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Biogeographical notes on the genus *Terebra* (Gastropoda: Terebridae) at Isla del Coco, Costa Rica

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Resumen: Se presentan nuevos registros para 11 especies del género *Terebra* (Gastropoda: Terebridae) en la Isla del Coco, Costa Rica, llevando a 13 el total. De éstas, once pertenecen a la Provincia faunística Panámica y dos a la Indo-Pacífica. Se evidencia una exitosa colonización y el mantenimiento de un flujo genético de estos terébridos a la isla, mediante un análisis biogeográfico que infiere sobre las condiciones ecológicas adecuadas para su desarrollo. Este considera al sistema de corrientes marinas que circundan la isla como uno de los medios de dispersión de elementos Panámicos e Indo-Pacíficos y toma en cuenta que las especies del género *Terebra* presentes en la isla tienen protoconchas multiespirales, por lo cual se inferiere que son especies con larvas planctotróficas y por consiguiente pueden ser teleplánicas (susceptibles de transporte pasivo a largas distancias).

During the past five years the authors have studied the molluscan fauna of Isla del Coco, Costa Rica, more commonly known as Cocos Island.

Cocos is a relatively recent volcanic island, formed in the Late Pliocene and located on the central part of the northwestern flank of the Cocos Aseismic Ridge, where it is the only outcrop protruding above sea level (5^o 30' 06" to 5^o 33' 26" N and 87^o 01' 47" to 87^o 05' 46" W). The nearest point on the continent is Cabo Blanco, Costa Rica, at 494 km distance; the nearest islands are Malpelo (Colombia) at 630 km, La Pinta = Abingdon (Galápagos, Ecuador) at 673 km, and Clipperton (France) at 2375 km distance. Cocos Island has a surface area of approximately 24 square kilometers.

Until 1983, only two species of *Terebra* Bruguiére, 1789, had been reported from Cocos Island (Montoya 1984): *Terebra maculata* (Linnaeus, 1758), reported by Emerson and Old (1964) and *Terebra berryi* Campbell, 1961, reported by Bratcher and Burch (1971). With the present study, the number of terebrids for the island is increased to thirteen species (Table 1 and Plate 1).

The initial steps of our research at Cocos Island included analyzing the bathymetric ranges for terebrids; as a result, we determined that there was an absence of these mollusks in the intertidal sand zone, one of the habitats mentioned in the literature (Bratcher and Cernohorsky 1987). This correlates with the fact that the sandy intertidal environments are extremely limited on Cocos. There are only a few hundred meters of beaches in incipient development, while the rest of the volcanic shore line is rocky.

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TABLE 1

Cocos Island Terebra. *Species collected to date *.*

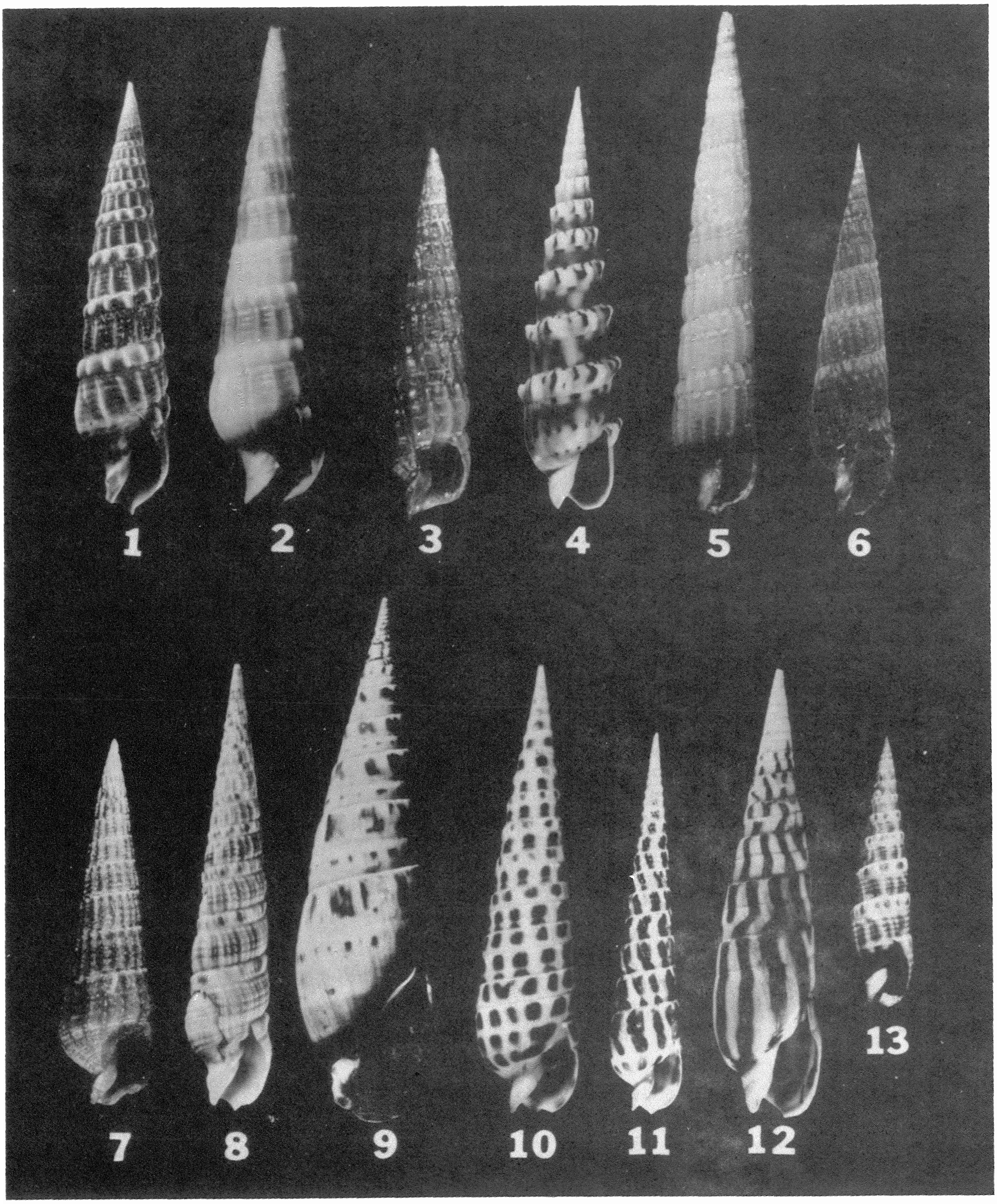
(156) *armillata* Hinds, 1844 Dredged and SCUBA collected. Chatham Bay 18 to 60 m on sand and coral rubble.	(Figure 1)
(174) *berryi* Campbell, 1961 Dredged, off Chatham Bay 35 to 60 m and Wafer Bay 30 m on sand and coral rubble bottom. Also night dive collected, Wafer Bay 20 m on sand.	(Figure 2)
(170) *corintoensis* Pilsbry & Lowe, 1932 Dredged, off Chatham Bay 135 m sand and coral rubble.	(Figure 3)
(011) *crenulata* (Linnaeus, 1758) SCUBA collected at night. Chatham Bay 25 m and East side of Manuelita Island 15 to 20 m on sand.	(Figure 4)
(172) *elata* Hinds, 1844 Dredged at night, off Chatham Bay 17 to 33 m and off Wafer Bay 18 to 60 m on sand and coral rubble.	(Figure 5)
(147) *glauca* Hinds, 1844 Dredged at night. Wafer Bay 18 to 33 m on sand.	(Figure 6)
(173) *guayaquilensis* (E. A. Smith, 1880) Dredged, off Chatham Bay 45 m on sand and light coral rubble.	(Figure 7)
(150) *hancocki* Bratcher & Burch, 1970 Dredged, off Chatham Bay 17 to 60 m on sand bottom and SCUBA collected, Manuelita Island 18 m on sand.	(Figure 8)
(015) *maculata* (Linnaeus, 1758) Dredged and SCUBA collected. Chatham Bay and Wafer Bays, Gissler Point, and Manuelita and Ulloa Island between 10 to 40 m on sand.	(Figure 9)
(139) *ornata* Gray, 1834 Dredged at night, off Chatham and Wafer Bays 25 to 60 m on sand. SCUBA collected. Manuelita Island 18 to 20 m on sand and light coral rubble.	(Figure 10)
(137) *robusta* Hinds, 1844 SCUBA collected at night, Chatham Bay 18 m. Manuelita Island 17 m and dredged, Wafer Bay 18 to 33 m on sand.	(Figure 11)
(141) *strigata* Sowerby, 1825 SCUBA collected at night and dredged, Chatham Bay 17 to 33 m on sand.	(Figure 12)
(152) *variegata* Gray, 1834 Dredged, off Chatham Bay 60 m on coral rubble.	(Figure 13)

* Parentheses indicate the species number of Bratcher and Cernohorsky (1987)

The most productive stations for terebrids were Chatham and Wafer Bays. These are protected areas with gentle slopes, consisting of coralline sand of variable coarseness and occasional areas of light to heavy coral rubble. The primary techniques used for collecting these mollusks included SCUBA diving at depths of fifteen to thirty meters and dredging to depths of 135 meters. Terebrids are mainly nocturnal sand dwellers and thus, our most effective collecting was done at night.

Of the thirteen species collected, eleven have a wide Panamic distribution extending from Baja California and the Gulf of California to Ecuador and Northern Peru. Six of these have been recorded at the Galápagos Archipelago (Finet 1985) and two, *Terebra maculata* (Linnaeus, 1758) and *T. crenulata* (Linnaeus, 1758) have Indo-Pacific faunal affinities.

Owing to their geologic origins, the knowledge of the composition and affinities of the molluscan faunas of the oceanic islands



Figs. 1-13. The genus *Terebra* at Cocos Island. Species collected to date. Fig. 1. *armillata* 50.0 mm. Fig. 2 *berryi* 16.1 mm. Fig. 3 *corintoensis* 10.4 mm. Fig. 4 *crenulata* 63.1 mm. Fig. 5 *elata* 26.6 mm. Fig. 6 *glauca* 27.8 mm. Fig. 7 *guayaquilensis* 73.0 mm. Fig. 8 *hancocki* 75.3 mm. Fig. 9 *maculata* 118.1 mm. Fig. 10 *ornata* 63.1 mm. Fig. 11 *robusta* 117.1 mm. Fig. 12 *strigata* 93.4 mm. Fig. 13 *variegata* 61.4 mm.

in the tropical Eastern Pacific allows a better understanding of genetic exchange and evolution in the Panamic faunal Province and in this particular case, of the molluscan assemblage of Cocos Island. We believe that the presence of a significant number of *Terebra* species at Cocos Island can be explained on the basis of three main factors.

TABLE 2

Cocos Island Terebra. *Protoconch characteristics**

Species	Whorl Number	Color, form & others
armillata	3 to 3 ½	conical, glassy shiny, light brown
berryi	4	subconical, glassy shiny, light brown
corintoensis	4 ½	conical, slender, shiny, amber
crenulata	3 ½ to 4 ½	conical, convex, shiny, brown
elata	3 ½	conoidal, smooth, glassy, amber
glauca	3	subconical, slender, glassy, light brown
guayaquilensis	3 ½ to 4	conical, smooth, glassy, dark brown
hancocki	3 ½	slightly convex, slender, shiny, amber
maculata	3 ½	conical, shiny and opaque, cream
ornata	2 ½ to 3	conical, shiny, 1½ brown and 1 light brown
robusta	3 ½ to 4 ½	conical, 2½ shiny and 2 opaque, brown
strigata	2 ½	slighty convex, translucent, light brown
variegata	3	conical, translucent shiny, light brown

* According to Bratcher (1979), Bratcher & Burch (1970 and 1971) and Bratcher & Carnohorsky (1987); and direct observations made by the authors.

First, the island marine environment (water temperature, salinity, substratum, etc.) offers the ecological conditions needed for terebrid development, and also allows the growth of the associated biota, such as hemichordate worms, capitellid and cirratulid polychaetes, which provide the trophic requirements of terebras.

Second, from December to April a complex system of marine surface currents generates off the Central and South American coast surrounding the island (Wyrtki 1963) which serves as a dispersal mechanism for Panamic faunal elements. During the remainder of the year the North Equatorial Countercurrent (NEC), which originates in the Western and Central Pacific, reaches Cocos with variable strength and penetration (Wyrtki 1965). According to Dana (1975), by using the maximum NEC speed given by Pickard (1963) of 60 cm/sec, passively floating invertebrate larvae would take roughly 125 days to make the journey from the Line Islands to the closest islands off the coast of Costa Rica.

Third, according to Bratcher and Cernohorsky (1987), reproduction involves planktonic veligers (planktotrophs) in the majority of Terebridae, although many species have direct development (nonplanktotrophs). This corresponds approximately to a proportion of 3:2 for all recent Terebridae, after analyzing information stated by those authors. The paucispiral protoconch indicates a species with direct development, while the multispiral protoconch indicates that such species have a long plaktonic life and therefore may be carried long distances by marine currents in the epipelagic waters of the open ocean before settling. Each of the thirteen terebrid species collected at Cocos has a multispiral protoconch (Table 2) indicating planktotropic larvae. For most of these species it is possible to infer teleplanic characteristics (long-distance dispersal) in the sense of Scheltema (1971).

Presumably the association of these three main factors made possible the occurrence of a high number of *Terebra* species at the small, isolated, oceanic Cocos Island. This situation supports the Scheltema (1986) hypothesis: volcanic island outcropping through a pre-existing ocean floor (in this case the Cocos Plate) require that their original colonization result from long-distance dispersal. Therefore among most tropical, shoal-water, sediment-dwelling invertebrates, such dispersal was largely accomplished by means of planktotrophic larvae.

The occurrence of two Indo-Pacific terebrids at Cocos requires additional explanation. *Terebra maculata* is the most common terebrid in the island. It was found abundantly in different growth stages, indicating that the species is fully established. The only other location in the Eastern Pacific where it has been previously reported is Socorro Island, a part of the Revillagigedo Archipelago, off the west coast of Mexico. This finding was originally described as *Terebra (Subulata) roosevelti* Bartsch and Rehder, 1939, and later synonymized with *T. maculata* by Bratcher (1970). While *T. crenulata* is not as abundant on Cocos, it has also been reported at Socorro and Clarion islands of the Revillagigedo Group (Bratcher 1970) and at Clipperton Island (Hertlein and Allison 1960, Salvat and Ehrhardt 1970).

J. B. Taylor (cited by Kay 1979) indicated that the veligers of *Terebra maculata* hatch when one whorl is complete, add two more whorls while plaktonic, and settle when three to three and one half whorls are complete. Bratcher and Cernohorsky (1987) indicate that *Terebra crenulata* have a protoconch with three and one-half to four and one-half conical whorls and settle when their length is approximately one millimeter. These characteristics of the two species imply a relatively long plaktonic life, susceptible to transport by marine surface currents and therefore give these species the possibility of long-distance dispersal.

Both *Terebra maculata* and *crenulata* develop their plaktonic life from April through September in the Central Pacific (J. B. Taylor, cited by Bratcher and Cernohorsky 1987), a time when the North Equatorial Countercurrent (NEC) reaches Cocos. This current is here hypothesized to be the dispersal mechanism explaining the occurence of these Indo-Pacific elements at Cocos Island.

The present analysis of the terebrid assemblage at Cocos Island provides evidence of a successful colonization by Panamic and Indo-Pacific terebrids (thirteen established species) and subsequently the maintenance of a continuous genetic flow needed to prevent changes and speciation/extinction through time.

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