Subterranean fauna of Christmas Island: habitats and salient features

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Abstract. A review is presented of the history of subterranean fauna exploration, the nature of the subterranean environments of Christmas Island and the biogeographical significance of members of the subterranean and springdependent species. The island, which has probably been emergent since the mid-Miocene, has a basalt core largely covered by Tertiary carbonates which have undergone intense karstification owing to the high rainfall on tropical forest, and through mixing corrosion as relative sea level changed and marine terraces formed as a result of tectonic uplift of the island. As a result, surface water is largely absent and drainage is largely as submarine groundwater discharge, however, there is a perched underground stream tapped for water on the plateau and some spring discharge on lower terraces where basalt intercepts the carbonate surface. Together these provide a range of subterranean habitats including terrestrial, freshwater streams and anchialine systems, in addition to springs and spring rills. Terrestrial caves shelter glossy swiftlets that support a rich guano-based community. Sediment banks and the tree root mats spreading over them support a community, thus far not rich, but containing troglobitic species, including the cockroach Metanocticola (Blattodea), scorpion (Ischnuridae), pseudoscorpions (Chthoniidae), microwhipscorpion (Hubbardiidae), spiders (from families Symphytognathidae; Trochanteriidae; Ochyroceratidae; Oonopidae; ?Desidae) and a variety of oniscoid isopods. As expected on an isolated seamount, it supports a procaridiid-type anchialine fauna characterised by an endemic species of *Procaris* (Procarididae). Unexpectedly, it is the only seamount supporting, in addition, representatives of a remipede-type anchialine fauna, namely *Humphreysella* (formerly *Danielopolina*) (Myodocopa: Thaumatocyprididae) and Halosbaena (Thermosbaenacea). In addition, the anchialine system supports the only known extant population of Microceratina (Podocopida: Cytheruridae). The freshwater subterranean stream and spring outlets support an extraordinary diversity of Darwinulidae (Ostracoda). A number of invasive species of fish have been introduced to freshwater areas and if established in springs could have a detrimental impact of stygiofauna and potentially invade anchialine waters. Direct anthropogenic impacts on caves is low owing to minimal caving activity on the island but the most sensitive to trampling are root mats and sediment banks in some caves, and especially guano piles, the disturbance to which could extend to glossy swiftlet colonies. Indirect impacts on fauna may occur owing to changes to the spring discharges as a result of water abstraction which could also impinge on the anchialine system by changing the hydrodynamic relationships between freshwater outflow and seawater, and through contaminants arising from land or sea.

Key words. troglobites, stygobites, anchialine, Thermosbaenacea, Thaumatocyprididae, Darwinulidae

INTRODUCTION

This paper explores some salient features of the subterranean environments of Christmas Island and their contained fauna. It encompasses aspects of terrestrial and aquatic systems, the latter including anchialine caves, but does not address fully marine caves, such as those studied by Hanomura & Kase (2001) and Kano & Kase (2002), that have insufficient freshwater input to develop the pronounced halocline characteristic of anchialine caves. The paper is not intended to provide a comprehensive list of subterranean fauna but does reference the main sources of this information.

The cave fauna of Christmas Island is a significant component of the island's biodiversity (Beeton et al.,

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© National University of Singapore ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print) 2010). The troglobitic fauna (obligate subterranean fauna living in air-filled voids) contains an array of cave-dwelling species and one of only two blind scorpions described from Australia, a group of arachnids whose troglobitic members are concentrated in Mexico, with outliers in Ecuador and Sarawak, and from Barrow Island and Christmas Island in the Indian Ocean (Harvey & West, 1998; Volschenk et al., 2001). However, the troglobitic fauna remains relatively poorly known and surveyed, a situation that also exists with the stygofauna (subterranean fauna living in freshwater-filled voids) and anchialine fauna (subterranean fauna occurring in a water body with connections to the ocean). Some aquatic taxa are endemic to Christmas Island (Namiotko et al., 2004; Bruce & Davie, 2006), while others have much broader affinities such as the Brown Spine-cheek Gudgeon Eleotris fusca which occurs in caves on many Indo-Pacific islands (H. Larson, pers. comm. 2013), and the shrimp *Macrobrachium lar* (Fabricius) that is found in waters and freshwater springs on Christmas Island (Humphreys & Eberhard, 1998), and are closely related to populations in the Pacific (A. Duffy, pers. comm. 2005 in Humphreys & Danielopol, 2006). Christmas

Island has an anchialine community of the procarididtype which are restricted to isolated seamounts (known elsewhere from Bermuda, Ascension Island and Hawaii: Bruce & Davie, 2006; Humphreys & Danielopol, 2006). Remarkably, the Christmas Island anchialine system also has the thaumatocyprid ostracod *Humphreysella* (formerly Danielopolina (Kornicker et al., 2006; Humphreys et al., 2009 and transferred by Iglikowska & Boxshall, 2013), in a clade (Iglikowska & Boxshall, 2013) typical of the Remiped-type anchialine community, elsewhere restricted to epicontinental areas; Christmas Island is the only seamount globally where representatives of both types of anchialine community cooccur (Humphreys & Danielopol, 2006). Humphreysella baltanasi (Kornicker, 2009) of Christmas Island belongs to a different genus from the only other Indian Ocean (and Australian) member of the clade, Welesina kornickeri (Danielopol et al., 2000) the latter being known sympatrically with Kumonga (formerly Lasionectes) exleyi (Kumongidae) a monotypic family of Remipedia in Bundera Sinkhole, Australia (Hoenemann et al., 2013), now in the Ningaloo Coast World Heritage Area. The general compositions of both types of anchialine community are predictable, even to the generic level, however far apart in the world they occur (Jaume et al., 2001).

SUBTERRANEAN ENVIRONMENT

Christmas Island is the emergent part of an isolated seamount that rises 4.5 km from the ocean floor. The island is now a carbonate cover island (sensu Mylroie et al., 2001; Jensen et al., 2002) in which the basalt core of the emergent volcano has become encased with carbonates, although in places these are inter-bedded with basalts of Eocene to Quaternary age. Grimes (2001) provided a detailed account of karst features on the island (Fig. 1). The island, which now reaches an altitude of 361 m ASL, has been subject to both tectonic uplift and eustatic changes that have resulted in major sea level changes relative to the island. These processes have resulted in a coast that is mostly cliffed and which rises through a series of up to four terraces to a plateau between 180 and 240 m ASL.

Generally, in such a situation karst development could be expected in the carbonate collar of the island to a depth of about 140 m below current sea level representing the formation of salt water interface caves expected to have been formed by mixing corrosion (Mylroie & Mylroie, 2007) during stadia in Pleistocene low sea levels (Siddall et al., 2006) and which may subsequently have been exposed by cliff retreat to form flank margin caves (sensu Mylroie, 2008). However, the rate of tectonic uplift of the island is about 0.14 m per 1000 years (Woodroffe, 1988) which represents an uplift of 18 m since the Late Quaternary (shore terrace limestones, 124 ka), 259 m since the start of the Quaternary (the age of the coastal terraces, see Grimes, 2001) and 576 m since the mid-Pliocene. Pleistocene sea level minima of ca. -120 m occurred at about 140 ka and 20 ka BP (Pillans et al., 1998) but, due to the uplift, the lowest cave development will now be somewhat shallower than these minimum Pleistocene sea level stands. In addition to

subterranean habitat formed in carbonate by karst processes, the basalt core of the island is probably fractured by rifts (Polak, 1976) and this may provide a fractured rock habitat for both air and water breathing subterranean animals.

FRESHWATER ECOSYSTEMS

The high rainfall percolates through the karstic limestone to the basalt core and drains to the sea largely as submarine groundwater discharge. Falkland (1999) modelled recharge using data from a number of sites on Christmas Island and estimated recharge to be 975 mm yr⁻¹, being 51% of the mean annual rainfall of 2017 mm. With a shoreline of 86.3 km and a surface area of 135 km², and effectively no surface run-off, the average submarine discharge along the shore should be about 4.5 m³ m⁻¹ d⁻¹. However, being a monsoonal climate, there is a marked seasonality in the rainfall between a mean of 42 mm in August and 347 mm in February. This seasonality will influence the balance between freshwater outflow and seawater intrusion and, in consequence, the location of the salt-water interface in the anchialine system is likely to migrate respectively landward or seaward on an annual basis.

A subterranean stream provides much of the potable water supply on Christmas Island coming from Jedda Cave [CI-5 (see Appendix 1): which accesses a cave stream midway between the subterranean flow from Grants Well (CI-11) and Jane-Up Cave (CI-6)] (Barrett, 2001). Recent investigation, based on scant data, has suggested the presence of a limited amount of perched groundwater (above volcanic rock) in the north east part of the island, while there is a substantial fresh groundwater system (basal aquifer) to the north of the Smithson Bight, at and below sea level, that is similar in quality to the perched water from where it flows (Falkland, 1999). Springs occur in a few places where basalts intercept the limestone surface above sea level, such as Ross Hill Gardens [fed by Hewan's and Harrison's (Nos 1 and 2) Springs], and Waterfall (fed by three separate springs, namely, Waterfall, Freshwater and Jones Springs) (Falkland & Usback, 1999). These rheocrene springs feed short rills mostly discharging to the coast, some across extensive areas of tufa with gour (rimstone) pools, such as the Dales on the west coast. Although some springs are tapped by the water utilities for human use the rills still flow, some discharging to the sea and others being lost below ground after short

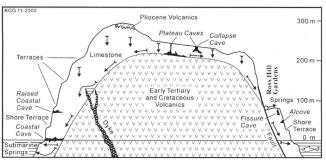


Fig. 1. Diagrammatic cross-section of Christmas Island, showing volcanic core, limestone capping, water flow lines (arrows) and typical cave development. Vertical scale is exaggerated $\times 10$. From Grimes (2001).

runs. Cave streams discharging to the coast are intertidal and those parts not directly connected with the sea form part of the anchialine system with the exception of the Daniel Roux Gusher, a forceful conduit with a minimum flow of about 15 Ls⁻¹ (Falkland, 1999), that emerges in the intertidal of Daniel Roux Cave. Owing to its location, minor engineering would be required to position a sampling net to undertake prolonged sampling, a view reinforced by the 'significant technical challenge' (Falkland, 1999) that would be needed to develop it as a water supply.

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 & Polak, 1979), although the basis of the latter report is unknown. Attempts to locate freshwater outflows along the coastline using thermal imagery or salinity readings taken along the coast were not successful (Falkland, 1999). In 2013, a technical diving team explored short areas of the ocean wall to 130 m depth in an attempt to locate reported deep resurgences and hypothesized flank margin caves at Pleistocene low sea level stadia but without success.

Some atolls are also known to support anchialine fauna, for example, *Parhippolyte uveae* Borradaile, *Periclimenes pholeter* Holthuis, and *Spelaeomysis servatus* (Fage) occur on Aldabra, Seychelles (Fransen & Tomascik, 1996; Pesce & Iliffe, 2002), a raised reef atoll. However, there has been no research directed at potential anchialine habitats on the more low lying Cocos (Keeling) Islands despite good access in places to a thin groundwater lens (Jacobson, 1976).

KARSTIFICATION

The carbonate cover of the island has highly developed karst and many large caves open from the cliffs (e.g., Daniel Roux, CI-5; Lost Lake, CI-7; Full Frontal, CI-20) and the lower terraces (Bishops Cave, CI-8; Smiths Cave, CI-9; Freshwater Cave, CI-10), many of which have extensive phreatic development (Fig. 2). On the plateau small diameter sinkholes give access to a karst stream (Jedda Cave, CI-5;

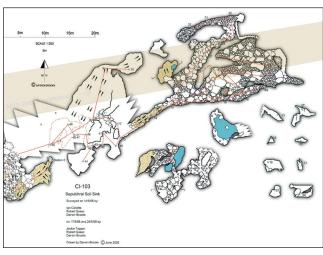


Fig. 2. Cave survey of CI-103 showing the complex nature of the caves on the lower terrace. With permission from Darren Brooks.

Jane-up Cave, CI-6; Grants Well, CI-11) (Fig. 3). Examination of bore logs (Falkland, 1999) shows that void development in the carbonates is present at all altitudes and that there is no trend in void size with altitude (Fig. 4). This indicates that karstification has been rather uniform through time despite the eustatic and tectonic changes affecting the island. Consequently, habitat for subterranean fauna should be widely available within the limestone. However, as subterranean systems typically rely on allochthonous energy sources. normally in the form of dissolved organic carbon (Culver & Pipan, 2009), the amount of energy to support populations of subterranean animals may decline with distance from the source, typically the surface. However, as anchialine systems are known to support chemolithotrophic extremophile microbial communities (Pohlman, 2011; Humphreys et al., 2012), this potential energy source should not be excluded.

FAUNA COLLECTIONS

Other than the cave exploration associated with finding water supplies (Barrett, 2001), there have been a number of fully or partially cave-focused collecting trips since 1987, three centred on the Western Australian Speleological Group, two funded by Parks Australia, and the most recent, a cave diving trip in 2013 funded by National Geographic. Most trips have involved museum staff or associates (Western Australian Museum, Raffles Museum of Biodiversity Research and Queensland Museum) and have involved numerous volunteer cavers and/or cave divers. The timing and nature of these episodes of cave research are outlined in Table 1 together with some of the significant fauna records. During a more prolonged WASG expedition in 2006, considerable effort to locate *Humphreysella* (then *Danielopolina*) and *Procaris*

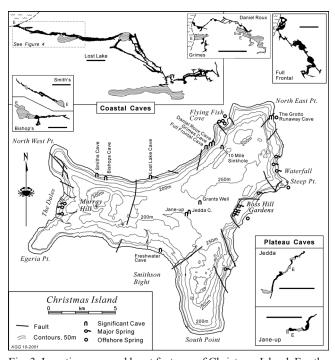


Fig. 3. Location map and karst features of Christmas Island. For the cave maps: the scale bar in each map is 100 m; black is solution passage; collapse areas are shaded; "E" marks an entrance (from Grimes, 2001, with permission).

Table 1. Main periods of collections of cave fauna, approximate specimen lot numbers, and main collectors/sponsors, together with significant cave fauna. Column two shows the number of specimen lots, amounting to more than 2000 specimens, collected from caves and karst waters on Christmas Island between 1987 and 2006. **Most** have not been formally identified and are deposited in the Western Australian Museum. Abbreviations: CI, Christmas Island; WASG, Western Australian Speleological Group; PANCI, Parks Australia North.

Year No. lots		Organisation and collectors	Significant fauna	
1987	2	WASG – N. Plumley (SEXI, 1987)	First troglobitic Ischnurida scorpion and the first troglobitic scorpion from Australia (Volschenk et al., 2001).	
1998	254	PANCI – W.F. Humphreys & S.M. Eberhard ¹	Recognition of diversity of CI cave fauna and especially the presence of an anchialine fauna (Humphreys & Eberhard, 1998, 2001). Procarididae recorded (Bruce & Davie, 2006), still the sole specimen. Finding of plurality of unusual and unusually located ostracods; genus <i>Microceratina</i> (Eucytherurinae), and families Darwinulidae and Thaumatocyprididae (Namiotko et al., 2004; Humphreys & Danielopol, 2006; Martens & Rossetti, 2002).	
2001	6	R.D. Brooks, M. Jefferies	Tyrannochthonius sp. nov. (Pseudoscorpiones)	
2004	120	R.D. Brooks, M. Jefferies	Danielopolina (now <i>Humphreysella</i>) collected (Humphreys & Danielopol, 2006; Kornicker et al., 2006).	
2006	591	WASG – R.D. Brooks, J. Anderson. Brooks (2006)	Danielopolina more widespread (Humphreys et al., 2009). Recognition of unique juxtaposition of representatives of epicontinental and seamount faunas (Humphreys & Danielopol, 2006; Humphreys et al., 2009).	
2010 and 2011	_	Raffles Museum of Biodiversity Research, Singapore (Ng et al., 2010, 2011)	A number of cave-adapted crustaceans and a fish were added to the fauna list from these Raffles Museum visits.	
2013		National Geographic. T.M. Iliffe, W.F. Humphreys /Texas A&M/ Western Australian Museum with technical cave diving team ² Dry cavers J. & R. Anderson & D. Smith	Prionospio, Halosbaena	

¹Also reports on cave use management (Spate & Webb, 1998), Geotechnical Hazard Assessment (Coffey Partners International, 1998) and Karst Geology (Grimes, 2001).

(the latter known from a single specimen) yielded only two juveniles of the former and no specimen of the latter despite up to 20 successive days of sampling of the original collection site and others. A subsequent cave diving trip in 2013 added only four additional *Humphreysella*, including adults for the first time, but no *Procaris*. However, it did record *Prionospio*, a genus of spionid Polychaeta, known from anchialine waters in Bundera Sinkhole in Western Australia and Lanzarote in the Canary Islands, Spain, but

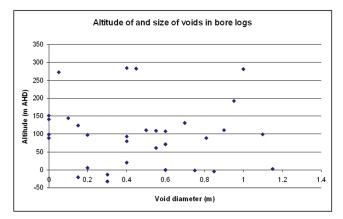


Fig. 4. Size of voids with altitude above datum; data extracted from the bore logs in Douglas Partners (1996).

which is also widespread in the ocean (Sigvaldadóttir, 1998) and brackish water of estuaries (Radashevsky et al., 2006). In addition, this expedition also recorded *Halosbaena* (Thermosbaenacea, restricted to subterranean waters) which has a similar distribution to the anchialine *Prionspio*.

AGE OF ISLAND FOR COLONISATION

Karst development of the type seen on Christmas Island requires that the island be at least partly emergent from the sea, as does the presence of endemic subterranean fauna in freshwater, anchialine and terrestrial systems (Grimes, 2001; Humphreys & Eberhard, 2001). Grimes (2001) made a careful assessment of evidence for the duration of aerial exposure of the island. He combined global sea level curves from the Pliocene onwards and the uplift rate of the island—due to its progression northwards over the lip of the Java Trench—based on age of the shore terrace (124 ka) and the current elevation of the highest point (Murray Hill, 360 m) (Woodroffe, 1988). Grimes (2001) concluded that the island could have had dry land for 2-3 million years. However, Pliocene rocks also seem to have been subaerial (Barrett, 1989) and so the island could have also been emergent at that time (5-3 Ma). Deposition of the main limestones on Christmas Island ceased during the

²See Acknowledgements.

low sealevel in mid-Miocene (10 Ma) when the limestone would have been emergent and exposed to karstification for several million years. The lack of extensive Pliocene and Pleistocene limestones suggests that there was then no extended submergence of the island (Grimes, 2001). In essence, there is no evidence of prolonged deep submergence from the mid-Miocene onwards but short periods of shallow submergence cannot be discounted.

METHODS

Owing to the very low energy environment characteristic of most subterranean habitats, with the exception of the fauna on guano piles (Poulson & Lavoie, 2000; Culver & Pipan, 2009), the populations of cave-adapted animals are very sparse and so irregular methods are typically used to sample them. 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 visual searching and hand collection into a vial, but guano samples were collected and examined for fauna in the laboratory or the fauna was concentrated from guano deposits by means of temporary pit-fall traps. Aquatic fauna was sampled by hand or hand-net following visual sighting, or by plankton nets (mesh size 350 and 60 μm) of appropriate dimensions hauled through the water column (Fig. 5), and by the use of traps—working on the principle of cray pots—baited with a variety of baits and left in place overnight. Snorkelers and divers visually searched for animals and collected them individually in vials, else they towed plankton nets through the water to concentrate animals. In cave streams and springs, the entire stream was filtered through nets for 24 hours or more (Fig. 6). Samples were mostly examined under a dissecting microscope while the specimens were alive in order to enhance the recovery and quality of specimens. Specimens were preserved in 75% ethanol, formalin or Bouin's solution as appropriate, while specimens for molecular work were stored in 95% ethanol.

NATURE OF SUBTERRANEAN LIFE

Animals occurring in caves have varying degrees of cave dependence, some being there by chance while others are highly adapted to permanent subterranean habitation. They



Fig. 5. Jay Anderson netting rootlet mass in CI-54, Whip Cave. Photo: Ross Anderson.

can be classified according to their apparent 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 underground they do not reproduce there. Trogloxenes spend part of their life cycle in caves, as for example, glossy swiftlets that roost and nest in caves but emerge to seek food outside—their excreta may form the basis of distinct guanodwelling 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 (Hamilton-Smith, 1971). Troglobites are species which obligatorily spend their entire lives within caves-troglodytes are people inhabiting caves-and are highly specialised to life underground and they cannot survive on the surface for any length of time. They are of interest to scientists because of their degree of specialisation, and because they are frequently found to be climatic or phylogenetic relicts that have survived in subterranean habitats long after their surface-dwelling ancestors have become extinct (Humphreys, 2000). In addition, entrapped in the geological context by their adaptations to subterranean life, repeated independent colonisation of the subterranean environment can serve as powerful models by which to explore the processes of evolution (Leijs et al., 2012; Vergnon et al., 2013). However, this does not preclude active colonisation of caves by their epigean ancestors (Rouch & Danielopol, 1987; Hoch & Howarth, 1999). Troglobites display a number of characteristic convergent morphological



Fig. 6. Stygofauna net filtering the entire flow of the subterranean stream passing through the notched weir in Grants Well in 2006. Photo: Ross Anderson.

traits involving the reduction or loss of characters (regressive evolution) such as the loss of eyes, pigment, sclerotisation and wings. This trend is complimented by the enhancement of other non-visual, sensory 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 information, and by physiological changes such as reduced metabolic rate. Collectively, these traits are referred to as troglomorphies (Christiansen, 1962). It is convenient to distinguish those subterranean fauna restricted to water by the prefix stygo- (sometimes stygio-), 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, but see discussion in Sket (2008) who proposes the hierarchical terms trogloxene, subtroglophile, eutroglophile and troglobiont as terms for increasing adaptation to subterranean life.

FAUNA

The fauna from some of the earlier work has been reported elsewhere (Humphreys & Eberhard, 1998, 2001) and here I simply make reference to these lists but focus attention to certain of the more interesting results that have emerged from those and subsequent studies, largely presented here in the context of specific habitats. There are many samples collected in caves, not necessarily cave-adapted species, that have not been formally identified but which are deposited in the Western Australian Museum (Table 2).

Anchialine (or anchihaline) ecosystems. These near-coastal groundwaters within a karst or pseudokarst matrix that occur circum-globally, largely in tropical and subtropical coastal areas in oceanic islands and less commonly on peninsulas. They are accessed through caves, bores or karst windows or anchialine pools (especially on the Hawaiian Islands (www. usgs.gov/ecosystems/pierc/files/factsheets/pools.pdf). They contain tidally influenced, stratified layers of fresh to brackish waters, overlying hypoxic bottom water of fully marine salinity. Extensive networks of submerged passageways often extend from collapse cave entrance pools locally referred to as "blue holes" in the Bahamas and "cenotes" in the Yucatan Peninsula. This type of habitat was recognised by Holthuis (1973) but formalised by Sket (1981) and Stock et al. (1986).

Anchialine systems often support an extraordinarily diverse cave-adapted fauna, primarily found below a halocline and so inhabiting the deeper, marine layers of water. They mainly comprise a diverse array of crustacean higher taxa that are often endemic to anchialine ecosystems (Jaume et al., 2001). They have been categorised as procarid-type and remipede-type anchialine faunas occurring on isolated seamounts and in epicontinental seas respectively (Humphreys & Danielopol, 2006), the types being named after prominent higher taxa often associated with each, the family Procarididae and class Remipedia respectively. Procarids are found on Hawaii, Ascension Island, Bermuda,

and Christmas Island, whereas remipedes, which have an amphi-Atlantic distribution (Caribbean and Canary Islands) and north-western Australia, are considered to show a full tethyan track distribution suggesting that the ancestors of this fauna existed in the Tethys Sea since the Mesozoic (Iliffe et al., 1983, 1984) and that their present distribution could have occurred by vicariance as a result of plate tectonics (Jaume et al., 2001), a hypothesis currently under intense debate (Maderspacher, 2012; Bauza-Ribot et al., 2013; de Bruyn et al., 2013; Phillips et al., 2013). The general composition of each type of anchialine fauna is predictable, often to the generic level, however far apart and isolated they occur (Jaume et al., 2001) but the fauna composition differs between the two type types of anchialine system (Humphreys & Danielopol, 2006).

Although access to the anchialine system on Christmas Island is quite limited and the full salinity profile not reached (see Humphreys et al., 2009), the presence of a procarid-type anchialine fauna was established as a result of the expedition in 1998 (Humphreys & Eberhard, 1998, 2001) through the discovery of a procarid for the first time in the Indian Ocean, the Christmas Island endemic, Procaris noelensis Bruce & Davie, along with alpheid, hippolytid and atyid shrimps, characteristically associated with procarids (references in Humphreys & Danielopol, 2006). In 2004 and 2006 juvenile specimens of a specimens of the thaumatocypridid ostracod, Humphreysella (then Danielopolina) baltanasi Kornicker were found (Fig. 7)—the first time the genus had been found in a procaridid anchialine community on an isolated seamount (Humphreys & Danielopol 2006)—together with calanoid, cylopinid and harpacticoid copepods, and a nerillid polychaete. The evidence suggests that there should be a broad band of caverns, and associated crevicular habitat, from above the ocean to a depth of at least 100 m (Humphreys & Eberhard, 1998, 2001; Grimes, 2001; Namiotko et al., 2004; Humphreys & Danielopol, 2006) that could have,

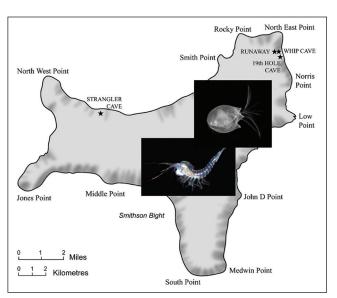


Fig. 7. Location of major anchialine caves (capital letters) on Christmas Island (map from Humphreys et al., 2009). Insets: upper, *Humphreysella baltanasi*, photo: Ross Anderson; lower, *Halosbaena* sp., photo: Douglas Elford, WAM.

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Table 2. Oniscidean isopods collected from Christmas Island caves (determined by S. Taiti). Distributions of genera from Schmidt & Leistikow (2004). Most species unclassified. Ep, epigean; Tx, trogloxene; Tp2, second level troglophile.

Family	Species	Cave no. 6CI-	Distribution
Armadillidae	Cubaris murina Brandt	54, 103	Pantropical
Armadillidae	Myrmecodillo n. sp. 1 Tx	5, 6, 10, 19	Genus: Madagascar, South Africa, Tonga, Hawaii, Mauritius, New Britain, Queensland Australia
Armadillidae	Myrmecodillo n. sp. 2 Tx	Coastal water bore #2 Smithsons Bight	_
Armadillidae	Myrmecodillo n. sp. 3	2, 56	_
Armadillidae	Myrmecodillo n. sp. 4	12, 99	_
Armadillidae	Venezillo parvus (Budde-Lund)	19	Tropics and subtropics, Europe
Eubelidae	Elumoides monocellatus Taiti & Ferrara Ep	Coastal water bore #2 Smithsons Bight	Mauritius, Reunion, Seychelles
Eubelidae	Elumoides sp. (n. sp. $?? ?)$	19	Genus: Seychelles, Réunion, Mauritius, Kribi?, Ascension
Halophilosciidae	Littorophiloscia cf. pallida Taiti & Ferrara	99	Genus: Atlantic coast of North America, East Africa, Southeast Asia, Egypt, St. Helena, Ivory Coast
Olibrinidae	Olibrinus antennatus (Budde-Lund) coastal shore	20	Southern Asia
Philosciidae	Anchiphiloscia pilosa (Budde-Lund)	10, 11, 99	Chagos, Solomon Islands
Philosciidae	Burmoniscus orientalis Green, Ferrara & Taiti	11, 12, 13, 16, 64	Southern Asia
Philosciidae	Indet, with eyes & pigment	54	_
Philosciidae	Papuaphiloscia n. sp. 1 Tp2	2, 5, 11, 12, 13, 19, 100	Genus: Bismarck Archipelago; China: Hubei, Hainan Dao; Guadalcanal; Hawaii; New Guinea; Japan: Okinawa; New Zealand
Philosciidae	Papuaphiloscia n. sp. 2	2, 13	_
Platyarthridae	Trichorhina heterophthalma Lemos de Castro	54	Pantropical

and in places may currently support, anchialine fauna on Christmas Island, and that this cavernous/crevicular collar would have provided continuous anchialine habitat during isostatic and eustatic changes.

Procarididae. The first occurrence of *Procaris* in the Indian Ocean is notable because morphological and molecular analyses have confirmed that the genus belongs to a basal infraorder, the Procarididea Felgenhauer & Abele, 1983, that diverged from its sister lineage, the Caridea, in the Early Carboniferous 333 MYA (285–403 MY, 95% confidence interval) (Bracken et al., 2010). This ancient family comprises only five known species, all from anchialine environments found largely on isolated seamounts—Hawaii, Ascension Island, Christmas Island and Bermuda—and Cozumel Island, Mexico.

Humphreysella (formerly Danielopolina). The thaumatocyprid Myodocopa genus Humphreysella (Kornicker & Danielopol in Kornicker et al., 2006) is a member of the core anchialine fauna suite found in epicontinental areas, together with other crustacean taxa such

as remipedes, thermosbaenaceans of the genus Halosbaena and epacteriscid copepods (Iglikowska & Boxshall, 2013). Recent phylogenetic analysis has recognised that the type species Danielopolina carolynae Kornicker & Sohn from the Atlantic deep benthic, is the only valid member of the genus and that all other members of the genus Danielopolina comprise a separate clade of anchialine thaumatocypridids which have accordingly been transferred to a new genus Humphreysella containing 10 anchialine species, and a new monotypic genus Welesina as W. kornickeri (Danielopol et al., 2006) from Western Australia (Iglikowska & Boxshall, 2013). These thaumatocyprids are considered to be closely related to *Pokornyopsis* which, during the Jurassic, inhabited submarine fissures in the northern Tethys, now in central Europe (Aubrecht & Kozur, 1995; Aubrecht & Schlögl, 2011). On Christmas Island H. baltanasi is known from several adjacent caves near North East Point (Runaway CI-2, 19th Hole CI-19, Whip CI-54), and two caves at the base of West Point (Bishops CI-8 and Strangler CI-16) 14 km away in direct line or 17 km through the mooted anchialine system (Fig. 7); this wide distribution suggests that Humphreysella may be expected to be widely present in the anchialine system of the island.

Microceratina: Cytheruridae. Of particular significance is the finding of the cytherurid ostracod genus *Microceratina* (as *M. martensi* Namiotko, Wouters, Danielopol & Humphreys, 2004), which is recorded for the first time ever with soft body parts from Christmas Island. The genus occurs, as *M. pseudoamfibola* Mazzini & Gliozzi, 2000, in an anchialine cave in southern Italy, although it is known only from valves. However, the genus has a long fossil record from the Late Cretaceous to Recent. *Microceratina martensi* is known from the organic rich anchialine system in Whip Cave (CI-54; Fig. 8).

Prionospio sp.: Polychaeta. The genus includes about 80 species in the oceans where it has a cosmopolitan distribution (Sigvaldadóttir, 1998). However, other than Christmas Island (Whip Cave), the genus is known from anchialine caves only on Lanzarote (Canary Islands: Wilkens et al., 2008) and Bundera Sinkhole (northwestern Australia: Wilson & Humphreys, 2001). In life these sediment-inhabiting cave species repeatedly swim (wriggle) up into the water column and fall back to the sediment; the significance of the behaviour is not known but may be related to the extremophile environments encountered in anchialine systems (Humphreys, 1999; Seymour et al., 2007; Humphreys et al., 2012) and other habitats commonly inhabited by members of the genus *Prionospio* (Gaudron et al., 2010).

Thermosbaenacea. The order Thermosbaenacea is restricted to subterranean waters including thermal springs in fresh water, brackish water and anchialine habitats (Jaume, 2008), and the hyporheic and chemoautotrophic systems, and includes about 36 species within seven genera (Wagner, 1990; Poore & Humphreys, 1992; Shimomura & Fujita, 2009; Por et al., 2013). Four species in the genus *Halosbaena*, each restricted to one area, are described from anchialine systems of the Caribbean, Lanzarote in the Canary Islands (Wagner, 1990), Minamidaito-jima, Okinawa, Japan (Shimomura & Fujita, 2009) and from the coastline of the southern North West Shelf, Australia, where it extends from anchialine habitats into freshwater systems to ca. 300 m altitude (Poore & Humphreys, 1992; Humphreys, 2008). The distribution of the genus has been considered consistent with the spread



Fig. 8. Whip Cave (CI-54), the site of greatest anchialine fauna diversity recorded on Christmas Island; diver is Richard 'Harry' Harris. Photo: Bill Humphreys.

of the Tethys during the break-up of Pangaea but recent records from the isolated sea mounts of Christmas Island (*Halosbaena* sp.) and Minamidaito-jima, Japan (Shimomura & Fujita, 2009) challenges this hypothesis and suggests more recent dispersal (Humphreys & Danielopol, 2006).

Decapoda. The varunid crabs, *Orcovita orchardorum* Davie & Ng and *Orcovita hicksi* Davie & Ng are anchialine specialists and represent the first occurrence of the genus in the Indian Ocean. They are known from Runaway and Whip Caves and the 19th Hole, these caves being within 250 m of each other and probably interconnected, as well as from Freshwater Cave on the south coast on Smithson Bight, 13 km direct line or 28 km through mooted anchialine systems. Their sympatric occurrence and widely separated locations suggests that they, like *Humphreysella*, will occur widely in the anchialine system of Christmas Island.

As reported in Davie & Ng (2012), both new species of Orcovita were collected with other decapods including the alpheid shrimp *Metabetaeus minutus* (Whitelegge) (see Anker, 2010), a possible new species of hippolytid shrimp, Parahippolyte sp., a new species of Macrobrachium (Palaemonidae), and an atyid shrimp *Antecaridina* (?) *lauensis* (Edmondson). Besides these, numerous other aquatic species had previously been reported within the same wider cave systems including: an unidentified Scyllidae sp. (Polychaeta); Nerilla sp. (Archiannelida: Nerillidae); Microceratina martensi (Ostracoda: Cytheruridae); Humphreysella baltanasi (Thaumatocyprididae: Halocyprida) (Humphreys & Danielopol, 2006; Humphreys et al., 2009; Iglikowska & Boxshall, 2013); Nitocrella/Nitokra complex (Harpacticoida: Ameiridae); Bryocyclops muscicola (Menzel)(Cyclopoida: Cyclopinidae); a new copepod genus (Calanoida: Arietellidae); Leucothoe sp. (Amphipoda: Leucothoidae); Macrobrachium lar (Decapoda: Palaemonidae); Gobioidae indet. (Pisces: Perciformes); unidentified Eleotridae (Pisces: Perciformes) (see Humphreys & Eberhard, 2001; Namiotko et al., 2004); Eleotris (?) fusca (Eleotridae) (Humphreys & Eberhard, 2001; Namiotko et al., 2004). Three species of eels, Anguilla bicolor (Anguillidae), Echidna unicolor (Muraenidae), and Congresox talabonoides (Muraenesocidae) were also present in Whip and Runaway Caves (Tan et al., 2014.). This very diverse anchialine assemblage lies on the northeast corner of Christmas Island in the zone of most intense anthropogenic

Marine species in caves. Marine caves are commonly inhabited by widespread species such as the xanthid *Neoliomera cerasinus* and portunid *Atoportunus gustavi* both of which occur in caves on Christmas Island as well as Guam and Ryukyus Islands, Japan (respectively Ng, 2002; Ng & Takeda, 2003). The latter species occurs primarily on coral rubble but also in caves (hence they are both chalicophilous and cavernicolous) and possess all the features associated with an obligate cavernicolous lifestyle, namely, reduced colouration, elongated appendages and reduced eyes (Ng & Takeda, 2003); *Metabetaeus* has also been collected in anchialine systems and *M. mcphersonae* in coral (Anker, 2010). In this respect they mirror terrestrial subterranean

fauna which show well developed troglomorphies even in the shallow subterranean habitat (Culver & Pipan, 2009). The possibility that a chalicophilous life style may pre-adapt species for colonisation of anchialine caves suggests that sampling deep within coral rubble, say by Bou-Rouch pumps developed for studying hyporheic habitats (Bou & Rouch, 1967) or similar, may be rewarding for those interested in the colonisation of anchialine caves and the dispersal of anchialine species.

Species-rich anchialine caves on Christmas Island, especially Whip Cave which is about 75 m from the ocean with its diverse cave fauna with at least 22 species (see varunid crabs section above), also have fully marine species such as the pelagic harpacticoid copepod *Macrosetella gracilis* (Dana) that is typically associated with colonies of a bloomforming nitrogen-fixing (diazotrophic) cyanobacterium *Trichodesmium* sp. found in tropical and subtropical waters (O'Neil et al., 1996).

The aquatic fauna in Whip Cave contains coexisting fauna that can occupy a wide range of habitats. It contains typical anchialine fauna (*Humphreysella*, *Halosbaena*), but also semi anchialine taxa such as *Metabateus* (*M. minutus* also occurs further inland in Runaway Cave), and probably accidental occurrences of the pelagic *Macrosetella*

Freshwater. As discussed above, access to subterranean strictly freshwater subterranean ecosystems on Christmas Island is limited to the plateau karst stream that flows between Grants Well and Jedda Cave where nets can be positioned to filter the water flow. Springs occur in a few places where basalts intercept the limestone surface above sea level and, together with their rills and tufas, these sites can be sampled directly or by interception stream flow through nets. The freshwater habitats support significant and unusual taxonomic entities, especially freshwater fish and decapods (*Macrobrachium microps*, CI-3, CI-10) and *M. lar*, CI-54, Cl-64, the latter 80 m above sea level) (Short & Meek, 2000), as well as a host of introduced species.

Darwinulid ostracods. The Darwinulidae are considered to have been asexual for millions of years and in consequence to have a very slow evolutionary rate resulting in a very conservative morphology (see discussion in Rossetti et al., 2011). About 35 living species in six genera are recognised world wide. The presence of several new species and a new genus on Christmas Island is an unexpected and significant finding, representing an extraordinary diversity in one location, one likely to be enhanced by the use of molecular techniques (Schön et al., 2012). The darwinulids all occur in freshwater, variously in subterranean streams, springs or tufa flows: Vestalenula sp. E: (danielopolispecies group, provisional), Grants Well CI-11; Isabenula humphreysi Rossetti, Pinto & Martens, 2011 (genus endemic to Christmas Island), Hughs Dale CI-77; Penthesilenula sp. (africana-species group, provisional), CI-11, Hendersons Spring CI-64, CI-77.

Fish of inland waters. A number of fish (and a 'terrapin') have been reported from the inland waters of Christmas Island, typically associated with the karst features such as anchialine waters, springs and spring rills, as well as water tanks. The fish comprise the platy, Xiphophorus maculatus (Gunther) mosquito fish, Gambusia affinis (Baird & Girard) guppy, Poecilia reticulata Peters tilapia (Oreochromis sp.); and the Asian bony tongue, Scleropages formosus (Schlegel & Müller). Populations were prolific in some of the Dales and at Ross Hill Gardens in 1998 but the current status of the populations is unknown. Although they are presumably all introduced species, they are likely to have a significant influence on the invertebrate fauna of the karst and cave habitats. A number of these species are prolific breeders (Allen, 1991) and are known to become pests of native fauna: guppies are likely to eliminate the native fauna when they enter natural fresh or brackish waters (G. Allen, pers. comm. 1993); tilapia because of its destructive behaviour (Allen, 1991); and mosquito fish which often take over, crowding out the native species (Allen, 1991). A number of these species are known to invade anchialine systems in Hawaii (Ridgley & Chai, 1990) and Cape Range in Western Australia (W. F. Humphreys, unpublished) including Gambusia sp., Poecilia sp. and Oreochromis sp. (Ridgley & Chai, 1990). Predictions that feral fish locally contained in artificial ponds were likely to invade the anchialine system on the Cape Range peninsula, Western Australia (Humphreys, 1994), had been fulfilled by 1997 (Humphreys, 2010), where the land management agency has not yet succeeded in eliminating this threat. Invasion of the anchialine system is possible by direct invasion from freshwater habitats but is most likely by human agency.

The brown gudgeon, *Eleotris fusca* (Bloch & Scheider) (Perciformes: Eleotridae) is native to Christmas Island where pale forms have been reported from the dark zone of Daniel Roux Cave. A species of cave-dwelling pygmy goby (*Trimma*: Gobiinae) is recorded in the current volume (Tan, 2014).

Asian bony tongue. Scleropages formosus (Teleostei: Osteoglossoidei: Osteoglossidae) is probably introduced; it has been recorded from an unspecified location and its present status on Christmas Island is unknown. These mouthbrooders are widely distributed in Southeast Asia, Sumatra and Borneo and represent an ancient group of primary freshwater fish having remained in freshwater throughout their history. They are included as endangered in the IUCN Red List of threatened animals, being an endemic species of very restricted distribution now threatened by overfishing. There is disagreement as to whether the species comprised one or four species prior to the description of the Myanmar population (Pouyaud et al., 2003; Kottelat & Widjanarti, 2005).

Tilapia. Oreochromis sp. (Percoidei: Cichlidae). This widely introduced genus has been recorded in Ross Hill pond; it is an omnivorous mouth brooder that is tolerant of hypersaline waters and eating small invertebrates (Getachew, 2006) and so may be more widely invasive and threaten karst invertebrate fauna.

Guppy. Poecilia reticulata and platy, Xiphophorus maculatus (introduced in Ross Hill pond) and Gambusia affinis (Cyprinodontiformes: Cyprinodontoidei: Poeciliidae), swamp above waterfall at the Dales. Guppy, in particular, has been recognised as a serious threat to the anchialine systems as they are known to be able to invade estuarine waters. The closely related Atlantic Molly, Poecilia mexicana, is able to colonise and adapt to cave systems, including extreme sulphurous environments (Parzefall, 2001; Plath et al., 2004; Korner et al., 2006; Plath, 2007). Consequently, the presence of guppy in karst pools on Christmas Island for prolonged periods should be considered a threat to the anchialine ecosystem as a whole through potential predation and competition by this highly invasive predator, and by its potential to introduce a parasite (Asian fish tapeworm) that could threaten at least the electrid fish populations (Dove & Fletcher, 2000; W. F. Humphreys, 2010, unpublished report). The Gambusia on mainland Australia is G. holbrooki but it is likely that Gambusia would have been introduced to Christmas Island from SE Asia where G. affinis is widespread, whereas G. holbrooki has only been reported there from Singapore (Global Invasive Species Specialist Group, viewed 1 May 2013, www.issg.org/database/).

Ross Hill Gardens. The overflow from the spring infrastructure has yielded two species of ameirid harpacticoid copepods, *Nitokra* sp. 2 and also a member of the *Nitocrella/Nitokra* complex and the cyclopoid *Bryocyclops* (*Bryocyclops*) *muscicola* (Menzel) a widely distributed tropical species known from interstitial, cave and moss habitats. Podocopid ostracods also occur, a darwinulid *Penthesilenula* [provisional *africana*-group (Rossetti et al., 2011) and candonid *Stenocypris* sp. In addition, mayflies (Ephemeroptera) and shrimps (Decapoda: Caridea) were collected (Short & Meek, 2000).

Terrestrial Fauna

Amphipoda. Talitridae of the genus *Floresorchestia* have been found in damp caves and adjacent to anchialine pools but, as they are fully eyed, are probably widely distributed across the island.

Isopoda: Oniscidea. Sixteen species of oniscidean isopods are known from caves on Christmas Island belonging to 10 genera distributed amongst six families, namely, Armadillidae (6 species), Eubelidae (2), Halophilosciidae (1), Olibrinidae (1), Philosciidae (5), and Platyarthridae (1). A few are broadly distributed in the tropics (Table 2) whereas others are known only from Indian Ocean islands. However, there are a number of undescribed species, belonging to the genera Myrmecodillo, Elumoides and Papuaphiloscia that may be endemic to Christmas Island. The species of *Papuaphiloscia* have some troglomorphic features (depigmentation and lack or reduced eyes) but these might be because they also live deep in the soil. Nothing is known of the onsicid fauna outside caves in Christmas Island and so it is problematic to assign them to troglomorphic categories. Members of the genus Myrmecodillo genus are usually soil-dwelling, with reduced eyes and pigment, and can be categorised as endogean. The other species in Table 2 are epigean and if found in caves are certainly trogloxene (S. Taiti, pers. comm. 2013).

Blattodea. An endemic genus of troglobitic cockroach, *Metanocticola christmasenesis* Roth has been recorded from Jedda and Jane Up caves that differs from the tropical genus *Nocticola* Bolívar in having a sex gland in the metanotum, a character unique amongst cockroaches (Roth, 1999).

Formicidae. The introduced Yellow Crazy Ant, Anoplolepis gracilipes (Smith) has formed supercolonies on Christmas Island and the behaviour of the ants has resulted in a cascade of change that has resulted in an 'ecological meltdown'; one such behaviour is the 'farming' of hemiptera that feed in the forest canopy, protecting them from predators and parasites and resulting in their superabundance (O'Dowd et al., 2003). Cave-dwelling ants, belonging to the genus Paratrechina are known elsewhere also farm Fulgoromorpha and both parties may even be restricted to subterranean habitats (Humphreys, 1998; Hoch et al., 2006) and so it is pertinent to consider whether ants may also affect the subterranean ecosystems on Christmas Island. Using the collections from a comprehensive island-wide survey, Framenau & Thomas (2008) recorded 52 species of ants in 24 genera and 7 subfamilies, none endemic to Christmas Island and many being worldwide tramp species some of which have resulted in significant ecological damage in other parts of their range. Thirteen of the species have been recorded from caves on Christmas Island, namely, Dolichoderinae: Tapinoma melanocephalum (Fabricius). Formicinae: Anoplolepis gracilipes (Smith); Camponotus Kirby; Paratrechina bourbonica (Forel). Myrmicinae: Monomorium cf. subcoecum Emery; Pheidole sp. (variabilis group); Tetramorium insolens (Fr. Smith); T. simillimum (Smith); Hypoponera punctatissima (Rogers); Pachycondyla (Brachyponera) christmasi (Donithorpe); Pachycondyla (Trachymesopus) darwinii (Forel); Platythyrea sp. (parallela (Smith) group); Ponera swezeyi (Wheeler). Only the two ponerines, H. punctatissima and P. (T.) darwinii are known on Christmas Island only from caves. The presence of *P. bourbonica* outside caves indicates that an obligate subterranean mutualism between Paratrechina and Hemiptera may not occur on Christmas Island.

Arachnida

Spiders and their allies are a major component of cave faunas (e.g., Harvey et al., 1993) but few of those known from Christmas Island exhibit overt troglomorphies.

Scorpiones. The most notable is the troglobitic ischnurid scorpion *Liocheles polisorum* Volschenk, Locket & Harvey, 2001 (Fig. 9). As mentioned in the introduction, few caveadapted scorpions are known, especially outside Mexico. On Christmas Island, the species is known from caves CI-8, CI-10, CI-19 and CI-103, which are situated to the east, west and south of the island and thus the species is probably widespread but not abundant and so rarely seen as would be expected from a relatively large invertebrate top predator.

Pseudoscorpiones. They are commonly found in caves in mainland Australia where many new cave-dwelling species occur belonging to several families (e.g., Harvey, 1993; Harvey & Volschenk, 2007). Two undescribed species of chthoniid pseudoscorpions of the genus *Tyrannochthonius*, one eyeless and the other with reduced eyes, have been taken from caves CI-10, CI-19 and CI-103.

Amblypygida. The charontid *Charon gervaisi* Harvey & West occurs in caves (CI-2, CI-19, CI-84, CI-103) but it is not troglobitic. The species is described from specimens collected from a woodpile in the Settlement on Christmas Island and it is considered likely that the Christmas Island species is introduced, a view supported by the lack of specimens from caves distant from habitation and that is found in Java, only some 360 km away (Harvey & West, 1998).

Schizomida. On mainland Australia, schizomids are very speciose in the subterranean environments of the arid zone and in surface environments in rain forests (Harvey, 1992, 2001; Harvey et al., 2008). Only one species of hubbardiid schizomid in the genus *Apozomus* is known from Christmas Island, in caves CI-19 and CI-103 where it is troglobitic and endemic to Christmas Island (M. S. Harvey, pers. comm. 2013).

Araneae. Although true spiders are often found in caves, few on Christmas Island have been located having overt troglomorphies.

An eyeless species of *Anapistula* (Symphytognathidae) was taken from the main chamber of Daniel Roux Cave (CI-3). This cave contain water supply infrastructure including a long fixed ladderway. The species is eyeless and probably undescribed, although the genus is globally distributed (Harvey, 1998).

The trochanteriid spider on Christmas Island, known from caves CI-5, CI-6, CI-9, CI-10, CI-11 and CI-19, has been included in *Olin platnicki* Deeleman-Reinhold, 2001 by Platnick (2002). However, the Christmas Island specimens



Fig. 9. The blind ischnurid scorpion *Liocheles polisorum* collected by Rob Susac in Freshwater Cave (CI-10). Chela length ca. 15 mm. Photo: Ross Anderson.

entirely lack eyes, whereas those from caves on the type locality (Pulau Talata Koh, Togian Islands, Sulawesi) have eyes "possibly reduced in size as a consequence of the lightless environment of the cave". Platnick (2002: 72) considered it likely that the species may be widespread on Indian Ocean Islands. This ambiguity may not be resolved until a male is collected from Christmas Island, or specimens suitable for DNA extraction are obtained from Sulawesi. An Acarina parasitic on *O. platnicki* in CI-5 may itself be troglobitic by association.

Eyeless members of the family Ochyroceratidae are known from caves CI-10, CI-11 and CI-19. Members of this family of small spiders (0.5–3 mm long) occur widely in tropical caves and forest litter, especially in the Indo-Pacific, where they construct irregular sheet-webs and carry their egg sacs in the jaws until they hatch. If parthenogenesis, present in one of the species (Edwards, 2003), is widespread in the family, that would facilitate its widespread distribution throughout the tropics.

Goblin spiders (Oonopidae) occur worldwide with more than 1000 species known in 88 genera. They are found in leaf litter, and eyeless species occur in both termite nests and in caves. They are tiny, cryptic spiders rarely observed and some species are apparently parthenogenetic which may account for some species having established after introduction. *Ischnothyreus velox* Jackson, found on Christmas Island (cave CI-19; CI-103), has a pantropical distribution and has been introduced to Europe. *Opopaea lena* Suman was collected in a plankton net held for 24 hours over the overflow of Hendersons Spring. There is a blind *Ischnothyreus* sp. from CI-5 and a blind *?Opopaea* from CI-19.

There is also a blind spider of uncertain status, possibly Desidae, from caves CI-10 and CI-19.

Pholcidae are commonly found in caves on Christmas Island but none is overtly troglomorphic, although elsewhere they are among the spiders most consistently found in caves and where they are often blind and commonly with reduced eyes (Huber, 2000). As several species of various genera are independently preadapted to live and spread with humans, as is evidenced by the numerous synanthropic species from various genera worldwide (Huber, 2000), it is likely that some cosmopolitan species occur in Christmas Island caves.

Terrestrial vertebrates. These are not a conspicuous feature of Christmas Island caves save for the occurrence of the endemic, echolocating, Christmas Island glossy swiftlet (*Collocalia esculenta natalis* Lister) (Apodiformes: Apodidae) in several caves (CI-9, CI-30, CI-50, CI-53, CI-56). This species is an important source of guano that supports a substantial population of guanobites, especially in upper Daniel Roux Cave (CI-56).

Historically, the Christmas Island glossy swiftlet was recorded in large numbers over the whole island, being more common on shore terraces than the plateau (Gibson-Hill, 1947). They were most numerous on the west side of South Point and least numerous along the coast from Egeria Point to West White Beach. The subspecies is endemic to Christmas Island although many other subspecies and species occur through Southeast Asia, Queensland and Pacific islands. The species is treated extensively in the main text of Humphreys & Eberhard (1998). Collocalia esculenta natalis nests in colonies in several of the caves on Christmas Island where they build closely packed masses of cup-shaped nests high in the roof of the cave. Lichens and other fine threads are woven together, and cemented to the roof with saliva (Gray, 1995). Guano—mostly insect exoskeletons—accumulates beneath the colonies and supports an assemblage of invertebrate species. Nests fall off the wall if the moisture content of the air falls below 70% relative humidity (Nguyen Quang et al., 1998) and for this reason, amongst many, vegetation clearance should not occur in the vicinity of caves.

The nests of Collocalia species in Southeast Asia and India are intensively harvested for the goumet delicacy 'birds nest soup' (Nguyen Quang et al., 1998). The Christmas Island swiftlets use smaller quantities of saliva to cement their nests than their Southeast Asian relatives. However, there is anecdotal evidence which suggests that nests of Christmas Island swiftlets may once have been harvested; Brooks (1990) drew this conclusion after observing that the arrangement of poles lodged high in the roofs of caves occupied by swiftlets at South Point was similar to those used by bird nesters elsewhere. Daniel Roux Cave is clearly a major nesting site, containing several hundred individuals and where a large, well-developed guano mound testifies to its use by a large number of birds over a long period of time and providing an extensive habitat for guanobites. Being the only guano producer in caves on Christmas Island, the invertebrate communities that establish on guano are themselves dependent on the persistence of the swiftlets.

SENSITIVITY OF CAVE FAUNA

Finally, I address the conservation of this unusual subterranean fauna. Humphreys & Eberhard (2001) provided a breakdown of the habitats and associations of spring and cave fauna on Christmas Island and characterised their vulnerability to caver impacts as well as the main external threats. Further, they used this to assess and to rate vulnerability of particular caves accordingly (Humphreys & Eberhard, 1998: Appendix 3) and provided a summary table for 25 of the caves (Humphreys & Eberhard, 2001). The potential impact of cavers was rated from low (e.g., anchialine and springs) through medium (e.g., sediment banks) to high impact (e.g., tree roots in caves, freshwater pools). They rated the guano deposits in Daniel Roux Cave Upper (CI-56) both of high biological significance and high vulnerability to caver impact owing to trampling on the guano piles deposited by glossy swiftlets.

The presence and location of anchialine habitats in a given geomorphologic context depends on the balance between seawater inflow and freshwater outflow and is indicated by the location of the halocline (the halocline will occur progressively deeper the further inland it occurs). Reducing the flow of freshwater (by water abstraction, diversion or climate change) will allow the halocline to migrate inland and vice versa. If inland migration (or sea level change) moves the halocline to unsuitable geology (basalt on Christmas Island) or seaward migration moves it to the shore, then anchialine habitat would be lost entirely in that area.

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Humphreys: Subterranean fauna of Christmas Island

Appendix 1. Cave Names and Karst Index numbers where fauna has been collected on Christmas Island (CI). The numbers have prefix 6, denoting Western Australia, which is shown only for first location. 6CI-1, The Grotto; CI-2, Runaway Cave; CI-3, Daniel Roux Cave lower; CI-5, Jedda Cave; CI-6, Jane Up Cave; CI-7, Lost Lake Cave; CI-8, Bishops Cave; CI-9, Smiths Cave; CI-10, Freshwater Cave; CI-11, Grants Well; CI-12, unnamed sinkhole; CI-13, unnamed sinkhole; CI-16, Strangler Cave; CI-19, 19th Hole; CI-20, Full Frontal Cave; CI-21, unnamed sinkhole; CI-30, Swiftlet Cave; CI-50, Manager's Alcove; CI-53, Grimes Cave; CI-54, Whip Cave; CI-55, unnamed; CI-56, Daniel Roux Upper C; CI-59, Small spring and pool; CI-64, Hendersons Spring (The Pumphouse); CI-77, Hughs Dale (Dale No. 2); CI-78, Andersons Dale No. 5; CI-79, Small Cave near CI-78; CI-84, Dale No. 7; CI-85, Freshwater Spring; CI-86, Jones Spring; CI-99; CI-100; CI-103, Sepulchral Soil Sink; Coastal water bore 1; Coastal water bore 2.