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MURICIDAE (MOLLUSCA: GASTROPODA) OF THE ESMERALDAS BEDS, NORTHWESTERN ECUADOR

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ILLUSTRATIONS

I. ABSTRACT

Inasmuch as the Bolivar Trough, or Atrato Strait, of Colombia and Ecuador is probably the largest and most long-lasting trans-American Tertiary seaway, a study of the muricid gastropods of the Pliocene Esmeraldas beds of Ecuador was undertaken to compare relationships with the contemporaneous Caribbean fauna. The results show much less correlation with the Caribbean fauna than anticipated; only seven of the 21 species studied occur in the Pliocene of the western Atlantic. The greatest number in common with any fauna proves to be 11 that are still living on the coast of western America. But, of these, six no longer occur in Ecuador (one is confined to the Galápagos, one to California, two are found only in the Gulf of California, and two do not extend south of Panama). Of the 21 species treated systematically, three are new: *Murexsul pitti* and *Ceratostoma notiale*, both confined to the Esmeraldas beds; and *Murex (Haustellum) ruthae*, from the Esmeraldas beds and the Recent fauna of the Gulf of California.

In terms of presumed ancestry, 12 of the species have unmistakable Caribbean ancestors, and an additional three are worldwide Tethyan genera that may have come from the Caribbean. However, three are northern California-Japanese in relationship, two probably came directly from West Africa, and one seems to be endemic to the tropical eastern Pacific.

II. INTRODUCTION

It is generally agreed that the opening between the eastern Pacific Ocean and the Caribbean Sea was closed by Late Pliocene time, about 3.3 million years ago. Saito (1976) suggested closure by 3.5 m.a. (latest Early Pliocene; late planktic

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foraminiferal zone N.19) on the basis of foraminiferal differences in the two regions. Keigwin (1978) argued, on the basis of foraminiferal biostratigraphy, that it might be as late as 3.1 m.a. (N.20). This writer (Vokes, 1966, p. 68) once suggested that the faunal differences seen between the mid-Pliocene (N.20)* Pinecrest beds** and the Late Pliocene Caloosahatchee Formation in southern Florida are a reflection of temperature changes brought about by the creation of the Gulf Stream as a result of this closure and, thus, would serve to date the time of closing.

The reasons for accepting times of closure ranging from 5.7 m.a. to 1.8 m.a. have been summarized by Jones and Hasson (1985, pp. 343-348) and they conclude that 3.5 m.a. is still the most likely date for restriction of migration "of most or all microfauna." The data based on other phyla is less precise, for a variety of reasons, but "total emergence of the entire isthmus probably did not occur until sometime after 3.0 m.a., in the latest Pliocene or earliest Pleistocene" (*ibid.*, p. 349).

It is also generally conceded that much of the marine molluscan fauna of the Tropical East Pacific is directly derived from the Caribbean Tertiary fauna. Woodring (1966) did an extensive study of the interchanges and, although his age assignments tend to be a little too old in the current chronology (his Middle Miocene is Pliocene; his Pliocene is Pleistocene), the comparisons are still valid. As he predicted, we have since discovered some of his "paciphiles" (*i. e.*, taxa that are extinct in the Caribbean but still living in the eastern Pacific) in the Recent fauna of the western Atlantic; but the relatively high number of paciphiles remains impressive. In the Muricidae, for example, there are at least six paciphile groups: *Homalocantha*, *Purpurellus*, *Ceratostoma*, *Pterorytis*, *Bizetiella*, and *Vitularia*.

Given that the longest lasting and probably largest sea connection between the Caribbean and the eastern Pacific was the Bolivar Trough, or Atrato Strait, in western Colombia and Ecuador, an investigation of the late Tertiary Mollusca of the area at the Pacific end of the strait should be expected to reveal a fauna nearly identical to that of correlative faunas in the Caribbean.

Although outcrops with well-preserved fossil mollusks are rare on the Pacific Coast, along the northwestern coast of Ecuador (text-fig. 1) there is a remarkable occurrence of a series of gravity-flows (here termed the Esmeraldas beds) that bring shallow-water mollusks into the Early Pliocene deep-water clays of the Onzole Formation. Therefore, a study of the Esmeraldas fauna, in particular the members of the family Muricidae, was undertaken to compare the Pacific terminus of the strait with the much better known Caribbean faunas.

The Mio-Pliocene beds along the coast of northwestern Ecuador consist of deep-water, blue-gray silty-shales, with many pelagic foraminifera and sparse megafossils, primarily *Dentalium* shells. However, locally, at Punta Gorda (text-fig. 2), just west of Esmeraldas, and along Rio Camarones, about 10 km east of Esmeraldas, there are interlayered gravity-flow

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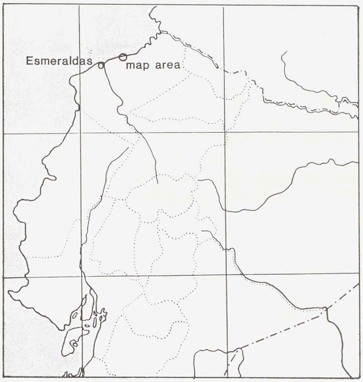
*Technically there is no "Middle" Pliocene; the era is divided into Early and Late. But the planktic zone N.20 lies athwart the boundary (see Berggren, 1973, fig. 1). Therefore, to distinguish between the unequivocal N.19-zoned beds of the Esmeraldas area and others, the informal term mid-Pliocene will here be used for beds that are placed in Zone N.20.

**Petuch (1986, p. 392) pointed out that the name Pinecrest Formation has been used previously for a Triassic unit in Utah (see Wilmarth, 1937, p. 1662). Although the North American Stratigraphic Code (Art. 7c) states "Priority in publication is to be respected, but priority alone does not justify displacing a well-established name by one neither well-known nor commonly used," he proposed to replace it with the name Buckingham Formation (there is also a previous Buckingham Gneiss, from the Pre-Cambrian of Quebec; see Wilmarth, 1937, p. 284). The Buckingham and the Tamiami Limestone, proposed at the same time, are facies of each other, with the Tamiami being the indurated limestone of which the Buckingham is the non-indurated phase. Both carry a fauna of predominately pectens, oysters, barnacles, and echinoderms and presumably represent a more offshore facies than the sandy Pinecrest. Until a definitive study of the southern Florida stratigraphy resolves the nomenclatural problem, the name "Pinecrest beds" will continue to be used to refer to the sandy, highly fossiliferous mid-Pliocene beds of southern Florida.

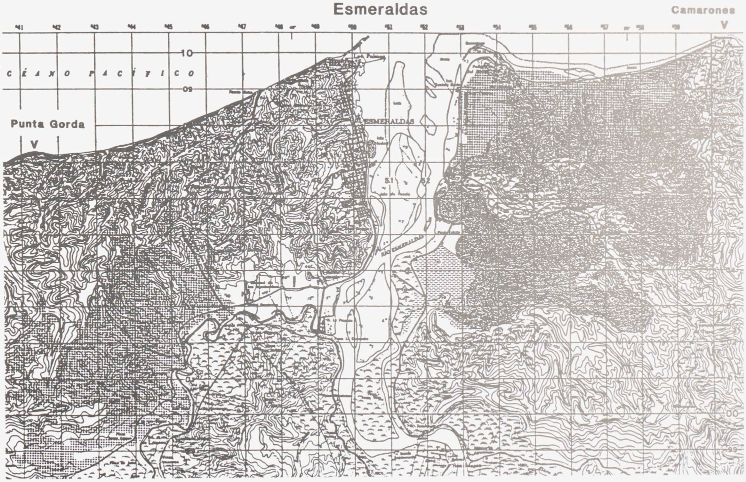


Text-figure 1. Map of northwestern Ecuador, showing study area.

lenses that are virtually coquinas of benthic forams and mollusks in a coarse sand matrix.

The only detailed study of the Esmeraldas mollusk fauna is that by Olsson (1964), who recognized the gravity-flow nature of the fossiliferous lens at Punta Gorda, stating: "The rubble lens is considered to be merely the terminal end of a large rock or mud flow produced by a major landslide which moved glacier-fashion across the shore into the sea, plowing up the bottom and gathering debris as it moved out into deeper water. Thus the littoral shells gathered in shallow water are battered and worn while the deeper water ones are generally in perfect shape" (1964, p. 14).

The name "Esmeraldas Formation" was proposed by Olsson (1942a, p. 260) for the "highly foraminiferal, tuffaceous shales so extensively exposed along the coast of Esmeraldas and along the Esmeraldas river itself." In the Second Edition of the *Lexique Stratigraphique* (1977) Bristow and Hoffstetter admit the name "Esmeraldas Formation" of Olsson, 1942, but state that "Olsson thought that the Esmeraldas Facies was equivalent to the Borbón Formation, differing only by the depositional zone. But in reality the Esmeraldas For-



Text-figure 2. Map of Esmeraldas area, Ecuador.

mation is the Onzole Formation" (1977, p. 142, *translated*). These authors consider the Onzole Formation to include beds from Middle Miocene through Pliocene (N.13 to N.19) in age, with a thickness stated to range up to 550 m. The Esmeraldas beds, which are at the top of the section, have been dated as N. 18-19 (Haman and Kohl, 1986, p.181) on the basis of calcareous nannofossils, or 3.6 to 3.2 m.a. on planktic foraminifera (Rosenberg, 1984, p. 84).

The present writer finds it hard to accept the name Onzole Formation for the beds at Esmeraldas, as they clearly represent a distinct lithologic change from the underlying hundreds of meters of deep-water clays; however, this is the terminology adopted by the Ecuadorian Geological Survey and is being used on all current geological maps.* Therefore, for the purposes of this paper, the term "Esmeraldas beds" will be used for the mollusk-rich shallow-water gravity-flows in northwestern Ecuador located at the top of the Onzole Formation. This is essentially the view adopted in a recent work by Hasson and Fischer (1986), who treat what they call the "Miocene Borbón Formation," and the "Pliocene Esmeraldas Formation." They note (1986, p. 32): "The Borbón Formation [*i.e.*, Onzole Formation] consists mainly of porous, tuffaceous, coccolith-rich diatomites and diatomacous mudstones. It lacks the macrofauna so characteristic of the Esmeraldas Formation."

We were originally apprised of the molluscan localities in the vicinity of Camarones by William Pitt, of Sacramento, California, who visited the site in 1980 and sent the muricids he collected to the writer for examination. His description of the area sounded so fascinating that in January, 1982, we made a visit of about one week to Esmeraldas. Just preceeding this time extensive roadwork had been undertaken by the Ecuadorian government to construct a new road along the coast from Esmeraldas to Punta Verde and ultimately to La Tole, at the mouth of the Rio Santiago. At the time we did not fully appreciate the new outcrops created by this work, until a second trip made with Mr. and Mrs. Pitt, in May, 1986, when we discovered all of the previous localities were completely overgrown.

This unfortunate circumstance nevertheless had a good effect, for not being able to collect at the previous sites, we were able to spend more time exploring other places. In particular, we walked for about 3 kms along the periphery of Punta Gorda (text-fig. 3), searching for Olsson's locality; but it is gone. As Bristow and Hoffstetter have reported (1977, p. 257), it was a localized lens that has been completely eroded away by the sea. But the exposures at low tide along Punta Gorda are amazing. There are a few scattered megafossils, but the main "traces of former life" comprise a spectacular array of ichnofossils (text-figs. 4-6). Olsson observed that "molluscan fossils are sparingly scattered through the formation exposed in the shore platform opposite Punta Gorda, all species having deep-water characteristics . . . A small deep-water *Nassarius* of the *Profundinassa* group is common and often in nestlike aggregates" (text-fig. 7) and "amongst other invertebrate fossils is a simple coral *Flabellum* . . . [of] the *F. japonicum* group [text-fig. 8], a late Tertiary to Recent group of species living in waters ranging from 80 to 1750 fathoms depth" (*ibid.*, p. 13).

Our principal collecting area for shallow-water mollusks is near Camarones (text-fig. 9), a small coastal village about 10 km east of Esmeraldas, or about 20 km by the new paved road. The best locality is the cut-bank of the Rio Camarones, just east of the village (TU 1397, text-figs. 10, 11) – the Quebrada Camarones of Olsson (1964), where large blocks with mollusks fall down from above. But the road-cuts along the highway were excellent during the 1982 construction period, and that at the mouth of the Quebrada (TU 1398, text-figs. 12, 13) showed the sedimentary structures of the gravity-flows especially well. The cliffs to the west of town along the road (TU 1399), also very good in 1982, were almost completely overgrown by 1986.

Within the small area at Camarones, there is a noticeable difference in the depth ranges of the transported faunas. Locality TU 1399 seems to be the most shallow but TU 1397 is moderately deep-water. In general, the same species of mol-

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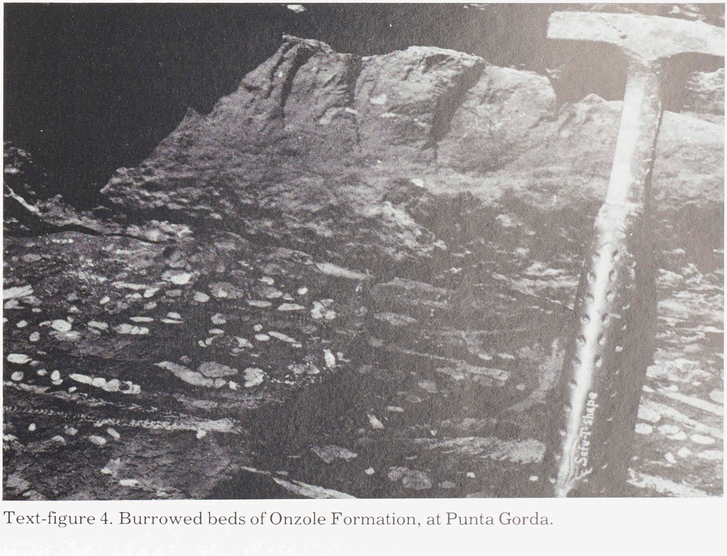
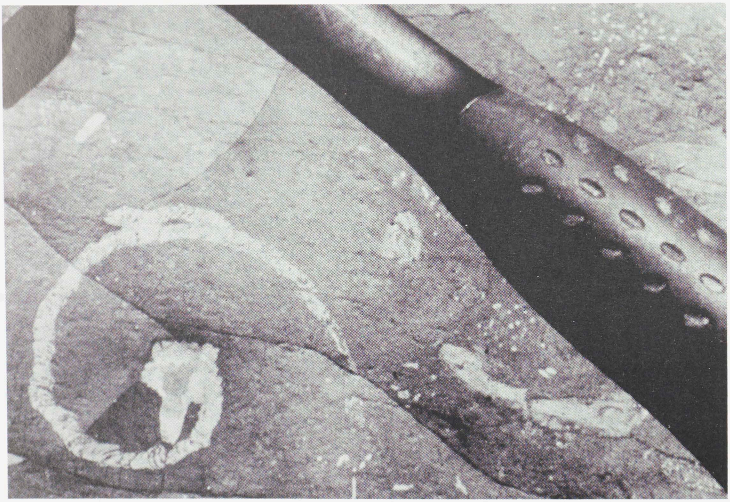
*For discussions of the currently accepted stratigraphical nomenclature in the area see Bristow, 1976, and Evans and Whittaker, 1982.

Text-figure 3. Punta Gorda, viewed from east, showing wave-cut platform exposed at low tide.

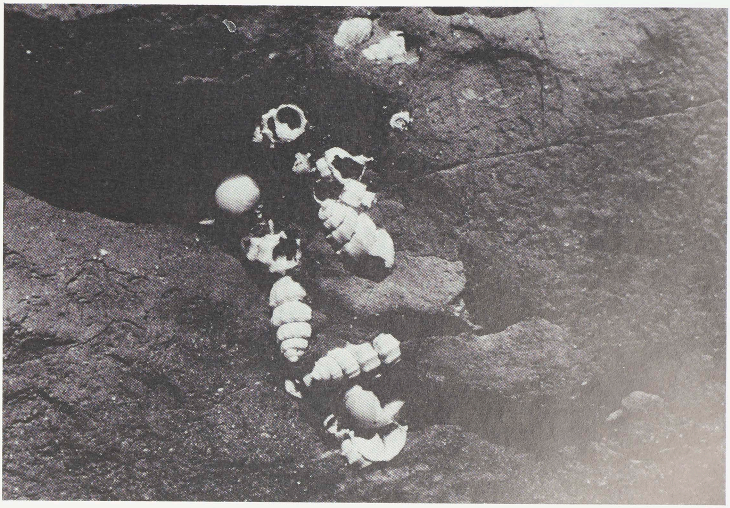


Text-figure 4. Burrowed beds of Onzole Formation, at Punta Gorda.

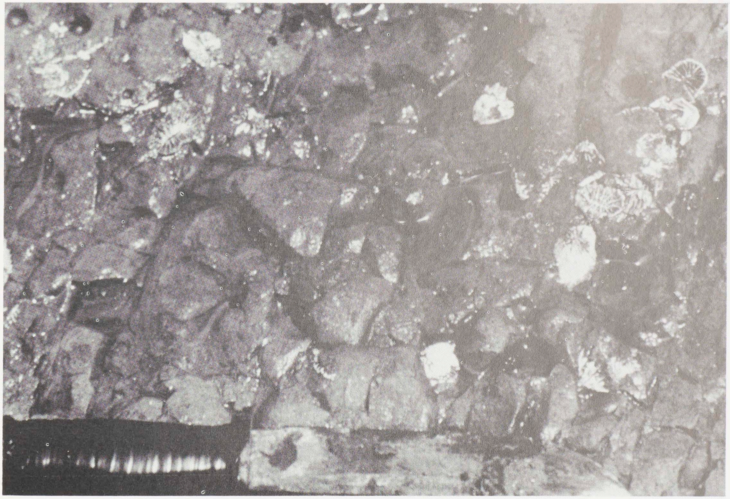
Text-figure 5. Burrow in Onzole Formation, Punta Gorda.



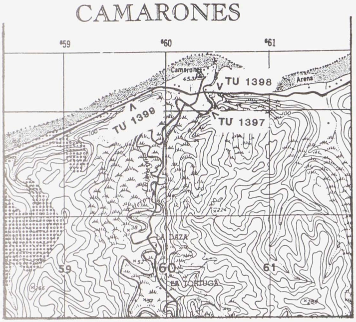
Text-figure 6. Burrow in Onzole Formation, Punta Gorda.



Text-figure 7. Cluster of specimens of *Profundinassa*, perhaps filling a burrow; Onzole Formation, Punta Gorda.



Text-figure 8. Specimens of *Flabellum*, a solitary coral; Onzole Formation, Punta Gorda.



Text-figure 9. Map of Camarones area, northwestern Ecuador; showing Tulane University (TU) collecting localities.

lusk occur at both places, but in differing quantities. For example, at TU 1399 various species of *Oliva* are abundant (62 specimens, in contrast to 5 at TU 1397) but *Cantharus scissus* Olsson is rare at TU 1399 (4 specimens) and common at TU 1397 (45 specimens). A closely related living species is one that Olsson named as type of a new subgenus, *Cantharus (Muricantharus) panamicus* (Hertlein and Strong), in a subsequent work (Olsson, 1971, p. 61), where he noted the depth of the living species averages 73 meters.

Thus, we may postulate that at locality TU 1399 the original slide began in relatively shallow water, almost intertidal, sweeping down into depths of perhaps 1000 m; but the slide at TU 1397 began in somewhat deeper water, on the order of 75 m, then washed into the deeper water.

Inasmuch as the Esmeraldas fauna is Early Pliocene in age, it should be closely allied with a correlative sequence in the Dominican Republic, where we have been working several years (Vokes, in press). The beds in the Dominican Republic contain facies from shoreline (Bulla Conglomerate) through shallow-water (Cercado Formation) to deep-water (Gurabo Formation) and ecologically are very nearly identical to the Esmeraldas beds. One would expect the faunas also to be nearly identical but they are not.

In his 1964 study, Olsson included five muricid species (one only as "unnamed turrid sp.") from the Esmeraldas beds, one from the Picaderos Formation and two from the Angostura Formation. Of these, all have now been found in the Esmeraldas beds except *Eupleura* sp. cf. *thompsoni* Woodring, which we have taken at Punta Verde, in the Angostura Formation.

Our work has added 14 additional muricid taxa, but, contrary to the anticipated results, there is just one species in common with the Dominican fauna, and only eight of the 21 occur in any other Pliocene faunas. Two of these, *Hexaplex brassica* and *Vitularia salebrosa* (as *ecuadorana*) are from the Pacific coast. The others are Caribbean: *Murex polynematicus* and *Typhis latipennis* from the Gatun Formation, Panama; *Chicoreus (Phyllonotus) globosus*, *Hexaplex hertweckorum*, and *Muricopsis oxytata* from the Pinecrest and Caloosahatchee units of southern Florida; *Vitularia salebrosa* again (as *linguabison*) from the Pinecrest beds and the Agueguexquite Formation of Mexico; and *Typhis alatus* from the Gurabo Formation, Dominican Republic, and the Gatun Formation, Panama. The largest number of taxa in common with another fauna is 11, which are still living in the eastern Pacific.

Table I shows the species involved and their affiliations. The prefix "R" indicates species occurring in the Recent Pacific fauna, but an asterisk indicates those that no longer live on the Ecuadorian coast. A lower case "r" indicates living Atlantic species.

In overall makeup, the majority of the Esmeraldas fauna is indeed allied with the Caribbean province, 12 of the muricid species have unmistakable Caribbean relatives. Of these, three are from the "Gatunian," or "southern Caribbean province" but three are from the "Caloosahatchian," or "northern Caribbean province," suggesting that Petuch's (1982, p. 282) conclusions on the origins of the eastern Pacific fauna as exclusively "Gatunian" may be unwarranted. Three taxa represent world-wide Eocene (Tethyan relics) and two species apparently came directly from West Africa, which is not unexpected

TABLE 1.
ELEMENTS OF THE MURICID FAUNA OF THE "ESMERALDAS BEDS"

I.	Caribbean		
	1.	(R)	MUREX (HAUSTELLUM) RECURVIROSTRIS (Charco Azul Formation)
	2.		MUREX (HAUSTELLUM) POLYNEMATICUS (Gatun Formation)
	3.	(R)*	MUREX (?HAUSTELLUM) RUTHAE, n. sp.
	4.	(r)	CHICOREUS (PHYLLONOTUS) GLOBOSUS (Pinecrest beds and Caloosahatchee Formation; Recent, Venezuela)
	5.		CHICOREUS (PHYLLONOTUS) sp.
	6.	(R)*	ATTILIOSA NODULOSA
	7.	(r)	MURICOPSIS OXYTATA (Pinecrest beds, Caloosahatchee and Bermont formations; Recent, western Atlantic)
	8.	(R)	MUREXIELLA LAPPA
	9.	(R)*	ACANTHOTROPHON SORENSENI
	10.	(R)	VITULARIA SALEBROSA (Daule and Charco Azul formations, Pinecrest beds, and Agueguexquite Formation)
	11.	(R)*	TYPHIS (TALITYPHIS) LATIPENNIS (Gatun Formation)
	12.		TYPHIS (TALITYPHIS) ALATUS (Gurabo and Gatun formations)
II.	World-wide Tethyan relics, probably Caribbean		
	1.	(r)	POIRIERIA (POIRIERIA) ACTINOPHORA (Recent, western Atlantic)
	2.	(R)*	POIRIERIA (PAZIELLA) MERIDIONALIS (as GALAPAGANA in Recent)
	3.		MUREXSUL PITTI, n. sp.
III.	California-Northern Pacific		
	1.		CERATOSTOMA NOTIALE , n. sp.
	2.	(R)*	PTEROPURPURA (PTEROPURPURA) MARKSI (as TRIALATA in Recent)
	3.		PTEROPURPURA (OCINEBRELLUS) ECUADORIA
IV.	Direct from West Africa?		
	1.	(R)	HEXAPLEX BRASSICA (Charco Azul and Jama formations)
	2.	(r)	HEXAPLEX HERTWECKORUM (Pinecrest beds; as H. DUPLEX in Recent, eastern Atlantic)
V.	Endemic?		
	1.	(R)	HEXAPLEX AMBIGUUS

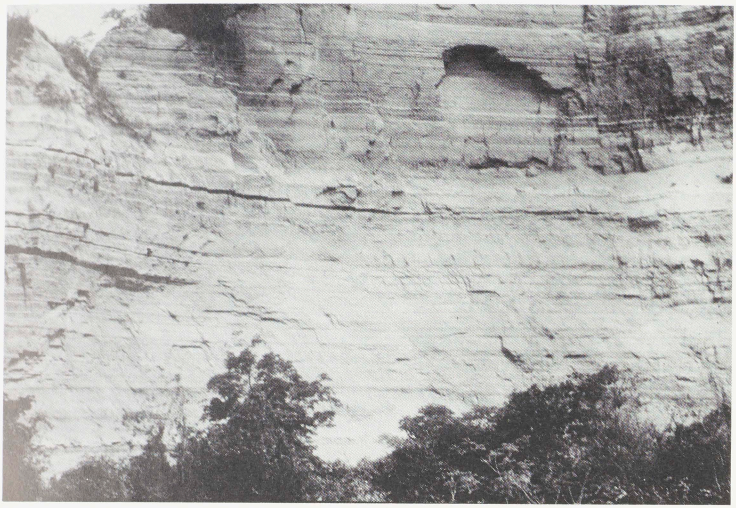
21 species total

R – living in eastern Pacific; *no longer on Ecuador coast

r – living in Atlantic

in light of similar distribution in genera such as *Harpa* (*H. doris* in Africa, *H. crenata* in eastern Pacific) and *Purpurellus* (*P. gambiensis* in Africa, *P. pinniger* and *P. macleani* in eastern Pacific). Both of these genera are good examples of "paciphiles" with representatives in the Gurabo Formation of the Dominican Republic, but no longer extant in the western Atlantic. Three taxa are clearly from a more northern Pacific province and are most closely related to living cooler-water species of California and Japan. This corroborates the findings of Hasson (*in* Jones and Hasson, 1985, p. 345), who noted the changes in microfauna from the tropical Miocene "Borbón Formation" [*i.e.* lower Onzole] to the temperate Pliocene "Punta Gorda Formation" [*i.e.*, Esmeraldas beds], which has a microfauna similar to that of California.

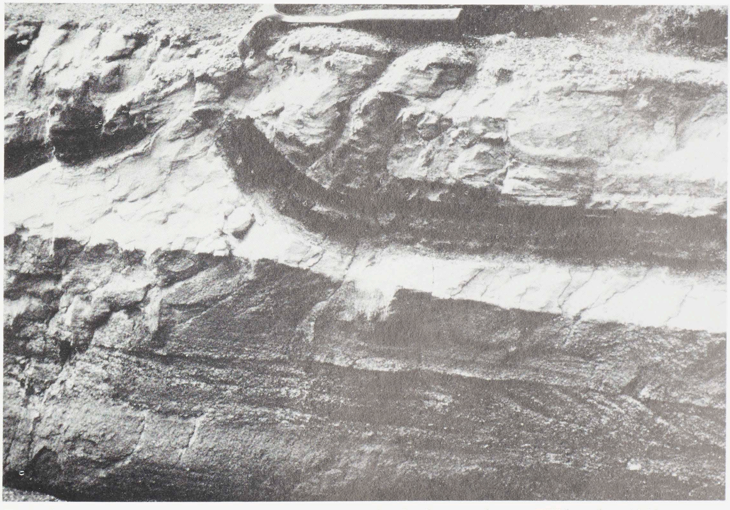
Although 11 species (or their very close descendants) still live in the eastern Pacific, six of these are no longer in the Esmeraldas area. Presumably the loss of the Caribbean current after closure of the seaway changed the temperature just enough that some of the species now do not extend as far south. The Ecuador-Peru border is essentially the boundary between the



Text-figure 10. Cut-bank on Rio Camarones; TU locality 1397.

Text-figure 11. Large blocks fallen from above; TU locality 1397.

Text-figure 12. Exposure in road-cut at mouth of Rio Camarones; TU locality 1398.



Text-figure 13. Detail of "escape structure" in beds shown above; TU locality 1398.

Tropical East Pacific and the cooler-water Peruvian Province. The mollusk fauna of Ecuador is at the southern extremity of the Tropical province and would be expected to show a diminution in numbers.*

As Jones and Hasson (1985, p. 350) have indicated, the question of how rapidly populations separated by a geographic barrier diverge is central to the process of speciation. Considering the large proportion of still living forms in the Pliocene Esmeraldas beds, it would seem that a longer period than just 3.5 million years was necessary to evolve the array of cognate species that are present in the Tropical Eastern Pacific Province as a whole. Thus, although the Atrato Strait was closed last, it seems probable that the majority of the elements were already in place before the Pliocene and were initially introduced farther north, probably in the Costa Rica region.

This is demonstrated by the *Murex messorius* complex, which by the Early Pliocene had already differentiated into *M. recurvirostris* and, presumably, the northern *M. lividus* and *M. tricoronis* as well. The form that has been called "*Murex elenensis*" in the Gulf of California is not that species and is here named *Murex ruthae*. It is this member of the lineage that occurs at Esmeraldas, suggesting that it is the ancestral form from which the living *M. elenensis* evolved.

But the most striking case is that of *Hexaplex ambiguus*. Although the shell cited under that name by Olsson (1964, p. 138, pl. 29, fig. 5) is not *H. ambiguus*, true *H. ambiguus* also occurs in the Esmeraldas beds. The origin of this species complex (*H. radix*, *nigritus*, and *ambiguus*) is obscure, and until now it was assumed to have been derived from *H. hertweckorum* (*H. fulvescens* of authors). Discovery of an example of *H. ambiguus* occurring with *H. hertweckorum* in the Esmeraldas beds casts doubt upon this idea. Regardless of the origin, presumably western Africa, the separation of the *H. hertweckorum*-*H. ambiguus* lines must have preceded the Esmeraldas fauna by considerable time. Again, the entry point for the *H. ambiguus* line was almost certainly the Costa Rica area. Today, *H. ambiguus* extends northward from Costa Rica to the Gulf of California, where *H. nigritus* occurs sympatrically in the northern portion of the range. Southward, it extends to Ecuador, but in the Bay of Panama it is found sympatrically with a local descendant, *H. radix*.

In the Recent fauna of Ecuador there are several muricid groups for which there is no known Esmeraldas equivalent. Some of this is an artifact of collecting, but the groups that have not been found represent ancient lines (*e.g.*, *Homalocantha*, *Favartia*, and *Purpurellus*), which occur in the Lower Miocene of the western Atlantic and which would have been presumed to have made the move into the Pacific earlier than some of the other groups. Although *Favartia* still lives in the Caribbean, both *Homalocantha* and *Purpurellus* no longer occur there but are still living in West Africa.

One final observation on the composition of the Tropical East Pacific muricid fauna is the inexplicable *lack* of certain groups that are well-represented in the Caribbean fauna. These include *Chicoreus* s.s., *Chicoreus (Siratus)*, *Pterynotus* s.s. and *Poirieria (Panamurex)*. These groups have numerous species in both the fossil and living Caribbean faunas, but for some reason never made the transition to the East Pacific Coast.

III. ACKNOWLEDGMENTS

This study has been in progress for a number of years, since our first visit to Esmeraldas in 1982, and has involved the reevaluation of a number of Recent species from both the western Atlantic and the eastern Pacific, in addition to the expected fossil species. As a result, the writer is indebted to an unusually large number of persons, from various institutions, including John Taylor and Kathie Way, of the Mollusca Section, British Museum (Natural History), for their kindness while work was being done at the Museum and subsequently; and Peter Jung, of the Naturhistorisches Museum, Basel, Switzerland, for the use of his Esmeraldas collections. For the loan of specimens she is

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*Of the 75 West Coast species of muricid listed by Keen (1971, pp. 514-524; excluding Galápagos endemics) only 22 are found in Ecuador. Of these, two are confined to the Ecuador-Peru area, the other 20 extend as far north as Mexico.

grateful to the late Joseph Rosewater, M.G. Harasewych, Thomas R. Waller, and Warren Blow, all of the United States National Museum of Natural History; James McLean and Gale Sphon, Los Angeles County Museum of Natural History; Peter R. Hoover, Paleontological Research Institution, Ithaca, New York; and Elana Benamy, Academy of Natural Science, Philadelphia. The late Ruth Purdy, San Diego, California, was always extremely generous with Mexican Recent material, much of which is figured herein. Other colleagues, who provided a variety of information concerning ages of formations, as well as location, etc., of type specimens, include: Roger Bristow, British Geological Survey, Exeter, England; W.H. Akers, formerly of Chevron USA, now retired, and Barry Kohl, also of Chevron USA, New Orleans; Robert H. Stewart, formerly of the Panama Canal Company, now retired; Ruth Turner and Ronald Eng, of the Harvard Museum of Comparative Zoology; Michael Kellogg, California Academy of Sciences; William K. Emerson, American Museum of Natural History, New York; Richard Preece, University Museum of Zoology, Cambridge; and Patrick Nuttall, British Museum (Natural History). Finally, William and Lois Pitt, Sacramento, California, deserve the greatest thanks of all, for locating the sites originally, collecting much of the material, and for being delightful field companions.

Abbreviations for Repository Institutions

ANSP - Academy of Natural Sciences, Philadelphia
BMNH - British Museum (Natural History)
CAS - California Academy of Sciences
LACM - Los Angeles County Museum of Natural History
NMB - Naturhistorisches Museum, Basel, Switzerland
PRI - Paleontological Research Institution
UCMP - University of California, Berkeley, Museum of Paleontology
USNM - United States National Museum of Natural History

IV. SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Order NEOGASTROPODA
Superfamily MURICACEA
Family MURICIDAE Rafinesque, 1815
Subfamily MURICINAE Rafinesque, 1815
Genus MUREX Linnaeus, 1758

Murex LINNAEUS, 1758, Syst. Nat., ed. 10, p. 746.

Type species: *Murex tribulus* Linn., 1758, by subsequent desig., Montfort, 1810.

Subgenus HAUSTELLUM Schumacher, 1817

Haustellum SCHUMACHER, 1817, Essai Nouv. Syst. Vers Test., p. 213.

Type species: *Murex haustellum* Linn., 1758, by tautonomy.

MUREX (HAUSTELLUM) RECURVIROSTRIS Broderip

Plate 1, figs. 1, 2

Murex recurvirostris BRODERIP, 1833, Zool. Soc. London, Proc., pt. 2, p. 174; SOWERBY, 1834, Conch. Illus., *Murex*, pl. 59, fig. 9; REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 19, fig. 75; SOWERBY, 1879, Thes. Conch., v. 4, *Murex*, fig. 16; TRYON, 1880, Man. Conch., v. 2, p. 80 (in part), pl. 11, fig. 193 only; OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, pp. 163, 171; KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 352, fig. 336; KEEN, 1971, *ibid.*, ed. 2, p. 514, fig. 976; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 70, pl. 11, fig. 11; FAIR, 1976, *Murex* Book, p. 71, pl. 3, fig. 28; D'ATTILIO and HERTZ, 1979, Festivus, v. 11, no. 8, p. 61, figs. 3, 5; not fig. 6 (= *M. lividus* Carpenter).

Murex (Murex) recurvirostris Broderip. HERTLEIN and STRONG, 1955, Amer. Mus. Nat. Hist., Bull., v. 107, Art. 2, p. 252.

Murex (Haustellum) recurvirostris Broderip. VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 210, back cover color photo.

INCORRECT REFERENCES TO *M. recurvirostris:*

Murex recurvirostris Broderip. GABB, 1873, Amer. Phil. Soc., Trans., (N.S.) v. 15, pt. 1, p. 201; PILSBRY, 1922, Acad. Nat. Sci. Phila., Proc., v. 73, p. 353 (Baitoa, Cercado, and Gurabo formations, Dominican Republic = *M. messorius* Sowerby).

Murex recurvirostris Broderip. GABB, 1881, Acad. Nat. Sci. Phila., Jour., (Ser. 2) v. 8, pt. 4, p. 349 (Moín Formation, Costa Rica = *M. olssoni* Vokes).

Murex recurvirostris Broderip. BAKER 1890, Acad. Nat. Sci. Phila., Proc., v. 42, p. 70, fig. 9 (protoconch); M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 2 (in part), pl. 1, fig. 2 (Recent, "Dominican Republic"), text-fig. k (after Baker, 1890) (= *M. rectirostris* Sowerby).

Murex (Murex) recurvirostris Broderip. WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 288, pl. 17, figs. 7, 8 (Bowden Formation, Jamaica = *Chicoreus (Siratus) formosus* Sowerby).

Murex recurvirostris Broderip. RUTSCH, 1934, Schweizer. Paleont. Gesell., Abh., v. 54, no. 3, p. 64, pl. 4, fig. 1; v. 55, no. 1, p. 136 (Pta. Gavilan Formation, Venezuela = *M. donmoorei* Bullis).

Murex recurvirostris Broderip. WOODRING *in* DURHAM, *et al.*, 1955, Geol. Soc. Amer., Bull., v. 66, p. 984 ("Coatzacoalcos Formation," Mexico = *M. messorius* Sowerby).

Murex recurvirostris Sowerby *[sic]*. KAICHER, 1957, Indo-Pacific Sea Shells, Muricacea, Buccinacea, pl. 2, fig. 6 (Recent, China, Japan = *M. rectirostris* Sowerby).

Murex (Murex) recurvirostris recurvirostris Broderip. WOODRING, 1959, U.S. Geol. Surv., Prof. Paper 306-B, p. 214, pl. 35, figs. 5, 8; pl. 36, figs. 11, 12 (Gatun Formation, Panama = *M. messorius* Sowerby).

Murex (Murex) recurvirostris Broderip. PERRILLIAT MONTOYA, 1960, Paleontologia Mex., no. 8, p. 21, pl. 3, figs. 10, 11 (Agueguexquite Formation, Mexico = *M. bellegladeensis* Vokes).

Murex (Murex) recurvirostris recurvirostris Broderip. WEISBORD, 1962, Bulls. Amer. Paleontology, v. 42, no. 193, p. 278, pl. 26, figs. 3, 4 (Mare Formation, Venezuela = *M. donmoorei* Bullis).

Murex (Murex) recurvirostris recurvirostris Broderip. PERRILLIAT [MONTOYA], 1972, Paleontologia Mex., no. 32, p. 79, pl. 39, figs. 5-9 ("Santa Rosa beds," Mexico = *Chicoreus (Siratus)* sp. or spp.)

Lectotype: BMNH 1964347 (here designated); height 55 mm, diameter 26 mm. (This is the specimen figured by Sowerby, 1834, pl. 59, fig. 9. According to Broderip, 1833, p. 174, the type is "long. 3, lat. 1 6/8 poll." or 76 mm in height and

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PLATE 1

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1, 2. *Murex (Haustellum) recurvirostris* Broderip 13
  1. (X 1 1/2) USNM 418037; height 30.8 mm, diameter 23.7 mm.
     Locality: TU 1399; Esmeraldas beds, Ecuador.
  2. (X 1 1/2) USNM 859918; height 39.8 mm, diameter 21.3 mm.
     Locality: TU R-186; Palo Seco, Panama; Recent.

3. *Murex (Haustellum) messorius* Sowerby 16
   (X 1 1/4) USNM 859919; height 54.4 mm, diameter (including spines) 27.8 mm.
   Locality: TU R-109; Bahia de las Minas, Panama (Atlantic); Recent.

4, 5. *Murex (?Haustellum) ruthae* E. H. Vokes, n. sp. 18
  4. (X 1 1/4) USNM 859920 (paratype B); height 47.6 mm, diameter (including spines) 24.3 mm.
     Locality: Off Guaymas, Sonora, Mexico; Recent.
  5. (X 1 1/4) USNM 418038 (paratype C); height (incomplete) 24.7 mm, diameter 22.0 mm.
     Locality: TU 1397; Esmeraldas beds, Ecuador.

6. *Murex (Haustellum) polynematicus* Brown and Pilsbry 17
   (X 1 1/4) UCMP 38138; height 44.6 mm, diameter 27.6 mm.
   Locality: Unnamed formation; Dept. of Nariño, Colombia.

7, 8. *Hexaplex hertweckorum* Petuch 24
  7. (X 1) USNM 645613; height 64.0 mm, diameter 43.5 mm.
     Locality: TU 797; Pinecrest beds, Florida.
  8. (X 1) USNM 643954; height 67.0 mm, diameter 45.0 mm.
     Locality: Punta Gorda; Esmeraldas beds, Ecuador.

9. (X 1/2) *Hexaplex duplex* (Röding) 25
   Vokes Coll.; height 125 mm, diameter 93 mm.
   Locality: Off Dakar, Senegal; Recent.

10, 11. *Hexaplex ambiguus* (Reeve) 25
  10. (X 3/4) USNM 859921; height 70.4 mm, diameter 64.0 mm.
      Locality: TU R-173; Puntarenas, Costa Rica; Recent.
  11. (X 1/2) USNM 418039; height (incomplete) 52.0 mm, diameter 63.5 mm.
      Locality: TU 1399; Esmeraldas beds, Ecuador.

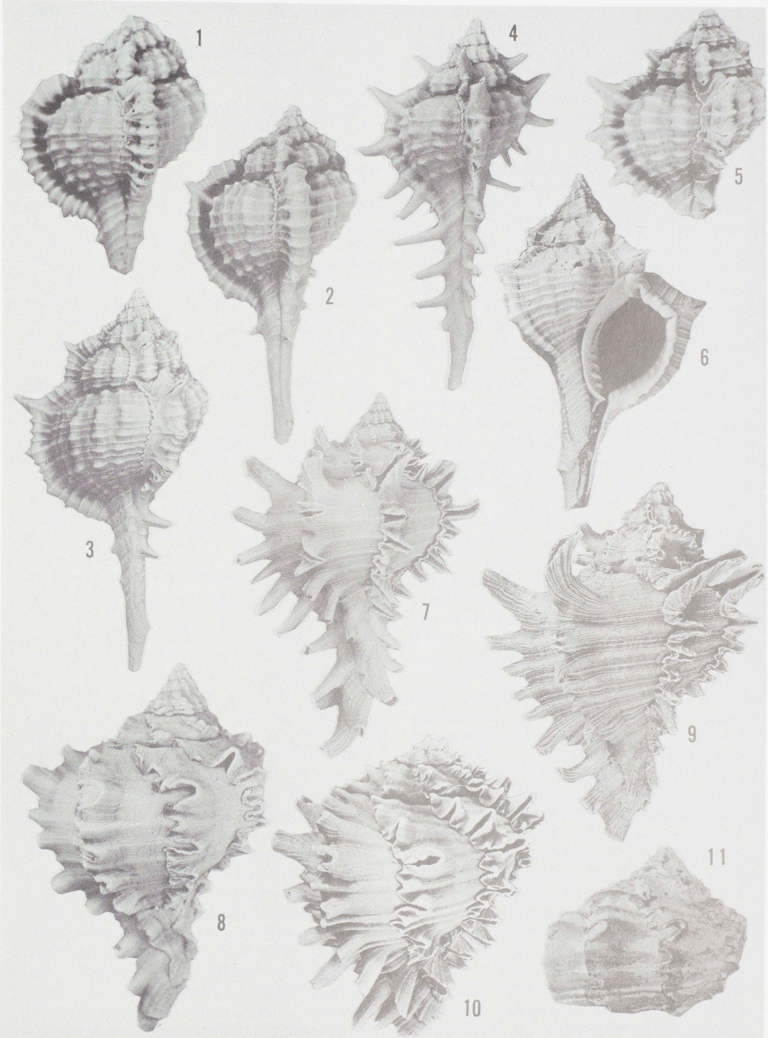

PLATE 1

44 mm in diameter. This is obviously a mistake, as one "poll." equals one inch and other measurements in the same paper agree with this interpretation. The largest specimen of *M. recurvirostris* seen by this writer is only 66 mm in height.)

Type locality: Gulf of Nicoya, Costa Rica.

Occurrence: Esmeraldas beds, Ecuador. Pleistocene, Panama. Recent, southern Mexico to Ecuador.

Figured specimens: Fig. 1, USNM 418037; height 30.8 mm, diameter 23.7 mm; locality TU 1399. Fig. 2, USNM 859918; height 39.8 mm, diameter 21.3 mm; locality TU R-186.

Discussion: Because *M. recurvirostris* was the first species of its group to be described from the New World there has been a tendency to use the name for every "*Murex*" species that occurs in the area, from Miocene to Recent, Atlantic or Pacific. Although Gabb (1873, 1881) was the first offender, the true culprit was Tryon (1880, p. 81) who included in synonymy: *M. messorius* Sowerby, 1841, with its synonyms, *M. funiculatus* Reeve, 1845, and *M. nigrescens* Sowerby, 1841, from the western Atlantic; *M. lividus* Carpenter, 1857, from the eastern Pacific; *M rectirostris* Sowerby, 1841, from the Indo-Pacific; and *Chicoreus (Siratus) articulatus* Reeve, 1845, (as "*motacilla* Sowerby") with its synonyms, *C. nodatus* (Reeve, 1845) and *C. antillarum* (Hinds, 1844) as well as *C. (S.) similis* (Sowerby, 1841) all from the western Atlantic.

It is little wonder that subsequent workers have been confused, as seen from the extended synonymy of *erroneus* references to *M. recurvirostris*. Among its eastern Pacific congeners, *M. recurvirostris* may be distinguished by the strong rugae on the inner lip, a trait not found in any other eastern Pacific species, nor in *M. rectirostris*, from the Indo-Pacific.

Atlantic species that have been included in synonymy are: *M. messorius; M. olssoni* Vokes, 1967; *M. donmoorei*, Bullis, 1964; and *M. bellegladeensis* Vokes, 1963. The latter lacks the labial rugae; the first three do have these rugae but both *M. olssoni* and *M. donmoorei* are much more spinose than *M. recurvirostris*. Only *M. messorius* is actually very close, and it may be distinguished by the lack of the deeply excavated varices characteristic of *M. recurvirostris*. In summary: *M. recurvirostris* has labial rugae, deeply excavated varices, and almost no spines; *M. messorius* has rugae and few spines, but no excavated varices; *M. olssoni* and *M. donmoorei* have rugae, many spines and no excavated varices; *M. bellegladeensis, M. lividus*, and *M. rectirostris* do not have labial rugae.

The ancestral form of this species-complex is the Atlantic *M. messorius*, which first appears in the Early Miocene Baitoa Formation, Dominican Republic. This species must have moved into the eastern Pacific relatively early, for the shell that occurs in the Esmeraldas beds is unequivocally referable to *M. recurvirostris* and not to *M. messorius* (*cf.* pl. 1, fig. 1, with figs. 2 and 3 - *recurvirostris* and *messorius*, respectively). The eastern Pacific species *M. lividus* is morphologically similar to the ancestral line, but lacks the labial rugae. The subspecies *M. lividus tricoronis* Berry, 1960, a more spinose form, also lacks the labial rugae. The latter two taxa are apparently confined to the Baja California and Gulf of California region; however, there are specimens from the Panama-Costa Rica area that are very similar to *M. lividus* or even *tricoronis*, in that they have spines, weakly excavated varices, and marked red spiral lines, but they retain the labial rugae. In fact, except for the red spiral lines, they are almost indistinguishable from the spinose forms of *M. messorius* that occur off Atlantic Panama (see Vokes, 1967a, pl. 2, especially fig. 6). The same form occurs in the Pleistocene Charco Azul Formation (TU 1499), suggesting that these atavists represent the remnants of the ancestral *messorius* line still surviving in the Panama region, as the original point of entry. From this species have evolved the northern *M. lividus* and *tricoronis*, losing the rugae, and *M. recurvirostris*, which has developed excavated varices.

In the collections from Esmeraldas, *M. recurvirostris* is not common, as we have a half-dozen, mostly broken, specimens. The species lives today in very shallow water (intertidal to about 7 m) and is interpreted as one of the transported members of the Esmeraldas fauna. Pilsbry and Olsson (1941) did not report this species from the Jama Formation, but Olsson did list it from the Charco Azul (1942b, p. 171) and Armuellas (*ibid.*, p. 163) formations of the Burica Peninsula. We have a number of specimens from the Charco Azul, where they occur together with the above-mentioned forms of *M.* cf. *messorius*, in beds that also represent gravity-flows of shallower material into deep-water beds.

MUREX (HAUSTELLUM) POLYNEMATICUS
Brown and Pilsbry
Plate 1, fig. 6

Murex (Murex) polynematicus BROWN and PILSBRY, 1911, Acad. Nat. Sci. Phila., Proc., v. 63, p. 353, pl. 26, fig. 1; OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 137, pl. 29, figs. 2, 2a.

Murex (Murex?) polynematicus Brown and Pilsbry. WOODRING, 1959, U.S. Geol. Surv., Prof. Paper 306-B, p. 215, pl. 36, figs. 2, 3; pl. 37, figs. 6,9.

Murex (Murex) gilli polynematicus Brown and Pilsbry. VOKES, 1963, Tulane Stud. Geol., v. 1, no. 3, p. 101, pl. 2, fig. 5.

Murex messorius Sowerby. VOKES, 1963, Tulane Stud. Geol., v. 1, no. 3, pl. 3, fig. 8 only (*not* of Sowerby).

Chicoreus (Siratus) gilli polynematicus (Brown and Pilsbry). VOKES, 1965, Tulane Stud. Geol., v. 3, no. 4, p. 183.

Not *Murex (Murex) polynematicus* Brown and Pilsbry. JUNG, 1965, Bulls. Amer. Paleontology, v. 49, no. 223, p. 520, pl. 69, fig. 6 (=*M. gilli* Maury).

Holotype: ANSP 1719; height 54.5 mm, diameter 33.7 mm.

Type locality: Gatun Formation; Gatun Locks, Panama.

Occurrence: Angostura Formation and Esmeraldas beds, Ecuador. Gatun Formation, Panama; unnamed formation, Nariño, Colombia; Pliocene.

Figured specimen: UCMP 38138; height 44.6 mm, diameter 27.6 mm; locality, Rio San Luis, 10 km south of confluence with the Rio Iseuande, Dept. of Nariño, Colombia.

Discussion: In 1963 the writer suggested that *M. gilli* (Maury, 1910) was so similar to *M. polynematicus* that the two could be separated only at the subspecific level. Since then she has examined much more material and has determined that *M. polynematicus* is a much larger species, with a lower spire and a smaller aperture than *M. gilli*, and there is a tendency toward a secondary varical spine at the periphery in *M. polynematicus*. These distinguishing features are readily apparent in the example figured by Jung (1965, pl. 69, fig. 6) from the Cantaure Formation of Venezuela, which is correlative with the Early Miocene Chipola Formation of Florida and not the Pliocene Gatun Formation, as he thought at the time. The Venezuelan specimen is better referred to *M. gilli*, in spite of the geographic proximity to *M. polynematicus*.

Woodring (1959, p. 214) stated that a specimen of what he termed "*Murex recurvirostris*" from the middle Gatun Formation had a protoconch of two and three-quarter whorls. It was this specimen (USNM 643766) that was figured by the writer as the protoconch of *M. messorius* (Vokes, 1963, pl. 3, fig. 8). Additional material has demonstrated that this shell is actually *M. polynematicus; M. messorius* has the one and one-half whorl protoconch Woodring attributed to the specimen of "*M. recurvirostris*" from the upper part of the Gatun Formation.

Both *M. messorius* and *M. polynematicus* occur in the Gatun Formation, although *M. messorius* is always less common than *M. polynematicus*. Thus, it was surprising to find in the Esmeraldas beds *M. polynematicus* with *M. recurvirostris* instead of *M. messorius*.

Given the very common occurrence of *M. polynematicus* in Panama (we have over 300 specimens from 6 localities: TU 757, 958, 961, 1431, 1432, 1433), one would expect that the species would still be living in the Caribbean, as most of its contemporaries are. But the line seems to be extinct. The nearest species is the Venezuelan *M. chrysostoma* Sowerby, 1834, which is also a member of the group of *M. gilli-polynematicus*, but which has been a separate species for at least as long as *M. polynematicus*. In the collections of the Museum of Paleontology, University of California, Berkeley, there are numerous Pliocene examples of *M. chrysostoma* from Isla Margarita, Venezuela.

The generic placement of this species has been a problem to the writer. Originally assigned to *Murex* s.s. (Vokes, 1963), it obviously does not belong there. Later (Vokes, 1965), all of the species assigned in 1963 to *Murex* s.s., which had deflected canals, were transferred to *Chicoreus (Siratus)*. This left *M. gilli* and *M. polynematicus* in an awkward position, as they do not fit readily with either group. Since that time, the writer has worked extensively on the Indo-Pacific members of

Murex s.s. and, as a result (Ponder and Vokes, 1988), has come to the conclusion that *all* New World species formerly attributed to *Murex* s.s. are better placed in *Haustellum*. This removes the difficulties encountered with *M. gilli* and *M. polynematicus*, as they, of all the species involved, are the most closely akin to the type of *Haustellum (M. haustellum* Linnaeus). Unfortunately, it creates even more serious problems in the case of *M. cabritii* and *M. elenensis*, which must result from convergence of the New and Old World lines.

In the Esmeraldas collection, we have but one fragment of *M. polynematicus*, but the surface ornamentation is so characteristic there is no hesitation is assigning it to this species. The form was reported by Olsson from the type area of the Angostura Formation on the Rio Santiago and we have collected several examples of the species in the Angostura beds at Punta Verde (TU 1507), 20 km north-east of Rio Camarones. In the collections of the Berkeley Museum of Paleontology, there are several examples from Nariño, southern Colombia (see pl. 1, fig. 6) that are also referable to this species. This is a common form in the shallow-water Gatun Formation of Panama and is another of the transported members of the Esmeraldas fauna.

MUREX (?HAUSTELLUM) RUTHAE
E. H. Vokes, n. sp.

Plate 1, figs. 4, 5; Plate 2, figs. 1, 2.

Murex plicatus Sowerby. CARPENTER, 1857, Cat. Mazatlan, p. 518 (*not* of Sowerby).

Murex elenensis Dall. DURHAM, 1950, Geol. Soc. Amer., Mem. 43, p. 111, pl. 35, fig. 8; M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 2, pl. 4, fig. 2 (not fig. 12, as stated); KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 351, fig. 335; KEEN, 1971, *ibid.*, ed. 2, p. 514, fig. 975; DUSHANE and POORMAN, 1967, Veliger, v. 9, p. 428; DUSHANE and SPHON, 1968, Veliger, v. 10, p. 242; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 66 (in part), pl. 11, fig. 13 only (not pl. 13, fig. 1 = *M. tricoronis* Berry); FAIR, 1976, *Murex* Book, p. 39, pl. 3, fig. 3; D'ATTILIO and HERTZ, 1979, Festivus, v. 11, no. 8, p. 60 (in part), fig. 1 (not fig. 4 = *M. elenensis* Dall) (*not* of Dall).

Murex sp. cf. *elenensis* Dall. VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 210, note 3.

Description: Shell with eight adult whorls, plus a protoconch of one and one-half rounded whorls, ending at a small, sharp, varix. Axial ornamentation on first three teleoconch whorls of nine or ten rounded ridges; by third or fourth teleoconch whorl every third ridge developed into a spined varix, three varices to each whorl, with the two intervening ridges remaining as intervarical nodes. Spiral ornamentation beginning with three equal cords, gradually adding alternate minor threads. On body whorl, six low rounded cords, all of approximately the same strength, alternating with smaller threads. Where the spiral cords cross the varices, spines produced; that at the shoulder the strongest, a slightly weaker one at the periphery, and two smaller ones between periphery and base of the body whorl. In addition, anterior to the two stronger spines, the two remaining spiral cords give rise to small spinelets. In young specimens varical spines nearly perpendicular to shell axis, but with increasing age these spines tend to bend forward and diminish in size, especially that at the periphery, until the shoulder spine and the anterior-most spine on the body whorl are the longest, with those between them greatly reduced. Aperture oval, inner lip smooth,

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PLATE 2

Figures Page

1, 2. *Murex (?Haustellum) ruthae* E. H. Vokes, n. sp. 18
   1. (X 1) USNM 859922 (holotype); height 81.0 mm, diameter 37.2 mm.
      Locality: Off Guaymas, Sonora, Mexico; Recent.
   2. (Fig. 2a, X 1 1/4; fig. 2b, X 10) LACM 2247 (paratype A); height 34.9 mm, diameter 16.6 mm.
      Locality: Between Loreto and Carmen Island, Baja California Sur, Mexico; Recent.

3, 4. *Murex (?Haustellum) elenensis* Dall 20
   3. (X 1 1/4) USNM 859923; height 55.7 mm, diameter 29.5 mm.
      Locality: TU R-478; Puerto de Cayo, Ecuador; Recent.
   4. (X 1) BMNH 1964-351 (lectotype-*M. plicatus* Sowerby); height 80.0 mm, diameter (including spines) 42.8 mm.
      Locality: Gulf of Nicoya, Costa Rica; Recent.

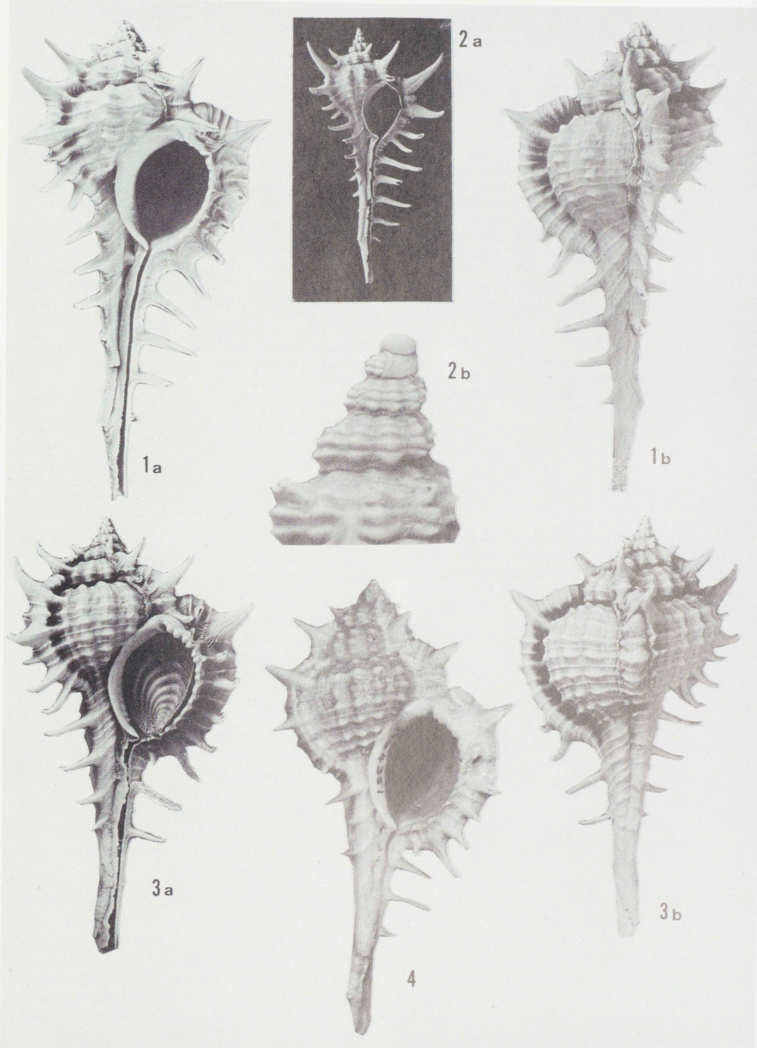

PLATE 2

free-standing anteriorly, appressed at posteriormost portion only. Outer lip crenulated along margin, otherwise smooth, except for a pair of nodes at posterior end, giving rise to a small anal notch. Siphonal canal long, straight, only slightly deflected at distal end; former canals fused into a tube, open by a narrow slit; ornamented by three rows of long spines, usually four in each row, rarely three or five. Color beige, with diffuse darker bands at the shoulder and base of the body whorl; rarely a third band at the periphery. Spiral cords topped with golden lines. Aperture white except for the darker bands showing through. Operculum reddish-brown, typically muricoid, with a terminal nucleus.

Holotype: USNM 859922; height 81.0 m, diameter 37.2 mm; locality, off Guaymas, Sonora, Mexico (shrimpers). (Plate 2, fig. 1)

Paratype A: LACM 2247; height 34.9 mm; diameter 16.6 mm; locality 27-45 m, channel between Loreto and Carmen Island, Baja California Sur, Mexico (Ariel Expedition, 29 August 1960). (Plate 2, fig. 2)

Paratype B: USNM 859920; height 47.6 mm, diameter 24.5 mm; locality, off Guaymas, Sonora, Mexico (shrimpers). (Plate, 1, fig. 4)

Paratype C: USNM 418038; height (incomplete) 24.7 mm, diameter 22.0 mm; locality TU 1397. (Plate 1, fig. 5)

Type locality: Channel between Loreto and Carmen Island, Baja California Sur, Mexico (locality of paratype A; the only one with certain locality data, most examples come from shrimpers and data are consequently rather vague. See ICZN Code art. 72(h)i.)

Occurrence: Esmeraldas beds, Ecuador. Pleistocene and Recent, Gulf of California only?

Discussion: The Gulf of California species that has universally been referred to *M. elenensis* Dall, 1909 (n. n. pro *M. plicatus* Sowerby, 1834, *non* Gmelin, 1791, etc.) is not the same as the typical form, which comes from Ecuador (Sta. Elena Bay – type locality of *M. elenensis*) to as far north as the Gulf of Nicoya (type locality of *M. plicatus*). This northern form is here named *M. ruthae* in honor of the late Ruth (Mrs. Ben) Purdy, who was always extremely generous with specimens and who contributed most of the material figured here. Comparison of the two forms shows that the Gulf of California species is larger, heavier, with a coarser sculpture. There are usually two (rarely three) intervarical nodes, in contrast to the three or four of *M. elenensis*, and the varices of the California shell are much less deeply excavated abaperturally. The spines of *M. ruthae* are longer, heavier, straighter, and extend farther down the siphonal canal.

Radwin and D'Attilio (1976, p. 66) included in the synonymy of "*Murex elenensis*," by which name they treated *M. ruthae*, both *M. lividus* Carpenter and *M. tricoronis* Berry. The principal similarity in the three forms is color: *M. lividus* has the diffuse dark bands of *M. ruthae* (lacking in true *M. elenensis); M. tricoronis* lacks the dark bands but has the gold-topped spiral cords. However, *M. lividus* has only short spines; *M. tricoronis* is more spinose but still has only one or two short spines on the siphonal canal, in contrast to the usually four of *M. ruthae*, as may be seen by comparing the illustrations in Radwin and D'Attilio (pl. 11, fig. 13 = *M. ruthae;* pl. 13, fig. 1 = *M. lividus tricoronis*).

This new species appears to be confined to the Gulf of California, usually in depths of 5 to 10 meters, and is taken mostly by shrimpers. The habitat of *M. elenensis* is essentially the same, but the species, so far as is known, does not get north of the Gulf of Nicoya, Costa Rica. Thus, it was a great surprise to find the Gulf of California species in the Esmeraldas beds, rather than the present day Ecuadorian form. In the collection from Esmeraldas, we have only two broken examples, but they lack the deeply excavated varices and "crisp" intervarical nodes of *M. elenensis* (*cf.* pl. 2, fig. 3b). It is assumed that *M. ruthae* is the ancestral form, which has now retreated to the Gulf of California, perhaps due to the warmer water there. If the presence of deeply excavated varices is parallel in *M. recurvirostris* and *M. elenensis* (which is by no means certain) then the non-excavated *M. messorius* and *M. ruthae* would represent the more "primitive" condition and the excavated forms the more "advanced."

Unfortunately, there is little fossil record for the New World *Murex* species-group with spinose canals. *Murex elenensis* occurs in the Pleistocene Charco Azul Formation of Panama (TU 1499). In the western Atlantic the cognate of *M. elenensis* is *M. cabritii* Bernardi, 1859. The only fossil occurrence of the latter is in the Pleistocene Moín Formation of Costa Rica (TU localitites 953, 954, 1240, and 1307).

Likewise, *M. ruthae* has been reported from the Pleistocene of Baja California (Durham, 1950, p. 111, pl. 35, fig. 8, as *M. elenensis* Dall, from Sta. Inez Bay). The occurrence in the Esmeraldas beds pushes the line back to the Early Pliocene but obviously the group has a much older history. It is assumed that these American spinose species are independently derived from the *M. messorius* stock and resemble the true *Murex* s.s. members of the Indo-Pacific region only as a result of convergence.

The presence of only these two incomplete examples in the Esmeraldas beds, together with the shallow habitat of the living forms, indicates this is another of the transported specimens in the fauna. The occurrence of this same form in the Gulf of California, together with the other species that are also confined to the area north of Panama today, suggests that the shallow water, at least, was probably warmer during Esmeraldas time than it is now.

Genus CHICOREUS Montfort, 1810

Chicoreus MONTFORT, 1810, Conchyl. Syst., v. 2, p. 611.

Type species: *Murex ramosus* Linn., 1758, by original desig.

Subgenus PHYLLONOTUS Swainson, 1833

Phyllonotus SWAINSON, 1833, Zool. Illus., (2) v. 3, expl. to pl. 100.

Type species: *Murex imperialis* var. *a* Swainson, 1833, by subsequent desig., Swainson, 1833 (*M. imperialis* var. *a* Swainson = *M. imperialis* Swainson, 1831, *non M. imperialis* Fischer, 1807 = *M. margaritensis* Abbott, 1958).

CHICOREUS (PHYLLONOTUS) GLOBOSUS (Emmons)

Plate 3, figs. 1, 2

Murex globosa EMMONS, 1858, Rept., North Carolina Geol. Surv., p. 247, fig. 105A.

Murex (Phyllonotus) pomum Gmelin. GARDNER, 1948, U.S. Geol. Surv., Prof. Paper 199, p. 219 (in part), pl. 29, figs. 22, 24; OLSSON and HARBISON, 1953, Acad. Nat. Sci. Phila., Mon. 8, p. 234 (in part), pl. 34, fig. 1 (*not* of Gmelin).

Phyllonotus globosus (Emmons). OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, p. 549, pl. 82, fig. 2; FAIR, 1976, *Murex* Book, p. 46, pl. 9, fig. 120; PETUCH, 1976, Veliger, v. 18, p. 325, text-figs. 3, 5, 6.

Chicoreus (Phyllonotus) globosus (Emmons). VOKES, 1967, Tulane Stud. Geol., v. 5, no. 3, p. 148, pl. 4, figs. 1-3; pl. 5, figs. 1-3 (see for additional references for the species in western Atlantic); VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 212, front cover color photo.

Phyllonotus cf. *globosus* (Emmons). PETUCH, 1987, New Caribbean Moll. faunas, p. 89, pl. 19, figs. 1, 2.

Holotype: not found.

Type locality: Waccamaw Formation; Cape Fear River (probably Neils Eddy Landing), Columbus County, North Carolina.

Occurrence: Esmeraldas beds, Ecuador. Pinecrest beds and Caloosahatchee Formation, Florida; Waccamaw Formation, North and South Carolina; ? Imperial Formation, California; Pliocene. Recent, Venezuela.

Figured specimens: Fig. 1, USNM 418040; height (incomplete) 29.0 mm, diameter (incomplete) 22.1 mm; locality TU 1397. Fig. 2, USNM 418041; height 45.3 mm, diameter 27.4 mm; locality TU 768.

Discussion: On the basis of the three fragmentary specimens we have of this species, it is presumed to be *C. globosus;* however, the possibility exists that it might be *C. pomum* (Gmelin, 1791). At this small size the two forms are difficult to distinguish, especially when as poorly preserved as the material at hand. They are definitely not the Recent eastern Pacific *C. peratus* (Keen, 1960), the cognate of *C. pomum*, as the Esmeraldas fragments clearly show no anal notch, no sharply pointed intervarical nodes and lack the shagreened surface of *C. peratus*.

Whether the fragments are referred to *C. globosus* or *C. pomum*, the implications are the same, as both are Caribbean species. The ancestor to both *C. pomum* and *C. peratus* is an undescribed species in the Dominican Republic, which has the body shape of *C. pomum* but the protoconch of *C. peratus*. It is unknown if it is also ancestral to *C. globosus*, but as there is not really any other contender we will assume that it is, as well as being ancestral to the other *Phyllonotus* species living on the West Coast: *C. regius* (Swainson, 1821) and *C. erythrostomus* (Swainson, 1831). (For a comparison of the various species the reader is referred to Vokes, 1984).

In the Pliocene beds of southern Florida *C. globosus* is a common species but today it is confined to the northern coast of Venezuela in shallow water (about 5 m). It is closely related to the similar *C. margaritensis* (Abbott, 1958) type of the subgenus, but differs from the latter in having only three or four varices in contrast to the five of *C. margaritensis;* it is also a lighter shell, with a higher spire. The more wide-spread *C. pomum* always has three varices and a relatively heavier shell.

CHICOREUS (PHYLLONOTUS) sp.
Plate 3, fig. 5

Figured specimen: USNM 418043; maximum diameter (as is) 29.0 mm; locality TU 1397.

Discussion: A single battered incomplete specimen from Quebrada Camarones is unlike any known species, bearing only a generic resemblance to the members of *Phyllonotus*. Undoubtedly, this is partly a result of the incomplete condition of the shell. But it is possible to see that, although the earliest whorls have been broken away and plugged by the animal in life, on the first whorls present the shell has a dozen axial nodes per whorl. By analogy with *C. erythrostomus*, to which it seems the most nearly related, this means that all of the earlier teleoconch whorls, three or four in number, were ornamented by twelve equal axial ridges and on the (probably) fifth post-nuclear whorl these began to develop into small varices, with three varices per whorl and two intervarical nodes between each pair.

This differs from *C. erythrostomus*, which develops four varices per whorl, with one node between each pair, and which also has a strong sharp spine at the shoulder of each varix. The varices in the fragment show no evidence of any spines but just raised welts where the spiral cords cross over. However, these two species have the same type of strongly projecting intervarical nodes, unlike those of the other three-varixed members of the group, such as *C. globosus*, *C. pomum* and *C. peratus*. The spire in the fragment is also lower than any of the known forms, only *C. erythrostomus* approaching the extremely inflated whorls of the Esmeraldas shell.

Genus HEXAPLEX Perry, 1810

Hexaplex PERRY, 1810, Arcana, expl. to pl. 23 (genus without species); 1811, Conchology, pl. 8.

Type species: *Hexaplex foliacea* Perry, 1811, by subsequent desig., Iredale, 1915 (= *Murex cichoreum* Gmelin, 1791).

PLATE 3

Figures — Page

1, 2. *Chicoreus (Phyllonotus) globosus* (Emmons) 21
  1. (X 1 1/2) USNM 418040; height (incomplete) 29.0 mm, diameter (incomplete) 22.1 mm.
     Locality: TU 1397; Esmeraldas beds, Ecuador.
  2. (X 3/4) USNM 418041; height 45.3 mm, diameter 27.4 mm.
     Locality: TU 768; Caloosahatchee Fm., Florida.

3, 4. *Hexaplex brassica* (Lamarck) 28
  3. (X 3/4) ANSP 15205; height 89.0 mm, diameter (including spines) 74.6 mm.
     Locality: Puerto Jama; Jama Fm., Ecuador.
  4. (X 1 1/2) USNM 418042; length (as is) 25.0 mm, width (as is) 13.0 mm.
     Locality: TU 1399; Esmeraldas beds, Ecuador.

5. *Chicoreus (Phyllonotus)* sp. 22
   (X 1 1/2) USNM 418043; maximum diameter (as is) 29.0 mm.
   Locality: TU 1397; Esmeraldas beds, Ecuador.

6, 7. *Acanthotrophon sorenseni* (Hertlein and Strong) 38
  6. (X 2) USNM 418044; height 27.7 mm, diameter 18.1 mm.
     Locality: TU 1399; Esmeraldas beds, Ecuador.
  7. (X 1 1/2) CAS 9611 (holotype); height 32.2 mm, diameter (including spines) 20.0 mm.
     Locality: Off Cabo San Lucas, Baja California Sur, Mexico; Recent.

8. *Acanthotrophon panamensis* (Olsson) 38
   (X 1 1/2) USNM 701162 (holotype); height 32.0 mm, diameter (including spines) 25.3 mm.
   Locality: Bay of Panama, Panama, 84 m; Recent.

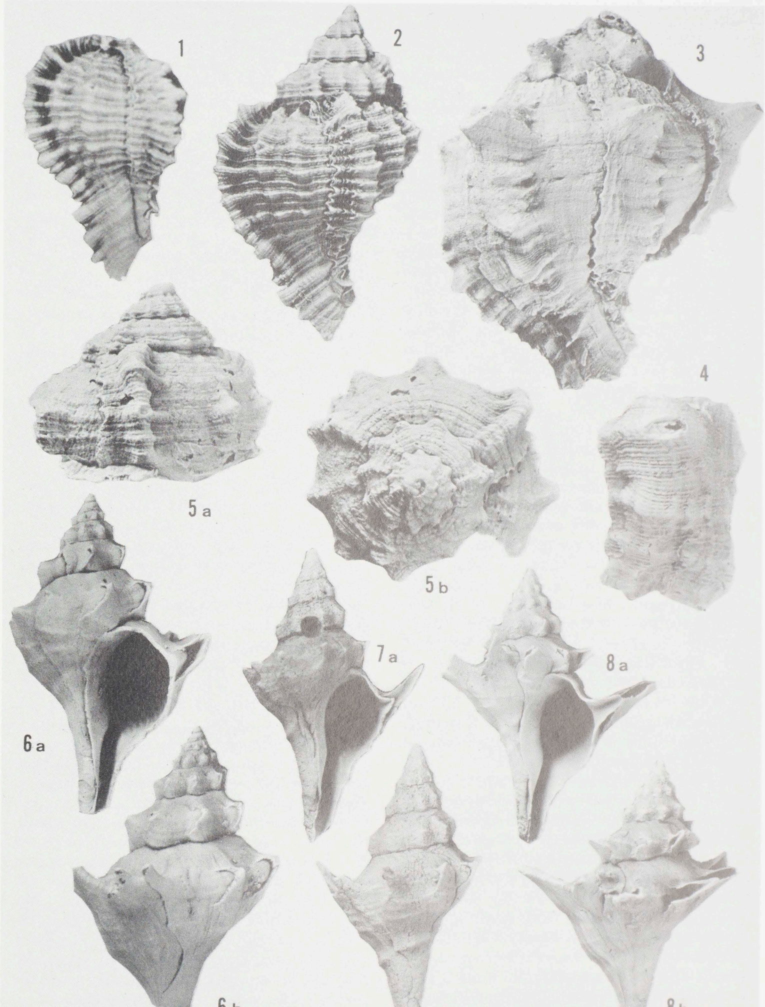

PLATE 3

Muricanthus SWAINSON, 1840, Treatise on Malacology, p. 296. New name for *Centronotus* Swainson, 1833, non Schneider, 1801 (Pisces).

Type species: *Murex radix* Gmelin, 1791, by subsequent desig., ICZN Opinion 911, 1970.

Discussion: The question of the validity of the subgenus *Muricanthus* is one that persists, as well as which species are to be included therein. Radwin and D'Attilio (1976, p. 75) included in *Muricanthus* several West African forms, as well as the New World forms usually placed herein. These authors, in fact, place only the type of *Hexaplex (H. cichoreum)* and *H. stainforthi* (Reeve, 1843) in *Hexaplex*, dividing the other possible members into various genera, especially *Phyllonotus*, although they give no reasons for the generic distinctions or rationale for which is placed where.

To this writer, if the taxon *Muricanthus* were to be considered valid, the only species assignable to it are the three eastern Pacific members of the "*Murex*" *radix* complex – *radix*, *ambiguus*, and *nigritus*. And, when one compares these with *H. cichoreum*, there is no morphologic basis upon which the two may be separated. The spines in *H. radix* and *H. nigritus* are short and spike-like but those of *H. ambiguus* are as frilly and recurved as many examples of *H. cichoreum*. Both "groups" have a labral tooth (well figured in Radwin and D'Attilio, 1976, text-figs. 27 and 44) and identical radulae (*ibid.*, text-figs. 26 and 43). Both have dark and light spiral stripes. In short, there is no reason that can be singled out to justify separation.

Curiously, the Panamic *H. radix* seems to have made its way into the Atlantic waters of the Lesser Antilles. Originally described as *Murex strausi* by Verrill (1950, p. 4) from Dominica, the illustration (a rather bad drawing) looked too much like *H. radix* for anyone to take seriously. More recently, Sutty (1986, p. 57, fig. 57) reported two examples from 21 feet (6.4 m) off Martinique. Her excellent color photographs show a small shell (32 mm) that is identical to juvenile specimens of *H. radix* of the same size. There may be a colony of *H. radix* in the Lesser Antilles but personally the writer suspects the hand of man was involved in some fashion.

HEXAPLEX HERTWECKORUM (Petuch)
Plate 1, figs. 7, 8

Muricanthus ambiguus (Reeve). OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 138, pl. 29, fig. 5 (*not* of Reeve).

"*Muricanthus ambiguus* (Reeve)" Olsson. VOKES, 1968, Tulane Stud. Geol., v. 6, no. 3, p. 87 (*not* of Reeve).

Hexaplex (Hexaplex) fulvescens (Sowerby). VOKES, 1968, Tulane Stud. Geol., v. 6, no. 3, p. 104 (in part), pl. 3, fig. 1; pl. 4, figs. 1,2 only (*not* of Sowerby).

Muricanthus hertweckorum PETUCH, 1988, Bull. Paleomalacology, v. 1, no. 1, p. 18, pl. 3, figs. 1-3.

Holotype: USNM 424261; height 40 mm, diameter 35 mm.

Type locality: APAC Pit (Macasphalt Pit #0800826), Sarasota, Florida (= TU 1000).

Occurrence: Esmeraldas beds, Ecuador. Pinecrest beds, Florida; Pliocene.

Figured specimens: Fig. 7, USNM 645613; height 64.0 mm, diameter 43.5 mm; locality TU 797. Fig. 8, USNM 643954; height 67.0 mm, diameter 45.0 mm; locality, Punta Gorda, Ecuador.

Discussion: In the Pliocene Pinecrest beds of southern Florida there are numerous examples of a species that this writer earlier (Vokes, 1968) referred to *H. fulvescens*. However, the two forms are not identical, differing in the nature of the spines. *Hexaplex fulvescens* has straight, pointed spines, which are very nearly closed, leading to placement in the subgenus *Muricanthus* by some. However, the fossil specimens are more typically *Hexaplex*, with more open, distinctly recurved spines. In addition, the whorls of the fossil examples are more inflated and the spiral ornamentation is less pronounced. The Esmeraldas specimen that was referred to the Recent West Coast *H. ambiguus* (Reeve) by Olsson, differs from that species in much the same way. As can be seen from pl. 1, figs. 8 and 10, *H. ambiguus* has many more "prickly" spines, plus a labral tooth not found in the fossil example. In fact, this labral tooth is confined to those eastern Pacific species of the *H. radix* complex (*i.e.*, *H. radix*, *ambiguus*, and *nigritus*) and does not occur in *H. fulvescens* or *H. princeps*, its eastern Pacific cognate.

Comparison of the Ecuadorian specimen with the Pinecrest material shows that they are identical, and are neither *H. fulvescens* nor *H. ambiguus*. The most closely related form is the West African *H. duplex* (Röding, 1798), which differs solely in lacking the secondary spines between the shoulder and the suture (see pl. 1, fig. 9). It would appear that members of this species traveled more or less directly to the eastern Pacific from West Africa, but at the same time another group moved northward into Florida. There they flourished for a time, as we have numerous examples from many different Pinecrest localities (especially TU 1000, where it is common). But then it seemingly disappeared during the Late Pliocene Caloosahatchee time (we have no examples in our collections) and reappears in the Early Pleistocene Bermont Formation as true *H. fulvescens*. It is still very rare during this time, as we have it from only one Bermont locality (TU 578). Presumably, the lack of the form during the interval between the Pinecrest and the Recent is a result of environment. The Pinecrest is a muddy-sand/sandy-mud, similar to the modern environment of the living *H. fulvescens*, and most of the Caloosahatchee and Bermont localities are carbonate banks.

It is true that there are specimens, especially young examples, of *H. fulvescens* that get very close to the Pliocene form but, in general, the two species are readily separable. (One assumes that if any Late Pliocene examples are ever found they will be maddeningly intermediate.) Nevertheless, there is no known ancestor for the line in the Caribbean prior to the appearance of these Pinecrest specimens, and the line almost certainly came directly from West Africa. On the West Coast, there is no living representative of this line, unless it is *H. princeps* (Broderip, 1833), which still occurs in Ecuador, but which is noticeably different.

HEXAPLEX AMBIGUUS (Reeve)

Plate 1, figs. 10, 11

Murex ambiguus REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 13, fig. 51; REEVE, 1846, Zool. Soc. London, Proc., pt. 13, p. 86.

Murex nitidus Broderip. REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 17, fig. 70 (? not of Broderip).

Murex (Phyllonotus) nigritus "Meusch." [= Philippi]. CARPENTER, 1857, Cat. Mazatlan, p. 521 (in part).

Murex (Phyllonotus) nitidus Broderip. TRYON, 1880, Man. Conch., v. 2, p. 105 (in part), fig. 242 only.

Muricanthus ambiguus (Reeve). KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 354, fig. 343; KEEN, 1971, *ibid.*, ed. 2, p. 521, fig. 999.

Muricanthus callidinus BERRY, 1958, Leaflets in Malac., v. 1, no. 15, p. 84; KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 354, fig. 343a (= Reeve, fig. 70); KEEN, 1971, *ibid.*, ed. 2, p. 521, fig. 1000 (upper fig. = holotype; lower fig. = Reeve, fig. 70); DUSHANE and POORMAN, 1967, Veliger, v. 9, p. 428.

Not *Muricanthus ambiguus* (Reeve). OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 138, pl. 29, fig. 5 (= *H. hertweckorum*).

Hexaplex ambiguus (Reeve). VOKES, 1968, Tulane Stud. Geol., v. 6, no. 3, p. 87; FAIR, 1976, *Murex* Book, p. 20, pl. 12, fig. 149.

Muricanthus radix (Gmelin). RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 77 (in part), pl. 12, fig. 1 only.

Holotype: Not found.

Type locality: Unknown.

Occurrence: Esmeraldas beds, Ecuador. Recent, Guaymas, Mexico (*fide* DuShane and Poorman, 1967, p. 428) to Paita, Peru (*fide* Hertlein and Strong, 1955, p. 257).

Figured specimens: Fig. 10, USNM 859921; height 70.4 mm, diameter 64.0 mm; locality TU R-173. Fig. 11, USNM 418039; height (incomplete) 52.0 mm, diameter 63.5 mm; locality TU 1399.

Discussion: There have been discussions since the time of Reeve as to whether the various forms of "Black *Murex*" that occur along the west coast of tropical America are all one species or three (even four) valid taxa. Reeve (1845, expl. to pl. 13) gives a long discussion, concluding: "The true *Murex radix* is a round particularly solid heavy shell with a short, though sharply acuminated spire, with not less than ten varices, in which the fronds are numerous, somewhat laterally compressed, comparatively short, and sharp pointed; the species described by Dr. Philippi under the title of *Murex nigritus* (for which see [Reeve, 1845] Pl. 12, Sp. 47), has but eight or nine varices and the fronds are not branched, those on the upper angle of the whorls being tubercularly squamate, those in the middle flat and very obscure, whilst those of the base are long and horn-shaped." He then described a new species, *Murex ambiguus*, stating: "The shell is of somewhat light structure and the fronds are large, open, and flowery. It certainly presents a modification of character intermediate between the *Murices radix* and *nigritus* but is always easy to be distinguished."

Unknown to Reeve is that there is a valid geographic distribution of the three forms, even though it is not as simple as we once thought. Furthermore, it appears that *H. ambiguus* is the ancestral species for two local forms: *H. nigritus*, from the Gulf of California to as far south as the Gulf of Tehuantepec; and *H. radix*, only in the Bay of Panama. The ancestral *H. ambiguus*, however, lives throughout the entire length of the range. Here is a case where "geographic subspecies" is not the solution to the taxonomic problem, for the oldest name *(radix)* is confined to a small area and to use it as the primary taxon is misleading both geographically and stratigraphically. As the three forms are readily separable and, as the Laws of Nomenclature will not allow the stratigraphical solution of "*H. ambiguus* s.s.," "*H. ambiguus radix*" and "*H. ambiguus nigritus*" it seems best to accept the three as valid species.

A fourth name, *Muricanthus callidinus*, was erected by Berry, 1958, for the shell illustrated by Reeve (1845, pl. 17, fig. 70) as *Murex nitidus* Broderip. In this form, the spines are straighter than in the typical *H. ambiguus* but otherwise there are no discernable differences and *M. callidinus* is here considered as a synonym of *H. ambiguus*.

The juvenile specimen named by Broderip as *Murex nitidus* (1833, p. 176) and illustrated by Sowerby (1834, pl. 58, fig. 4), from "Real Llejos, Cent. Am." (= Corinto, Nicaragua) is probably a young example of *H. princeps*, as suggested by Sowerby (1841, p. 6) rather than "*M. callidinus*" as indicated by Reeve (1845, pl. 17, fig. 70). As Keen (1958, p. 358) noted, *Murex nitidus* "is apparently the young of one of the species of *Muricanthus*, but authors are not in agreement as to which one. We are saved the necessity of guessing, as the name is preoccupied by *M. nitidus* Pilkington, 1804."

The identification of the southern members of the group is confused. Reeve stated that his specimen of "*Murex radix*" (1845, pl. 17, fig. 69) was from "Bay of Caraccas,

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PLATE 4

Figures		Page
1, 2.	*Poirieria (Paziella) meridionalis* (Olsson)	32
1.	(X 2) USNM 418045; height 27.4 mm, diameter 15.5 mm.	
2.	(X 3) USNM 418046; height 12.0 mm, diameter 7.9 mm. Locality of both: TU 1397; Esmeraldas beds, Ecuador.	
3-5.	*Poirieria (Poirieria) actinophora* (Dall)	29
3.	(X 2 1/2) USNM 430478; height 20.6 mm, diameter (including spines) 14.3 mm. Locality: Virgin Islands, 550-600 meters; Recent.	
4.	(X 2 1/2) USNM 418047; height 18.2 mm, diameter 8.7 mm.	
5.	(X 2 1/2) USNM 418048; height 17.5 mm, diameter 9.3 mm. Locality of both: TU 1397; Esmeraldas beds, Ecuador.	
6.	*Murexsul pitti* E. H. Vokes, n. sp. . . . . (X 1 1/2) USNM 418049 (holotype); height 30.0 mm, diameter 19.5 mm. Locality: TU 1397; Esmeraldas beds, Ecuador.	37
7, 8.	*Murexiella lappa* (Broderip)	37
7.	(X 3) USNM 859924; height 14.7 mm, diameter 9.0 mm. Locality: TU R-166; Barra de Navidad, Jalisco, Mexico; Recent.	
8.	(X 3) USNM 418050; height 13.7 mm, diameter 8.0 mm. Locality: TU 1397; Esmeraldas beds, Ecuador.	
9, 10.	*Muricopsis oxytata* (M. Smith)	34
9.	(X 2) NMB H 17338; height 28.0 mm, diameter 14.7 mm. Locality: K-493, Trans-Ecuadorian Pipeline; Esmeraldas beds, Ecuador.	
10.	(X 3) USNM 418051; height 19.3 mm, diameter 9.0 mm. Locality: TU 726; Caloosahatchee Fm., Florida.	

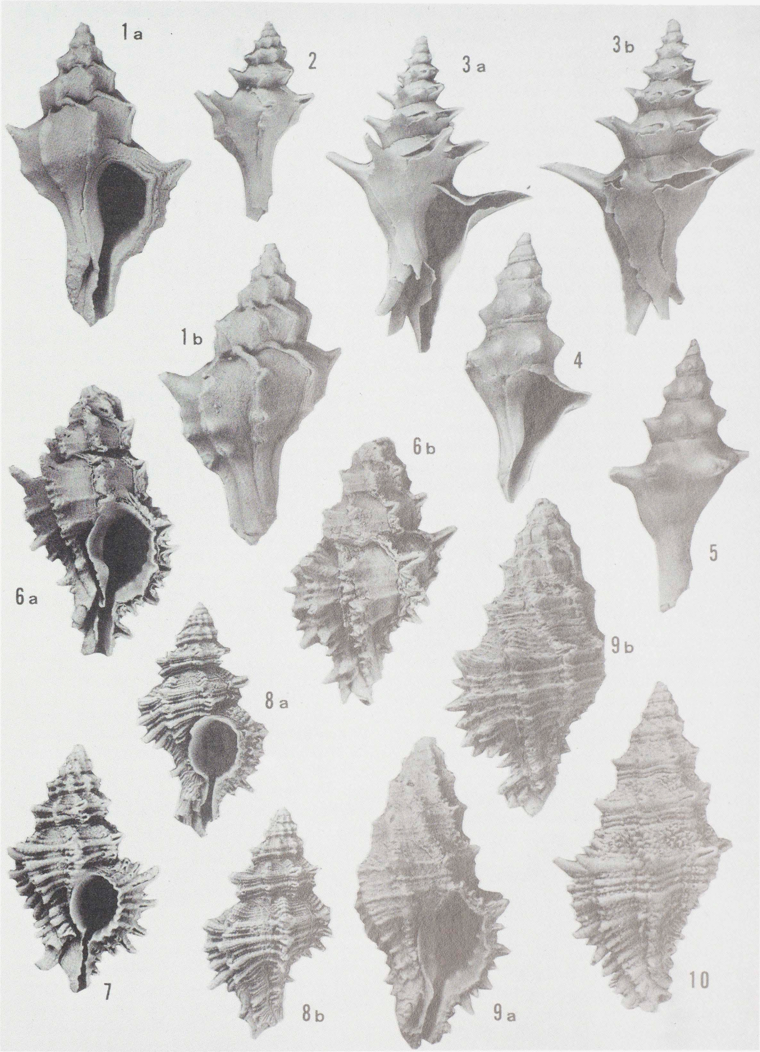

PLATE 4

West Colombia," which is assumed to be Bahía de Caraquez, just north of Manta, Ecuador. Other authors have cited "*radix*" as occuring from Panama to Ecuador (Keen, 1958, p. 356) or to Peru (Radwin and D'Attilio, 1976, p. 78; Hertlein and Strong, 1955, p. 257). Reeve's specimen appears to be typical *H. radix*, but the writer has seen no other examples, except from the Bay of Panama. Thus, there are three conclusions possible: the Reeve locality is incorrect, as are many others in the Cuming material; our intrepretation of where it is located is incorrect (no such name can now be found); or true *radix* does occur south of Panama. All southern specimens that we have collected (R-56, Tumaco, Colombia; R-381 and R-553, Sta. Elena Bay, Ecuador; R-552, Ayungue, Ecuador; and R-484, Camarones, Ecuador) are *H. ambiguus*.

In any case, the sole example of this group taken in the Esmeraldas beds is *H. ambiguus*, which would tend to confirm the idea that this is the ancestor from which the others diverged. The real problem is where did *H. ambiguus* originate? Only generically similar to the contemporaneous *H. hertweckorum*, the two must be assumed to have a earlier common ancestor. But there is no known form anywhere that would qualify. The only species that is remotely related is the common Indo-Pacific *H. cichoreum* (Gmelin, 1791), which shares the strong dark and light spiral banding, and a pronounced labral tooth. The spines of *H. cichoreum* are longer and more recurved and the maximum shell size is smaller, but otherwise the resemblance to *H. ambiguus* is stronger than anyone has ever been willing to admit. Perhaps this is because the two descendant forms, *H. radix* and *H. nigritus*, are much more distinctive.

This resemblance is further evidence that there is no justification for the recognition of *Muricanthus* (type species: *Murex radix*) as a valid subgenus. The only possible distinction is that "*Muricanthus*" has more varices than *Hexaplex* – the name "*Hexaplex*" is misleading, *H. cichoreum* has seven varices as often as six. But how many is enough to be "more?" Specimens of *H. fulvescens* may have from six to ten varices; *H. ambiguus* usually has about eight or nine; *H. nigritus* has six to eight; *H. princeps* has five to eight. Only *H. radix* itself would qualify, having more than ten, as a rule. Keen (1958, p. 356; 1971, p. 521, and personal communication) believed that the strongly looped anal notch of *H. cichoreum* was significant, but this varies even among members of the species *H. cichoreum* itself; some are strong, some almost invisible.

All living members of the group are inhabitants of very shallow water, usually from intertidal to as much as 30 m (Gulf of Tehuantepec–Don Shasky Coll.). This fits with the occurrence of this single Esmeraldas specimen at TU 1399, which is overall a much shallower fauna than is seen at the other localities.

HEXAPLEX BRASSICA (Lamarck)
Plate 3, figs. 3, 4

Murex brassica LAMARCK, 1822, Anim. s. Vert., v. 7, p. 167; SOWERBY, 1834, Conch. Illus., *Murex*, pl. 67, fig. 56; KIENER, 1843, Coq. Viv., v. 7, *Murex*, p. 68, pl. 26, fig. 1, pl. 27, fig. 1; REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 14, fig. 56; SOWERBY, 1879, Thes. Conch., v. 4, *Murex*, fig. 166.

Murex ducalis BRODERIP and SOWERBY, 1829, Zool. Jour., v. 4, no. 15, p. 377.

Murex (Phyllonotus) brassica Lamarck. CARPENTER, 1857, Cat. Mazatlan, p. 523; TRYON, 1880, Man. Conch., v. 2, p. 100, pl. 22, fig. 200; M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 8, pl.4, fig.1.

Phyllonotus brassica (Lamarck). PILSBRY and OLSSON, 1941, Acad. Nat. Sci. Phila., Proc., v. 93, p. 37; OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, p. 169; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 88, pl. 16, fig. 5; FAIR, 1976, *Murex* Book, p. 27, pl. 10, fig. 124.

Hexaplex brassica (Lamarck). KEEN, 1958, Sea Shells Trop. West Amer., p. 352, fig. 338; KEEN, 1971, *ibid.*, ed. 2, p. 516, fig. 979; OLSSON, 1964, Neogene Moll. Northwest. Ecuador, pl. 29, fig. 4 (not in text); DUSHANE and POORMAN, 1967, Veliger, v. 9, p. 428.

Chicoreus (Phyllonotus) brassica (Lamarck). VOKES, 1967, Tulane Stud. Geol., v. 5, no. 3, p. 160; VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 212.

Holotype: Not found.

Type locality: Mazatlan, Mexico (designated by Kiener, 1843, p. 69).

Occurrence: Jama Formation and Esmeraldas beds, Ecuador. Charco Azul Formation, Panama; Pleistocene. Recent, Gulf of California to Peru.

Figured specimens: Fig. 3, ANSP 15205; height (incomplete) 89.0 mm, diameter (including spines) 74.6 mm; locality, Puerto Jama, Ecuador. Fig. 4, USNM 418042 (fragment); length (as is) 25.0 mm, width 13.0 mm; locality TU 1399.

Discussion: In the Esmeraldas collection there is a single fragment that can be referred without hesitation to an unmistakable species, "*Murex*" *brassica* Lamarck, 1822. This form was also reported by Pilsbry and Olsson (1941, p. 37) from the Pliocene Jama Formation of Ecuador and was figured by Olsson (1964, pl. 29, fig. 4) from beds that he considered to be Pliocene in age from the Burica Peninsula, Panama. The Burica beds are now known to be Pleistocene in age (R.H. Stewart, in litt., 24 Jan. 1985) but comparison of the Jama specimens (see pl. 3, fig. 3) and the Panamanian one shows no differences. Both the Pliocene and Pleistocene specimens do differ slightly from the usual appearance of Recent specimens in that the varices in the fossil examples are noticably stronger than in most Recent examples, where the varix is closely appressed to the whorl and scarcely visible except along the forward margin. However, this may be an ecologic factor, for specimens dredged from the Gulf of Chiriqui in 35-60 meters also have the stronger varices.

In an earlier paper (Vokes, 1967b, p. 160), the writer considered the problem of where to put *brassica* generically and concluded that the nature of the varices, lacking open spines, together with the strong labrum in front of the varix, much like that seen in *C. (P.) erythrostomus*, which also has a surface ornamentation similar to that of *brassica*, permitted (not mandated) placement in *Phyllonotus*. This was a compromise, for the form is distinctly intermediate between *Hexaplex* and *Phyllonotus*.

In terms of relationship, the only species closely related to *H. brassica* is the Mediterranean *H. trunculus* (Linnaeus, 1758). The generic placement of *H. trunculus* has also been a problem to many authors, some of whom have attempted to solve the problem by creating a new genus for the form. The names include *Purpura* Röding, 1798 (not *Purpura* Bruguière, 1789), *Truncularia* Monterosato, 1917 (not *Truncularia* Wiegmann, 1832), *Trunculariopsis* Cossmann, 1921 (new name for *Truncularia* Monterosato), and *Murithais* Grant and Gale, 1931. However, as the writer as discussed elsewhere (Vokes, 1968, p. 86), *H. trunculus* is just the end member of a group of muricids that goes back without change to the Eocene and cannot, in her opinion, be generically separated from *Hexaplex* s.s.

Obviously, *H. brassica* is descended from a West African form that made its way to the eastern Pacific without leaving a trace in the Caribbean. In the description of *H. etheringtoni* (Vokes, 1968, p. 102), it was suggested that perhaps this Colombian species was ancestral to the *H. brassica* line. However, the Tubará beds are now known to be Pliocene and not Miocene as originally thought, and are approximately contemporaneous with the Esmeraldas fauna. Thus, the two species probably represent different, although related, lineages. Nevertheless, both probably came directly from West Africa, as did *H. hertweckorum*.

Genus POIRIERIA Jousseaume, 1880

Poirieria Jousseaume, 1880, Le Naturaliste, Année 2, no. 42, p. 335.

Type species: *Murex zelandicus* Quoy and Gaimard, 1833, by original desig.

Actinotrophon DALL, 1902, U.S. Natl. Mus., Proc., v. 24, p. 534.

Type species: *Boreotrophon actinophorus* (Dall, 1889), by original desig.

Subgenus POIRIERIA s.s

POIRIERIA (POIRIERIA) ACTINOPHORA (Dall)

Plate 4, figs. 3-5

Trophon (Boreotrophon) actinophorus DALL, 1889, Harvard Mus. Comp. Zool., Bull., v. 18, p. 206, pl. 15, fig. 2; DALL, 1889, U.S. Natl. Mus., Bull. 37, p. 120, pl. 15, fig. 2 (entire plate is copy of previous); M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 19, pl. 9, fig. 2 (after Dall).

Boreotrophon (Actinotrophon) actinophorus (Dall). DALL, 1902, U.S. Natl. Mus., Proc., v. 24, p. 534.

"Unnamed." OLSSON, 1964, Neogene Moll. Northwest. Ecuador, pl. 20, figs. 5, 5a (not in text).

Trophon actinophorus Dall. BULLIS, 1964, Tulane Stud. Zoology, v. 11, no. 4, p. 107; RIOS, 1975, Brazilian Marine Moll. Icon., p. 88, pl. 25, fig. 361 (after Dall).

Murex (Paziella) actinophorus (Dall). BAYER, 1971, Bull. Marine Sci., v. 21, no. 1, p. 157, text-figs. 30, 35D (radula).

Actinotrophon actinophorus (Dall). RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 176, text-fig. 116 (after Dall); D'ATTILIO, 1980, Festivus, v. 12, no. 4, p. 61, fig. 1.

Poirieria actinophorus (Dall). RIOS, 1985, Seashells of Brazil, p. 83, pl. 29, fig. 361 (after Dall).

Holotype: Harvard Mus. Comp. Zool. 7313; height 17.5 mm, diameter (including spines) 14.0 mm.

Type locality: "Blake" Station 143, off Santa Cruz (St. Croix, V.I.), in 248 fms [453.5 m].

Occurrence: Esmeraldas beds, Ecuador. Recent, western Atlantic from Bahama Islands to Brazil, Panama and Colombia (fide Bayer, 1971, p. 159).

Figured specimens: Fig. 3, USNM 430478; height 20.6 mm, diameter (including spines) 14.3 mm; locality, Virgin Islands, Recent. Fig. 4, USNM 418047; height 18.2 mm, diameter 8.7 mm; locality TU 1397. Fig. 5, USNM 418048; height 17.5 mm, diameter 9.3 mm; locality TU 1397.

Discussion: In his study of the Esmeraldas fauna, Olsson included two figures of a poorly-preserved specimen he identified only as "Unnamed," including it among the Turridae. Our collections added another two, somewhat better, specimens and it is obvious that the species is not a turrid but a peculiar muricid, living today in the deep waters (averaging 440 m, Bayer, 1971, p. 159) of the Caribbean Sea.

Originally described as a *Trophon*, the species has been so considered until 1971, when Bayer studied the radula and observed that it was identical to that of *Poirieria (Paziella)*. Conchologically the shell differs from *Paziella* in having an open outer lip and no spines encircling the siphonal canal, exactly the features that separate *Paziella* from *Poirieria* s.s.

Although the appearance of a species of *Poiriera* in the Esmeraldas is of great interest, it is not too significant. The genus *Poirieria* appears first in the Paleocene of Alabama (Vokes, 1971, p. 37), occurs in the Lower Eocene of England, and the Middle Eocene of New Zealand (Maxwell, 1971, p. 764). The living species that is type of the genus, *Murex zelandicus*, differs little from the Eocene forms and obviously this is an extremely conservative group that has survived with little change in deeper waters. Indeed, the Caribbean *P. actinophora* is virtually identical to the New Zealand *P. delli* Maxwell (1971, p. 771, figs. 1, 28-30), from the Lower Miocene, a species that

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PLATE 5

Figures Page

1, 2. *Pteropurpura (Ocinebrellus) ecuadoria* (Olsson) 41
  1. (X 1 1/2) USNM 418052; height (incomplete) 36.3 mm, diameter 28.0 mm.
  2. (X 3) USNM 418053; height 18.4 mm, diameter 9.6 mm.
  Locality of both: TU 1397; Esmeraldas beds, Ecuador.

3. *Pteropurpura (Ocinebrellus) acanthophora* (A. Adams) 41
  (X 1 1/2) BMNH (holotype); height 38.7 mm, diameter 24.3 mm.
  Locality: Tsusaki, Japan, 37 fms (68 m); Recent.

4. *Pteropurpura (Pteropurpura) trialata* (Sowerby) 41
  (X 1 1/2) USNM 859925; height 41.6 mm, diameter 22.0 mm.
  Locality: Southern California; Recent.

5. *Pteropurpura (Pteropurpura) marksi* Olsson 41
  (X 1 1/2) USNM 418054; height 38.0 mm, diameter 25.5 mm.
  Locality: TU 1397; Esmeraldas beds, Ecuador.

6, 7. *Ceratostoma notiale* E. H. Vokes, n. sp. 40
  6. (X 2 1/2) USNM 418055 (holotype); height 19.5 mm, diameter 11.0 mm.
  7. (X 2) USNM 418056 (paratype); height (incomplete) 22.5 mm, diameter (incomplete) 11.0 mm.
  Locality of both: TU 1399; Esmeraldas beds, Ecuador.

8. *Ceratostoma nuttalli* (Conrad) 40
  (X 2 1/2) USNM 859928; height 19.1 mm, diameter 10.3 mm.
  Locality: Baja California, Mexico, *ca.* 160 km (100 miles) south of San Diego, California; Recent.

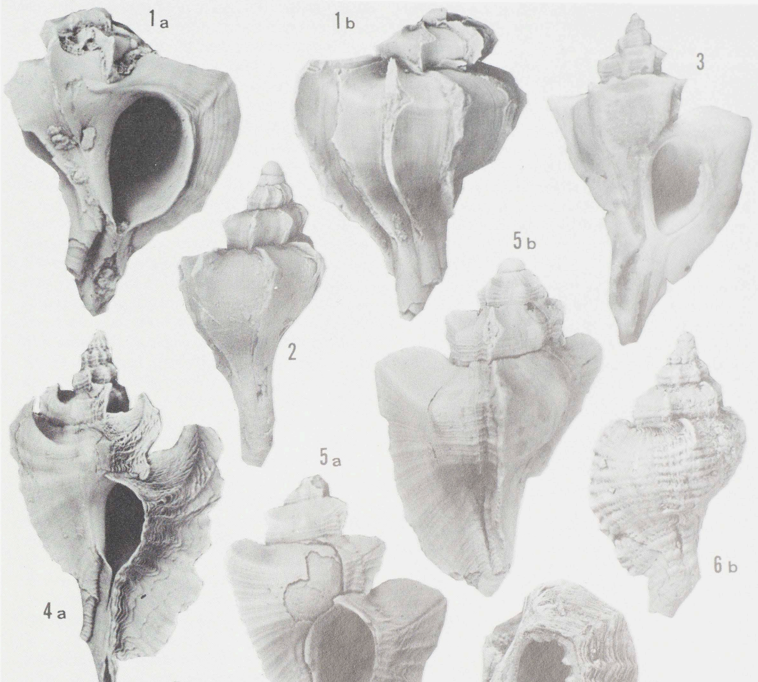

PLATE 5

Maxwell considers to be most closely related to the Recent *P. kopua* Dell, 1956, found in the deeper waters off New Zealand (600-700 m *ex* Dell, 1963, *in* Maxwell, 1971, p. 764).

Thus, *P. actinophora* is one of a group of Tethyan relics that survives throughout the world. Its presence in the Esmeraldas fauna is of interest primarily from the aspect that the group, so far as is known, no longer occurs in the eastern Pacific fauna, making it one of the few "caribphiles" as named by Woodring (1966, p. 430), who observed that the percent of caribphiles is much lower than paciphiles.

Considering the habitat of the Recent examples of *P. actinophora*, it is obvious that the Esmeraldas specimens lived at a similar depth when overwhelmed by the influx of shallower material.

Subgenus PAZIELLA Jousseaume, 1880

Paziella JOUSSEAUME, 1880, Le Naturaliste, Année 2, no. 42, p. 335.

Type species: *Murex pazi* Crosse, 1869, by original desig.

Bathymurex CLENCH and PÉREZ FARFANTE, 1945, Johnsonia, v. 1, no. 17, p. 41.

Type species: *Murex (Bathymurex) atlantis* Clench and Pérez Farfante, 1945, by original desig.

POIRIERIA (PAZIELLA) MERIDIONALIS (Olsson)
Plate 4, figs. 1, 2

Boreotrophon meridionalis OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 140, pl. 26, figs. 5, 5a.

Holotype: USNM 644138; height 32.2 mm, diameter 19.3 mm.

Type locality: Esmeraldas beds; Punta Gorda, Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Figured specimens: Fig. 1, USNM 418045; height 27.4 mm, diameter 15.5 mm. Fig. 2, USNM 418046; height 12.0 mm, diameter 7.9 mm. Locality of both: TU 1397.

Discussion: The species that Olsson referred to *Boreotrophon* is not of that group, but it is a deep-water form, nonetheless. In the Galápagos Islands, there is a living species named as "*Murex*" *galapaganus* by Emerson and D'Attilio (1970, p. 271, pl. 39, figs. 3-6), which is extremely close to *P. meridionalis*, so close that it can be no more than a subspecies at best. The only discernable difference is an extra spiral cord, with a resulting spinelet on each varix, seen in the younger form. This latter species occurs in depths of 150-200 meters, suggesting a similar environment for *P. meridionalis*.

The generic assignment for "*M.*" *galapaganus*, and by extension "*B.*" *meridionalis*, was discussed by the original authors, who noted that in shell morphology it is closest to *Bathymurex* and *Paziella*, but the heavy chalky intritacalx is most like *Takia* Kuroda, 1953, which, however, lacks the spinose varices. The operculum and radula they felt were closest to two Japanese species, "*Boreotrophon*" *gorgon* Dall, 1913, and "*B.*" *echinus* Dall, 1918. The latter subsequently have been placed in the genus *Nipponotrophon* Kuroda and Habe, 1971; thus, Radwin and D'Attilio (1976, p. 83) transferred "*M.*" *galapaganus* to *Nipponotrophon*.

Nipponotrophon is superficially similar to *Paziella* in shell morphology but has a radula almost identical to that of *Boreotrophon* (*cf.* Radwin and D'Attilio, 1976, text-figs. 48 and 121). However, "*M.*" *galapaganus* has a radula (see Emerson and D'Attilio, 1970, text-fig. 3) most like that of *Poirieria zelandica* (see Radwin and D'Attilio, 1976, text-fig. 57). The operculum (Emerson and D'Attilio, 1970, text-fig. 4) is not like any of the aforementioned genera, having a sublateral nucleus. But the operculum is not as critical a criterion as the radula, given the variation seen within other muricine genera (*e.g.*, *Murex* s.s.).

The only known species of *Nipponotrophon* are those from the western Pacific, whereas *Paziella* is now found only in the New World, although it was worldwide in earlier geologic times. The eastern Pacific forms are most like three species in the Caribbean that would be assigned to *Bathymurex* Clench and Pérez Farfante, 1945, if that taxon were considered to be sufficiently distinct from *Paziella* to be recognized. These include two fossil species: *P. dominicensis* (Gabb, 1873), occuring in the Early Pliocene Gurabo Formation of the Dominican Republic and the mid-Pliocene Concepcion Inferior Formation of Mexico, and *P. septima* Vokes, 1970, from the same Concepcion Inferior; and the Recent "*Murex*" *atlantis*, type of *Bathymur-*

ex. These three species differ from typical *Paziella* in lacking the spines encircling the base of the shell, and differ from the eastern Pacific species in that the spiral cords are more pronounced in the intervarical area but do not produce spinelets at the varices, except on the shoulder.

In *P. dominicensis* many of the specimens seem to have an outer organic layer that causes pyrite deposition on the shell; all of the Ecuadorian specimens are badly decorticated; and there is but one dead-taken specimen known of *P. atlantis*. Thus, it is possible that the heavy intritacalx of *P. galapagana* is characteristic of the group. If more examples of *P. atlantis* should demonstrate this, then the taxon *Bathymurex* could be redefined for those few species of *Paziella* lacking the spines on the canal and having the heavy intritacalx. For the present, they will be assigned to *Paziella*.

It should be noted that "*Nipponotrophon galapaganus*" from the Gulf of California, reported by Skoglund (1983, p. 107, figs. 3,4) is obviously not that species, as the specimen, among other differences, has very strong spines on the siphonal canal. Her shell is probably a new species of *Muricopsis*.

Poirieria (Paziella) atlantis is another deep-water form, the holotype coming from about 350 meters, off Cuba (Clench and Pérez Farante, 1945, p. 41). Examples of *P. dominicensis* are from beds that, on the basis of the other fauna, are assumed to be of comparable depth. As *P. meridionalis* is one of the few muricid species relatively common in the Esmeraldas beds (24 specimens from TU 1397; one from TU 1399), it is probable that it too was a member of the deeper Esmeraldas fauna.

Genus ATTILIOSA Emerson, 1968

Attiliosa EMERSON, 1968, Veliger, v. 10, p. 380.

Type species: *Coralliophila incompta* Berry, 1960, by original desig. (*C. incompta* Berry = *Peristernia nodulosa* A. Adams, 1855).

ATTILIOSA NODULOSA (Adams)

Plate 6, figs. 5, 6

Peristernia nodulosa A. ADAMS, 1855, Zool. Soc. London, Proc., (1854), p. 313; HEDLEY, 1908, Linnean Soc. New South Wales, Proc., v. 33, p. 486, pl. 8, fig. 11 (syntype).

Coralliophila nodulosa (Adams). MELVILL, 1891, Manchester Lit. Phil. Soc., Proc., (Ser. 4) v. 4, pp. 409, 410.

Coralliophila incompta BERRY, 1960, Leaflets in Malac., v. 1, no. 19, p. 119; DUSHANE and POORMAN, 1967, Veliger, v. 9, p. 429; DUSHANE and SPHON, 1968, Veliger, v. 10, p. 242, pl. 35, fig. 11.

Attiliosa incompta (Berry). EMERSON, 1968, Veliger, v. 10, p. 380, pl. 53, figs. 1 (holotype), 2-5; text-figs. 2-3 (radula), 4, 5 (operculum); KEEN, 1971, Sea Shells Trop. West Amer., ed. 2, p. 529, fig. 1021; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 26, pl. 3, fig. 1, text-fig. 10 (radula).

Attiliosa nodulosa (Adams). BULLOCK, 1976, Tulane Stud. Geol. Paleont., v. 12, no. 3, p. 133, pl. 1, figs. 6-8 (syntypes); RADWIN and D'ATTILIO, 1978, Tulane Stud. Geol. Paleont., v. 14, no. 3, p. 32, figs. 5, 5a (radula); VOKES and D'ATTILIO, 1982, Veliger, v. 25, p. 69; VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 212, pl. 1, fig. 21.

Holotype: Stanford University Paleo. Type Coll. 9512; now CAS 043915; height 33.5 mm, diameter 20.3 mm.

Type locality: Isla Angel de la Guarda, Baja California.

Occurrence: Esmeraldas beds, Ecuador. Recent, Baja California to Panama (*fide* Keen, 1971, p. 530).

Figured specimens: Fig. 5, USNM 859927; height 31.5 mm, diameter 19.0 mm; locality, off Guaymas, Sonora, Mexico, Recent. Fig. 6, USNM 418059; height 25.7 mm, diameter 16.6 mm; locality TU 1399.

Discussion: Keen (1971, p. 530) states that this species occurs as far south as Panama, in depths of 18-80 meters; however, according to Emerson (1968, p. 380), most material has been taken in about 30 meters. Thus, this single specimen from TU 1399 is another member of the shallow-water fauna that predominates at that locality.

Subfamily MURICOPSINAE

Radwin and D'Attilio, 1971

Genus MURICOPSIS

Bucquoy and Dautzenberg, 1882

Muricopsis BUCQUOY and DAUTZENBERG *in* BUCQUOY, DAUTZENBERG and DOLLFUS, 1882, Moll. Mar. Roussillon, v. 1, p. 19.

Type species: *Murex blainvillei* Payraudeau, 1826, by original desig.

Muricopsis oxytata (Smith)
Plate 4, figs. 9, 10

Murex hexagonus LAMARCK, 1816, Tableau Encycl. Meth. (Vers), v. 3, pl. 418, fig. 3; LAMARCK, 1822, Anim. s. Vert., v. 7, p. 169; KIENER, 1843, Coq. Viv., v. 7, *Murex*, p. 96, pl. 8, fig. 3; REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 27, fig. 120; SOWERBY, 1879, Thes. Conch., v. 4, *Murex*, fig. 257 (*non M. hexagonus* Gmelin, 1791).

Murex hexagonus oxytata M. SMITH, 1938, Nautilus, v. 51, p. 89, pl. 6, fig. 6.

Muricopsis hexagonus (Lamarck). OLSSON and HARBISON, 1953, Acad. Nat. Sci. Phila., Mon. 8, p. 247, pl. 37, fig. 4 (including *M. hexagonus oxytata* in synonymy); ABBOTT, 1954, Amer. Seashells, ed. 1, p. 209, pl. 25h.

Muricidea hexagonus (Lamarck). M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 11, pl. 6, fig. 3.

Muricopsis oxytata/oxytatus (Smith). ABBOTT, 1958, Acad. Nat. Sci. Phila., Mon. 11, p. 63; WARMKE and ABBOTT, 1961, Caribbean Sea Shells, p. 106, pl. 19e; ABBOTT, 1974, Amer. Seashells, ed. 2, p. 197, fig. 1957; HUMFREY, 1975, Sea Shells of the West Indies, p. 137, pl. 16, figs. 2, 2a; FAIR, 1976, *Murex* Book, p. 64, pl. 17, fig. 226; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 169, pl. 27, fig. 5; VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 214, back cover color photo.

Muricopsis lyonsi PETUCH, 1986, Jour. Coastal Resh., v. 2, no. 4, p. 404, pl. 4, figs. 12, 13.

Holotype: Not found; height 22 mm (*fide* Smith, 1938).

Type locality: Caloosahatchee Formation; Clewiston, Hendry County, Florida.

Occurrence: Esmeraldas beds, Ecuador. Tubará Group, Colombia; Pliocene. Pinecrest beds, Caloosahatchee and Bermont formations, Florida; Plio-Pleistocene. Moín Formation, Costa Rica; Pleistocene. Recent, western Atlantic, Florida to northern South America, Panama and Costa Rica.

Figured specimens: Fig. 9, NMB H 17338; height 28.0 mm, diameter 14.7 mm; locality, K-493, Trans-Ecuadorian Pipeline. Fig. 10, USNM 418051; height 19.3 mm, diameter 9.0 mm; locality TU 726.

Discussion: As the name *Murex hexagonus* of Lamarck is preoccupied by that of Gmelin, 1791, the next available name for the species is *M. oxytata* for, although Smith distinguished the Florida form as a subspecies, the distinction is not valid (Abbott, 1958, p. 63). The spelling "*oxytatus*" is used by many authors, thinking the ending should agree with the generic taxon; however, "*oxytata*" is a noun, meaning "spiny daddy," evidently in reference to what Smith assumed was its ancestral relationship to the Recent "*M. hexagonus.*"

PLATE 6

Figures Page

1, 2. *Typhis (Talityphis) latipennis* Dall 44
  1. (X 2) USNM 418057; height 27.0 mm, diameter 20.4 mm.
     Locality: TU 1397; Esmeraldas beds, Ecuador.
  2. (X 2) USNM 859926; height 32.5 mm, diameter 19.0 mm.
     Locality: El Dorado, Jalisco, Mexico, 28 fms (51 m); Recent.

3, 4. *Typhis (Talityphis) alatus* Sowerby 46
  3. (X 2) USNM 418058; height 26.7 mm, diameter (incomplete) 13.2 mm.
     Locality: TU 1399; Esmeraldas beds, Ecuador.
  4. (X 2) USNM 323910; height 27.7 mm, diameter 17.2 mm.
     Locality: TU 1212; Gurabo Fm., Dominican Republic.

5, 6. *Attiliosa nodulosa* (A. Adams) 33
  5. (X 1 1/4) USNM 859927; height 31.5 mm, diameter 19.0 mm.
     Locality: Off Guaymas, Sonora, Mexico; Recent.
  6. (X 1 1/2) USNM 418059; height 25.7 mm, diameter 16.6 mm.
     Locality: TU 1399; Esmeraldas beds, Ecuador.

7-9. *Vitularia salebrosa* (King and Broderip) 42
  7. (X 1) PRI 20481 (holotype - *V. ecuadorana* Marks); height 59.1 mm, diameter 30.5 mm.
     Locality: Daule Basin; Daule Fm., Ecuador.
  8. (X 2) USNM 418060; height 20.9 mm, diameter 13.8 mm.
  9. (X 2) USNM 418061; height 19.1 mm, diameter 10.6 mm.
     Locality of both: TU 1399; Esmeraldas beds, Ecuador.

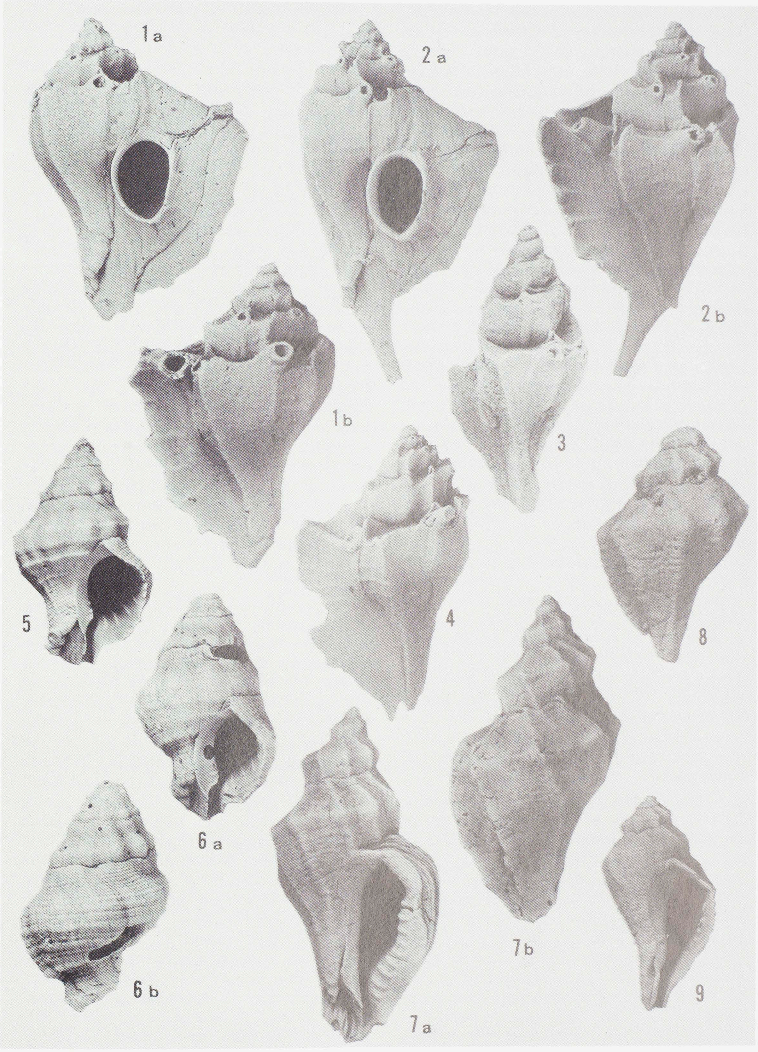

PLATE 6

This is a widespread species in both the fossil and Recent record of the western Atlantic. In addition to the many localitites in the Plio-Pleistocene of southern Florida, we also have several examples from both the Pleistocene Moín Formation and the Recent of Costa Rica, and in the collections of the Museum of Paleontology, University of California, Berkeley, there is a single example from the mid-Pliocene Tubará Group, at Punta Pua, Dept. of Bolivar, Colombia. Undoubtedly, the reason it is absent in the Gatun Formation is that it is almost totally confined to coralline facies. In the Recent fauna of the eastern Pacific the cognate species is *M. armatus* (Adams, 1854), which may be distinguished by having the varices irregularly aligned up the spire in contrast to the perfect hexagonal alignment of *M. oxytata*. Although Keen (1971, p. 523) indicated the species is confined to the Gulf of California, we have examples from Isla Gobernador, Panama. But everywhere, it occurs under stones at low tide; evidently upon moving into the non-coralline eastern Pacific the ancestral form was forced to make an adjustment in habitat.

In an Ecuadorian collection made by Peter Jung, of the Naturhistorisches Museum, Basel, Switzerland, there is a single specimen of what proves to be *M. oxytata*, not *M. armatus*. His locality is not the same as ours, being at K-493 on the Trans-Ecuadorian Pipeline, or about 10 km south of Esmeraldas (near the road to the bridge over the Rio Esmeraldas); however, the associated fauna indicates that the outcrop is identical to that at Camarones.

A new species, *M. lyonsi*, was described by Petuch (1986, p. 404, pl. 4, figs. 12, 13) from the mid-Pliocene of the Miami area, which he stated differs from *M. oxytata* in lacking the varical spines, having instead large varical scales. In our collections, we have a number of these short-spined forms from several localities, both correlative with the type material (TU 541, 1000) and younger (TU 202-Caloosahatchee Fm.; TU 1240-Moín Fm.). Examination of topotypic material (TU 1493) suggests that the differences are only ecological – perhaps rougher water.

Genus MUREXSUL Iredale, 1915

Murexsul IREDALE, 1915, New Zealand Inst., Trans., Proc., v. 47, p. 471.

Type species: *Murex octogonus* Quoy and Gaimard, 1833, by original desig.

Discussion: The genus *Murexsul* is one of the original muricid genera, going back to the Eocene when it was distributed worldwide. At the time the writer originally discussed ths genus (Vokes, 1968, pp. 87, 106), she considered it a subgenus of *Hexaplex*. But additional work on the history of the Muricidae (Vokes, 1971) and work on the nature of the radula, which resulted in Radwin and D'Attilio (1971) separating those forms with a three-dimensional rachidian tooth into a subfamily Muricopsinae, shows that this assignment was incorrect. However, the shell morphology in many cases remains discouragingly similar and the early fossil species, such as the *Hexaplex engonatus* (Conrad) complex, may well be members of *Murexsul*. But, in general, the two may be separated by the presence of an anal notch in *Hexaplex*, not seen in *Murexsul*, and the fact that the shoulder spine is usually longer than the other spines in *Hexaplex* but they are all of about the same length in *Murexsul*.

Ponder (1972, p. 237) took issue with Vokes's statement (1964, p. 19) that *Murexsul* might be separated from the similar *Muricopsis*, "by the extreme development of the denticles on the outer lip," stating that he felt this was not a valid distinction. However, as the two groups have been separate since the Eocene (there is a good Eocene species of *Muricopsis* in California – *Muricopsis vistanensis* Givens and Kennedy, 1976), plus the presence of the denticles on the *inner* lip of *Muricopsis* and its subgenus *Risomurex* Olsson and McGinty, 1958 (see Vokes and Houart, 1986), little is gained by combining the two groups. Nevertheless, Ponder is correct in observing that the two are very closely related.

The genus *Murexsul*, has not previously been recognized in the living western Atlantic fauna, until Petuch (1987, p. 100, pl. 21, figs. 11, 12) described *Murexsul harasewychi* from 35 meters depth off the coast of Colombia. In addition, the Brazilian *Muricopsis oxossi* Petuch, 1979, is extremely like the Mediterranean *Murexsul aradasii* (Monterosato *in* Poirier, 1881; a synonym of *Murex medicago* Watson, 1897; see Fair, 1976, p. 21, pl. 17, fig. 244 - type of *medicago*), and both are better placed in *Murexsul* than in *Muricopsis*.

In the Pleistocene Moín Formation of Costa Rica and the Late Pliocene Waccamaw Formation of South Carolina there are undescribed species of *Murexsul*, in addition to the mid-Pliocene *M. thalmanni* (Vokes, 1968) from the Agueguexquite Formation of Mexico. In the eastern Pacific, there is the Galapagan *M. jacquelinae* Emerson and D'Attilio, 1969, and the recently recognized "*Murex*" *dipsacus* Broderip, 1833 (see Vokes, 1984, note 8). So, the presence of *Murexsul* in the Esmeraldas beds is not unexpected. What is a bit disappointing is that it is not the same species as is found in the Mexican Pliocene.

MUREXSUL PITTI E. H. Vokes, n. sp.
Plate 4, fig. 6

Description: Shell large for the New World members of the group, attaining a height of 30 mm; early whorls unknown, as is total number, but probably seven adult whorls. On earliest whorls preserved, spiral ornamentation consisting of two weak cords, best seen as spines where the varices are crossed, that at the shoulder stronger; a weak thread between the pair. On body whorl, three major spiral cords, each drawn out into spines at the varices; alternating with weaker cords, also making shorter spines where they cross the varices, each of these flanked by even smaller spinelets. One strong cord on siphonal canal, also drawn into spines at varices. Axial ornamentation of seven low varices on each whorl present; these visible principally where the spiral cords are developed into spines. The adapertural faces of the varices formed by multiple layers of shell material, each folded into the inner side of the open spines. Area between varices almost smooth, unworn examples probably covered with a shagreened surface. Aperture circular, no anal notch; inner lip free-standing, smooth; outer lip crenulated at outer margin into the varical spines, with about eight small nodules on inner side. Siphonal canal deflected at the distal end, forming a small umbilical chink.

Holotype: USNM 418049; height 30.0 mm, diameter 19.5 mm. (Plate 4, fig. 6)

Type locality: TU 1397, Esmeraldas beds; Quebrada Camarones, cut-bank on east side of canyon, which is at east side of the village of Camarones, 20 km (by road) east of bridge over Rio Esmeraldas, Prov. of Esmeraldas, Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Discussion: This new species, named for William D. Pitt, our co-worker in Ecuador, is represented by two battered specimens from Quebrada Camarones. It is most similar to *M. thalmanni* (Vokes, 1968), from the mid-Pliocene Agueguexquite Formation of Veracruz, Mexico, but differs by its much larger size – none of the dozen specimens we have from Mexico measures more than 16 mm in height. The surface in the latter is also more scabrous, with both major and minor spiral cords being well developed in the intervarical spaces.

Unfortunately, for paleo-depth indications, this new species is not closely related to any of the extant members of the genus. But most species occur in moderate depths (*M. octogonus*, the type species, 18-64 m; *jacquelinae*, 30-100 m; *aradasii*, 30-50 m; *medicago*, 91 m [50 fms]; *oxossi*, 25 m; *dipsacus*, 23 m [12 fms]) so we may assume that the Esmeraldas species did the same. Likewise, its presence does not help our understanding of the origins of the Esmeraldas fauna, as the genus is another Tethyan relic with worldwide distribution for most of the Cenozoic.

Genus MUREXIELLA
Clench and Pérez Farfante, 1945

Murexiella CLENCH and PÉREZ FARFANTE, 1945, Johnsonia, v. 1, no. 17, p. 49.

Type species: *Murex hidalgoi* Crosse, 1869, by original desig.

MUREXIELLA LAPPA (Broderip)
Plate 4, figs. 7, 8

Murex lappa BRODERIP, 1833, Zool. Soc. London, Proc., v. 2, p. 177; SOWERBY, 1834, Conch. Illus., *Murex*, pl. 60, fig. 15; REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 30, fig. 142; SOWERBY, 1879, Thes. Conch., v. 4, *Murex*, fig. 238.

Murex (Phyllonotus) lappa (Broderip). M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 13, pl. 13, fig. 7.

Ocenebra lappa (Broderip). KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 359, fig. 356.

Murexiella lappa (Broderip). VOKES, 1970, Veliger, v. 12, p. 325; KEEN, 1971, Sea Shells Trop. West Amer., ed. 2, p. 519, fig. 990; FAIR, 1976, *Murex* Book, p. 53, pl. 19, fig. 269; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World; p. 158, pl. 26, fig. 5;

VOKES, 1984, Shells and Sea Life, p. 212, pl. 2, fig. 7.

Lectotype (here designated): BMNH 1964439/1 (specimen figured by Sowerby, 1834, fig. 15); height 30.1 mm, diameter (including spines) 20.7 mm.

Type locality: Bahía de Sta. Elena, Ecuador.

Occurrence: Esmeraldas beds, Ecuador. Charco Azul Formation, Pleistocene; Panama. Recent, Gulf of California to Peru.

Figured specimens: Fig. 7, USNM 859924; height 14.7 mm, diameter 9.0 mm; locality TU R-166. Fig. 8, USNM 418050; height 13.7 mm, diameter 8.0 mm; locality TU 1397.

Discussion: In an earlier study of the west coast members of *Murexiella*, Vokes (1970, p. 327) suggested that several of the nominal species might be synonyms of *M. lappa*. But a subsequent visit to the British Museum (Nat. Hist.) disclosed that the type specimens of the various species are now being recognized in the collections with the result that *none* of the species originally listed as "probable" synonyms really is so. The type of "*Murex*" *dipsacus* Broderip, 1833, proves to be a *Murexsul* (see note 8 in Vokes, 1984, p. 215; pl.2, fig. 25 is the type specimen). "*Murex*" *exiguus* Broderip, 1833, is a valid species (type figured in Vokes, 1984, pl. 2, fig. 3) and "*Murex*" *radicatus* Hinds, 1844, is a synonym of it, with both being characterized by flattened spiral cords.

However, *M. lappa* may still be the "ancestor" of the lot, as the species that occurs in the Esmeraldas is *M. lappa*, and the three and one-half whorl protoconch indicates that this is the primitive form, with the widest geographical distribution. It lives from intertidally under stones (Panama, Vokes Coll.) to 37 m (Keen, 1971, p. 519). The three specimens taken at TU 1397 are undoubtedly transported elements of the fauna.

Genus ACANTHOTROPHON Hertlein and Strong, 1951

Acanthotrophon HERTLEIN and STRONG, 1951, Zoologica, v. 36 (East. Pacific Exped. New York Zool. Soc., XLIII. Moll. West Coast Mexico and Central Amer., Part X), p. 86.

Type species: *Trophon (Acanthotrophon) sorenseni* Hertlein and Strong, 1951, by original desig.

ACANTHOTROPHON SORENSENI (Hertlein and Strong)
Plate 3, figs. 6, 7

Trophon (Acanthotrophon) sorenseni HERTLEIN and STRONG, 1951, Zoologica, v. 36 (East. Pacific Exped. New York Zool. Soc., XLIII. Moll. West Coast Mexico and Central Amer., Part X), p. 86, pl. 2, fig. 1; KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 364, fig. 371 (holotype); KEEN, 1971, *ibid.*, ed. 2, p. 537, fig. 1043 (holotype).

Acanthotrophon sorenseni (Hertlein and Strong). RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 20, text-fig. 2 (holotype); RADWIN and D'ATTILIO, 1978, Tulane Stud. Geol. Paleont., v. 14, no. 3, p. 132; VOKES, 1980, Veliger, v. 23, p. 11, figs. 13, 14 (holotype), 15 (protoconch).

Acanthotrophon sentus Berry. RADWIN and D'ATTILIO, 1978, Tulane Stud. Geol. Paleont., v. 14, no. 3, in part, figs. 3, 3a only (*not* of Berry).

Holotype: CAS 9611; height 32.2 mm, diameter 20.0 mm.

Type locality: Gorda Banks, off Cabo San Lucas, Baja California Sur, Mexico.

Occurrence: Esmeraldas beds, Ecuador. Recent, Gulf of California.

Figured specimens: Fig. 6, USNM 418044; height 27.7 mm, diameter 18.1 mm; locality TU 1399. Fig. 7, CAS 9611 (holotype).

Discussion: Radwin and D'Attilio (1978, p. 132) have demonstrated that the species referred to the genus *Acanthotrophon* are not to be placed in the Trophoninae, but are members of the subfamily Muricopsinae. The type species, *A. sorenseni*, is the least muricopsine-appearing of the group, but other species, such as *A. carduus* (Broderip, 1833), have a much more scabrous, "typical" muricopsine shell.

There is another species of "Trophoninae" that is probably also to be referred to this genus. This is *Austrotrophon panamensis* Olsson (1971, p. 68, figs. 36, 37), described from 84 meters in the Bay of Panama. Although Olsson compared his new species to *Austrotrophon cerrosensis* (Dall, 1891), type of that genus, the Panamian shell lacks the varical flanges extended along the entire length of the siphonal canal, having instead only open spines at the shoulder. This is the only obvious conchological feature that seems to distinguish *Austrotrophon* from *Acanthotrophon*. But the two are readily separable by the radula (thaidine in *Au-*

strotrophon, muricopsine in *Acanthotrophon*) and the operculum (purpuroid in *Austrotrophon*, muricoid in *Acanthotrophon*). Unfortunately, the sole example of *A. panamensis* was not taken live and we are not sure of the proper placement for the species. But comparison of the shells (see pl. 3, figs. 7 and 8) seems to indicate that *A. panamensis* is closely akin to *A. sorenseni*. The difference is only in the degree of strength of the spiral cords on the body whorl. However, *A. sorenseni* is variable in this feature (see the two specimens illustrated in a previous paper on the subject – Vokes, 1980, figs. 13,14). The type of *A. panamensis* also lacks lirations within the outer lip but these are often lacking in specimens of *A. sorenseni* and are always only weakly developed (Vokes, 1980, p. 11).

Therefore, although not positive it is probable that *A. panamensis* is to be referred to *Acanthotrophon;* what is more, the form may be a synonym of the more northern *A. sorenseni*, but we lack comparative material to verify this. If the type specimen of *A. panamensis* had been taken in the Gulf of California it probably would have been referred to the latter species.

This possibility is supported by the discovery of a single specimen in the Esmeraldas beds that must be referred to *A. sorenseni*. As several other species found in the Esmeraldas beds today occur from the Gulf of California to Panama, the possibility that *A. sorenseni* also ranges this far exists and the probability that *A. panamensis* is a synonym is plausible.

The type specimen of *A. sorenseni* was taken in 109 m; the type of *A. panamensis* in 84 m. Other material of *A. sorenseni* was reported by Vokes (1980, p. 14) from 36 to 100 m. Thus, this is another of the moderately deep-water elements in the Esmeraldas fauna.

Subfamily THAIDINAE Jousseaume, 1888

Discussion: In a work on the muricid fauna of the Mio-Pliocene of the Dominican Republic, Vokes (in press) presents the arguments for and against recognition of a separate family Thaididae, in contrast to placement as a subfamily within the Muricidae, and concludes that the latter course is preferable. Therefore, the subfamily Thaidinae is defined as those muricid species that have a calcitic shell, a purpuroid operculum, and a pentacuspidate rachidian radular tooth. By this definition, there is no distinction by which the subfamily Ocenebrinae may be recognized, as it is identical except for the presence of varices, which can be demonstrated to be meaningless, and it is here synonymized with the subfamily Thaidinae.

Genus CERATOSTOMA Herrmannsen, 1846

Cerostoma CONRAD, 1837, Acad. Nat. Sci. Phila., Jour., v. 7, p. 263.

Type species: *Murex (Cerostoma) nuttalli* Conrad, 1837, by monotypy.

Ceratostoma HERRMANNSEN, 1846, Indicis Generum Malakoz., v. 1, p. 206. New name for *Cerostoma* Conrad, 1837, *non* Latreille, 1802.

Discussion: When the writer originally (Vokes, 1964) presented a revision of the supraspecific groups of what was then the Muricidae and "Tritonaliinae" (now Ocenebrinae, ICZN Opinion 886, 1969) she placed all of the ocenebrine genera with a labral tooth (or ceratus) in the genus *Jaton* Pusch, 1837, with *Ceratostoma* and *Pterorytis* Conrad, 1863, as subgenera. But this is certainly an artificial grouping, as the labral tooth appears repeatedly in various muricid taxa and its presence clearly does not imply close relationship. Thus, it seems now that *Jaton* is a *Pteropurpura* with a tooth; *Pterorytis* is an *Ocinebrellus* with a tooth; and *Ceratostoma* is an *Ocenebra* with a tooth.

Unfortunately, because of the Law of Priority, in every case mentioned above, the toothed form is an earlier name. Therefore, one has the choice of making these well-known junior taxa subgenera of the older named taxa, or accepting all as valid genera. The latter course will be followed here.

In the case of *Ceratostoma* and *Ocenebra* there are other substantive differences, including the usually three (*C. rorifluum* has four), usually winged (but not always) varices, and especially the presence of strong denticles on the inner side of the outer lip in *Ceratostoma*, which are not present in

Ocenebra. The shell in *Ceratostoma* is also much less scabrous than in *Ocenebra*.

CERATOSTOMA NOTIALE E.H. Vokes,
n. sp.
Plate 5, figs. 6, 7

Description: Shell of average size, probably five teleoconch whorls in adult and a protoconch of two and one-half large whorls (diameter 1.5 mm). Spiral ornamentation on the first postnuclear whorl of two strong cords, gradually weakening until by third or fourth whorl only faint grooves demarcating the former cords, about a dozen on immature specimens, but adult shell almost completely smooth. Axial ornamentation on first teleoconch whorl of about ten equal ribs, these diminishing in number on each successive whorl and developing into rounded varices, with four on the body whorl of the adult. Varices on mature whorls little more than rounded ribs with a small flange at the shoulder, but that at aperture forming a moderately wide, thickened varix, the apertural face consisting of multiple shell laminae, each crenulated into the almost invisible spiral cords. At juncture of body whorl and siphonal canal a narrow, sharp labral tooth, directed adaperturally, with the varix infolded behind it. Aperture ovate, inner lip smooth, free-standing anteriorly, appressed posteriorly, no anal notch. Outer lip crenulated at margin, inner side with seven or eight strong elongate denticles. Siphonal canal of moderate length, sealed over by an extension of shell material from columellar side, distal end recurved. Shell composed of calcite on exterior, with aragonitic cortex, causing the surface to decorticate readily.

Holotype: USNM 418055; height 19.5 mm, diameter 11.0 mm. (Plate 5, fig. 6)

Paratype: USNM 418056; height (incomplete) 22.5 mm, diameter (incomplete) 11.0 mm; locality same as holotype. (Plate 5, fig. 7)

Type locality: TU 1399, Esmeraldas beds; roadcut on west side of village of Camarones, which is 20 km (by road) east of the bridge over Rio Esmeraldas, Prov. of Esmeraldas, Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Discussion: One of the unusual finds in the Esmeraldas beds is a new species of *Ceratostoma*, most closely related to the common *C. nuttalli* (Conrad), which generally occurs subtidally in the cooler waters of the California Province, extending only as far south as Santa Maria Bay (*fide* McLean, 1978, p. 42), Baja California (the more southerly non-winged form, which extends the range to the southern part of Baja California only, is referred to *C. monoceros* [Sowerby] or *C. unicorne* [Reeve] – see Keen, 1971, p. 534).

Although widespread in the fossil record, with species in the Late Oligocene of North Carolina and the Miocene of Italy, Austria, Mexico, California, and the Far East, by Pleistocene time the group of *Ceratostoma* seems to have constricted its range to the northern Pacific, from Korea and Japan to California. This is the first report of any species in South America – hence the name *notialis*, meaning *southern*.

This new species is most closely related to the California *C. nuttalli* (see pl. 5, fig. 8) but may be distinguished by the (presumably) four varices in the adult (our only adult specimen is incomplete but it seems to have had four varices, as do the immature examples) and by the nature of the protoconch, which in *C. nuttalli* is smaller (about one-half the diameter, or 0.7 mm in *C. nuttalli*) and of only one and one-half almost keeled whorls with much the same appearance as the protoconch of *Ocenebra seftoni* Chace, as figured by Radwin and D'Attilio (1976, text-fig. 74). The protoconch in *C. notiale* is very large for a muricid, and has exactly the appearance of *Phyllonotus pomum* (Gmelin), also as figured by Radwin and D'Attilio (*ibid.*, text-fig. 54).

Except for these differences, the shells are extremely similar and the assumption is made that the two probably lived in similar fashion. All living *Ceratostoma* species tend to occur in shallower water, examples taken from deeper water have conspicuous extended varices. This assessment agrees with the presence of five of the six known specimens of the Ecuadorian form coming from TU 1399, the more shallow-water gravity-flow (see Introduction). One juvenile was found at Quebrada Camarones (TU 1397).

Genus PTEROPURPURA Jousseaume,
1880

Pteropurpura JOUSSEAUME, 1880, Le Naturaliste, Année 2, no. 42, p. 335.

Type species: *Murex macropterus* Deshayes, 1839, by original desig.

Subgenus PTEROPURPURA s.s.

PTEROPURPURA (PTEROPURPURA) MARKSI Olsson

Plate 5, fig. 5

Pteropurpura marksi OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 139, pl. 29, fig. 6.

Holotype: USNM 643955; height 54.3 mm, diameter 37.1 mm.

Type locality: Esmeraldas beds; Punta Gorda, Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Figured specimen: Fig. 5, USNM 418054; height 38.0 mm, diameter 25.5 mm; locality TU 1397.

Discussion: When Olsson described *Pteropurpura marksi* he compared it only to *Purpurellus pinniger* (Broderip, 1833), which is not even in the same subfamily. Perhaps *Purpurellus pinniger* is the only trialate species that occurs off Ecuador today, but this is scarcely a valid criterion. Certainly *Pteropurpura centrifuga* (Hinds, 1844), which extends as far south as Panama, would be a better choice, the principal difference being the presence in the latter of stronger spiral cords that cause the varices to have three distinct digitations along the margins. But the species that bears the most resemblance to *P. marksi*, indeed from which it scarcely can be separated, is the Californian *P. trialata* (Sowerby, 1834) (cf. pl. 5, figs. 4, 5).

According to Olsson (1964, p. 139), this species was common at Punta Gorda (he had 10 specimens) and it is also at Quebrada Camarones, where we have 20 examples. There are none, however, from the more shallow fauna at TU 1399, suggesting that this is another of the species from a slightly deeper water fauna. In California, the species *P. trialata* is found from intertidally to somewhat offshore (18 m [10 fms], Keep, 1935, p. 235). But its more southern congener *P. centrifuga* is commonly taken by shrimpers in depths of 80-180 m (45-100 fms, DuShane and Poorman, 1976, p. 428). The nearest geographical occurrence to the Ecuadorian coast is *P. deroyana* Berry, 1968, which differs only subspecifically if at all from *P. centrifuga*, described from 46 m (25 fms) in the Galápagos Islands. So, the *Pteropurpura* line probably follows a temperature cline from deeper water off Ecuador to shallower water in California.

Subgenus OCINEBRELLUS Jousseaume, 1880

Ocinebrellus JOUSSEAUME, 1880, Le Naturaliste, Année 2, no. 42, p. 335.

Type species: *Murex eurypteron* Reeve, 1845 (= *M. falcatus* Sowerby, 1834), by original desig.

PTEROPURPURA (OCINEBRELLUS) ECUADORIA (Olsson)

Plate 5, figs. 1, 2

Trophon ecuadorius OLSSON, 1964, Neogene Moll. Northwest Ecuador, p. 140, pl. 29, figs. 7, 7a, 7b.

Holotype: USNM 643958; height 49.0 mm, diameter 33.3 mm.

Type locality: Esmeraldas beds; Punta Gorda, Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Figured specimens: Fig. 1, USNM 418052; height (incomplete) 36.3 mm, diameter 28.0 mm. Fig. 2, USNM 418053; height 18.4 mm, diameter 9.6 mm; locality of both, TU 1397.

Discussion: Although Olsson named this species as *Trophon* and compared it to *T. lamellosus* (Gmelin, 1791), there is only a superficial resemblance to that group. In the trophons, the varical formation always consists of a single lamina of shell material, overlapped in an adapertural direction. This is true in all of the genera of true Trophoninae, as well as the pseudotrophons, including *Stramonitrophon* Powell, 1951 (of which *lamellosus* is the type, as *M. laciniatus*) and *Austrotrophon* Dall, 1902, which are both thaidines in disguise (see Radwin and D' Attilio, 1976, p. 176), most closely related to *Forreria* Jousseaume, 1880.

The Ecuadorian species shares with the above-mentioned groups a calcitic shell, which decorticates readily, but it also has varices with a thickened apertural face and a closed siphonal canal. The calcitic shell, seven wing-like varices and closed canal indicate placement in the thaidine subgenus *Pteropurpura (Ocinebrellus)*. Indeed, the species has a marked resemblance to the Japanese *P. (O.) acanthophora* (A. Adams, 1863) (see the type specimen of the latter: pl. 5, fig. 3). Although this species usually has been placed in the synonymy of *"Murex" falcatus* Sowerby, 1834, type of *Ocinebrellus*, *P. acanthophora* differs from *P. falcata* and *P. adunca* (Sowerby, 1834), a closely related form, in having a larger, more open aperture, with small denticles on the inner side. The Ecuadorian species, in turn, differs from *P. acanthophora* in having an even larger aperture, which sometimes has small denticles, but not in all specimens (including that figured here). *Pteropurpura adunca* and *P. falcata* usually have four varices per whorl; *P. acanthophora* has five, and *P. ecuadoria* has about seven in the adult, although all the species tend to have a larger number in the earlier stages, eight or nine in *P. ecuadoria*.

This is the most common muricid at Quebrada Camarones; between Pitt's and our collections we have 61 specimens. But there are only four from TU 1399, emphasizing what was said in the Introduction concerning the differences in fauna between the two localities. Olsson (1964, p. 140) had three examples from Punta Gorda, and Jung collected two at the Trans-Ecuadorian Pipeline locality mentioned under *Muricopsis oxytata* (above).

Depth data for the Japanese species is sketchy, but in the American Museum of Natural History and the Vokes collections *P. adunca* seems to be the shallower form (6-45 m) and *P. falcata* is slightly deeper (70-130 m). *Pteropurpura acanthophora* was described from 37 fms (68 m), suggesting that it too is a deeper form, and this is probably the depth that the Quebrada Camarones material originally came from (see Introduction).

Genus VITULARIA Swainson, 1840

Vitularia SWAINSON, 1840, Treatise on Malacology, p. 297.

Type species: *Vitularia tuberculata* Swainson, 1840, by original desig. (= *Murex vitulinus* Lamarck, 1816, *fide* Swainson, = *Murex miliaris* Gmelin, 1791).

VITULARIA SALEBROSA (King and Broderip)
Plate 6, figs. 7-9; text fig. 14

Murex salebrosus KING and BRODERIP, 1832, Zool. Jour., v. 5, p. 347; SOWERBY, 1834, Conch. Illus., *Murex*, pl. 58, fig. 5 (as "var."); pl. 65, fig. 48; KIENER, 1843, Coq. Viv., v. 7, *Murex*, p. 121, pl. 47, figs. 1, 1a; REEVE, 1845, Conch. Icon., v. 3, *Murex*, pl. 24, figs. 98a, 98b.

Murex (Vitularia) salebrosus King and Broderip. ADAMS and ADAMS, 1853, Gen. Recent Moll., v. 1, p. 74; TRYON, 1880, Man. Conch., v. 2, p. 133, pl. 35, figs. 394, 396, 398 (as *salebrosa*).

Vitularia salebrosa (King and Broderip). CARPENTER, 1857, Cat. Mazatlan, p. 485; BRANN, 1966, Illus. to "Cat. Mazatlan," pl. 51, figs. 612, 2290, 2294, 2298, 2301, 2302; KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 363, fig. 370; KEEN, 1971, *ibid.*, ed. 2, p. 536, fig. 1040; DUSHANE and POORMAN, 1967, Veliger, v. 9, p. 429; VOKES, 1967, Tulane Stud. Geol., v. 5, no. 2, p. 90; RADWIN and D'ATTILIO, 1976, *Murex* Shells of the World, p. 173, pl. 7, fig. 14, text-figs. 113 (radula), 114 (protoconch), 115 (microsculpture); FAIR, 1976, *Murex* Book, p. 74, pl. 20, fig. 283; VOKES, 1977, Tulane Stud. Geol. Paleont., v. 13, no. 4, p. 192, text-fig. 5 (protoconch); VOKES 1986, Conch. Amer. Bull., v. 14, no. 2, p. 19, figs. 1, 7; BALDAZZI *et al.*, 1986, La Conchiglia, v. 18, nos. 212-213, p. 6.

Vitularia cf. *salebrosa* (King and Broderip). OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, p. 170.

Vitularia salebrosa extensa M. SMITH, 1947, Nautilus, v. 61, p. 54, pl. 2, fig. 5.

Vitularia ecuadorana MARKS, 1951, Bulls. Amer. Paleontology, v. 33, no. 139, p. 389, pl. 50, fig. 12; VOKES, 1967, Tulane Stud. Geol., v. 5, no. 2, p. 90; VOKES, 1977, Tulane Stud. Geol. Paleont., v. 13, no. 4, p. 192 (as "*equadorana*"); VOKES, 1986, Conch. Amer. Bull., v. 14, no. 2, p. 19, fig. 2 (holotype).

Muricidea (Vitularia) salebrosa (King and Broderip). M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 12, pl. 4, fig. 11.

Vitularia linguabison VOKES, 1967, Tulane Stud. Geol., v. 5, no. 2, p. 91, text-fig. 1; VOKES, 1977, Tulane Stud. Geol. Paleont., v. 13, no. 4, p. 192, text-fig. 4; VOKES, 1986, Conch. Amer. Bull., v. 14, no. 2, p. 19, figs. 4, 8; PETUCH, 1986, Jour. Coastal Resh., v. 2, no. 4, p. 396, figs. 8-11 (figs. 10, 11 as *V.* cf. *linguabison*).

Lectotype (?): BMNH 1986297; height 90.1 mm, diameter 50.3 mm ("long. 3 7/16; lat. 2; poll."). See discussion below.

Type locality: "Southern coasts of South America" (King and Broderip, 1832); "Panama (found under stones); Cuming" (Reeve, 1845, pl. 24).

Occurrence: Daule Formation (of Marks, 1951) and Esmeraldas beds, Ecuador. Pinecrest beds, Florida; Agueguexquite Formation, Mexico; Pliocene. Charco Azul Formation, Panama; Pleistocene. Recent, Baja California to Súa, Ecuador (TU R-532), and Galápagos (*fide* Radwin and D'Attilio, 1976, p. 174).

Figured specimens: Fig. 7, PRI 20481 (holotype – *V. ecuadorana* Marks); height 59.1 mm, diameter 30.5 mm; locality, Daule,

Text-figure 14. *Vitularia salebrosa* (King and Broderip). a) Illustration from Sowerby, 1834, *Conchological Illustrations*, pl. 65, fig. 48 (height 90 mm). b,c) Possible type material in British Museum (Natural History); b, lectotype?; height 90.1 mm, diameter 50.3 mm; c, paralectotype?; height 79.7 mm, diameter 36.2 mm.

Ecuador. Fig. 8; USNM 418060; height 20.9 mm, diameter 13.8 mm; locality TU 1399. Fig. 9, USNM 418061; height 19.1 mm, diameter 10.6 mm; locality TU 1399.

Discussion: The writer (Vokes, 1986) has discussed the identity of three "species" of *Vitularia: V. linguabison* Vokes, from the mid-Pliocene beds of Florida and Mexico; *V. ecuadorana* Marks, from the mid-Pliocene "Daule Formation" of Ecuador; and the Pleistocene to Recent *V. salebrosa*. The conclusion was that all three are the same species, for which *V. salebrosa* is the oldest name.

This conclusion was largely brought about by the discovery, in the Esmeraldas beds, of two small examples of *Vitularia*, one with protoconch preserved, that demonstrate the link between *V. ecuadorana* and *V. salebrosa*. At about the same time, additional high-spired examples of the Atlantic *V. linguabison* indicated that this form was also part of the same complex. As the Atlantic and Pacific *V. linguabison* and *V. ecuadorana* are now known to be correlative in age, this is not unreasonable.

Thus, we have another species in common between the Esmeraldas beds and the mid-Pliocene Pinecrest beds of Florida.

According to Keen (1971, p. 536), the Recent *V. salebrosa* ranges only as far south as Gorgona Island, Colombia; however, Baldazzi *et al.* (1986, p. 6) have reported the occurrence at Camarones, Ecuador, and we have beach specimens from Súa, Ecuador (TU R-532). This is another of the down-slope transported elements of the Esmeraldas fauna; DuShane and Poorman (1967, p. 429) report that the species was taken "just below low tide on base of gorgonians; dredged 15-17 fms [27-31 m] on rock bottom."

In the collections of the British Museum (Nat. Hist.) there is a lot of three specimens, which may be the type material of this species. The original label with these shells reads: "*M. salebrosus* King, Zool. Jour., p. 347, Sow. Con. Ill. f. 5 var. f. 48 – Southern coast of America." But examination of the specimens shows that the Sowerby drawing given in fig. 48 is evidently a composite of the two larger shells (see text-fig. 14); however, the third is not the one in his fig. 5. Because the dimensions of the largest specimen so nearly match those in the original description, it seem probable that this is the type lot, and the largest specimen is here tentatively designated as lectotype.

Subfamiy TYPHINAE Cossmann, 1903

Genus TYPHIS Montfort, 1810

Typhis MONTFORT, 1810, Conchyl. Syst., v. 2, p. 614-615.

Type species: *Typhis tubifer* (Bruguière, 1792), by original desig.

Subgenus TALITYPHIS Jousseaume, 1882

Talityphis JOUSSEAUME, 1882, Rev. Mag. Zool., (Ser. 3) v. 7, p. 338.

Type species: *Typhis expansus* Sowerby, 1874, by original desig.

TYPHIS (TALITYPHIS) LATIPENNIS Dall

Plate 6, figs. 1, 2; text-fig. 15

Typhis latipennis DALL, 1919, U. S. Natl. Mus., Proc., v. 56, no. 2295, p. 339; M. SMITH, 1953, Illus. Cat. Recent Species Rock Shells, p. 18, pl. 14, fig. 9 (holotype).

Typhis (Talityphis) latipennis Dall. WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 295; KEEN, 1943, San Diego Soc. Nat. Hist., Trans., v. 10, no. 2, p. 53, pl. 3, figs. 17, 21, 24, 25; KEEN, 1958, Sea Shells Trop. West Amer., ed. 1, p. 367, fig. 382; KEEN, 1971, *ibid.*, ed. 2, p. 539, fig. 1049; KEEN and CAMPBELL, 1964, Veliger, v. 7, p. 50, pl. 9, fig. 13; Vokes, 1984, Shells and Sea Life, v. 16, no. 11, p. 214, pl. 1, fig. 25.

Talityphis latipennis (Dall). RADWIN and D'ATTILLIO, 1976, *Murex* Shells of the World, p. 201, pl. 30, figs. 13, 14, text-fig. 147 (radula).

Holotype: USNM 96653; height (incomplete) 28.9 mm, diameter 23.8 mm (this specimen is now lost, see discussion below).

Type locality: U. S. Fish Comm. Station 2822, Bahía de La Paz, Baja California, 21 fms (38 m).

Occurrence: Esmeraldas beds, Ecuador. Gatun Formation, Panama; Pliocene. Recent, Gulf of California to Panama.

Figured specimens: Fig. 1, USNM 418057; height 27.0 mm, diameter 20.4 mm; locality TU 1397. Fig. 2, USNM 859926; height 32.5 mm, diameter 19.0 mm; locality, El Dorado, Jalisco, Mexico, 51 m.

Discussion: In the Plio-Pleistocene of the western Atlantic there are three species of *Talityphis* that have given authors no end of trouble, as they are all extremely similar in morphology. The oldest (stratigraphically) of the group is *T. obesus* Gabb, 1873, described from the Early Miocene Baitoa Formation of the Dominican Republic (see Vokes, 1979, p. 112), but also occurring in the correlative Early Miocene Chipola Formation of Florida and the mid-Pliocene Gatun Formation of Panama. But the first named is *Typhis alatus* Sowerby, 1850, which was described from the Gurabo Formation of the Dominican Republic but also has been taken in the Gatun (Vokes, 1983, p. 124) and in the "Picaderos" [=Onzole] Formation of Ecuador by Olsson (1964, p. 141). Because of priority, the name *T. alatus* has been used for a variety of occurrences of other species of *Talityphis*, such as that of *T. expansus* Sowerby, 1874, in the Pleistocene of Bowden, Jamaica (Woodring, 1928, p. 294, pl. 18, figs. 3, 4, as *T. alatus obesus*), and Moín, Costa Rica (Olsson, 1922, p. 132, pl. 13, fig. 15), and in the Recent (Bullis, 1964, p. 107).

Although all are similar, there are differences that may be used to distinguish these three forms. *Typhis obesus*, as the name indicates, is very inflated, with a relatively low spire compared to the other two. Between the two narrower, high-spired forms, *T. alatus* may be distinguished immediately by the swelling or axial node adjacent to the intervarical tube. It is also less triangular in outline than either *T. obesus* or *T. expansus*.

Into this picture comes *Typhis latipennis* Dall, heretofore only known from the Recent fauna from Baja California to Panama. But in the collections from the Esmeraldas area we have several specimens (TU 1397-3; TU 1399-6) that prove to be *T. latipennis* and not, as might be anticipated, either *T. obesus* or *T. alatus*. Again, the differences between the forms are extremely subtle, and no one has ever attempted to define them. Dall, in the original description of *T. latipennis* simply says: "It is obviously distinct from either of the species yet described from this region." Radwin and D'Attilio (1976, p. 236) in their description of *Talityphis perchardei* (a synonym of *T. expansus;* see Vokes, 1984, note 17) say only that their new species "must be considered a Caribbean cognate of the Panamic *T. latipennis*."

In a comparison of cognate species, the writer (Vokes, 1984, pl. 1, figs. 25, 26) has given illustrations of *T. latipennis* and *T. expansus*, which show that the main difference between the two is a less triangular shape in *T. expansus* (due to the fact that the varix is less recurved dorsally) with a greater distance between the tube and the varical spine and stronger spiral ornamentation also in the Caribbean species. The aperture is relatively larger in *T. latipennis*, and this suggests that *T. latipennis* is closer to *T. obesus* than it is to *T. expansus*. If one compares the specimen of *T. obesus* figured by Vokes (1983, pl. 1, fig. 4) from the Gatun Formation, with *T. latipennis*, it may be seen that the two differ only in the even larger aperture in *T. obesus*. The not-so-close relationship between *T. latipennis* and *T. expansus* is more dramatically demonstrated by illustrations of the quite different radulae of the two species, given by Radwin and D'Attilio (1976, text-figs. 147 and 192, respectively).

Because of the same confusion of *T. alatus/obesus* and *T. expansus*, Keen (1943, p. 54) compared her new species *T. lampada* to the specimen of "*T. alatus*" figured by Olsson (1922, pl. 13, fig. 15) from the "Gatun Formation" of Toro Cay, Panama. But Olsson's shell is a specimen of *T. expansus* from the Pleistocene Moín Formation and not *T. obesus* (or *T. alatus*). Keen's *T. lampada* is very close to *T. obesus*, differing in having an even larger aperture than either *T. obesus* or *T. latipennis*. Thus, one may make the assumption that *T. obesus* was the ancestral stock, which entered the Pacific early in the Neogene, there to give rise to *T. lampada* in the north (Round Mountain Silt, Miocene, of Kern Co., California) and *T. latipennis* in the more tropical area.

Text-figure 15. *Typhis (Talityphis) latipennis* Dall. Holotype, USNM 96653; height (incomplete) 28.9 mm, diameter 23.8 mm (X 2).

In the Pleistocene Charco Azul Formation of the Burica Peninsula, Panama/Costa Rica, there is another species of *Talityphis: T. olssoni* Keen, 1943 (new name for *T. costaricensis* Olsson, 1942b, *non T. costaricensis* Olsson, 1922). Known only from the holotype (PRI 4064) this species is much like *T. latipennis*, but seems to have a narrower shell, with stronger spiral ornamentation. Without more material it will not be placed in synonymy, but the possibility should be noted.

Typhis (Talityphis) latipennis is another Esmeraldas species that occurs today only as far south as Panama. It is generally found in moderate depths of about 50 m.

This is the same depth as the Atlantic *T. expansus* and so it is assumed that *T. latipennis* is the ecologic cognate of *T. expansus*, even though it may result from parallel evolution from an ancestral *T. obesus*, which appears to have occupied much shallower water.

The holotype of *T. latipennis* was a badly damaged specimen, with most of the siphonal canal missing. The verb *was* is used here because while the specimen (USNM 96653) was in the hands of the writer, in preparation of this paper, it suffered what insurance companies term a "mysterious disappearance." In a word, it was lost! Dall never figured the species, but an apertural view of the holotype was subsequently figured by M. Smith (1953, pl. 14, fig. 9). An abapertural view is given here in text-fig. 15. A replacement specimen has been placed in the collections of the USNM (USNM 859929), but it is not a neotype, as the ICZN Code (Art. 75a) specifically advises that a neotype is only to be designated when it is necessary "in the interests of stability of nomenclature." As there is no question about the identity of *T. latipennis* Dall, the replacement is simply a "reference specimen."

TYPHIS (TALITYPHIS) ALATUS Sowerby
Plate 6, figs. 3, 4

Typhis alatus G. B. SOWERBY, 1850, Geol. Soc. London, Quart. Jour., v. 6, p. 48, pl. 10, fig. 4.

Typhis (Talityphis) alatus Sowerby. OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 141; GERTMAN, 1969, Tulane Stud. Geol. Paleont., v. 7, no. 4, p. 159, text-fig. 3 (holotype); VOKES, 1983, Tulane Stud. Geol. Paleont., v. 17, no. 4, p. 124, pl. 1, figs. 1-3.

Holotype: British Museum (Nat. Hist.) GG. 20084; height 29.5, diameter 18.0 mm.

Type locality: Gurabo Formation; Rio Yaque, Dominican Republic (designated by Gertman, 1969, p. 160).

Occurrence: Esmeraldas beds, Angostura, and "Picaderos" [=Onzole] formations, Ecuador. Unnamed Middle Miocene Formation, Dominican Republic. Gatun Formation, Panama; Gurabo Formation, Dominican Republic; Pliocene.

Figured specimens: Fig. 3, USNM 418058; height 26.7 mm, diameter (incomplete) 13.2 mm; locality TU 1399. Fig. 4, USNM 323910; height 27.7 mm, diameter 17.3 mm; locality TU 1212.

Discussion: Olsson (1964, p. 141) reported a single specimen of *Typhis alatus* from the "Picaderos" Formation on the Rio Santiago, Ecuador. Although it is obvious from his synonymy that he included both *T. obesus* and *T. expansus* in his concept of the species, examination of his specimen (USNM 645453) shows that it is *T. alatus*, although of smaller than normal size.

Collections made by us in Ecuador yielded a second specimen of *T. alatus* from the Angostura Formation at Punta Verde (TU 1507), and a third rather battered and incomplete example from TU 1399, west of Camarones. The presence of *T. alatus* in these beds is a slight geographic extension of range, but as the species occurs in the Middle Miocene of the Dominican Republic (unnamed formation, figured in Vokes, in press), the Early Pliocene Gurabo Formation and in the mid-Pliocene Gatun Formation of Panama (see Vokes, 1983), it does not provide any new stratigraphic information.

In the Atlantic the species usually is found in deeper water deposits than the correlative *T. obesus*, although we have a single example from the shallowest beds of the Gatun (TU 1431; see Vokes, 1983, pl. 1, fig. 2). The beds at Picaderos would seem to be similar in environment of those of the Gurabo Formation, as Olsson (1964, p. 10) listed *Sconsia laevigata* (Sowerby), a common Gurabo form that usually occurs with *T. alatus* in beds that are judged to be deposited in between 50 and 150 meters, and *Gemmula vaningeni* (Brown and Pilsbry), which the writer has previously noted (Vokes, 1983, p. 123) is most closely related to the Recent *G. hindsiana* Berry, living in depths of 40 to 70 meters. Presumably the specimen at Camarones was collected by a gravity-flow in its passage through waters of these depths.

V. LOCALITY DATA

The following are Tulane University fossil locality numbers:

202. Caloosahatchee Fm., south bank of Caloosahatchee River, about two miles west of La Belle (SE 1/4 Sec. 12, T43S, R28E), Hendry Co., Florida.

541. Pinecrest beds and Caloosahatchee Fm. mixed, Miami Canal spoil banks, two miles

north of pumping station at Broward County line, Palm Beach Co., Florida.

705. Bowden Fm., type locality, Bowden, east of Port Morant, Parish of St. Thomas, Jamaica.

726. Caloosahatchee Fm., Hendry County rock pit, 1/2 mile north of Florida Highway 80, three miles west of La Belle (SE 1/4 Sec. 14, T43S, R28E), Hendry Co., Florida.

757. Gatun Fm., roadcut on south side of Boyd-Roosevelt Highway at junction of road to "Refinería Panamá, S.A.," just east of Cativá, Prov. of Colón, Panamá.

768. Caloosahatchee Fm. and Bermont Fm. mixed, spoil banks north side of Caloosahatchee River, 5 1/2 miles west of Ortona Lock (NW 1/4 Sec. 35, T42S, R29E), Glades Co., Florida.

797. Pinecrest beds, material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T49S, R32E), Collier Co., Florida.

953. Moín Fm., type locality, Moín Hill, railroad cut and adjacent ditches on road to Sandoval, 4.5 km west of Puerto Limón, Costa Rica.

954. Moín Fm., hill cut immediately behind Standard Fruit Co. box factory, just west of cemetery at Pueblo Nuevo, about 2 km west of Puerto Limón, Costa Rica.

958. Gatun Fm., hillslope on east side of road from Boyd-Roosevelt Highway to "Refinería Panamá, S.A.," about 1/2 km north of junction, just east of Cativá, Prov. of Colón, Panamá.

1000. Pinecrest beds, borrow pit at east end of 17th street, (variously Warren Bros., Macasphalt, etc.), (T36S, R19E), about 8 miles east of U.S. Highway 301 at Sarasota, Sarasota Co., Florida.

1212. Gurabo Fm., Rio Gurabo, east bank, third bluff below the ford on Los Quemados-Sabaneta road, Dominican Republic.

1240. Moín Fm., Barrio Los Corales, top of hill at end of road that passes Standard Fruit Co. box factory (see TU 954), 1.8 kms north of main highway at Pueblo Nuevo, which is 2 kms west of Puerto Limón, Costa Rica.

1307. Moín Fm., hill top approximately halfway between Puerto Limón and Barrio Los Corales and about 0.5 km north of highway at Pueblo Nuevo, Costa Rica.

1397. Esmeraldas beds, Quebrada Camarones, cut-bank on east side of canyon, which is at east edge of village of Camarones, 20 km (by road) east of bridge over Rio Esmeraldas, at Esmeraldas, *or* approximately 10 km east of mouth of Rio Esmeraldas, Prov. of Esmeraldas, Ecuador.

1398. Esmeraldas beds, roadcut at mouth of Quebrada Camarones, east side of bridge at village of Camarones, which is 20 km (by road) east of bridge over Rio Esmeraldas, at Esmeraldas, Prov. of Esmeraldas, Ecuador.

1399. Esmeraldas beds, roadcut on west side of village of Camarones, which is 20 km (by road) east of bridge over Rio Esmeraldas, at Esmeraldas, Prov. of Esmeraldas, Ecuador.

1431. Gatun Fm., hilltop construction site, 0.5 km northwest of intersection of Boyd-Roosevelt Highway and road to Puerto Pilon, at Sabanita, Prov. of Colón, Panamá.

1432. Gatun Fm., north side of Boyd-Roosevelt Highway, clearing behind Residential Martin Luther King (formerly Palo Quemado), approximately 1.5 km east of junction of road to "Refinería Panamá, S.A.," at Cativá, Prov. of Colón, Panamá.

1433. Gatun Fm., north side of Boyd-Roosevelt Highway, clearing behind Urbanization San Martin, approximately 0.5 km east of junction of road to "Refinería Panamá, S.A." at Cativá, Prov. of Colón, Panamá.

1493. Pinecrest beds, Arvita Pit, on Bird Road (= W. 40th St.), approximately 5 miles west of Florida Turnpike, on west side of Coral Gables, Dade Co., Florida.

1499. Charco Azul Fm., Burica Peninsula, beds exposed at low tide, 7 km south of dock at Charco Azul Terminal, Puerto Armuellas, Panamá.

1507. Angostura Fm., Punta Verde, large point just east of Rio Verde, or about 22 km east of Rio Esmeraldas, Prov. of Esmeraldas, Ecuador.

The following are Tulane University Recent locality numbers:

R-56. Beach at Playa de Boca Grande, about 10 miles south of Tumaco, Colombia.

R-109. Fill for refinary, Bahia las Minas, Isla Payardi, Panamá. (Radiocarbon dated at 7000 years B.P.)

R-166. Barra de Navidad, Jalisco, Mexico; rocky point across inlet from main sand bar.

R-173. Puntarenas, Costa Rica.

R-186. Rocks and beach in front of Palo Seco Leper Colony (formerly Canal Zone), Panamá (Pacific Ocean side).

R-381. Beach at Salinas, Bahía de Sta. Elena, Prov. of Guayas, Ecuador.

R-478. Beach at Puerto de Cayo, Prov. of Manabi, Ecuador.

R-484. Beach at Camarones, fishing village about 10 km (airline) east of Rio Esmeraldas, Prov. of Esmeraldas, Ecuador.

R-532. Beach at Súa, which is *ca.* 25 km (airline) west of Esmeraldas, Prov. of Esmeraldas, Ecuador.

R-552. Ayangue, southern end of Ensenada de Valdivia, Prov. of Guayas, Ecuador.

R-553. La Libertad, beach and rocks in front of hotel Samarina, Bahía de Sta. Elena, Prov. of Guayas, Ecuador.

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REVIEW

MIGRATION OF SEISMIC DATA, edited by Gerald H. F. Gardner. Published by the Society of Exploration Geophysicists, Tulsa, Oklahoma, Geophysics Reprint Series No. 4, 1985, viii + 462 pp., illustrated, paperbound, $19.00

This reprint volume includes thirty-three papers by a variety of authors, originally published between 1937 and 1984 and chronologically arranged to illustrate the evolution of migration interpretative concepts and methodology through the years. The original ruler-and-compass constructions used in the twenties and thirties have progressed to computer algorithms for depth migration in three dimensions in present interpretative seismology. This reprint series is quite useful in making reference material available on various subjects. The present volume is recommended for reference purposes.

—H.C.S.