Berry, 1988). The anchialine fauna of Christmas Island will have invaded from the sea: Many anchialine lineages have widespread pantropical, or wider, distributions where suitable habitats are found.

The Procaridae is a primitive, highly aberrant, family which appears to be restricted to anchialine caves and has only one other representative, *Vetericaris chaceorum* Kensley & Williams, 1986, from Bermuda, which poses interesting questions concerning the distribution and dispersion of these faunas. Boxshall (1989) proposed that the mid-oceanic ridge islands form a continuous route of dispersal around the globe, however there is not a simple connection between the crevicular system of mid-oceanic ridges and hot spot islands such as Christmas Island. The occurrence of procaridid, alpheid, hippolytid and atyid shrimps in the same anchialine system on Christmas Island mirrors that on Bermuda where the same four families occur in the anchialine system on the island (Hart and Manning, 1981) which is renown for the diversity of its anchialine fauna. In addition *Procaris* has always been recorded with another ancient family, the Atyidae, wherever it is found (only known from Bermuda, Ascension Islands, Hawai'i and Christmas Island). These co-occurrences of two primitive and presumably ancient caridean families support the contention that crevicular habitats have served as faunal refuges for long periods of time (Kensley and Williams, 1986).

The cave fauna and habitats are sensitive to disturbance from a number of threatening processes, including pollution, deforestation, mining, feral species and human visitors (Meek, 2001). The sensitivity and vulnerability varies depending on the characteristics of the fauna and habitat, its distribution and the nature of the threatening process (Table 5). Public education, habitat protection and monitoring are recommended for managing human visitors. For other, external threatening processes, survey and assessment of impacts on subterranean biota is required (Humphreys and Eberhard, 1998).

Table 5: Summary of fauna habitat/association types, their occurrence, vulnerability to human visitors, and main external threatening processes.

Habitat/association	Occurrence	Vulnerability to human visitors	Main external threats
Glossy swiftlet	Restricted	High	Deforestation
Guano	Restricted	High	Deforestation
Tree roots	Restricted	High	Deforestation, mining
Freshwater pools	Restricted	High	Deforestation, pollution
Freshwater streams	Restricted	Medium	Deforestation, pollution, mining, water abstraction, feral species
Sediment banks	Restricted	Medium	Deforestation, pollution, mining
Organic material	Restricted	Medium	Deforestation
Anchialine	Widespread	Low	Pollution, water abstraction, feral species
Marine	Widespread	Low	Pollution
Entrance/twilight	Widespread	Low	Deforestation, mining
Wall association	Widespread	Low	Deforestation
Springs	Restricted	Low	Water abstraction, pollution, feral species
Deep zone	Widespread	Variable	Deforestation, pollution

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REFERENCES

Adams, C.G. and Belford, D.J., 1974. Foraminiferal biostratigraphy of the Oligocene–Miocene limestones of Christmas Island (Indian Ocean). *Palaeontology* **17**: 457-506.

Allen, G.R., 1991. *Freshwater fishes of New Guinea*. Publication No. 9 of the Christensen Research Institute, Madang.

Andrews, C.W. et al., 1900. *A monograph of Christmas Island (Indian Ocean).* British Museum (Natural History), London.

Bailey-Brock, J.H. and Brock, R.E., 1993. Feeding, reproduction, and sense organs of the Hawaiian anchialine shrimp *Halocaridina rubra* (Atyidae). *Pacific Science* **47**: 338-355.

Berry, P.F., (ed.), 1988. *The marine fauna of Christmas Island, Indian Ocean.* Western Australian Museum, Perth.

Botosaneanu, L., (ed.), 1986. *Stygofauna Mundi: A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters. (including the marine interstitial)*. E.J. Brill, Leiden, The Netherlands. 740 pp.

Boxshall, G.A., 1989. Colonisation of inland marine caves by misophrioid copepods. *J. Zool., Lond*. **219**: 521-526.

Brock. R.E., Norris, J., Zeimann, D. and Lee, M.T. , 1987. Characteristics of water quality in anchialine pools of the Kona, Hawaii, coast. *Pacific Science* **41**: 200-208.

Brooks, S., 1990. Caving in paradise. *Australian Caver*, No. **124**: 11-13.

Chappell, J. and Thom, B.G., 1977. Sea levels and coasts. pp. 275-291. *in* J. Allen, J. Golson and R. Jones (eds*). Sunda and Sakul: Prehistoric studies in southeast Asia, Melanesia & Australia.* Academic Press, London.

Camacho, A.I., 1992. Sampling the subterranean biota. Cave (aquatic environment). *in* A.I. Camacho (ed.) *The Natural History of Biospeleology*: 135-168. Monografias Museo Nacional de Ciencias Naturales, Madrid.

Condé, B.,1998. First record of Campodeids (Diplura: Campodeidae) from caves in Australia. *Rec. Western Austr. Mus.* **19**: 145-152.

Deharveng, L. and Bedos, A., 2000. The cave fauna of Southeast Asia: origin, evolution and ecology. *In* H. Wilkens, D.C. Culver and W.F. Humphreys (eds*). Ecosystems of the World, vol. 30. Subterranean Exosystems*: 603-632. Elsevier, Amsterdam.

Du Puy, D.J., 1993. Christmas Island. pp 1-30 in *Flora of Australia Vol. 50, Oceanic Islands 2.* Australian Government Publishing Service, Canberra.

Gibert, J., Stanford, J.A., Dole-Olivier, M.-J. and Ward, J.V., 1994. Basic attributes of groundwater ecosystems and prospects for research. *In* J. Gibert, D.L. Danielopol and J.A. Stanford (eds). *Groundwater Ecology*: 7-40. Academic Press, London.

Gibson-Hill, C.A., 1947. The nature of the coast. *Bull. Raffles Mus., Singapore* **18**: 8-17.

Gray, H.S. (revised by R. Clark), 1995. *Christmas Island naturally.* Second edition. Christmas Island Natural History Association and Australian Nature Conservation Agency.

Green, P. T., 1997. Red crabs in rain forest on Christmas Island, Indian Ocean: activity patterns, density and biomass. *Journal of tropical ecology* **13**: 17-38.

GREEN, P.T., O'Dowd, D.J. and Lake, P.S., 1997. Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. *Ecology* **78**: 2474 -2486.

GRIMES, K., 2001. Karst features of Christmas Island (Indian Ocean). *Helictite* **37(2):** 41-58.

HAMILTON-SMITH, E., 1971. The classification of cavernicoles. *National Speleological Society Bulletin* **83**: 63-66.

HART, C.W. and MANNING, R.B., 1981. The cavernicolous caridean shrimps of Bermuda (Alpheidae, Hippolytidae, and Atyidae). *J. Crust. Biol.* **1**: 441-456.

HARVEY, M.S., GRAY, M.R., HUNT, G.S. and LEE, D.C., 1993. The cavernicolous Arachnida and Myriapoda of Cape Range, Western Australia. *Records of the Western Australian Museum,* Supplement **45**: 129-144.

HARVEY, M.S. and WEST, P.L.J., 1998. New species of *Charon* (Amblypygi, Charontidae) from northern Australia and Christmas Island. *J. Arachnol.* **26**: 273-284.

HARVEY, M.S. and YEN, A.L., 1989. *Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates.* Oxford University Press, Melbourne.

HOCH, H. and HOWARTH, F.G., 1999. Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae. *Zool. J. Linnean Soc.* **127**: 453-475.

HOWARTH, F.G., 1988. Environmental ecology of north Queensland caves: or why there are so many troglobites in Australia. pp. 76-84 *in* L. Pearson (ed.) *17th biennial conference, Australian Speleological Federation Tropicon Conference, Lake Tinaroo, Far North Queensland 27-31 Dec. 1988.* Australian Speological Federation, Cairns. 139 pp.

HOWARTH, F.G., 1983. Ecology of cave arthropods. *Ann. Rev. Entomol.* **28**: 365-389.

HOWARTH, F.G. and STONE, F.D., 1990. Elevated carbon dioxide levels in Bayliss Cave, Australia: implications for the evolution of obligate cave species. *Pacific Science* **44**: 207-218.

HUMPHREYS, W.F., 1991. Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. *J. Anim. Ecol.* **60**: 609-623.

HUMPHREYS, W.F., 1993. Cave fauna in semi-arid tropical Western Australia: a diverse relict wet-forest litter fauna. *Mémoires de Biospéologie* **20**: 105-110.

HUMPHREYS, W.F., 1994. *The subterranean fauna of the Cape Range coastal plain, northwestern Australia.* Unpublished report to the Australian Heritage Commission and the Western Australian Heritage Committee. 202 pp.

HUMPHREYS, W.F., 1995. *Limestone of the east Kimberley, Western Australia —karst and cave fauna.* Unpublished report to the Australian Heritage Commission and the Western Australian Heritage Committee. 190 pp.+ xix.

HUMPHREYS, W. F., 1999. Physico-chemical profile and energy fixation in Bundera Sinkhole, an anchialine remiped habitat in north-western Australia. *J. Roy. Soc. Western Austr.* **82**: 89-98.

HUMPHREYS, W.F. , 2000. Chapter 30. The hypogean fauna of the Cape Range peninsula and Barrow Island, northwestern Australia. *In* H. WILKENS, D.C. CULVER and W.F. HUMPHREYS (eds*). Ecosystems of the World, vol. 30. Subterranean Exosystems:* 581-601. Elsevier, Amsterdam.

HUMPHREYS, W.F. and EBERHARD, S.M., 1998. *Assessment of the ecological values and management options for cave use on Christmas Island: Project 97/002.* Unpublished. report prepared for Parks Australia North. 134 pp.

HUYS, R. and BOXSHALL, G.A., 1991. *Copepod Evolution.* Vol. 159, The Ray Society, London.

ILIFFE, T.M., 1992. Anchialine cave biology. *In* A. I. CAMACHO (ed.*). The Natural History of Biospeleology:* 614-636. Monografias Museo Nacional de Ciencias Naturales, Madrid.

ILIFFE, T.M., JICKELLS, T.D. and BREWER, M.S., 1984. Organic pollution of an inland marine cave from Bermuda. *Mar. Environ. Res.* **12**: 173-189.

JUBERTHIE, C. and DECU, V. (Eds), 1994. *Encyclopaedia Biospeologica , vol. 1.* Laboratoire souterrain du CNRS, Moulis, France.

KENSLEY, B. and WILLIAMS, D., 1986. New shrimps (families Procarididae and Atyidae) from a submerged lava tube in Hawaii. *J. Crust. Biol.* **6**: 417-437.

MACIOLEK, J.A., 1983. Distribution and biology of Indo–Pacific insular hypogeal shrimps. *Bull. Mar. Biol.* **33**: 606-618.

MACIOLEK, J.A., 1986. Environmental features and biota of anchialine pools on Cape Kinau, Maui, Hawaii. *Stygologia* **2**: 119-129.

MEEK, P.D., 2001. The history of Christmas Island and the management of its karst features. *Helictite,* **37(2):** 31-36.

Mylroie, J.E., Carew, J.L., Sealey, N.E. and Mylroie, J.T., 1991. Cave development on New Providence Island and Long Island, Bahamas. *Cave Science* **18**: 139-151.

Nguyen Quang, P. and Voisin, J.-F., 1998. Influence of cave structure, microclimate and nest harvesting on the breeding of the White-nest swiftlet *Collocalia fuciphaga germani* in Vietnam. *Ibis* **140**: 257-264.

Notenboom, J., Plénet, S. and Turquin, M.-J., 1994. Groundwater contamination and its impact on groundwater animals and ecosystems.*In* J. Gibert, D.L. Danielopol and J.A. Stanford (Eds). *Groundwater Ecology*: 477-504. Academic Press, London.

Pettifer, G.R. and Polak, E.J., 1979. Christmas Island (Indian Ocean), geophysical survey for groundwater, 1976. *Bureau of Mineral Resources, Geology and Geophysics Record* 1979/33.

Polak, E.J., 1976. Christmas Island (Indian Ocean), geophysical survey for groundwater, 1973. *Bureau of Mineral Resources, Geology and Geophysics Record* 1976/100.

Pospisil, P., 1992. Methods for describing and sampling the subterranean environment. *In* A.I. Camacho (ed.). *The Natural History of Biospeleology:* 107-134. Monografias Museo Nacional de Ciencias Naturales, Madrid.

Ridgley, M.A. and Chai, D.K., 1990. Evaluating potential biotic benefits from conservation: anchialine ponds in Hawaii. *The environmental Professional* **12**: 214-228.

Roth, L.M., 1999. New cockroach species, redescriptions, and records, mostly from Australia, and a description of *Metanocticola christmasensis* gen. nov., sp. nov., from Christmas Island (Blattaria). *Rec. Western Austr. Mus.* **19**: 327-364.

Rouch, R. and Danielopol, D.L., 1987. L'origine de la faune aquatique souterraine, entre le paradigme du refuge et le modèle de la colonisation active. *Stygologia*, **3**: 345-372.

Schwank, P., 1986. Microturbellaria from subterranean freshwater habitats. *In* L. Botosaneanu (Ed.). *Stygofauna Mundi: A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters. (including the marine interstitial):* 47-56. E.J. Brill, Leiden, The Netherlands. 740 pp.

Short , J.W. and Meek, P. 2000. New records of *Macrobrachium* (Crustacea: Decapoda: Palaemonidae) from Christmas Island, Indian Ocean. *Rec. Western Austr. Mus.***20**: 81-86.

Sket, B., 1981. Fauna of anchialine (coastal) cave waters, its origin and importance. *Proc. 8th Int. Congr. Speleol.* 646-647.

Sket, B., 1996. The Ecology of anchihaline caves. *Trends in Ecol. Evol.* **11**: 221-255.

Smith, G., 1998. Review of Australian Nicoletiinae (Zygentoma: Nicoletiidae). *Invert. Taxon.* **12**: 135-189.

Spate, A. and Webb, R., 1998. *Management options for cave use on Christmas Island.* Unpublished report to Parks Australia North Project 98/002. Australasian Karst Management Association Inc. 82 pp.

Thomas, M.L.H., Eakins, K.E. and Logan, A., 1991. Physical characteristics of the anchialine ponds of Bermuda. *Bull. Mar. Sci.* **48**: 125-136.

Thomas, M.L.H., Logan, A., Eakins, K.E. and Mathers, S.M., 1992. Biotic characteristics of the anchialine ponds of Bermuda. *Bull. Mar. Sci.* **50**: 133-157.

Veeh, H.H., 1985. Uranium-series applied to phosphate deposits on coral reef islands. *Proc. 5th Int. Coral Reef Congr.* **3**: 463-469. (Cited in Woodroffe 1988).

Vogel, P.N., Mylroie, J.E. and Carew, J.L., 1990. Limestone petrology and cave morphology on San Salavador Island, Bahamas. *Cave Science* **17**: 19-30.

Volschenk. E.S., Locket, N.A. and Harvey, M.S. 2001. First record of a troglobitic ischnurid scorpion from Australasia (Scorpiones: Ischnuridae). pp. 161-170 *In* V. Fet and P.A. Seldon (eds) Scorpiones 2001. *In Memoriam* Gary A. Polis. British Arachnological Society: Burnham Beeches, Bucks.

Woodroffe, C.D., 1988. Vertical movement of isolated oceanic islands at plate margins: evidence from emergent reefs in Tonga (Pacific Ocean), Cayman Islands (Caribbean Sea) and Christmas Island (Indian Ocean). *Z. Geomorph. Suppl.-Bd.* **69**: 17-37.

Yager, J. and Humphreys, W.F., 1996. *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. *Invert. Taxon.* **10**: 171-187.

APPENDIX 1: ANNOTATED SYSTEMATIC LISTING AND OCCURRENCE RECORDS OF CAVE FAUNA

The systematic listing largely follows the order and nomenclature of Botosaneanu (1986) and Harvey and Yen (1989). Occurrence records list the site and locality, or the cave name and/or number (eg. CI-54) as listed in Table 2. The assessed cavernicolous status of the taxa is recorded as: Ep – epigean, Tx – trogloxene, Tp1 – first level troglophile, Tp2 – second level troglophile, Tb – troglobite, Sb – stygobite including anchialine pool inhabitants, Gp – guanophile, Gb – guanobite. WAM refers to collections previously in the Western Australian Museum and ANIC refers to the Australian National Insect Collection, Canberra.

Phylum **PLATYHELMINTHES** — Flatworms
  Class **TURBELLARIA**
    'Microturbellaria' cf Schwank 1986, ?Sb
      Jane-up Well.

Phylum **ANNELIDA**
  Class **POLYCHAETA** det R. Wilson
    Family **SYLLIDAE**
      Indet.
      CI-54

  Class **ARCHIANNELIDA** det R. Wilson
    Family **Nerillidae**
      Nerilla sp.
      CI-54

  Class **APHANONEURA** det A. Pinder
    Coastal water bore #1, Smithsons Bight area; Jane-up Well.

  Class **OLIGOCHAETA** det A. Pinder
    Order **HAPLOTAXIDA**
    Family **Enchytraeidae**
      Coastal water bore #1, #2, Smithsons Bight area.

    Family **Tubificidae**
      Indet.
      Freshwater Spring (CI-85).

    Order **OPISTHOPORA** (Earthworm)
    Family Indet.
      Indet.
      Smiths Cave (CI-9).

Phylum **MOLLUSCA** det S.M. Slack-Smith
  Class **GASTROPODA, Ep**
  Sub-class **PROSOBRANCHIA**
    Family **Truncatellidae**
      Truncatella guerinii A. & J.B. Villa, 1841
      Runaway Cave (CI-2); Smiths Cave (CI-9); 19th Hole (CI-19); CI-55.

    Family **Cyclophoridae**
      Leptopoma sp. (?*L. mouhoti* (Pfeiffer, 1861)
      CI-55

    Family **Assimineidae**
      Assiminea sp. (?*A. andrewsiana* Smith,1900)
      Grants Well (CI-11).

  Sub-class **PULMONATA**
    Family **Ellobiidae**
      Pythia scarabaeus (Linnaeus, 1758)
      Runaway Cave (CI-2); Jedda Cave (CI-5); 19th Hole (CI-19); CI-55.

    Family **Vertiginidae**
      Nesopupa (?*Insulipupa*) sp.
      Coastal water bore #2.

    Family **Subulinidae**
      Subulina octona (Bruguiere, 1792)
      Jedda Cave (CI-5); Strangler Cave (CI-16).

      Subulina ?*octona* (Bruguiere, 1792)
      Jedda Cave (CI-5). Anterior end of shell broken off.

      ?*Subulina* sp.
      Strangler Cave (CI-16).

      Lamellaxis gracilis (Hutton, 1834)
      Jane-up Cave (CI-6).

      ?*Lamellaxis* sp.
      Grants Well (CI-11).

      Opeas ?*pumilum* (Pfeiffer, 1840)
      Freshwater Spring (CI-85).

    Family **Helicarionidae**
      Microcystis sp.
      Jane-up Cave (CI-6); CI-55.

    ?Family **Ferussaciidae**
      Cecilioides sp
    OR ?Family **Subulinidae**
      Ochroderma sp. OR *Prosopeas* sp.
      Freshwater Spring (CI-85).

  Class **BIVALVIA**
    Family **Isognomonidae**
      Isognomon ?*ephippium* (Linnaeus, 1758)
      (CI-20).

Phylum **CRUSTACEA**
  Class **OSTRACODA**
    Order **PODOCOPA**
      Jane-up Well; Jedda Cave (CI-5); Grants

Well (CI-11); CI-54; Henderson’s Spring (CI-64); Hugh’s Dale (CI-77); Freshwater Spring (CI-85).

Subclass **Copepoda**
Order **Calanoida** det. G.L. Pesce
Indet.
CI-54. Anchialine system.

Order **Cyclopoida**
Family **Cyclopinidae**
(CI-54). Anchialine cave
Bryocyclops (*Bryocyclops*) *muscicola* (Menzel, 1926)
Coastal water bore #1, #2, Smithsons Bight area; Jedda Cave (CI-5); Jane-up Well; Grants Well (CI-11); (CI-54); Hendersons Spring pumphouse outflow (CI-64).

Order **Harpacticoida**
Family **Ameiridae**
Nitocrella/*Nitokra* complex det. G.A. Boxshall
Coastal water bore #2; CI-54; Hendersons Spring (CI-64).

Nitokra cf. *spinipes* det. G.L. Pesce
Hendersons Spring (CI-64).

Family **Canthocamptidae** det. G.A. Boxshall
Indet.
Full Frontal Cave (CI-20).

Family **Phyllognathopodidae** det. G.A. Boxshall
Indet.
Coastal water bore #2, Smithsons Bight area.

Class **Isopoda**
Order **Oniscidea** det S. Taiti
Family **Armadillidae**
Myrmecodillo n. sp. 1 **Tx**
Jedda Cave (CI-5), Jane-up Cave (CI-6), Freshwater Cave (CI-10).

Myrmecodillo n. sp. 2 **Tx**
Coastal water bore #2, Smithsons Bight area.

Family **Eubelidae**
Elumoides monocellatus Taiti & Ferrara, 1983
Coastal water bore #2, Smithsons Bight area.

Family **Olibrinidae**
Olibrinus antennatus (Budde-Lund, 1902)
Full Frontal Cave (CI-20).

Family **Philosciidae**
Burmoniscus sp. (prob. *B. orientalis* Green, Ferrara & Taiti, 1990.
Hendersons Spring (CI-64).

Papuaphiloscia n. sp. **Tp2**
Jedda Cave (CI-5).

Class **Amphipoda**
Indet.
CI-54.

Class **Malacostraca**
Order **Decapoda**
Infraorder **Caridea**
Family **Procarididae** det. J. Short
Procaris (undescribed species), Sb Runaway Cave.

Family **Alpheidae** det. J. Short
?three species.
CI-54.

Family **Palaemoninae** det. J. Short
Macrobrachium, either *M. lar* or *M. microps*.
CI-54; Hendersons Spring (CI-64).

Macrobrachium microps Holthuis, 1978.
Freshwater Cave (CI-10).

Family **Atyidae** det. S. Choy
Antecaridina lauensis (Edmondson, 1935)

Family **Hippolytidae** det. J. Short
Parahippolyte (?*P. uveae* Borradaile, 1899).
Runaway Cave.

Infraorder **Anomura**
Family **Coenobitidae**
Birgus latro Linnaeus.
The robber crab, is nocturnal and they are occasionally found in the dark zone of caves on the plateau and especially down by the water in the small anchialine caves (e.g. CI-19 and CI-54).

Infraorder **Brachyura**
Several species of crab are found in the caves, all but Jackson’s crab superficially.

Family **Gecarcinucidae**
Gecarcoidea natalis (Pocock, 1888), the red crab.
Diurnal and ubiquitous on the ground on Christmas Island is rarely found even in the twilight zone of caves.

Cardisoma hirtipes Dana, the blue crab.
Occurs around soaks associated with springs

at Ross Hill Gardens, The Dales and Waterfall.

Family **Grapsidae**
Sesarma jacksoni Balss, jackson's crab,
Lost Lake Cave (CI-7), Freshwater Cave (CI-10), Grimes Cave (CI-53), Full Frontal Cave (CI-20), Runaway Cave (CI-2), 19th Hole (CI-19) and Smiths Cave (CI-9).

Ptychognathus pusillus Heller, the freshwater crab.
Found in running freshwater at Dolly Beach and Waterfall spring, has not been encountered in subterranean streams.

Phylum **CHELICERATA**
Class **ARACHNIDA**
Order **SCORPIONIDA**
Family **Ischnuridae**
Liocheles polisorum, Tb
Bishops Cave (CI-8), 19th Hole (CI-19).

Order **ARANEAE**
Family **Pholcidae**
Indet. **Tp2**
Runaway Cave (CI-2); Jedda Cave (CI-5); Jane-up Cave (CI-6); Bishops Cave (CI-8); Smiths Cave (CI-9); 19th Hole (CI-19); coastal water bore #2, Smithsons Bight area.

Family **Uloboridae** det. J.M. Waldock
Zosis sp., Ep
Smiths Cave (CI-9); Freshwater Cave (CI-10).

Family **Scytodidae** det. J.M. Waldock
Indet.
19th Hole (CI-19); CI-54.

Family **Theridiidae** det. J.M.Waldock
Indet. **Tp**
Smiths Cave (CI-9), Bishops Cave (CI-8).

Family **Oonopidae** det. J.M. Waldock
Opopaea sp. **Ep**
Hendersons Spring (CI-64).

Family **Gnaphosidae** det. R. Raven
Indet. **Tb**
Jedda Cave (CI-5).

Family **Heteropodidae** det. J.M. Waldock
Indet.
Smiths Cave (CI-9).

Order **AMBLYPYGI**
Family **Charontidae**
Charon gervaisi Harvey & West 1998, Tp1
Runaway (CI-2); 19th Hole (CI-19); CI-54.

Order **OPILIONIDA**
Family **Phalangodidae**
Indet., Tp1
Freshwater Cave (CI-10).

Order **ACARINA** det. M.S. Harvey
Indet., Ectoparasite
From the plumage of a Glossy Cave Swiftlet.

Indet., Ep
Grants Well (CI-11).

Indet., Ep
Jedda Cave (CI-5).

Indet., Ep
Coastal water bore #2, Smithsons Bight area.

Indet., Gp
Grimes Cave (CI-53).

Indet., Commensal/parasite, possibly Tb by association.
Jedda Cave (CI-5), on troglobitic gnaphosid spider.

Phylum **UNIRAMIA**
Class **DIPLOPODA**
Subclass **PENICILLATA**
Order **POLYXENIDA**
Indet.
Jedda Cave (CI-5); Jane-up Cave (CI-6); 19th Hole (CI-19).

Subclass **CHILOGNATHA**
Infraclass **HELMINTHOMORPHA**
Superorder **ANOCHETA**
Order **SPIROBOLIDA**
Family **Spirobolellidae** Brolemann, 1913 or **Pseudospirobolellidae** Brolemann, 1913
Indet.
Coastal water bore #2, Smithsons Bight area.

Superorder **MEROCHETA**
Order **POLYDESMIDA** det. W.S. Shear
Family **Paradoxosomatidae**
Subfamily **Paradoxosomatinae**
Tribe **Cnemodesmini**
Oxidus gracilis (C.L. Koch, 1847)
Smiths Cave (CI-9).

Superfamily **Polydesmidae**
Family **Haplodesmidae**
Cylindrodesmus hirsutus Pocock
Jedda Cave (CI-5); Jane-up Cave (CI-6).

Superorder **Ommatophora**
Order **Polyzoniida**
Family **Indet.**
19th Hole (CI-19).
Phylum **Uniramia**
Superclass **Hexapoda**
Class **Collembola**
Order **Collembola**
Indet.
Runaway Cave (CI-2); Jane-up Well; The Grotto (CI-1); Coastal water bore #1, Smithsons Bight area; Grants Well (CI-11), 19th Hole (CI-19); CI-54.

Family **Paronellidae** det. P.M. Greenslade
Cyphoderopsis Carpenter 1917, sp. indet..
Jedda Cave (CI-5).

Class **Diplura**
Order **Diplura**
Family **Campodeidae** det B. Condé
Cocytocampa sp. nov. 2, ?Tb

Order **Thysanura** det. G. Smith
Family **Nicoletiidae**
Subfamily **Nicoletiinae**
Metrinura Mendes (*sensu* Smith, 1998) Tb?
Jedda Cave (CI-5).

Class **Insecta**
Order **Blattodea** det L.M. Roth
Family **Nocticolidae**
Metanocticola christmasensis Roth 1998, Tb
Jedda Cave (CI-5); Jane-up Cave (CI-6).

Family **Blattellidae**
Gen. indet.
Freshwater Cave (CI-10).

Periplaneta americana L., Ep
Jedda Cave (CI-5); Smiths Cave (CI-9); Strangler Cave (CI-16); Upper Daniel Roux Cave (CI-56).

?New genus, Tb
Bishops Cave (CI-8).

Order **Orthoptera**
Superfamily **Grilloidea**
Grimes Cave (CI-53); Upper Daniel Roux Cave (CI-56).

Family **Myrmecophilidae**
Indet.

Order **Phthiraptera**
Suborder **Amblycera**
Family **Menoponidae**
Indet., Ectoparasite
From wing feathers of Glossy Cave Swiftlet.

Order **Hemiptera**
Suborder **Auchenorrhyncha**
Superfamily **Fulgoroidea**
Indet.
Grants Well (CI-11); 19th Hole (CI-19); CI-55.

Order **Coleoptera**
Family **Histeridae** det. ANIC
Carcinops sp., Gp
Upper Daniel Roux Cave (CI-56).

Family **Tenebrionidae** det. ANIC
Alphitobius laevigatus (Fabricius)., Gp
Upper Daniel Roux Cave (CI-56).

Order **Diptera**
Suborder **Nematocera**
Division **Culicomorpha**
Family **Culicidae** det. ANIC
Indet.
Strangler Cave (CI-16).

Family **Chironomidae** det. ANIC
Ablabesmyia notabilis type
Freshwater Spring (CI-85).

Polypedilum 'K3'
Freshwater Spring (CI-85).

Family **Ceratopogonidae** det. ANIC
Subfamily **Ceratopogonini**
Indet.
Freshwater Spring (CI-85).

Family **Simuliidae** det. ANIC
?*Austrosimulium* sp.
Freshwater Spring (CI-85).

Division **Bibionomorpha**
Family **Sciaridae** det. ANIC
?*Lycoriella* sp.
Jane-up Cave (CI-6).

Family **Mycetophilidae**
Indet., Tp1
Jane-up Cave (CI-6) and Jedda Cave (CI-5).

Suborder **Brachycera**
Division **Cyclorrhapha**
Family **Phoridae** det. ANIC
Indet.
Bishops Cave (CI-8).

Family ?**Drosophilidae** det. ANIC
Indet., Gp
Upper Daniel Roux Cave (CI-56).

Superfamily Chloropoidea
Family **Chloropidae** det. ANIC
Indet., Gp
Upper Daniel Roux Cave (CI-56).
Superfamily **Muscoidea**
Family ?**Fanniidae** det. ANIC
?*Fannia* sp.
19th Hole (CI-19).

Family **Muscidae** det. ANIC
Indet., Gp
Grimes Cave (CI-53); Upper Daniel Roux Cave (CI-56).

Order **LEPIDOPTERA**
Family **Pyralidae** det. ANIC
Pyralinae or Epipaschiinae indet., Gp
Smiths Cave (CI-9).

Family **Tineidae** det. ANIC
Indet., Gb
Smiths Cave (CI-9); Upper Daniel Roux Cave (CI-56).

Order **HYMENOPTERA**
Family **Formicidae** det. ANIC
Subfamily **Formicinae**
Anoplolepis gracilipes (Smith)
Runaway Cave (CI-2).

Subfamily **Ponerinae**
Pachycondyla sp., Gp
Upper Daniel Roux Cave (CI-56).

Phylum **CHORDATA**
Subphylum **VERTEBRATA**
Class **OSTEICHTHYES**
Infraclass **TELEOSTEI**
Order **PERCIFORMES**
Suborder **GOBIOIDEI**
Family **Eleotridae**
Eleotris fusca (Bloch & Scheider), brown gudgeon, Tp1
Upper Daniel Roux Cave (CI-56).

Subclass **AVES**
Order **APODIFORMES**
Family **Apodidae**
Collocalia esculenta natalis Lister, 1888.
Upper Daniel Roux Cave (CI-56); Smiths Cave (CI-9); Managers Alcove (CI-50); Grimes Cave (CI-53); Swiftlet Cave (CI-30).