Anchialine podocopid Ostracoda of the Galapagos Islands

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Water-filled fissures and lava tubes on Isla Santa Cruz and Isla Isabela provide anchialine habitats for 1 species of podocopid and pleopodcopid Ostracoda, most with Atlantic and West Indian affinities. Their ancestors may have been carried to earlier islands in the Galapagos system by trans-Atlantic currents on vegetation or large animals, or by migrating waterfowl. None are derived from present-day Pacific coastal faunas of North, Central or South America. Two species of Cytheroidea, a new species of Anchialoidea (Bairdiaea), and one of Cytherilla (Platyopila) are described.

KEY WORDS: Anchialine – Ostracoda – Galapagos – Podocopida.

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INTRODUCTION

The term "anchialine" was first proposed by Holthus (1973) to describe "pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides". A broader and more strictly interpreted ecological definition of the term has since been suggested by Stock, Iliffe & 75

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Williams (1986): "Isles of haline water, usually with a restricted exposure to open air, always with more or less extensive substratum connections to the sea, and showing noticeable marine as well as terrestrial influences". Anachialine habitats include land-locked open pools, similar pools in the interior of caves, and entirely submerged cave passages.

Anachialine habitats in the Galápagos Islands consist of deep pools in tectonic faults, partially flooded lava tubes, and small water-filled depressions in lava flows. Owing to the highly fractured and fissured nature of solidified lava, a contiguous hypogean groundwater biotope exists. Although some anachialine pools are open to sunlight, others are roofed over and in total darkness. Water in these anachialine pools has salinities ranging from nearly fresh to fully marine. Steep salinity gradients across halodines are present in the deeper pools. The period and range of tidal fluctuations are dependent upon proximity to the sea.


In order to study more extensively the biology of anachialine habitats in the Galápagos, the junior author used specialized cave diving techniques during a two-month expedition to these islands in 1987 (Hilse, in press). In addition to the troglobidan podocopid and platycopid ostracods described here, also discovered were a new chaumatocyprid ostracod, Damiopinna siss Kornicker & Hilse, 1989, with troglobitic congeners in the West Indies, Mexico and the Canaries Islands; a new cypriocid ostracod, Sisyphuria galapagensis Kornicker & Hilse, 1989, the first troglobitic member of this family; two new amphipods, Valvastella canariensis Stock & Hilse, 1990, and Aristoniscus serrata Stock & Hilse, 1990, belonging to families predominantly inhabiting the deep sea; and a new cypriocid copepod Eumysaphera galapagensis Bousfield & Hilse, 1990, with anachialine congeners on other oceanic islands on the opposite side of the Pacific in Palau and in the Canaries Islands in the Atlantic.

Four of the 31 podocopid and platycopid ostracod species collected (representing superfamilies Baidellacea, Cytheracea, and Cytherellacea) are described below. Two new genera and species of Pontocyprididae will be described in a second report (Maddocks, in press a), and the five species of Cyprididae (three new) will be analysed in a third report (Maddocks, in press b). For accuracy, those new names are used here, even though they are nomen nudum. All specimens have been deposited in the United States National Museum of Natural History in Washington, D.C.

HABITATS AND LIST OF STATIONS
Owing to the extensive faulting which has occurred in the Galápagos Islands, long systems of deep fissures are found, most notably along the southern coast of
Santa Cruz Island. Close to the coast, these deep faults extend below sea level and contain anchialine pools locally referred to as "grietias". Lava tubes—long conduits originally active in the transport of lava away from eruptive sites—may contain anchialine pools as well. Water-filled depressions in highly irregular lava flows close to the coast constitute a third type of anchialine habitat.

Podococid ostracods were collected from all three types of pools. The characteristics of these pools are summarized in Table 1, while their locations are given in Fig. 1. Ostracod species occurrences are summarized in Table 2.

**Deep Grieta** (Sm. 87-005), Tortuga Bay, south coast of Isla Santa Cruz: 3 May 1987, specimens collected with 33 µm mesh plankton net from water column in 6 to 12 m depths; 1 *Ambistegites dawsoni*, 3 *Cypredes simplicta*. This large grieta lies about 250 m east of the beach at Tortuga Bay and 40 m inland, behind a conspicuous round lava mound, and runs parallel to the coast. The pool, situated between 10 m high cliffs, is about 8 m wide by 40 m long and 12 m deep. Wedged breakdown blocks have covered the rear portion of the pool, keeping it in darkness. Several large root masses extend down into the water in this section of the pool. Salinity in the pools ranges from 0% at the surface to 25% at 12 m. Also collected here were the atyid shrimp *Typhlatya galapagensis*,

Table 1. Characteristics of anchialine pools in the Galápagos Islands from which podococid ostracods were collected. Depths, salinities, and temperatures refer to water samples from the bottom of the pools. Measurements were taken during May and June 1987.

<table>
<thead>
<tr>
<th>Station</th>
<th>Maximum depth</th>
<th>Surface salinity (%)</th>
<th>Surface temp. (°C)</th>
<th>Deep salinity (%)</th>
<th>Deep temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B7-005</td>
<td>1.0</td>
<td>0.8</td>
<td>26.4</td>
<td>20.0</td>
<td>23.1</td>
</tr>
<tr>
<td>E7-008</td>
<td>0.7</td>
<td>1.5</td>
<td>29.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E7-012</td>
<td>1.0</td>
<td>2.0</td>
<td>33.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E7-017</td>
<td>1.5</td>
<td>2.0</td>
<td>27.1</td>
<td>33.5</td>
<td>27.1</td>
</tr>
<tr>
<td>G7-014a</td>
<td>1.0</td>
<td>1.5</td>
<td>22.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G7-014b</td>
<td>1.0</td>
<td>1.5</td>
<td>22.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ocean</td>
<td>35.5-35.0</td>
<td>27.0</td>
<td>27.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Species occurrences. Explanations of symbols: *N* = Number of specimens * = = specimen, M = Madeira, B = Bermuda, W = West Indies, C = Clipper, Midway and Marshall Islands. The superscripts a and b refer to papers in which the cypridinid species will be described (Maddocks, in press a and b).

<table>
<thead>
<tr>
<th>Galapagos stations</th>
<th>E7-</th>
<th>Elsewhere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ostracod species</td>
<td>005</td>
<td>008 012 017 021 021a 021b</td>
</tr>
<tr>
<td><em>Ambistegites dawsoni</em></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Cypredes simplicta</em></td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Oxycluscapha sp.</td>
<td>8</td>
<td>*</td>
</tr>
<tr>
<td><em>Cypreella sp.</em></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Rifiluncus sp.</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Kauskia westoni</em></td>
<td>25</td>
<td>2</td>
</tr>
<tr>
<td><em>Ponagraphe crasselab</em></td>
<td>5</td>
<td></td>
</tr>
<tr>
<td><em>Ostracopia superba</em></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><em>Harpactes garmani</em></td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td><em>Harpactes galapagensis</em></td>
<td>64</td>
<td></td>
</tr>
<tr>
<td><em>Branchiostegella</em></td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>
the cypriolid ostracod *Skegeria galapagensis*, the thalassacteid ostracod *Dioecophila styx* and copepods still under study.

*Lava rock pool (Stn. 87-001)*, Puerto Villamil, Isla Isabela, 15 May 1987, specimens collected with small bottle from algae in 20 cm depth; *64 Strandonax stekii*. This pool is located on the southern coast of Isabela and is used as a source of water for washing clothes. It is located about 0.5 km inland. The 2 m long by 1 m wide by 70 cm deep pool is bounded on all sides by lava rock and overhung with vegetation. Water in the pool is nearly fresh, and mosquitos larvae were present.

*Lava rock pool (Stn. 87-012)*, Punta Tortuga, Isla Isabela, 26 May 1987, specimens collected with small dip net from water column in 0–3 m depth; *2 Cypridina stenopora*. This pool is located 1 km north of Punta Tortuga in a relatively recent lava flow on the west coast of Isabela. About 19 m long by 4 m wide by 1 m deep, this pool is situated about 150 m inland and is mostly open to sunlight. Salinity was 23.8°. Also collected were shrimp, isopods and copepods.

*Cueva de la Cadena (Stn. 87-017)*, Puerto Villamil, Isla Isabela, 31 May 1987, specimens collected with 55 μm mesh plankton net from water column and surface sediments in 0 to 1 m depth; *1 Diaphanosoma illecebrosum, 2 Kareocellina annhleri, 23 Palaemonetes macropus, 8 Oithona similis, 1 Cypridina sp.* Cueva de la Cadena is a lava tube located 2 km west of Puerto Villamil (Monteseddu-Pous & Ecoloa, 1978). The cave is in a paleochoe lava ridge which extends out into the sea. Depending on the level of the tides, sea water floods at least to the overhead collapse entrance of the cave or beyond. At low tide the lake within the tube is 93 m long with an additional 16 m of dry gallery behind the entrance. Maximum depth within the pool is 1.5 m. A completely submerged continuation of the tube extends seaward for about 15 m past the last air bell in the ceiling before becoming too low and being plugged with sediment. A slightly depressed surface salinity of 32% indicates the presence of some brackish runoff through the tube.

At 1 m, salinity and temperature were identical with the open sea. Tidal period and range in the cave appear to be identical with those of open waters. The presence of open-water fish in the pool indicates a direct connection with the sea must exist. Other collections from this cave pool included copepods, shrimp, crabs, polychaetes, molluscs, cumaceans and flatworms.

*Gruta north of trail to Tortuga Bay (Stn. 87-021a)*, Puerto Ayora, Isla Santa Cruz, 18–19 June 1987, specimens collected with 93 μm mesh plankton net from water column and root masses above halocline in 0 to 5 m depth; *2 Kareocellina annhleri, 2 Palaemonetes macropus, 4 Mysidopsis rosa, 31 Hansenocellina galapagensis*.

Also (Stn. 87-021b): specimens collected with 93 μm mesh plankton net from water column and bottom sediments below halocline in 9 to 10 m depth; *1 Mysidopsis rosa, 1 Hansenocellina galapagensis*. This is probably the same gruta visited by Peck & Peck (1986: 43). It is located about 100 m past the last house in Puerto Ayora on the trail to Tortuga Bay. Immediately on the north side of this trail is a sheer-walled fissure 1–2 m wide by 19 m deep. About 30 m along this fissure is a 30 m long pool divided by breakdown into two sections. Water is pumped from the pool, probably for domestic purposes. In the second part of the pool, a deep crack extends down under water past a marked halocline at 9 m before ending in a collapse at 10 m depth. Moderate tidal currents are present at the surface of the pool. The deepest part of the pool is in nearly total darkness, and is a narrow section of the fissure extending through the breakdown at either end of the
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pools. Salinity increases markedly at the halocline from 1.5 to 12.5%. Also present in the pool are Tpyhfhitsa galapagensis, Skagiaergia galapagensis, the melitrid amphipod Galapacaelurus teleforus, copepods, tanaidaceans and amphipod isopods. Plancktonic events in several other anchialine pools did not produce any podocopoid ostracods. Further investigations may show whether unsuitable conditions, competition from other organisms, or random factors are responsible. These included the following stations: 87-002, Grieta de Delfines, Puerto Ayora, Santa Cruz; brackish grieta near the coast with very open exposure to sunlight, salinity 16.5 to 31.5%; copepods. 87-006, Laguna del Junco, San Cristobal; crater lake. 290 m diameter and 6 m depth at 700 m elevation, freshwater; copepods. 87-016, Grieta de Calera de la Torta, south coast, Santa Cruz; 29 m deep grieta, salinity 8 to 19‰, one of the best collecting sites, with copepods, amphipods, polychaetes, shrimp, cumaceans. Danielopolisina, Skagiaergia. 87-020, Grieta Cave, Puerto Ayora, Santa Cruz; 2 m by 3 m by 1 m deep pool in darkness inside cave, salinity 7‰, copepods, amphipods. 87-022, Post Office Bay Cave, north coast, Floreana; 60 m long; 2 m deep pool in total darkness in lava tube, salinity 17 to 22‰; copepods.

PREVIOUS STUDIES

Both marine and freshwater podocopoid Ostracoda of the Galapagos Islands are poorly known, and the existing literature is highly habitat-specific. The only previous report from an anchialine environment is by Triebel (1956), who described Cyprididae s.s. and Xestoleberis arcuri from brackish Crater Lake Arcutus on Isla Genovesa (Fig. 1). The first species but not the second was represented in the collections reported here. Keyser (1977a, b) identified a species living in the Florida Everglades with C. s.s. More cryptically, he stated that X. arcuri is also living in Florida but did not present any evidence for this. Both records were uncritically repeated by Gottwald (1985). However, these identifications appear to be in error, and at present both species are thought to be restricted to the Galapagos.

Five dry offshore-marine sediment samples (Abalates stations 2813 and 2817, Ascan Bueno cruise 18B stations 791G and 794A, and Bahia de la Grande, Isla Santa Cruz; provided the material from which Pokorny (1968, 1969a, b, 1970; also Benson, 1976a, b) named 15 species and two subspecies of Radinella, nine species of Caudites and one of Brachinella (all superfamily Cytheracea). He attributed the very high number of sympatric congeneric species to repeated insular radiations and subsequent migrations. Madelocles (1969) described two deep-sea species of Paramesida and Batrachoididae (superfamily Bairdiacea) from Abalates station 1815 nearly. None of these species occur in the anchialine collections described here.

Bate, Whitaker & Mayes (1981) reported 26 species (14 new) from three collections of filamentous algae in littoral rock pools (at Pentia Espinosa on Fernandina Island, at Mosquera inlet between Baltra and North Seymour Island, and at Puerta Suarez on Isla Espanola; see Fig. 1). These included species of Cystotheleoida (order Platycopidea), Nannosida and Paramesida (superfamily Bairdiacea), Persphycythera, Paradactylida, Paramesida, Galapagocythera, Hemicythera, Radinella, Caudites, Palaearctia, Tarkoocythera, Lexocorocho and Xestoleberis (superfamily Cytheracea). They found only two species of Lexocorochoidea in
common with littoral algal samples they collected on the coast of Ecuador for comparison, and only one species of *Cytherelloidea* was identifiable with the Clipperton Island fauna described by Allison & Holden (1971). The absence of Cypridacea in their fauna is noteworthy. None of these phyltal species turned up in the anchialine collections described here.

Gottwald (1983) described 21 species of tiny interstitial cytheraceans (families Pammocorythidae, Cytheromastidae, Cobanocytheridae, Xestoleberididae and Parvocytheridae) from 1065 littoral and sublittoral sand samples from Fernandina, Marchena, Genovesa, Santiago, Bartholomé, Santa Cruz, Santa Fe, Floreana and Española islands (Fig. 1). Three of the species of *Cobanocythere* occur also on the coast of E. Salvador and Panama, but the others appear to be endemic. None were included in the anchialine collections described here.

Reviews of Pacific Ostracoda by Benson (1984) and Hartmann (1984) show that little is known of the living Ostracoda in the central and eastern Pacific. Allison & Holden (1971) described a fauna of 24 mostly reef species from Clipperton Island to the northwest. No Ostracoda have been studied from Isla del Coco and Isla de Malpelo, northeast of the Galapagos Archipelago, nor from
Isla de San Félix, Islas de Juan Fernandez, Isla Sula-y-Gomez, Easter Island, Pitcairn Island and Ducie Island, which are the easternmost islands in the South Pacific.

The anchialine fauna described here has no species in common with lagoonal, nearshore-marine, and fossil Pleistocene faunas described along the Pacific coast of the United States, Mexico, Central America, Gulf of Panama, and South America (Jardine, 1967; Skogsberg, 1928, 1950; Lucas, 1936; LeRoy, 1943; Smith, 1952; Hartmann, 1953, 1955, 1957, 1959a, b, 1962; Benson, 1959; Benson & Kaelser, 1963; Hartmann-Schröder & Hartmann, 1962, 1963; Swain & Gilby, 1964, 1967, 1974; McKenzie & Swain, 1967; Swain, 1967, 1969; Ishizaki & Gunther, 1974, 1976; Valentine, 1976; Maddocks & Steineck, 1967). However, it should be pointed out that the Ostracoda of coastal Columbia, Ecuador and Peru are virtually unknown, and that no anchialine faunas (if such faunas exist) have been described from the Pacific periphery of the Americas.

GALAPAGOS OSTRACODA AND ZOOGEOGRAPHY

These anchialine collections yielded ten podocopid and one platycopid ostracod species (Table 2), of which six species and two genera are new. One of the new genera (Illifaeonia) is represented by the same species in a cave in Bermuda, and the other genus (Karelomia) has affinities with Bermudian species. Of the five previously known species, one may be endemic to the Galapagos (Cleomela), two are known from Bermuda (I. liffii, P. cripta), one is common in pools and wells of the West Indies (S. (N.) stocki), and one is widely replete in young Cenozoic and modern reef environments from Madeira to Midway (O. angulata). While the closest taxonomic affinities of the new species are with Bermudian species, largely this reflects the need for taxonomic investigations of anchialine podocopid Ostracoda elsewhere. Most of the genera are circumtropical in occurrence or likely to be proven so when world anchialine habitats are better censused.

Overall, the affinities of Galapagos ostracods are with tropical Atlantic faunas. Until the Isthmus of Panama coalesced in the Late Miocene (Middle Pliocene (from 5 to 10 mya according to Smith, 1985; c. 3-4 mya according to Kreggpin, 1978 and Cronin, 1967, 1968), the Atlantic Equatorial Current swept unhindered into the Pacific and provided an easy westward route for passive dispersal of shallow-marine forms. The species-swarms of Candales and Radimella in the Caribbean-Gulf of Mexico region and eastern Pacific share ancestors in the Miocene and Pliocene formations of the south-eastern United States (Bate et al., 1981; Cronin, 1968). Islands suitable for colonization by ancestors of the present fauna are thought to have existed continuously in the neighbourhood for as long as 40 my (Holden & Dietz, 1972), although the present islands are no more than 4–5 mya (Hickman & Lipp, 1983). No doubt Oculonessograptus angustus, which ranges from Madeira and Bermuda in the Atlantic to Midway and the Marshall Islands in the Pacific (Cronin, 1988) reached the Galapagos Islands via this trans-Isthmian corridor, perhaps on floating seaweeds. Perhaps a similar case may be made for P. cripta and the ancestor of A. darwini.

The tiny troglobitic species, such as I. liffii, are more problematic. Perhaps these interstitial and cryptic species are present not only in the interstices of coralline sand and gravel but also in coralline rubble, hole-fasts of algae, and the
pores and passages of coraline limestone. Because most sampling programmes in reef environments have emphasized sedimentary facies and have neglected these cryptic microhabitats, our knowledge of the full distribution of these cryptic and hypogean forms lags behind that of epigean ostracods. According to this scenario, the hardfolds of reef seaweeds dislodged by storms would serve to transport these interstitial and cryptic taxa as well as phytal and epibenthic ostracods.

Fresh- or brackish-water species may have been transported by birds. Parthenogenensis, brood care, and production of desiccation-resistant resting eggs facilitate avian dispersal of ostracods (McKenzie & Hussainy, 1986; Sandberg, 1964; Sandberg & Plusquellec, 1974; DeDecker, 1977). This agency is well established for species of *Cyprideis* and may be invoked for the ancestor of *C. sinopora*. Broodballer (1983) reared S. (N.) tinctus from dried mud, showing that it, like many other freshwater Cyprididae, lays desiccation-resistant eggs suitable for dispersal by wind or birds.

The dispental modes of the Thalassocypodina and Remaneocypridina, which have smooth, fragile carapaces, dioecious reproduction, and no brood care, have never been investigated. Although we do not know whether their eggs resist desiccation, resting eggs, no species are known to have been raised from dried mud. The glass-smooth carapace sticks tightly by surface tension if it encounters the water surface, a device first invoked for dispersal of ostracods by Ebleon (1941). This property, combined with their preference for littoral habitats and their upward-swimming behaviour during each breaking wave (Wouters, 1984: 171), would readily facilitate coastal transport by longshore and tidal currents. Because most are euryhaline, it is possible that they could survive long-distance transport by oceanic currents. More realistically, the abundance of Thalassocypodina and Remaneocypridina in mangrove swamps, coastal grass beds, and other organic-rich strandline habitats suggests that they might ride floating vegetation, driftwood, mangrove seeds, and the like. Together with several Porocyprididae, certain Thalassocypodinae have been implicated as conomictic species of macroinvertebrate wood-living communities (Maddocks, 1968, 1979, 1987; Maddocks & Steinbeck, 1967; Steinbeck et al., 1990). Not should mobile and migratory animals be overlooked as possible vectors. Algae-encrusted sea turtles, fish, crocodiles, marine mammals such as the dugong, and larger arthropods could provide long-distance transport to coastal ostracods. Such hitch-hiking behaviour was speculatively invoked for deep-sea wood-land communities (Maddocks & Steinbeck, 1987; Steinbeck et al., 1990), which include pentocypridids and thalassocypodines of shallow-water affinities.

The occurrence of some close relatives of these Galapagos species in inland lakes (*Dileucypris tenuis* (Thelander, 1937) and Remaneocypris bohniensis Wouters, 1986, in Lake Taal on Luzon, Philippine Islands) and the far-thing distributions of some other thanalassocypodine species (*Magana mundi* Harding, 1962, on the Solomon Islands and the Comoros Islands (Wouters, 1986, 1987)) suggest dispersal by an aerial vector, either birds or wind. Transport by human agency (on encrusted hulls or in ballast-water of ships (Teeter, 1973); in seeds of rice or other agricultural plants (McKenzie & Moroni, 1986); or transplanted oysters (Kornicker, 1975)) seems unlikely in the case of the Galapagos fauna. Still, it should be kept in mind that European ships have visited these islands since the 16th century to careen their vessels and to clean and fill their water casks. The
survival of such inoculant populations would be favoured by the small size and isolation of these pools and the absence of competition from established species.

Finally, it is very likely that multiple dispersal nodes and colonization events have operated, not only for the different taxonomic elements of the Galapagos anchialine fauna but also for individual islands and localities. The anchialine pools of the volcanic Galapagos Islands are quite small and relatively isolated, and chance events may largely determine the residents of a given pool at any particular time. In fact, these anchialine pools are stands within islands in context of Equilibrium Biogeography Theory (MacArthur & Wilson, 1967; Simberloff, 1972).

SYSTEMATIC DESCRIPTIONS

Order Podococida Sars, 1866
Superfamily Bivalvinae Sars, 1880
Family Bivaliidae Sars, 1880
Subfamily Pussellinae Danielopol in Maddocks, 1976

1973 Family Pussellidae Danielopol: 143 (non nundam).
1976 Family Pussellidae Danielopol, Maddocks: 197; Danielopol, 1976: 26i

Remarks. The Pussellinae are small to medium-sized bairdiids adapted to phyial, interstitial and possibly cryptic marine habitats. The four genera form a morphoseries showing decrease in size, smoothing and streamlining of carapace, fusion of podomeres and loss of eyes. Orlovihiidaea McKenzie, 1977, which is the largest and least reduced, is well distributed in cold waters of the Southern Hemisphere. It includes O. angulata (Brady, 1870), O. arcifera (Swanson, 1979), O. anisata (Müller, 1900), Anchistroleches sp. aff. anisata of Maddocks (1969), and a large number of other living and Cenozoic fossil species (McKenzie, 1977). Anchistroleches is worldwide, mostly in tropical reef environments Danispellia Wouters, 1988, and Pussellia Danielopol in Maddocks, 1976, are interstitial or cryptic dwellers in reef environments and will probably prove to be circumtropical.

Genus Anchistroleches Brady & Norman, 1880
1880 Anchistroleches Brady & Norman: 110; Brady, 1890: 496; Müller, 1906: 100; Maddocks, 1969: 110; Maddocks, 1976: 199.

Remarks. Species of Anchistroleches are thought to be phyial, cryptic or interstitial in habit. Morphological adaptations for this life include the bevelled, angulate, hook-like tips of the terminal setae of the antennae and posterior legs for clinging tightly to or climbing irregular surfaces; the laterally compressed, streamlined, mirror-smooth, fragile carapace with broadened marginal zone of conception; the fusion of podomeres, loss of eyes, and somewhat juvenile aspect of appendage chaetotaxy; and the elongate, flexible, protrusible urobranch and hypostome, which probably allow feeding through a narrower gap between valves than in other Bivaliidae.

At present the genus Anchistroleches includes at least ten other species: A. janae (Brady, 1890) (Samoa, New Caledonia, Madagascar, perhaps Hawaii (Holden,
A. acroca Brady, 1868 [North Sea, Irish Sea, English Channel]; A. barnes Maddocks, 1976 [Bermuda]; A. benevolo Maddocks, 1969 [Walters Shald, south Madagascar Ridge]; A. brevica Scott, 1905 [Ceylon, Madagascar]; A. harrer Maddocks, 1976 [Bermuda]; A. meequadi Maddocks, 1976 [Flower Garden, Gulf of Mexico]; A. sp. 1 of Maddocks, 1969 [Madagascar]; A. sp. 1 of Bonaduce et al., 1980 [Gulf of Alguba]; and A. aff. A. sp. of Bonaduce et al., 1980, of Gabocho, Anguila & Babinono, 1986 [New Caledonia]. Several larger, less reduced species referred to Anchistchole by Maddocks (1976) have been reclassified in Orleabatida. As a result, Anchistcholes is now circumboreal in its distribution, while Orleabatida encompasses colder, deeper, more southerly residents (McKenzie, 1977).

**Anchistcholes darwini** Maddocks & Iliffe, sp. nov. (Figs. 2, 3A, B, 4-6)

**Derivation of name.** For Charles Darwin and for the marine station that bears his name.

**Material.** One adult male in alcohol.

**Types.** Holotype male specimen 3067M, USNM 193883.

**Type locality.** Deep Grotta, Tortuga Bay, Isla Santa Cruz.

**Occurrence.** One specimen in sample R7-005.

**Dimensions.** Holotype male 3067M, LVL 0.74 mm, LVH 0.38 mm, RVL 0.74 mm, RVH 0.37 mm.

**Diagnosis.** Carapace smooth, laterally compressed, thin-walled, nearly ovate in lateral view, with evenly rounded anterior margin, very broadly arched dorsal margin, obtusely tapering posterior margin, and wide, shallow ventral indentation; lateral profile lacking any angularities or abrupt truncations. Marginal zone of concrescence narrow; adductor muscle scar small, arranged in bythocyprid pattern; normal pore canals few, small, and simple.
Figure 3. Anchistochelus darwini Maskell & Hile, sp. nov., male specimen 3067M. A, B, Right and left sides of entire animal before dissection (× 83). C, D, Right and left sides of entire animal before dissection, showing eggs and musculature present in dorsum. E, F, Exteriors of partly desiccated organs and left valves (× 62). G, H, Exteriors of fragments of right and left valves (× 11). I, J, Right and left hemipenes and base of testes (× 280). K, Left exterior adductor muscle-scar pattern and V-shaped frontal scar (× 280).
Antennule robustly proportioned, with short, broad terminal podomeres, with podomeres 6 and 7 fused, and with numerous terminal setae of graduated lengths. Antenna with podomeres 4 and 5 separated by a conspicuous joint; two antennal setae of podomere 3 small, located at about middlelength; anterodistal seta of podomere 6 very tiny; postero-distal seta of podomere 6 short; terminal claw short, fairly thick, with angled terminal hook. Male fifth limb has small, oval vibratory plate, which has five unfeathered setae segregated proximally and seven feathered setae arranged around the distal and posterior margin; podomere 2 greatly elongated, with anterodistal setae located at middlelength; podomeres 3 and 4 totally fused, not separately identifiable; podomere 2 separated from podomeres 3 and 4 by an incomplete, inflexible suture and indented margin; podomere 5 flexibly articulated in the normal fashion, bearing a moderately long, tapering, angular claw. Furca sicrate, not tapering, thickened and angular distally, carrying two short ventrodistal setae and one smaller, distant proximal seta. Hemipenis with compact, almost hemispherical basal and median segments, which are strongly musculated, with margins prominently indented at articulatory joints, terminal segment consists of an oblong, arching, twisted, lamellar hood; cephalic tube thick, curved in sigmoid fashion. Tестes and vas deferens coiled in a broad disk within the flexible, protrusable end of the body.

Affinities. The male fifth limb of this species shows complete fusion of podomeres 2 and 3 and partial fusion of podomeres 3 and 4, which represents the greatest degree of transformation of this limb yet seen in the genus, subfamily and family. The swollen contours of podomere 4 also differ from the usual cylindrical limb. Although this could be a developmental pathology unique to this individual, the specimen is too abnormal in any other way. The vibratory plate of the fifth limb appears to have five unfeathered setae segregated proximally, rather than the usual four, although the portion of the legs on the dissecting slide does not permit complete certainty about this. Apparently, one of the eight distal and posterior feathered setae has migrated forward to join the four unfeathered segregated setae, producing 5 unfeathered plus 7 feathered rather than the usual 4 unfeathered plus 8 feathered setae. Such characters are reminiscent of *Zephyrocoptes* Maddocks, 1969, a depopera genus of Bythocypridinae (see Maddocks, 1969, 1973, 1976). As yet, one few species have been described in the various genera of the Pusselinii, Bairdiiinai and Bythocypridinae to delineate the subfamily boundaries with certainty. Davidelepel (personal communication) as one time suggested that the interstitial Pusselinii ought to be classified as a tribe within the largely deep-sea subfamily Bythocypridinae; his argument for this and others against were summarized by Maddocks (1976: 197). The characters of *A. darwini* show that the question remains open.

Comparison. The copulatory organ of *A. darwini* is somewhat more compact in its proportions than that of *A. harmani* and has a thicker, more sinuously curved copulatory tube but otherwise corresponds very closely in structure. In addition, *A. darwini* differs from *A. harmani* by larger size, ovate lateral outline with gently curving contours, shorter terminal claw and much shorter accessory setae on podomeres 3 and 6 of the antenna, fusion of podomeres 3, 4 and 5 on the fifth limb, longer terminal claw on sixth and seventh limbs, and less elongate furca.

The ovate carapace of *A. darwini* is very similar in shape to that of *A. fumata*. 
but slightly smaller. According to Brady’s (1890: 496) illustrations, *A. femur* has a longer terminal claw and two long accessory setae on the antenna, has podomeres 2 and 3 well separated, has a longer copulatory tube and more elaborate distal lobe on the copulatory organ, and has a distal seta on the furca in addition to two longer setae.
**Anchirotecheles darwini** is larger or much larger than *A. barnharti*, *A. monnadi* and *A. aeneus*. In lateral outline it is more elongate and more ovate than these rather quadrate species, with gently rounded rather than truncate anterior and posterior margins. Details of appendages and the narrow marginal zone of concrescence also easily distinguish *A. darwini* from these and other species.

**Remarks.** The sample was collected by plankton net from the water column, but the presence of this bentthic species shows that the net must have included some sediment, plants, or other substrate from the walls or bottom. The carapace of this specimen is weakly calcified, and the course of the inner margin and radial pore canals cannot be definitely traced.

Remarks. Species of Cyprides are well known to be tolerant of low, high and fluctuating salinities. Sandberg & Plusquellec (1974: 6) concluded that "Migratory birds comprise the most likely of all potential dispersal agents for Cyprides species". The brood care of young instars and tolerance for fluctuating salinities are important preadaptations of Cyprides for passive dispersal, and some species are distributed along waterfowl migration flyways for thousands of miles. There are more than two dozen living and late Cenozoic fossil species in the Americas, Africa and Europe (Sandberg, 1964; Sandberg & Plusquellec, 1974).

Because the appendage anatomy and even the male genitalia show only minute

Figure 6. Anchistodracaean darwini Maddocks & Iliffe, sp. nov., male specimen. A, Posterior end of body, with distally coiled onco and vas deferens, both tentipenes, and both furcae. B, Mandible. C, Suck region, with labrum and hypostome (all x 520).
differences between species, while the carapace is subject to considerable within- and between-population variability, species of this important genus have not always been accurately discriminated.

_Crepidula sternopora_ Triebel, 1956
(Figs 2, 3C-F, 7A-J)


**Material.** Five specimens in alcohol, including two females and three juveniles, USNM 119886-119888.

**Occurrence.** In sample 87-005, three specimens; in sample 87-012, three specimens.

**Dimensions.** Female 3068F, LVL 0.94 mm, LVH 3.54 mm, RVL 0.94 mm, RVH 0.53 mm. See also Fig. 2. These females are slightly larger than the range reported by Triebel (L 0.82–0.93 mm).

**Distribution.** In the present study, this species was collected from Deep Grotto in Tortuga Bay on Isla Santa Cruz and from a lava rock pool at Punta Tortuga on Isla Isabela, Triebel described a population of males, females and juveniles from Crater-Lake Arcturus on Isla Genovesa.

**Comparison.** Kreyer (1972a, b) reported a smooth species of _Crepidula_ living on mud substrates in the Florida Everglades under the name _C. heesoni_ Tresler & Smith, 1948, and he listed _C. sternopora_ [sic] with several other names as subjective synonyms of that species. However, the Everglades species illustrated by Kreyer was probably _Crepidula americana_ Sharp, 1908, which is well known in the Bahamas, Puerto Rico, the west coast of Florida, Texas, Louisiana, and New York, and in the Miocene and Pliocene of Mississippi and North Carolina (Sandberg, 1964; Sandberg & Plusquellec, 1974; Sanger & Teeter, 1982).

Females of _C. americana_ are slightly longer and perhaps slightly more elongate than females of _C. sternopora_; the more elongate-ovate shape is in part an illusion caused by the more sloping postero-dorsal margin and the more narrowly rounded, less truncate posterior margin of _C. americana_. Males of _C. americana_ also have a more sloping postero-dorsal margin and an obliquely angulate posterior margin rather than the more broadly rounded posterior margin of _C. sternopora_. Both sexes of _C. americana_ have nearly straight ventral margins, whereas the ventral margin of _C. sternopora_ is distinctly indented in the mouth region with convex anterioventral and posteroventral segments. Females of _C. americana_ are thickest posteriorly, while both sexes of _C. sternopora_ have subparallel sides in dorsal view according to Triebel’s illustration. The elongate, sometimes Y-shaped, stieve-type normal pore canals of _C. sternopora_ and _C. americana_ are not unique but occur in many other species as well. For example, in _C. torva_ (Jones, 1850) the irregularity of these pores varies inversely with salinity (Roosenfeld & Vesper, 1977).

(The true identity of _Crepidula heesoni_ remains uncertain, because the carapace outline of the female as illustrated by Tresler & Smith (1948: pl. 4, fig. 41) is rather unlikely, the carapace of the holotype is decalcified, and Sandberg (1964) was unable to re-collect topotype specimens. It may be a synonym of _C. americana_. The copulaeasty organ illustrated by Tresler & Smith (pl. 3,
fig. 30) is very similar to that figured for *C. americana* (Sandberg & Plusquellec, 1974: text-fig. 6a), and other appendages agree quite closely.

On the basis of present evidence, then *C. steppore* is not conspecific with the Florida species. Sandberg (1964) listed *C. steppore* as a valid species (without restudying it) and suggested that it might be endemic to the Galapagos.

Although endemism is not a usual attribute of species of *Cyprideis*, the known Pacific species are very distinct from *C. steppore*. *Cyprideis haememisis* (LeRoy, 1943) (widely distributed in British Columbia, Oregon, California, Baja California, southern Chile, Midway Island, the Hawaiian Islands, and a well in Utah; Sandberg, 1964; Sandberg & Plusquellec, 1974) is larger than *C. steppore*, has marginal denudations and a posteroventral spine, has an elongate-subquadrate shape with truncate female posterior end and arsulate male posterior end, has a nearly straight ventral margin, and has a posteroventral concavity in the male right valve, which presents a diagnostic asymmetry in dorsal view. *Cyprideis castae* Benson, 1959 (Baja California to Gulf of Panama) is
much smaller and more elongate, with posteriorly truncate females and angularly tapering males, and with sinuous, centrally constricted dorsal outlines, as well as a pitted exterior (Sandberg, 1964; Sandberg & Plusquellec, 1974; McKernie & Swaine, 1967). *Cypridella dentata* Klie, 1932 (Bonaire, Aruba, Curacao, Bermuda) is much larger than *C. simpsoni*, with greatest thickness located posteriorly in females and centrally in males, with occasional tiny marginal dimplications, with deeply incised, Y-shaped normal pore-canal pits, and with nearly straight ventral margin (Sandberg, 1964; Maddocks & Kornicker, 1986). *Cypridopsis multidentata* Hartmann, 1955 (Brazil, Argentina) is smaller than *C. simpsoni*, more elongate-recumbent to lateral outline, with a distinct dorsal angle in the male, has marginal dimplications, and has a posteroventral spine on the left valve (Sandberg, 1964; Sandberg & Plusquellec, 1974). *Cypridopsis pacifica* Hartmann, 1957 (El Salvador, Nicaragua) is smaller and more elongate, with ovate-subtriangular lateral outline, tapering posterior end, marginal denticles, and posteroventral spine on right valve (Sandberg, 1964; Sandberg & Plusquellec, 1974; Swartz & Gilby, 1967). The well-known *C. sulcata* van den Bold, 1963 (Louisiana, Texas, Gulf Coast of Mexico, Venezuela, Argentina, Hispaniola, South Carolina, New York, and Mocone to Pleistocene of Kansas, North Carolina, Louisiana, Florida and Trinidad) is larger, more heavily ornamented, much more variable in carapace ornament, has females that are thickest posteriorly in dorsal view, and has a characteristically sinuate ventral margin in the males. *Cypridopsis stephensi* Sandberg, 1964 (South Carolina, Georgia, east Florida, and Mocone to Pleistocene of Louisiana and the south-eastern United States) is much smaller and has elongate-subquadrate outlines in both male and female.

*Fam. Trachyleberidae* Chester-Bradley, 1948

*Genus Occulcythereis* Howes, 1951


Remark. The asymmetrical valves of males reflect corresponding asymmetry of the left and right fifth and sixth limbs, a feature found in few other Trachyleberididae (Triebel, 1961). Fossil species of *Occulcythereis* are common in the Cenozoic and probably the latest Cretaceous of Europe and North America. Another living species occurs in the Mediterranean, *O. lineata* (Müller, 1804).

*Occulcythereis angusta* van den Bold, 1963

(Figs 2, 3-G, K, 7-K, 8)

1961 *Cythereis deformis* Brady: 197; pl. 26 figs 6, 8 (not *Cythereis deformis* Baird, 1836).

1963 *Occulcythereis deformis* (Brady), Triebel: 206.

1963 *Occulcythereis angusta* van den Bold: 391, pl. 9, fig. 1-9, pl. 12, fig. 6; van den Bold, 1966a: 5; van den Bold, 1966b: plate 1; van der Bold, 1968: plate 8; van den Bold, 1971: tables 4, 6; Allison & Holden, 1971: 203, figs 27a-d; Teeter, 1973: table 1; Maddocks, 1974: 212, pl. 7, figs 3-5; van den Bold, 1975: tables 2, 5; Teeter, 1975: 452, figs 13F, 8, 44; van den Bold, 1977: table

9: van den Bold, 1988: 40, pl. 5, fig. 9: van den Bold, 1989: table 2; Cronin, 1988: 883, pl. 2, fig. 15.
1976 Ocealocyclus sp., Holde: F29, pl. 12, figs 22, 23 (after Cronin, 1988).
Material. Eight specimens in alcohol, including one male, six females, and one juvenile, USNM 193889-193890.
Occurrence. In sample 87-017, 8 specimens.

Dimensions. Male specimen 3065M, LVL 0.54 mm, LVH 0.24 mm, RVH 0.46+ mm, RVH 0.26 mm. See also Fig. 2.

Distribution. This species was originally described from Madeira at a depth of 70 fathoms (135 m). It is distributed widely throughout the Caribbean region and Gulf of Mexico in carbonate environments, including Bermuda, Nicaragua, Belize, Alacran Reef, and the Flower Gardens (van den Bold, 1963, 1989; Teeter, 1975; Maddocks, 1974, unpublished data). Its fossil record extends as far back as the Miocene in Jamaica, Dominican Republic, Trinidad, and Costa Rica (van den Bold, 1988). In the Pacific it was reported from reef sediments of Clipperton Island by Allison & Holden (1971); Cronin (1988) extended its range to the Miocene and Pliocene of the Marshall Islands and suggested that *Oculiulysithes* sp. of Holden (1976), from the Miocene of Hawaii, probably belongs to the same species. However, no one has restudied Brady’s types and compared populations from these localities to verify this broad species concept and to evaluate the visible differences in shape.

Comparisons. The only other species of this genus for which the soft parts have been partly described is *Oculiulysithes lineata* (Müller, 1894) in the Bay of Naples. *Oculiulysithes angusta* is slightly shorter than *O. lineata*, proportionally not as high, and has a concave rather than convex margin. The hemipenis of *O. angusta* has a more elongate, tapering terminal lobe, rather than the blunt, subquadrinate lobe of *O. lineata*, and has a lamellate expansion of the tip of the copulatory tube. The degree of asymmetry of the male fifth and sixth legs is approximately the same in *O. angusta*, as illustrated for *O. lineata*, but the right fifth and sixth legs and the seventh legs appear to have slightly more elongate podomere proportions and distal claws (see Müller, 1894: 577, pl. 29, figs 21, 26, pl. 31, figs 29–30, 33).

Order *Platyopoda* Sars, 1869
Superfamily *Cytherellaceae* Sars, 1866
Family *Cytherellidae* Sars, 1866
Genus *Cytherella* Jones, 1899
*Cytherella* sp.

Material. One female carapace in alcohol, USNM 193891.

Occurrence. In sample 87-017, one specimen.

Remarks. The empty carapace is small, smooth, elongate-ovate in shape, and otherwise nondescript. The specimen is fragmentary and could not be measured.

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REFERENCES


ANCHIALINE OSTRACODA OF THE GALAPAGOS


