

BIOGEOGRAPHIC RELATIONSHIPS OF GALAPAGOS MARINE ISOPOD CRUSTACEANS

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ABSTRACT

Thirty-five species of marine isopods are reported from the Galapagos region; 18 (51%) are endemic. Of the 17 nonendemic species, 6 are restricted to the Panamic Region, 4 occur in the Panamic Region and Californian Province, and 7 are widespread. For the most part, biogeographic relationships of the Galapagos endemic species are not yet known. Of four species for which sister-group relationships are hypothesized, one has its possible sister-species in Antarctica, one in the Panamic Region, one in Brazil/Australia, and one in New Caledonia (west Pacific). Seventeen species of shallow-water isopods are known from the Galapagos, 11 (65%) of which are endemic, 3 also occur in the mainland Panamic Region, and 3 occur in both the Panamic Region and Californian Province. There is no evidence from separate analyses of endemic and nonendemic species to support a vicariance hypothesis that the archipelago was once connected to the American mainland by shallow submarine corridors along the Carnegie or Cocos Ridge. All Galapagos isopods appear to owe their origin on the islands to dispersal from other regions. Only two species span the east Pacific barrier, and both are parasites on oceanic fishes. Other studies of Galapagos marine biogeography are briefly reviewed. All Galapagos marine taxa that have been examined biogeographically, except pycnogonids, gammarid amphipods and isopods, have a pelagic dispersal stage in their life history. Pycnogonids, gammarids and isopods exhibit higher endemism (75%, 35% and 51%) than any other suprageneric-level taxon yet analyzed from the Galapagos, suggesting a direct correlation between dispersal capabilities and levels of endemism on oceanic islands.

Four questions are addressed in the present paper: (1) How do levels of endemism in Galapagos marine isopods compare to those of other Galapagos marine invertebrate taxa? (2) Is there biological evidence to support the hypothesis of a former, shallow, submarine dispersal "corridor" between the mainland and the Galapagos along either the Cocos or Carnegie Ridge? (3) What are the biogeographic relationships of the nonendemic Galapagos marine isopods, and how do these compare to other nonendemic Galapagos taxa? (4) What are the biogeographic relationships of the endemic marine isopods of the Galapagos?

The Galapagos Archipelago comprises 13 major islands and numerous lesser islands and rocks. The islands are summits of giant shield volcanoes that rise from the crustal Galapagos Platform that rests atop the Nazca Plate. The Archipelago straddles the equator, extending from about 89°15'30"W to 92°01'00"W, and 1°36'S (Hood, or Espanola Is.) to about 1°40'N (Culpepper, or Darwin Is.). The Galapagos are isolated oceanic islands. The easternmost island, Chatham (San Cristobal), lies 970 km to the west of Ecuador. Farther to the west, in line with the eastward flowing waters of the tropical Pacific, the nearest substantial shallow water habitats are 7,000 km away, at Christmas Island Ridge, which bears several low islands and atolls (Christmas Is., Fanning Is.). The next major island chain westward is the Marshall-Gilbert Archipelago, which is 11,000 km from the Galapagos, and the Philippines are about 5,000 km farther west.

The islands and shield volcanoes of the Galapagos Archipelago were probably formed between 700,000 and 3.5 million years ago. The Galapagos Spreading Center passes several hundred kilometers to the north (Fig. 1), and crustal movement south of this center is about 3 cm/yr southward. This movement, coupled



Figure 1. Tectonic and geographic setting of the Galapagos Islands. Arrows indicate approximate direction of plate movements. Those portions of the Cocos and Carnegie Ridges above 1,000 fathoms (1,829 m) depth are stippled.

with the approximate 7 cm/yr eastward spread from the East Pacific Rise, results in a net east-southeast crustal movement of about 6–7 cm/yr for the Galapagos. Current opinion views the Galapagos Islands as derived from hot spot activity, and it seems likely that the Carnegie and Cocos Ridges, and perhaps the Malpelo Ridge, are also products of this activity.

Some authors have suggested that past emergent or shallow submarine dispersal corridors existed between the Galapagos and the mainland via the Cocos or Carnegie Ridge (Vinton, 1951; Van Dyke, 1953; Williams, 1966; Cox and Dalrymple, 1966; Dalrymple and Cox, 1968). Nevertheless, most geologists believe the islands themselves have never been any closer to the mainland than they are now, and are the products of ocean floor volcanism. Southeast drift is presumably moving the islands ever closer to the South American continent. For pertinent data and recent reviews of Galapagos geology see Wilson (1963), Morgan (1971;

1972a; 1972b), Holden and Dietz (1972), Anderson et al. (1975), Hey and Vogt (1977), Hey et al. (1977), and Hickman and Lipps (1985). For pertinent data¹ and recent reviews of radiometric dating see Cox and Dalrymple (1966), Dalrymple and Cox (1968), McBirney and Williams (1969), Bailey (1976), Bow (1979), Baitis and Lindstrom (1980), Hall et al. (1980), Cox (1983), Hall (1983), and Simkin (1984).

Durham's (1962; 1963; 1966) paleontological dating of a Santa Cruz island stratum as late Miocene is questionable in light of recent radiometric dating, but may indicate an older uplifted area deposited in shallow water prior to later emergence. Emergence of shallow subtidal areas of the Galapagos in recent times has been documented by Glynn and Wellington (1983), and late Miocene-Pliocene sea levels are known to have fluctuated significantly (Fairbridge, 1973; Vail and Mitchum, 1979).

The present marine climate of the Galapagos is generally classified as subtropical (Ekman, 1953; Abbott, 1966). As in other subtropical regions of the world (e.g., the Gulf of California and the Guayaquil region of Ecuador) the Galapagos Islands contain a mixture of tropical and temperate biotas and habitats, with the former predominating. As is typical of other subtropical areas (Brusca and Wallerstein, 1979a), annual surface water temperatures throughout the archipelago range from lows of around 16°C to highs of around 30°C. Although Galapagos surface water temperatures generally average between 18 and 27°C, they tend to be warmer year round in the north, ranging around 23–30°C. To the west, surface waters are cooler than elsewhere, typically ranging from 17–24°C. Most of the Galapagos Islands have well developed intertidal habitats. The yearly tidal range is about 2 m, unusually large for equatorial islands. The biological composition of Galapagos littoral and shallow-water communities has been discussed by Hedgpeth (1969), and Glynn and Wellington (1983).

Numerous oceanographic reviews of the Galapagos area are available. Particularly good works include Wooster and Cromwell (1958), Wooster and Reid (1963), Wyrski (1966), Wooster and Hedgpeth (1966), Abbott (1966), Glynn and Wellington (1983) and Houvenaghel (1984). Important recent data appear in Tsukchiya (1970), Stevenson et al. (1970), Pak and Zaneveld (1973), and Enfield (1975). In brief, the islands experience variable oceanographic conditions, since they lie in a region where several major currents, which vary in strength and position, meet or pass nearby. Three water masses predominantly influence the Galapagos: cool subtropical waters of the Equatorial Undercurrent (Cromwell Current), which upwell in the western region of the Galapagos; temperate waters of the South Equatorial Current, which bathe the islands year round; and warm waters that intrude from the region of the Panama Bight, doing so with particular intensity during El Nino years.¹

Only four published papers have specifically addressed the marine isopod crustaceans of the Galapagos Islands. Hansen (1897) described six species from deep benthic regions around the Archipelago that were collected by the Albatross Expedition in 1891. Richardson (1901; 1912) reported two additional benthic species from the area, and Van Name (1924) reported on the isopods collected by the Williams Galapagos Expedition. The 50 specimens reported by Van Name comprise the first collection of shore and terrestrial isopods taken from the islands themselves. Van Name's study brought the total number of Galapagan marine

¹ An unpublished, succinct, current review of Galapagos geological history and general oceanographic conditions is available from the author on request.

isopods to 12, 11 of which are deep water or open ocean species. A few additional records were added by Beddard (1886), Richardson (1914), Lincoln and Jones (1973), Fresi (1973), Coineau and Schmidt (1979), Brusca and Wallerstein (1979b), Brusca (1981; 1983), Delaney (1984), and Poore (1984).

METHODS

Isopod collections were examined from the Los Angeles County Museum of Natural History (LACM)—Allan Hancock Foundation (AHF), the California Academy of Sciences, and the U.S. National Museum. Principal sources of material were collections made by the AHF cruises of the *VELERO III* and *IV*, the LACM 1984 Galapagos expedition, and field work by R. C. Brusca (1986). The personal Galapagos isopod collections of Peter Glynn and Gary Robinson were also examined. A literature search for all distribution records from the region was made.

For the biogeographic analysis, the Galapagos region was defined as a $10^{\circ} \times 10^{\circ}$ square, 85°W to 95°W , by 5°N to 5°S . This square includes the Galapagos Platform and the adjacent deep sea bed, as well as the westernmost portions of the Cocos and Carnegie Ridges. Data for shallow-water and deep-water records are analyzed separately. Records specifically from hydrothermal vent communities are not included in the analysis. The term "Panamic Region" refers to the warm water Eastern Pacific Zoogeographic Region, which includes the subtropical Cortezian Province, and the tropical Mexican, Panamanian, and Galapagan Provinces (Briggs, 1974; Brusca and Wallerstein, 1979a). For purposes of the analysis, members of the families Cymothoidae and Aegidae are regarded as "parasites."

RESULTS

Thirty-six species of Galapagos marine isopods are herein reported (Table 1). One of these, a damaged *Munna*, cannot be further identified and is excluded from the following analysis, which is thus based on a total of 35.

Seventeen of the marine isopods known from the Galapagos are shallow-water species (littoral to 100 m). The remaining 18 species are pelagic, deep-water, and/or parasitic on pelagic or epibenthic fishes. Of the 17 shallow-water species, 11 (65%) are known only from the Galapagos, 3 (17.5%) also occur on the mainland coast of the Panamic Region, and 3 (17.5%) occur in both the Panamic Region and Californian Province. Of the 11 endemic shallow-water species, 10 are undescribed (Table 1).

Of the 35 species analyzed, 17 (49%) are nonendemic. Of these 17, 6 are restricted to the Panamic Region, 4 occur in both the Panamic Region and Californian Province, 6 are widespread in the Pacific, and 1 is circumtropical (Table 1).

Eighteen species (51%) are endemic to the Galapagos region. Of these 18, one is an open-ocean pelagic species (*Anuropus pacificus*), 1 is a fish parasite (*Aega longicornis*), 5 are benthic species taken from depths greater than 225 m, and 11 (31% of the total isopod fauna) are shallow-water species (littoral to 100 m).

DISCUSSION

Previous Studies on Galapagos Marine Biogeography.—Although the Galapagos Islands have a long history of terrestrial and marine ichthyological biogeographic studies, the marine invertebrate fauna has received surprisingly little attention (Table 2). I am aware of only 10 biogeographic analyses for marine invertebrates of the Galapagos (intertidal meiofaunal species are excluded from this discussion): amphipods (Barnard, 1979), brachyuran crabs (Garth, 1946), spirorbinid polychaetes (Bailey and Harris, 1968), pycnogonids (Child and Hedgpeth, 1971), spiny lobsters [Palinuridea] (Holthuis and Loesch, 1967), molluscs (Hertlein, 1937; Hertlein and Strong, 1955; Finet, 1985), and corals (Durham, 1966; Glynn and Wellington, 1983). These studies, and those on Galapagan fishes (Walker and Rosenblatt, 1961; Rosenblatt and Walker, 1963; Walker, 1966; Briggs, 1974;

Table 1. Marine isopods known from the Galapagos region. Shallow water = sublittoral to 100 m; shallow benthic = 100–500 m; benthic = 500–1000 m; deep benthic = deeper than 1000 m; * = new Galapagos records. New species are currently being described by the author as part of his on-going systematic research on tropical eastern Pacific shallow-water isopods

Suborder Flabellifera

Family Aegidae Dana, 1853

1. *Aega acuminata* Hansen, 1897. Panamic; deep benthic.
2. *Aega longicornis* Hansen, 1897. Endemic; benthic.
3. *Aega plebia* Hansen, 1897. Widespread in Panamic Region and N.W. Pacific temperate region; benthic to deep benthic.

Family Anuropidae Stebbing, 1893

4. *Anuropus pacificus* Lincoln and Jones, 1973. Endemic; pelagic.

Family Cirolanidae Hansen, 1890

5. **Cirolana diminuta* Menzies, 1962. Panamic and Californian; shallow water.
6. **Cirolana* n. sp. A. Endemic; shallow water.
7. **Cirolana* n. sp. B. Endemic; shallow water.
8. **Metacirolana* n. sp. [cf. *M. costaricensis*]. Endemic; shallow water.
9. **Metacirolana costaricensis* Brusca and Iverson, 1985. Panamic; littoral.

Family Corallanidae Hansen, 1890

10. **Excorallana houstoni* Delaney, 1984. Panamic; littoral and shallow water.
11. *Excorallana truncata* (Richardson, 1899) Panamic and Californian, littoral and shallow water.
12. **Excorallana* n. sp. Endemic; littoral and shallow water.

Family Cymothoidae Leach, 1818

13. *Anilocra meridionalis* Richardson, 1914. E. Pacific oceanic islands (Galapagos, Revillagigedos, Clipperton, and Hawaii).
14. *Nerocila excisa* (Richardson, 1901). TransPacific (Panamic, Galapagos, tropical west Pacific).
15. *Nerocila acuminata* Schioedte and Meinert, 1881. Panamic, Californian.
16. *Lironeca vulgaris* Stimpson, 1857. Wide ranging in northeastern Pacific (Oregonian and Californian Provinces, Panamic Region).
17. *Ceratothoa gaudichaudii* (Milne Edwards, 1840). Wide ranging in eastern Pacific (California, Panamic Region, Peruvian Province south to Cape Horn and around to Patagonia).
18. *Cymothoa exigua* Schioedte and Meinert, 1884. Panamic.
19. *Mothocya arrosor* Bruce, 1986. Circumtropical.

Family Sphaeromatidae Hansen, 1905

20. **Dynamenella* n. sp. A. Endemic; littoral.
21. **Dynamenella* n. sp. B. Endemic; littoral.
22. **Dynamenella* n. sp. C. Endemic; littoral.
23. **n. gen., n. sp.* [cf. *Dynamenopsis*] Endemic; littoral.

Suborder Gnathiidea

Family Gnathiidae Harger, 1880

24. **Gnathia trilobata* Schultz, 1966. Californian (and probably mainland Panamic); shallow water.

Suborder Valvifera

Family Idoteidae Fabricius, 1798

25. *Cleantioides occidentalis* (Richardson, 1899). Panamic; littoral and shallow water.

Family Astacillidae G.O. Sars, 1897

26. *Arcturus abyssicola* Beddard, 1886. Endemic; deep benthic.

Suborder Anthuridea

Family Anthuridae Leach, 1814

27. *Colanthuria* n.sp. (cf. *C. bruscai* Poore, 1984). Endemic; shallow water.
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Table 1. Continued

Suborder Asellota

Family Eurycopidae Hansen, 1916

28. *Storhyngura pulchra* (Hansen, 1897). Widespread in northeastern Pacific (Oregonian and Californian Provinces, Panamic Region); deep benthic.
 29. *Munnicope scabra* (Hansen, 1897). Endemic; deep benthic.

Family Munnidae Sars, 1899

30. *Munna* sp. Damaged specimen, I.D. not possible; shallow water.

Family Munnopsidae Sars, 1869

31. *Munnopsis longiremis* Richardson, 1913. Galapagos and Costa Rica; deep benthic.

Family Janiridae Sars, 1899

32. **Heterias* n.sp. Endemic; shallow water.

Family Gnathostenetroididae

33. *Maresiella barringtoniana* (Fresi, 1973). Endemic; benthic.

Family Microparasellidae

34. *Microcharon galapagos* Coineau and Schmidt, 1979. Endemic; littoral.

Suborder Epicaridea

Family Bopyridae Rafinesque, 1815

35. *Cryptone elongata* Hansen, 1897. Endemic; benthic; parasite of the crab *Nematocarcinus agassizii* Faxon.
 36. *Zonophyrxus similis* Richardson, 1914. Endemic; deep benthic.

Note: Richardson's (1905) record of *Colypurus agassizii* from the Galapagos apparently is in error; station data accompanying the type and only specimen indicate its collection near the coast of Panama. Richardson's (1905) record of the Caribbean *Excirolana mayana* (Ives, 1891) from the Galapagos was probably an incorrect identification.

McCosker and Rosenblatt, 1984), all arrived at the same conclusion: the Galapagos nearshore fauna is a mixture of species occurring in neighboring Pacific regions but is dominated by Panamic forms.

In fact, species-level affinities of Galapagan coastal marine life appear to be largely predictable with knowledge of local currents and oceanographic conditions. The principal currents capable of carrying marine organisms to the Islands from nearby land masses are the South Equatorial Current from the southeast, and the Panama Current (the "Panama Flow"), from the northeast. The latter sweeps southwestward from the region of the Panama Bight, and includes waters whose origins lie in the California Current and North Equatorial Countercurrent. Predictably, distributions and taxonomic affinities of the Galapagos species lie principally with the shores of the tropical/subtropical eastern Pacific (the Panamic Region), the Californian Province, and temperate western South America. Weaker ties exist with the tropical Indo-West Pacific region. A small number of circum-tropical and cosmopolitan species also inhabit the Islands.

Indo-West Pacific species probably reached the Galapagos principally by way of the Equatorial Undercurrent, which upwells on the western face of the Archipelago, and perhaps to a limited extent by way of the North Equatorial Countercurrent-Panama Current. Many west Pacific species that occur in the eastern Pacific are confined to island habitats in the latter region. For example, of the 48 species of Indo-West Pacific prosobranchs and bivalves reported in the eastern Pacific, 38 (79%) are confined to offshore islands, at least nine of which occur in the Galapagos (Emerson, 1978). Many marine invertebrate species are endemic to the Galapagos and Cocos Islands (and also often Malpelo Island) suggesting

Table 2. Numbers of known species and endemics of Galapagos marine biota. Isopod data are from the present study. Sources for other taxa are cited in text (for algae see Wellington, 1975, who updated Silva's 1966 analysis). Pycnogonids, molluscs, and amphipods cannot yet be considered well known in the Archipelago

Taxon	Total number species reported from the Galapagos	Number (and percent) of endemics
Fishes	306	44 (13%)
Algae	333	116 (35%)
Brachyuran crabs	117	25 (21%)
Ahermatypic corals	31	9 (30%)
Hermatypic corals	13	0
Molluscs	600	156 (26%)
Spiny lobsters	3	1 (33%)
Pycnogonids	12	9 (75%)
Gammaridean amphipods	49	17 (35%)
All isopods	35	18 (51%)
Shallow-water isopods	17	11 (65%)
Benthic deep-water isopods	9	6 (67%)

some degree of past geological or genetic continuity of these areas. Abbott (1966), and Glynn and Wellington (1983), provide discussions of probable routes and timing for oceanic immigration to the Galapagos.

The most recent summary of Galapagos marine fish biogeography (McCosker and Rosenblatt, 1984) reported 306 species in 91 families. Of these 306 species, the shorefish and nearshore pelagic fish fauna shares nearly 60% of its species with the tropical eastern Pacific and 14% with the Indo-West Pacific, while 8% are circumtropical species. Smaller percentages of the Galapagos shorefish fauna also occur in temperate South America and the Caribbean. Forty-four (13%) of the 306 species are Galapagos endemics, and 7 others occur only at the Galapagos, Cocos, and Malpelo Islands ("insular endemics"). McCosker and Rosenblatt claimed that Galapagos endemics tend to be in families possessing short-lived pelagic larval stages. They also reasoned that absence of certain "key mainland faunal elements" suggests that there has not been a close land connection to the Galapagos.

Wells (1983) reported 44 species of corals from the Galapagos (13 hermatypes and 31 ahermatypes). The hermatypic fauna is largely west Pacific in origin; none is endemic to the Galapagos and no species are shared with the Caribbean. Of the ahermatypic corals, 10 (32%) are endemic, 6 (19%) are Panamic, 12 (39%) are Indo-West Pacific, and 3 (10%) are Atlantic. Glynn and Wellington (1983) concluded that Galapagos coral reefs are young (1,000 to 5,000 years old), and are principally the product of Holocene dispersal events from east and west Pacific localities, rather than vicariant remnants of a Panamanian trans-isthmian track.

Of the 600 species of molluscs known from the Galapagos, about 26% are endemic. Of the nonendemic molluscs, about 68% are Panamic only, 10% Panamic-Californian, 9% Panamic-Peruvian, 4% Panamic-Californian-Peruvian, 1% Peruvian, 1% Panamic-Caribbean, 1% Panamic-Indo-West Pacific, 2% Indo-West Pacific, and about 4% widespread (Finet, 1985).² Hertlein and Emerson (1953) noted that trans-Pacific molluscs on offshore eastern Pacific Islands (Galapagos, Cocos, Clipperton, etc.) were predominantly in families such as the Cypraeidae,

² The mollusc data presented in James (1984) appear to be in error [323 species; 42% endemism].

Conidae, Bursidae and Cymatidae. Hertlein and Emerson suggested that this distributional pattern resulted from long pelagic larval lives in members of these families, although they presented no specific evidence in this regard.

Barnard's (1979) limited data on Galapagos gammaridean amphipods revealed 49 marine species, 17 (35%) of which were regarded as "provisional endemics." However, many of the endemics were regarded as scarcely distinct from their presumed sister-species on the eastern Pacific mainland. For this reason, and because the Panamic amphipod fauna is so poorly known, Barnard felt endemism in the Galapagos should be regarded as low until more collections had been made and analyzed. Although cladistic analyses were not performed, Barnard provided phylogenetic assessments of the endemic Galapagos species, which showed affinities mostly with eastern Pacific mainland forms, but also with certain Indo-West Pacific and widespread Pacific species complexes.

Of the 120 species of brachyuran crabs reported from the Galapagos by Garth (1946), 25 (21%) are endemic, 82 (68%) are Panamic species, and the remainder occur in temperate west America or the west Pacific. Of the 3 species of spiny lobsters known from the Galapagos, one is endemic, one is Indo-West Pacific (occurring from the Red Sea to Clipperton, Cocos and the Galapagos), and the third is a Panamic species (Holthuis and Loesch, 1967). Galapagos pycnogonids are poorly known, but of the 12 species reported from the Galapagos, 9 are endemic, one is Panamic, one is Caribbean, and one is Panamic-Caribbean. Bailey and Harris (1968) reported 12 species of Spirorbinae (Polychaeta: Serpulidae) from the Galapagos: 6 endemics, 5 Panamic species, and 1 widespread (probably cosmopolitan) species.

Galapagos Marine Isopods.—With the exception of pycnogonids, amphipods and isopods, all the Galapagos marine taxa discussed above undergo indirect development, with pelagic transport occurring during at least one stage of their life histories. Pycnogonids have a largely nonmotile, benthic larva (the protonymphon) that is often associated with cnidarians. Isopods (and gammaridean amphipods) have direct development and brood the young, thus lacking larval stages altogether. The majority are benthic crawlers that only occasionally swim off the ocean bottom, and then only for short periods of time. Exceptions are members of the families Aegidae and Cymothoidae, which take passage on epibenthic or pelagic host fishes, and the singular family Anuropidae, composed of 7 strictly pelagic species. One would predict chances of successful trans-oceanic jump dispersal to be low in species lacking pelagic life history stages, and that oceanic island endemism would be higher in taxa lacking pelagic stages than in taxa possessing this means of dispersal. Hence, if the Galapagos Archipelago never had a past shallow submarine connection to mainland America (via the Cocos or Carnegie Ridge), one would predict endemism in groups such as pycnogonids, amphipods and isopods to be higher than in groups with pelagic stages.

The only other summary of Galapagos marine isopods (Van Name, 1924) reported 12 species from the area. The present study reports three times this number, which must be regarded as a preliminary assessment of the total isopod fauna as collections from the Archipelago are still few in number. Certainly more species will be found, especially in deeper offshore regions. For example, Grassle et al. (1985) noted the high incidence of isopods (undescribed species) from the Galapagos rift area where this group was ranked third in overall abundance, in both numbers of individuals *and* numbers of species. By way of comparison, about 170 marine isopods have been reported from California waters, and I estimate that about 150 species occur in the Panamic Region. Thus, if more

intensive collecting doubled or even tripled the number of known Galapagos marine isopods, the fauna would still appear depauperate compared to adjacent mainland shores. Nonetheless, the 35 species now known from the Archipelago do provide a preliminary data base for addressing the four questions posed in the introduction.

First, endemism in Galapagos marine isopods is high. For all isopod species taken together it is 51%; for littoral/shallow-water species only it is even higher, 65% (Table 3). These endemism levels are higher than those reported for any other marine taxon (above the genus level) yet examined from the Galapagos, except pycnogonids. Nine deep-water species are known (depths greater than 100 m), 6 (67%) of which are so far known only from the Galapagos area. This suggests the possibility of an endemic deep water isopod fauna. However, it is impossible to generalize at this time because too few deep-water samples have been analyzed from this region.³

The apparent high endemicity of Galapagos marine isopods could be an artifact of sparse sampling. Pelagic species (*Anuropus*), and species that are carried about on fish hosts (Cymothoidae, Aegidae), might have ranges far greater than presently recognized. Similarly, deep benthic species might have much broader ranges than present data indicate (at least spanning the Cocos and Nazca Plates). If the pelagic, parasitic, and deep benthic taxa are all treated as nonendemics, Galapagos endemicity would drop to 11 species, or 31%. However, most biogeographers consider far less than 31% endemicity sufficient to recognize provincial status.

Second, there seems to be no biological evidence to support the hypothesis that shallow submarine corridors along the Cocos or Carnegie Ridge once connected the Galapagos Islands to the American mainland. The shallow-water isopod fauna appears depauperate and endemism is greater than that of almost all other coastal marine taxa, as predicted for a group that lacks a pelagic dispersal phase in their life history. Further shallow-water sampling in the Archipelago will continue to test this hypothesis.

Third, extra-Galapagos distributions of the nonendemic Galapagos marine isopods are similar to distribution patterns seen in other nonendemic Galapagos marine taxa (primarily the Panamic Region and Californian Province). It is notable, however, that only two species span the east Pacific ("Ekman") Barrier, *Mothocya arrosor* and *Nerocila excisa*, both parasites on oceanic fishes, attesting to the effectiveness of the virtually islandless eastern Pacific as a barrier to eastward dispersal in nonpelagic organisms. No isopod species are known to be common to the Galapagos and the Caribbean. Given the young age of the Archipelago, and the prevailing currents of the region, it is reasonable to hypothesize that the source of the nonendemic Galapagos species was extra-Galapagan (rather than species evolving in the Archipelago, then dispersing to mainland shores).

The fourth question addressed in this paper—"What are the biogeographic relationships of the endemic taxa"—is the most interesting and also the most difficult to address because of the lack of information on phylogenetic relationships. Before a historical biogeographic hypothesis can be proposed for an area, both phylogenetic analyses (cladograms) and geographic pattern analyses must be available. The predicament faced in the present study (and by all historical biogeographers) is the lack of available cladograms or sister-group hypotheses for most taxa. The need for cladograms becomes obvious when one asks the most

³ G. S. Wilson (in litt.) estimates the isopod fauna of the Galapagos hydrothermal vents area may eventually be shown to be as high as 80–120 species. However, organic enrichment may maintain a local diversity higher than that of the adjacent Nazca and Cocos Plates.

Table 3. Biogeographic relationships of Galapagos marine isopods with numbers of species and percent of total fauna in each of 4 categories

I. Endemic species:	18 (51%)
II. Nonendemic species:	17 (49%)
Panamic:	6 (35%)
Panamic-Californian:	4 (24%)
Widespread Pacific:	7 (41%)
III. Shallow water species:	17 (48.5%)
Endemic:	11 (65%)
Panamic:	3 (17.5%)
Panamic-Californian:	3 (17.5%)
IV. Deep water species (depth greater than 100 m):	9 (27%)
Endemic:	6 (67%)
Panamic:	2 (22%)
Panamic-Northeast Pacific:	1 (11%)

simple and fundamental questions of biogeographic origin regarding an endemic taxon: if we don't know what the sister-group is, and where it lives, how can we formulate a reasonable hypothesis regarding the geographic origin of the species in question?

This study has so far dealt only with patterns of geographic distribution among the nonendemic Galapagos marine isopods. Both predictions and empirical evidence indicate that the nonendemic Galapagos biota shares species-level similarities with the biotas of its adjacent geographic regions. Only endemic taxa, however, are useful in detecting area relationships which possibly derive from past vicariant events. The importance of identifying the phylogenetic sister-groups of endemic species is that it allows one to hypothesize past geological events that contributed more generally to the biotic history of the relevant region.

I suggest that if the Galapagos shallow-water marine biota is the product wholly of independent dispersal events and not vicariance, then endemic species sister-group relationships should be shared with a variety of source areas (i.e., be heterogeneous), as is the case with nonendemic species. If the shallow-water biota is partly or largely the result of vicariance, the sister-group relationships of the endemics should share a high degree of concordance (i.e., discrete tracks should be identifiable). If such a vicariance event comprised the fragmentation or sinking of a shallow submarine ridge connecting the Archipelago to mainland tropical America, sister-group tracts connecting these areas should be evident. Unfortunately, cladograms identifying sister-groups of Galapagos isopods do not yet exist, and 10 of the 11 shallow-water endemic species are undescribed. However, four species of Galapagos marine isopods belong to genera small enough that sister-species hypotheses (or at least estimates of most similar congener) can be deduced.

The pelagic genus *Anuropus* contains only 7 described species. The Galapagos species *A. pacificus* may be the sister-species of *A. antarcticus* Hale, 1952, of Antarctica (unpubl. analysis). The genus *Colanthura* comprises only 9 described species. The undescribed Galapagos *Colanthura* is probably a morphological variant of the Panamic *C. bruscai* Poore, 1984, or is its sister-species (Poore, in litt.). The genus *Heterias* contains only 3 known species, the marine Galapagos species reported, and two freshwater species, one from Australia (Victoria) and one from Brazil (Sayce, 1900; Richardson, 1904; Wolff, 1962; Lemos de Castro and Brasil Lima, 1977). The closest relative of *Microcharon galapagos* appears to be a New Caledonian form, *M. salvati* (Coineau and Schmidt, 1979).

The above 4 endemic taxa share their closest apparent relationships with (1) Antarctica, (2) the tropical eastern Pacific, (3) Brazil/Australia, and (4) the west Pacific (New Caledonia). Based on this admittedly small data base of 4 species, it would appear that area-relationships of the endemic marine isopods may also be heterogeneous, corroborating the relationships seen among the nonendemic taxa and suggesting that Galapagos endemic species arose by way of rare dispersal events rather than vicariance. This hypothesis can be further tested as corroborated cladograms of Galapagan genera become available.

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