

DANIELOPOLINA (OSTRACODA, THAUMATOCYPRIDIDAE) ON
CHRISTMAS ISLAND, INDIAN OCEAN, A SEA MOUNT ISLAND

BY

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ABSTRACT

The genus *Danielopolina* is reported from an isolated seamount, Christmas Island, Indian Ocean, where it is known, for the first time, in sympatry with a Procaridid Type of anchialine community. We explain the significance of the juxtaposition in this geographical and geological context and explore the role of active and passive dispersal in the colonization of remote seamount islands.

RÉSUMÉ

Le genre *Danielopolina* est signalé sur un mont sous-marin isolé (seamount), l'île Christmas dans l'océan Indien, où il est signalé pour la première fois en sympatrie avec une communauté anchialine de type Procaridide. La signification de cette juxtaposition dans un tel contexte géographique et géologique est expliquée et le rôle des dispersions actives et passives dans la colonisation des îles océaniques isolées est exploré.

INTRODUCTION

We report the occurrence of *Danielopolina* from the anchialine waters of an isolated seamount island, Christmas Island in the Indian Ocean. Its occurrence in this geographical and geological context is of such moment that we report it here despite the single larval individual known being insufficient for a formal species description. The genus *Danielopolina* is known from 11 species, 10 inhabiting epicontinental anchialine ecosystems and one being a deep-sea species (Kornicker & Iliffe, 1998) that may belong to a different genus (Danielopol et al., 2000).

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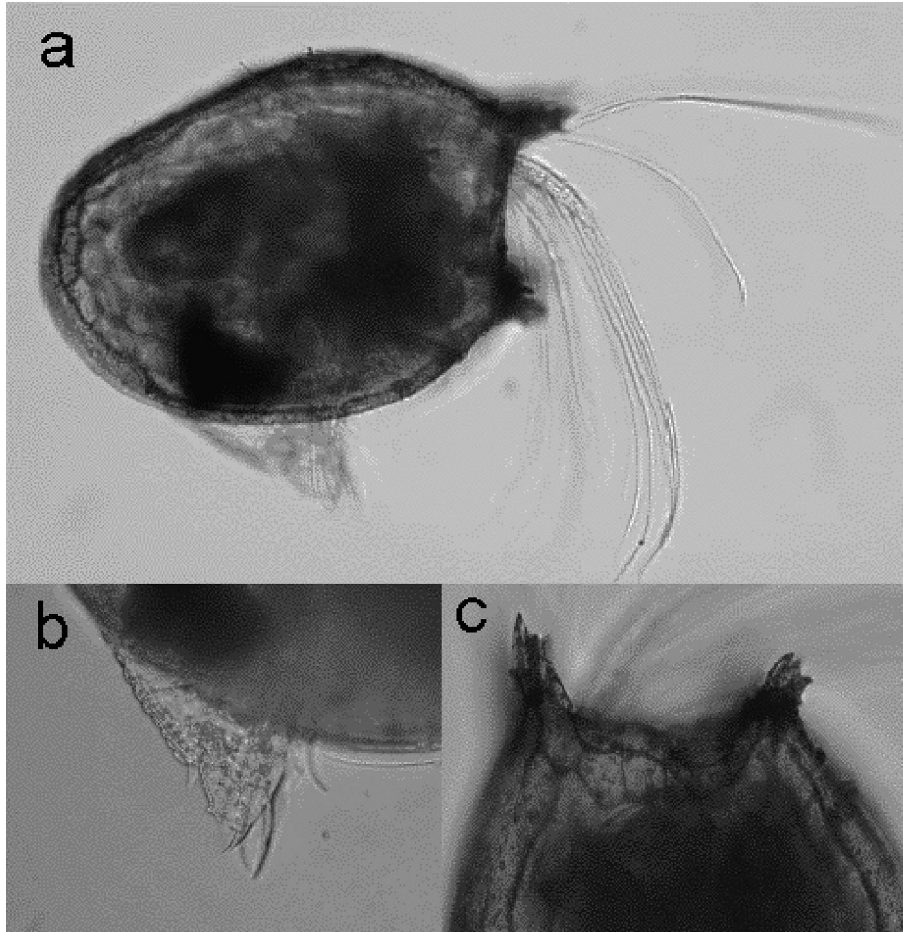


Fig. 1. Image of the *Danielopolina* sp. from Christmas Island, Indian Ocean. a, habitus; b, detail of furca; c, detail of anterior short processes. (Photo: Angel Baltanás.)

The individual, that we here refer to *Danielopolina* sp. (cf. *D. kornickeri* Danielopol, Baltanás & Humphreys, 2000), has a general shape and a carapace ornamentation resembling those of *Danielopolina kornickeri*. In lateral view the shape is more ovate than rounded, the valve surface ornamentation is represented by large polygonal ridges (fig. 1), and there is a presence of anterior short processes but an absence of postero-dorsal processes. The carapace length is 0.32 mm, without the 0.04 mm long antero-dorsal processes, and the height of the carapace is 0.20 mm. The distal part of the furca clearly indicates a juvenile stage equivalent to the second instar of *D. wilkensi* Hartmann, 1985 (cf. Kornicker & Iliffe, 1995: 23, fig. C), as it has one articulate claw and three short “Anlage” spines (fig. 1).

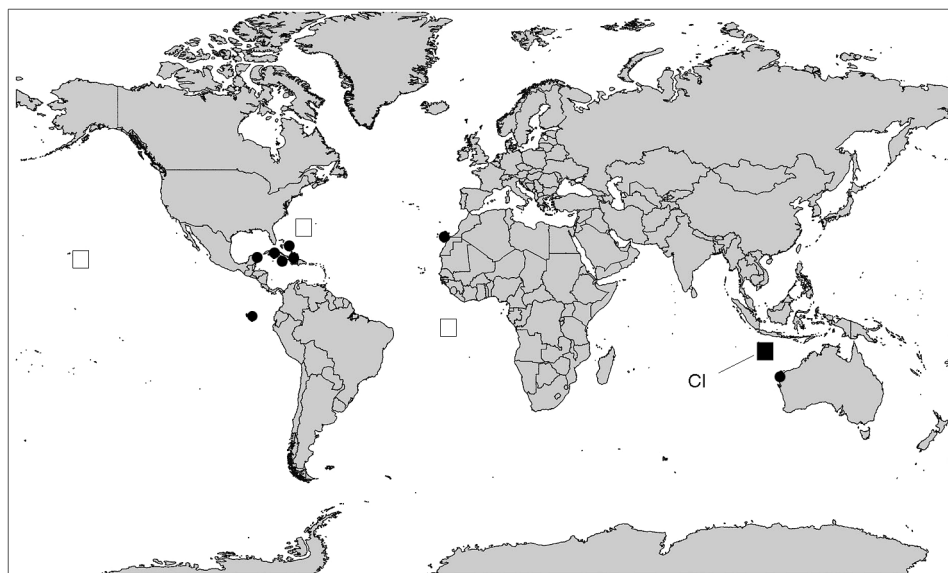


Fig. 2. World distribution of anchialine *Danielopolina* (●), and the Procariid Type anchialine fauna (□). CI denotes Christmas Island, Indian Ocean.

The long exopodal setae on the second antenna suggest that in this stage the animal is already able to swim.

Danielopolina kornickeri was described from an anchialine cave in Western Australia and was so far the only *Danielopolina* species occurring outside of the Western and Northern Hemispheres (Atlantic and islands of the eastern Pacific) where it represents a taxon of the primitive anchialine cavernicolous clade. The distribution and phylogenetic position of this species, together with its associated fauna, is consistent with the hypothesis that the anchialine troglobites originated from an ancient shallow marine fauna that existed in the Tethys Sea at least since the Mesozoic, rather than from deep-sea ancestors (Danielopol et al., 2000).

ANCHIALINE SYSTEMS

Anchialine habitats are inland mixohaline groundwaters affected by marine tides, usually with a reduced subaerial exposure (Stock et al., 1986); essentially they are groundwater estuaries. They are distributed circum-globally in tropical and subtropical latitudes, mostly in arid coastal areas (see Iliffe, 2000). The water column characteristically has a stable hydrological stratification with a marked thermo-halocline, separating a surface layer of fresh or brackish water from a warmer marine, oligoxic water mass occupying the deeper reaches. Anchialine habitats may support diverse crustacean assemblages, especially in the oligoxic

TABLE I
Characteristic higher taxa associated with the remipede¹⁾ and procaridid²⁾ anchialine communities:
disparate but predictable

Remipede community ¹⁾	Procaridid community ²⁾
Remipedia	Procarididae
Thermosbaenacea	Alpheidae (Decapoda)
Hadziidae (Amphipoda)	Hippolytidae (Decapoda)
Cirolanidae (Isopoda)	Atyidae (Decapoda)
Atyidae (Decapoda)	
Thaumatocyprididae (Ostracoda)	
Epacteriscidae, Pseudocyclopiidae, and Ridgewayiidae (Copepoda, Calanoida)	
Halicyclopinae (Copepoda, Cyclopoida, Cyclopidae)	
Speleophriidae (Copepoda, Misophrioida)	
Superornatiremidae (Copepoda, Harpacticoida)	
Quintana Roo, Mexico; some northern Caribbean Islands; Lanzarote, Canary Is.; Cape Range, Australia	Bermuda, Ascension Island, Hawaii, and Christmas Island (Indian Ocean) (<i>Procaris</i> also from Fiji) ³⁾

¹⁾ Sket, 1996; Iliffe, 1992, 2000; Wagner, 1994; Jaume et al., 2001; Jaume & Humphreys, 2001.

²⁾ Chace & Manning, 1972; Holthuis, 1973; Hart & Manning, 1981; Kensley & Williams, 1986; Humphreys & Eberhard, 1998.

³⁾ J. Short, pers. comm., 2001.

The distribution of anchialine habitats is given in Iliffe (2000).

reaches of the water column, and most of their members represent biogeographic and/or phylogenetic relicts (Sket, 1981, 1996). Such anchialine systems are the subject of widespread conservation assessment (for references see Humphreys, 2000b).

Two types of anchialine fauna have been identified, each of which contains a characteristic assemblage of taxa (table I), often predictable, even to the generic level, however far apart in the world they are found. The first, which we term the Remipede Type, is confined to epicontinental anchialine (var.: anchihaline) waters. The second, which we term the Procaridid Type, is confined to anchialine waters of seamount islands. Both types occur in Australia, in the sovereign sense, with the former type present in Cape Range, Western Australia, and the latter type on Christmas Island, Indian Ocean. This distinction mirrors the observation of Maciolek (1983) that the hypogeal shrimp species from islands and continents of the Indo-Pacific are entirely separate and exhibit numerous biological differences.

The various remipede habitats are on islands of largely Tertiary geology but they occur in near-continental waters underlain by much older basements, a factor that may explain the anomaly, suggested by some theories of their distribution

discussed below, of an apparently much older fauna than the geological context in which they are found. For example, the remipede habitat of the Canary Islands, on Lanzarote, is underlain by a Mesozoic basement (Boutin, 1994), and on Fuerteventura (also Canary Islands) the stygobitic species of the *Metacrangonyx panousei* Balazuc & Ruffo, 1953 lineage inhabit the only part of the island where Cretaceous sediments exist, while the rest of the island is formed by consolidated sediments of Tertiary age (Boutin, 1994). In Australia, the Tethyan fauna on the Cape Range peninsula (Yager & Humphreys, 1996) occurs in karst in Tertiary limestones sitting on a Jurassic basement, but not over the adjoining Carboniferous basement. The geological history of the Galapagos is controversial but biological and geological evidence suggest past close connections with the continental faunas of the Americas (Grehan, 2001), and also that it is part of the Tethyan realm (Kornicker & Iliffe, 1989) from the main part of which it is now isolated by the Isthmus of Panama.

FAUNA OF ANCHIALINE SYSTEMS

The remipede-type anchialine system characteristically comprises an assemblage of atyid shrimps, thermosbaenaceans, hadziid amphipods, cirolanid isopods, remipedes, thaumatocypridid ostracodes, and an array of copepods in the calanoid families, Epacteriscidae, Pseudocyclopiidae, and Ridgewayiidae, together with halicyclopine cyclopoids, speleophriid misophrioids, and superornatiremid harpacticoids (table I). The structure of this assemblage is predictable, often even at the generic level (Poore & Humphreys, 1992; Wagner, 1994; Jaume et al., 2001). This fauna is distributed from the Yucatán peninsula of Mexico, Cuba, the Bahamas, the Canaries (with some elements in the western Mediterranean), and northwestern Australia. This distribution follows the full Tethyan track (Jaume et al., 2001), and is considered to corroborate the hypothesis that the anchialine stygobites originated from an ancient epigeal fauna that existed in the Tethys Sea at least since the Mesozoic (Iliffe et al., 1983, 1984; Wilkens et al., 1986; Kornicker & Iliffe, 1989; Humphreys, 1993a, b; Danielopol et al., 2000). Aspects of the remipede-type of anchialine system in Australia have been addressed in more than 40 publications that can be sourced through Humphreys (1999, 2000b, 2002), Jaume et al. (2001), and Bradbury (2002).

The procaridid-type anchialine fauna, found on seamount islands, typically comprises procaridid, alpheid, hippolytid, and atyid shrimps. This type of anchialine fauna is known from Hawaii, Bermuda, Ascension Island, and Christmas Island, which are all isolated seamount islands, although Bermuda was derived from the mid-Atlantic Ridge. Other than from Christmas Island ("*Procaris noelensis*"

Bruce & Davie, *subm.*; Humphreys & Eberhard, 1998, 2001), the genus *Procaris* (Procarididae) is known only from the Pacific Ocean on Hawaii (*P. hawaiana* Holthuis, 1973), and the Atlantic Ocean and Caribbean on Ascension Island (*P. ascensionis* Chace & Manning, 1972), Bermuda (*Procaris chacei* Hart & Manning, 1986) and on Cozumel Island, Quintana Roo, Mexico (Kensley, 1988; Sternberg & Schotte, 2004), and possibly Fiji (J. Short, *pers. comm.*). Hart & Manning, (1986: 416) proposed that the similarity between the species of *Procaris* and their highly anomalous distribution in marine caves indicates an extremely slow rate of evolution and that the cryptic habitats they occupy are refugia. The Procarididae, a primitive and highly aberrant family (Chace & Manning, 1972; Holthuis, 1973), appear to be restricted to anchialine caves and include only one other described representative, *Vetericaris chaceorum* Kensley & Williams, 1986, from Hawaii. The feeding behaviour of *Procaris* is consistent with a pelagic history (Provenzano, 1978), as suggested by Chace & Manning (1972).

All described procaridids are sympatric with one or more species of atyid shrimps. The occurrence of procaridid, alpheid, hippolytid, and atyid shrimps in the same anchialine system on Christmas Island (Humphreys & Eberhard, 1998, 2001) mirrors that found on Bermuda (Hart & Manning, 1981), renown for the diversity of its anchialine fauna (Iliffe, 1994). The structure of this assemblage is predictable, sometimes even at the generic level (Hart & Manning, 1981; Humphreys & Eberhard, 2001). The co-occurrences of these apparently ancient caridean families have been proffered as support for the contention that crevicular habitats have served as faunal refuges for long periods of time (Kensley & Williams, 1986). However, Ascension Island is young, being constructed on a five to six million years old oceanic crust, and with whole rock dates suggesting that the oldest exposed rocks are only about one million years old (Weaver et al., 1996). Aspects of the procaridid-type of anchialine system in Australia have been addressed by Humphreys & Eberhard (1998, 2001), Namiotko et al. (2004), Short & Meek (2000), and Grimes & Humphreys (1998).

On Christmas Island, *Procaris* sp. was found in the same section of the anchialine system as *Microceratina martensi* Namiotko, Wouters, Danielopol & Humphreys, 2004 (Cytheridae); Syllidae *indet.* (Polychaeta); *Nerilla* sp. (Archiannelida, Nerillidae); Nitocrella/Nitokra complex (Harpacticoida, Ameiridae); *Bryocyclops* (*Bryocyclops*) *muscicola* (Menzel, 1926) (Cyclopoida, Cyclopinidae); ? new genus (Calanoida, Arietellidae); *Leucothoe* sp. (Amphipoda); Alpheidae (three species not determined: J. Short, *pers. comm.*); ? *Parhippolyte* ? *P. uveae* Borradaile, 1899 (Hippolytidae); *Antecaridina lauensis* (Edmondson, 1935) (Atyidae); *Macrobrachium lar* (Fabricius, 1798) (Decapoda, Palaemonidae); and ? *Eleotris fusca* (Forster, 1801) (Eleotridae) (Humphreys & Eberhard, 1998, 2001; Namiotko et al., 2004).

COLONIZATION ROUTE FOR CHRISTMAS ISLAND

Christmas Island lies in the Indian Ocean, about 350 km southwest of Java, separated from it by the Java Trench, and 1200 km west of the Australian continent. It is the exposed tip of an isolated seamount and the only exposed member of a series of volcanoes that formed from the middle Cretaceous, starting about 80 Ma (Grimes, 2001). It is a small (135 km²), isolated, uplifted volcanic island rising 4.5 km from the ocean floor and capped by a sequence of Tertiary limestones up to 250 m thick (Pettifer & Polak, 1979). There was reactivation of volcanism in the Eocene (35-40 Ma), from which date there is a poorly exposed series of carbonates, and there has been localized vulcanicity as recently as the Pliocene. Plate movement is causing the island to be rising over the lip of the Java Trench as a result of which it is flanked by a series of limestone terraces overlying the basaltic volcanics. The main exposures are a series of carbonates of late Oligocene to mid-Miocene age (Grimes, 2001). The geological history of Christmas Island has recently been considered by Grimes (2001) and the age of the exposed landmass discussed by Namiotko et al. (2004), in the context of *Microceratina*, another Tethyan ostracode, and this is summarized here. Owing to the steep submarine slopes on the island, the exposed landmass would never have been substantially larger than at present, but at times could have been both much smaller and fragmented, even submerged. The main limestones were laid down in shallow water with fossil dates from the Late Oligocene (Adams & Belford, 1974). Consideration of available evidence of several types suggests that there has been a shallow water to emergent habitat associated with Christmas Island for at least 26 Ma (Grimes, 2001). Christmas Island is currently a carbonate-cover island, sensu Mylroie et al. (2001) and Jensen et al. (2002).

Although Thaumatoocyprididae of the genus *Danielopolina* can swim like Remipedia, they are not planktonic. However, there is considerable evidence (Larwood & Whatley, 1993; Larwood et al., 1996; Allmon & Ross, 2001) that shallow benthic habitats of oceanic islands, including seamounts, were passively colonized from remote sources in the Tertiary to the Recent by a rich and diverse ostracode fauna. Even marine interstitial ostracodes could have arrived by passive drift to volcanic islands like the Galapagos (Danielopol & Bonaduce, 1990; Namiotko et al., 2004). Therefore, the colonization of Christmas Island by a *Danielopolina* species could have occurred from the Tertiary to the Recent, with cave colonization allowed by the karstification of the limestone during the Neogene.

Danielopolina styx Kornicker & Iliffe, 1989, on Galapagos, occurs in anchialine waters in association with the caridean shrimp, *Typhlatya galapagensis* Monod & Cals, 1970, a genus occurring in both *Procaris* (Ascension Island and Bermuda), and remipede regions (Caicos Island, Cuba, Yucatan), in addition to Barbuda,

Dominican Republic, and Puerto Rico (Mona Island) (Kornicker & Iliffe, 1989), which suggests that either or both types of community may occur in these latter areas, a view reinforced by the presence on the Galapagos of a red hippolytid shrimp (Kornicker & Iliffe, 1989). However, remipede type communities in the Caribbean region are, so far, restricted to areas of the North American Plate and its boundary with the Caribbean Plate.

Both *Danielopolina kornickeri* (cf. WFH, unpubl. data) and *D. styx* are found in mid-water in an anchialine cave, where they are collected in plankton nets, and “[b]ecause the anchialine caves are in contact with the marine shallow environment outside the caves one can presume that the continuity of some sandy gravelly or silty sediment habitats existed between the epigean and hypogean systems. The benthic ostracods could therefore easily colonize the hypogean habitats” (Danielopol, 1990: 140) and “may currently inhabit clastic sediments along continental coasts and as such could be transported passively to marine caves on oceanic islands . . .” (Danielopol et al., 2000). Two factors would appear to mitigate this. Firstly, *D. kornickeri*, together with sympatric speleophriid, epacteriscid, and pseudocyclopiid copepods, are found only at depth (>18 m) in suboxic waters but below layers of hydrogen sulphide and a cascade of N-species, conditions that mimic, on a much larger scale, those occurring in anoxic sediments (Humphreys, 1999). The Christmas Island *Danielopolina* and *D. kornickeri* (cf. Danielopol et al., 2000) have a small carapace of slightly rounded shape, strong antennae and furca, and, by analogy with Polycopidae, should be able to swim close to the bottom surface and so have the possibility to actively migrate into the interstitial space of coarse sand (see also Danielopol et al., 2000). The presence of *Danielopolina* in wells on the Canary Islands (Wilkens et al., 1986: 225) led Kornicker & Iliffe (2000) to deduce that they could migrate, at least short distances, through the crevicular spaces in volcanic rock, and that this lent support to the hypothesis of a deep-sea crevicular dispersal down slopes of seamount islands proposed by Hart et al. (1985). Such a route is an improbable source of *Danielopolina* on Christmas Island because it has no contiguous shallow platform as it plunges unbroken 4.5 km to abyssal depths surrounding the island. Below depths of c. 150 m the distribution of many hypogean species is probably limited by low temperature (Maciolek, 1983).

GENERAL EVIDENCE FOR OCEANIC DISPERSAL

Ostracodes of the family Cytheruridae are completely devoid of swimming capacity but have dispersed widely within the Pacific and arrived at various seamounts (Christmas Island: Namiotko et al., 2004). In contrast, the Procarididae,

Alpheidae, Hippolytidae, and Atyidae (infraorder Caridea) all have zoea larvae that can spend a short period swimming freely in the water column during which time they can be dispersed by water currents (Gruner, 1993). For example, *Atyaephyra desmarestii* (Millet, 1831), (Atyidae) has a pelagic life-style, and is able to spend about three weeks as a zoea in the water column (Gruner, 1993: 959).

Similar issues are raised by the presence on Christmas Island of ostracodes of the family Darwinulidae in both freshwater springs on the coast and cave streams on the plateau. These include *Vestalenula* sp. nov. and an enigmatic species having characteristics of *Vestalenula* and *Penthesilenula* (cf. K. Martens, pers. comm. to WH, 2001); both are ancient asexual lineages. Darwinulids generally, including *Vestalenula* representatives, are benthic forms that have a brood pouch and lack the capacity to swim in the water column. However, we know of species that live on remote islands in the Pacific, such as *Vestalenula daps* (Harding, 1962) from the Solomon Islands, which was found in fish stomachs (Harding, 1962), pointing to passive dispersal.

We present some other evidence that oceanic dispersal, as proposed also by Maciolek (1983), is applicable to seamount anchialine faunas, and by implication, that this is a possible route for *Danielopolina* spp. Large-scale dispersal patterns have been a major feature in the evolution of the freshwater prawn genus *Macrobrachium* (Palaemonidae) (cf. Murphy & Austin, 2005). *Macrobrachium lar* is the most widespread species in the genus, occurring naturally through much of the Indo-West Pacific, and was introduced in the Hawaiian archipelago and occurs there now as well. It is usually epigeal, and adults are generally found in freshwater rainforest streams, although the larvae/early postlarvae appear to be tolerant of high salinities. *M. lar* occurs on Christmas Island in both the anchialine system and freshwater springs (Humphreys & Eberhard, 1998). Molecular studies have demonstrated that *M. lar* from mainland Australia and Papua New Guinea constitute their own clade, whereas the Christmas Island *M. lar* belongs to the most widespread clade that stretches from Christmas Island, through Indonesia (Tioman Island and Sulawesi) into the Pacific (New Britain, Micronesia, New Caledonia, Vanuatu, Fiji, and Futuna), and as far east as the Samoan Islands (Western and American) (A. Duffy, pers. comm., 2005) thus spanning Huxley's line. This suggests that ocean currents have transported larvae of *M. lar* through the Indo-Melanesian archipelago, a view in accord with that of Smith & Williams (1981). By contrast, the giant freshwater prawn, *M. rosenbergii* (De Man, 1879), despite requiring estuarine conditions for larval development, possesses different clades on either side of Huxley's line, probably separated since the Miocene (De Bruyn et al., 2004), and this restricted marine dispersal is consistent with the molecular patterns of *M. rosenbergii* found across the Isthmus of Kra Seaway (De Bruyn et al., 2005).

Although Banarescu (1990) considered subterranean genera of Atyidae to be Tethyan marine relicts, a strong case can be made for oceanic dispersal in some genera. While atyids are not renowned for their salinity tolerance in either larval or subsequent life stages, salinity tolerance is high in the genera *Halocaridina*, *Antecaridina* and *Typhlatya*, which have widely disjunct distributions (discussed by Smith & Williams, 1981). The latter genus is from Madagascar and may possibly include, as a subgenus, *Stygiocaris* from Cape Range, Western Australia (Holthuis, 1960). While *Stygiocaris* has been considered a fresh- to brackishwater taxon (mean salinity of 25 sites c. 2700 mg l⁻¹ and a maximum of 20,000 mg l⁻¹ (Humphreys, 1994), they have recently been recorded in Bundera Sinkhole, the type and only locality for *Danielopolina kornickeri*, at a depth of 25-30 m in sea water at a salinity of 35,000 mg l⁻¹ (W. F. Humphreys, P. Hosie & P. Bowler, unpubl. data).

Other evidence for oceanic dispersal is found in the robber crab, *Birgus latro* (Linnaeus, 1758) (Anomura, Coenobitidae), that may occur in the dark zone of caves, especially near the water in anchialine caves (Humphreys & Eberhard, 1998). These land crabs are also genetically quite similar between Indian Ocean and Pacific populations, with a suggested migration rate between Christmas Island and the Solomon Islands of 0.3 individuals per generation, or one individual every 40 years (Lavery, 1991).

FINAL REMARKS

Kornicker & Iliffe (1989) considered *Danielopolina* to have originated in the Tethys Sea in the Mesozoic and that the “dispersal of its ancestors was greatly influenced by plate movement”, a view supported by later evidence (Baltanás & Danielopol, 1995; Danielopol et al., 2000). However, there has been a recent revival of interest generally in oceanic dispersal as a plausible mechanism, often of seemingly unlikely propagules (De Queiroz, 2005). The presence of *Danielopolina* sp. on Christmas Island is a major breakdown of this classification of anchialine habitats and fuels the debate on the distribution and dispersal of at least some elements of anchialine biotas. To distinguish between vicariance (earth history events) and dispersal (biological) events in the historical biogeography of anchialine faunas, where the comparisons are predominantly at the interspecific, or higher, taxonomic level, will require construction of congruent area cladograms and the independent support of molecular clock data. We conclude this note with a remark of Professor L.B. Holthuis, one of the pioneers of anchialine cave biology, “. . . I see the peculiar distribution of anchialine Crustacea as one of the many interesting problems, for which we have not (yet?) found explanation” (L. B. Holthuis: pers. comm. to DLD, 2005).

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