

NATICIDAE (MOLLUSCA: MESOGASTROPODA) FROM THE NEOGENE  
OF NORTHWESTERN ECUADORWILLIAM D. PITT<sup>1, 2</sup> and LOIS J. PITT<sup>2</sup>

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## I. ABSTRACT

The Bolivar Trough from Colombia to Ecuador was the longest lasting Neogene seaway allowing for the free movement of molluscan species between the Caribbean and Pacific faunal provinces. This paper is intended to show the relationship of the Ecuadorian Neogene naticid fauna to the fossil and Recent Caribbean and eastern Pacific faunas.

The naticid fauna from the Neogene formations of northwestern Ecuador consists of 17 species, including eight known from the Recent fauna of the Tropical East Pacific, four previously known only from the Caribbean Tertiary, one Caribbean Tertiary and Recent species, previously reported from Ecuador, three previously known only from the Ecuadorian Neogene, and one from the Tertiary of the northern Pacific.

Although it was anticipated that a majority of the species from the Ecuadorian Neogene would have their origin in the Caribbean fauna, only five of the seventeen species can be considered Caribbean species, with only one of those occurring in the Recent Caribbean fauna; however, several

others have analogues in the Caribbean and may have originated there, and two have California-Japanese relationships.

## II. INTRODUCTION

It is generally accepted that for much of the Tertiary Period the Caribbean Sea was connected to the Pacific Ocean through the Isthmus of Panamá. Saito (1976) has suggested that the closure took place about 3.5 million years ago. Jones and Hasson (1985) discussed reasons for accepting times between 5.7 Ma and 1.8 Ma, and concluded that 3.5 Ma was the most likely time when the migration of species ended, with total emergence of the isthmus at 3.0 Ma or later.

The faunas of the Neogene formations of northwestern Ecuador have a fairly large proportion of their species with either a direct or indirect relationship to Cenozoic species of the Caribbean or to the Recent eastern Pacific fauna. This paper will discuss the naticid species from four Neogene formations of northwestern Ecuador ranging in age from Late Miocene to Late Pliocene and their relationships to Caribbean and Pacific faunas.

The purpose of this study is to show the relationship of the Neogene naticids of northwestern Ecuador to the Caribbean and Pacific faunas, fossil and Recent. It is not intended to be a monograph of the Family Naticidae.

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Naticids are a taxonomically difficult group, as there are not many distinct morphological features or color patterns, leaving many species on a world-wide basis seemingly closely allied and possibly, in many cases, only ecological variants. One example is the close relationship between *Neverita (Glossaulax) reclusiana* (Deshayes) and the Japanese *N. (G.) didyma didyma* (Röding) (see Majima, 1989, p. 53-58). There is still much work to be done to sort out the differences among the world-wide naticids and until this is done it is appropriate to retain many local names.

Of the 17 species covered in this report only five have Caribbean counterparts; the largest group, consisting of eight species, is living in the eastern Pacific; three are endemic, known only from the Esmeraldas beds; one is known only from the northern Pacific fossil record. Table I shows the species involved and their affiliations.

Stratigraphic relationships have always been a problem in northwestern Ecuador. There have been a number of people that have worked on these problems in this part of Ecuador at different times and places. There has been no correlation between the known fossil localities, unless some of this work was done by early oil explorations, in which case the records are in company files and are unavailable.

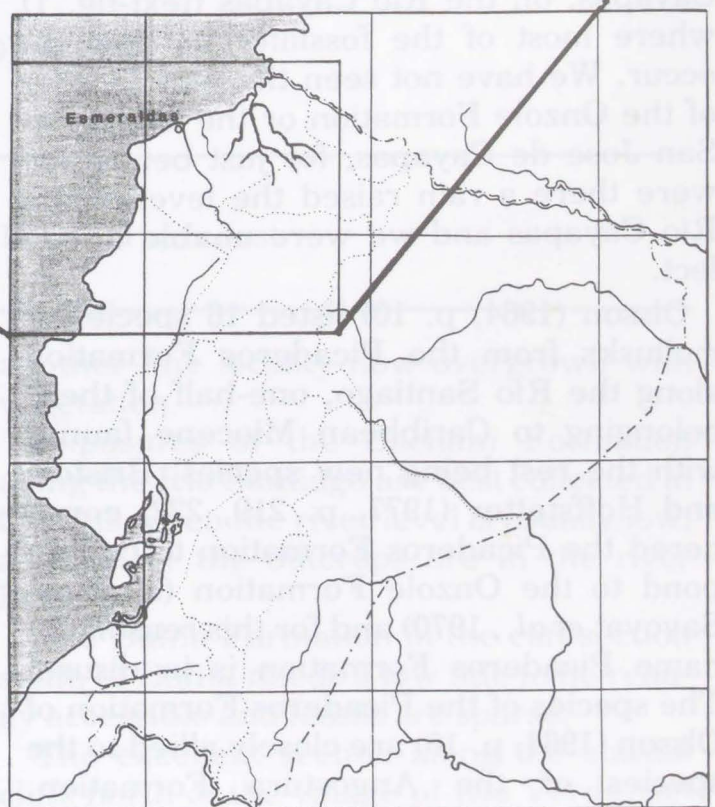
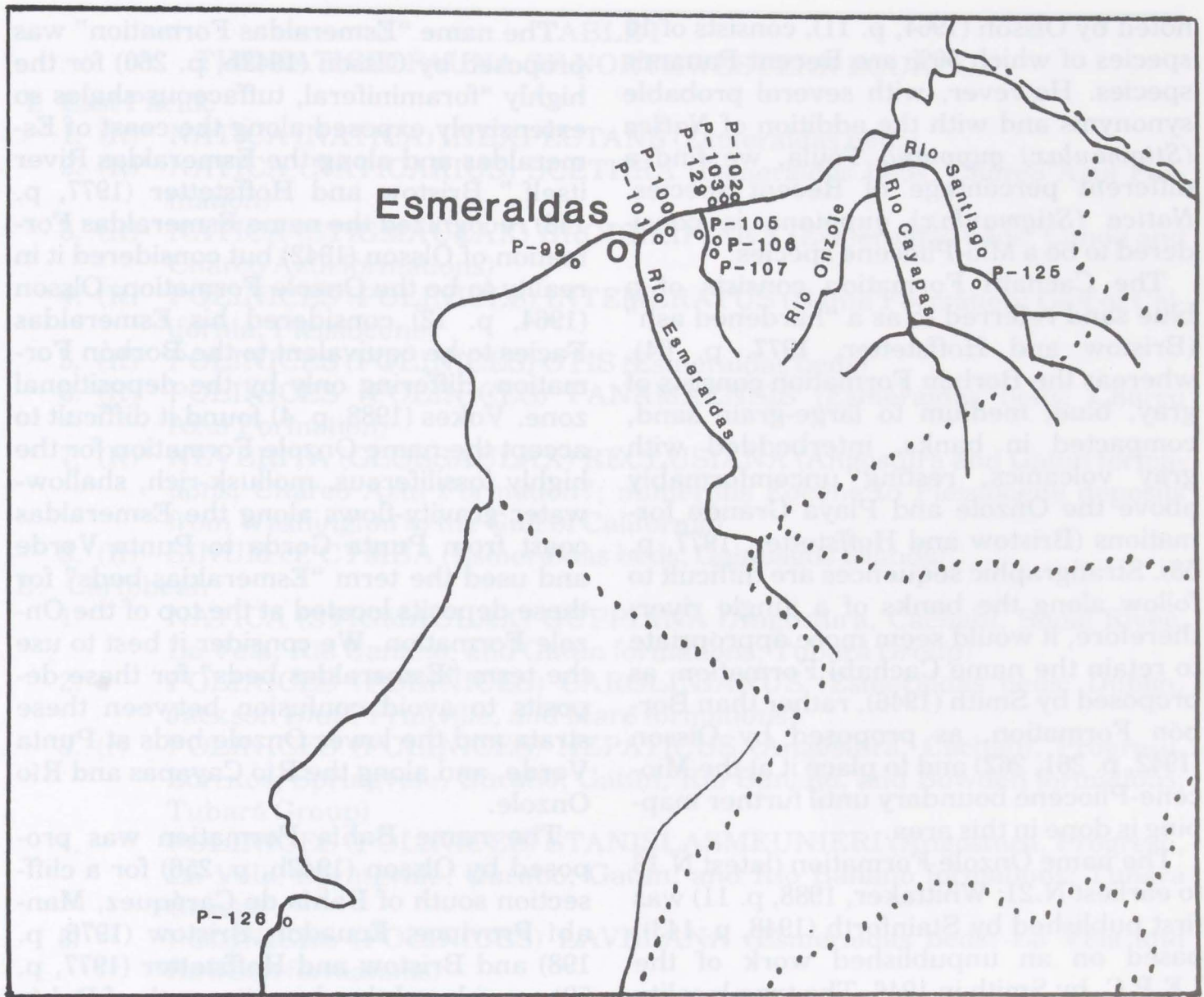
The Angostura Formation of Late Miocene age (planktic foraminiferal zone N.16) is the oldest formation discussed in this paper. This name was first published by Stainforth (1948, p. 142, 143, 146), following an unpublished work of the International Ecuadorian Petroleum Company (I.E.P.C.) by Smith in 1946 (*vide* Bristow and Hoffstetter, 1977, p. 32). The type locality of the Angostura Formation is in the gorge along the Río Santiago near the confluence with Estero Angostura, Esmeraldas Province, Ecuador (text-fig. 1). This locality is the "Cueva de Angostura" of Olsson (1942b, p. 262). Later, Olsson (1964, p. 8) noted that the formation consists predominantly of coarse sandstones and beds of conglomerates, adding that the beds are largely barren of fossils, but in places contain lenses of well preserved mollusks.

There is a fine outcrop of the Angostura Formation at Punta Verde (text-fig. 1, locality P-102), 2 1/4 km east of the village of Río Verde, about 30 km east of the city of

Esmeraldas. The outcrop was discovered by Roger Bristow and John Whittaker of the British Geological Survey and of the British Museum (Natural History), Department of Palaeontology, respectively. There are also several minor outcrops, one in the village of Palestina (text-fig. 1, P-105), a few kilometers west of Río Verde and others (text-fig. 1, P-106, P-107), along a road south from Palestina to El Alto. The Angostura Formation is the Ecuadorian equivalent of the Gatun Formation of Panamá and is considered to be Late Miocene (N. 16), by Whittaker (1988, p. 10). Woodring (1957, p. 47) placed the Gatun Formation in the Miocene but Vokes (1990, p. 4) noted that there is no positive dating of the Gatun Formation and considered the Gatun to be probably Early Pliocene in age. She believes that the resemblance between the Angostura and Gatun faunas is due more to facies than age.

The faunas at Punta Verde and Palestina vary somewhat and probably represent a facies rather than a time difference. Mollusk specimens are abundant at both localities, with *Turritella* the predominant genus. The outcrops along the road to El Alto contain few specimens, mainly pelecypod fragments and several examples of *Neverita (Glossaulax) reclusiana* (Deshayes). The deposits at Palestina afforded specimens of *Neverita (Glossaulax) pabloensis* (Clark) and *Neverita (Glossaulax) reclusiana* (Deshayes). There was mixing of these two species at some localities, but there were only a few specimens from any locality, making integration or separation of the two species impossible to determine based on specimens studied from these localities.

The name Cachabí Formation was first published by Mosquera (1949, p. 18, 21), following an unpublished work of the I.E.P.C. by Smith in 1946 (*vide* Bristow and Hoffstetter, 1977, p. 64), and was considered to be Pleistocene in age. Olsson (1964, p. 10, 11) considered the deposits at Barro Colorado, along the Río Santiago, which is very near the type locality of the Cachabí Formation, to be referable to the Borbón Formation, of Late Miocene or Early Pliocene age. Savoyat *et al.* (1970) considered the Cachabí Formation to be questionably Pliocene in age. The fauna near the village of Barro Colorado, as



Text-figure 1. Map of northwestern Ecuador; showing Pitt (P) collecting localities.

noted by Olsson (1964, p. 11), consists of 10 species of which 50% are Recent Panamic species. However, with several probable synonyms and with the addition of *Natica (Stigmaulax) guppiana* Toula, we find a different percentage of Recent species. *Natica (Stigmaulax) guppiana* is considered to be a Mio-Pliocene species.

The Cachabí Formation consists of a blue sand referred to as a "hardened ash" (Bristow and Hoffstetter, 1977, p. 64), whereas the Borbón Formation consists of gray, blue, medium to large-grain sand, compacted in banks, interbedded with gray volcanics, resting unconformably above the Onzole and Playa Grande formations (Bristow and Hoffstetter, 1977, p. 58). Stratigraphic sequences are difficult to follow along the banks of a jungle river; therefore, it would seem more appropriate to retain the name Cachabí Formation, as proposed by Smith (1946), rather than Borbón Formation, as proposed by Olsson (1942, p. 261, 262) and to place it at the Miocene-Pliocene boundary until further mapping is done in this area.

The name Onzole Formation (latest N.16 to earliest N.21; Whittaker, 1988, p. 11) was first published by Stainforth (1948, p. 143), based on an unpublished work of the I.E.P.C. by Smith in 1946. The type locality is on the Río Onzole to the east of the Río Cayapas, above the village of San Jose de Cayapas, on the Río Cayapas (text-fig. 1) where most of the fossiliferous deposits occur. We have not seen the type locality of the Onzole Formation or the locality at San Jose de Cayapas, for just before we were there a rain raised the level of the Río Cayapas and we were unable to collect.

Olsson (1964, p. 10) listed 16 species of mollusks from the Picaderos Formation along the Río Santiago, one-half of these belonging to Caribbean Miocene faunas with the rest being new species. Bristow and Hoffstetter (1977, p. 219, 232) considered the Picaderos Formation to correspond to the Onzole Formation (also see Savoyat *et al.*, 1970) and for this reason the name Picaderos Formation is in disuse. The species of the Picaderos Formation of Olsson (1964, p. 10) are closely allied to the species of the Angostura Formation. Savoyat *et al.*, (1970) placed the base of the Onzole Formation along the Río Santiago (see Bristow and Hoffstetter, 1977, p. 220).

The name "Esmeraldas Formation" was proposed by Olsson (1942b, p. 260) for the highly "foraminiferal, tuffaceous shales so extensively exposed along the coast of Esmeraldas and along the Esmeraldas River itself." Bristow and Hoffstetter (1977, p. 143) recognized the name Esmeraldas Formation of Olsson (1942) but considered it in reality to be the Onzole Formation. Olsson (1964, p. 12) considered his Esmeraldas Facies to be equivalent to the Borbón Formation, differing only by the depositional zone. Vokes (1988, p. 4) found it difficult to accept the name Onzole Formation for the highly fossiliferous, mollusk-rich, shallow-water gravity-flows along the Esmeraldas coast from Punta Gorda to Punta Verde and used the term "Esmeraldas beds" for these deposits located at the top of the Onzole Formation. We consider it best to use the term "Esmeraldas beds" for these deposits to avoid confusion between these strata and the lower Onzole beds at Punta Verde, and along the Río Cayapas and Río Onzole.

The name Bahía Formation was proposed by Olsson (1942b, p. 256) for a cliff-section south of Bahía de Caráquez, Manabí Province, Ecuador. Bristow (1976, p. 198) and Bristow and Hoffstetter (1977, p. 59) considered the deposits south of Bahía at Punta La Colorada (= Punta Mesita of recent maps) to be Borbón Formation. Whittaker (1988, p. 24) later re-introduced the term Bahía Formation to replace the "Upper Calcareous" Member of Marks (1951, p. 32) and the Borbón Formation of Bristow (1976, p. 195) and Bristow and Hoffstetter (1977, p. 58) for the cliff section south of Bahía.

The authors, along with Harold and Emily Vokes of Tulane University made collections at the following localities: AN-GOSTURA FORMATION – Punta Verde (text-fig. 1, P-102, P-103, P-129), Palestina (P-105), and (P-106, P-107), along the road to El Alto, from Palestina; ESMERALDAS BEDS – Quebrada Camarones (P-100), the road cut south of Camarones (P-101), and Punta Gorda (P-99); CACHABÍ FORMATION – Barro Colorado (P-125); and BAHÍA FORMATION – in the cliffs south of Bahía de Caráquez (P-126).

The Angostura Formation at Punta Verde needs a low Spring tide for collecting, as in the Fall it can be covered with sand. The locality is very good in terms of

TABLE I  
THE NATICID FAUNA OF NORTHWESTERN ECUADOR

- I. East Pacific
1. (R)\* NATICA (NATICA) INEXPECTANS (Esmeraldas beds)
  2. (R)\* NATICA (NATICARIUS) SCETHRA (Esmeraldas beds; Charco Azul Formation)
  3. (R) NATICA (STIGMAULAX) BRODERIPIANA (Esmeraldas beds; Canoa and Charco Azul formations)
  4. (R) POLINICES (POLINICES) INTEMERATUS (Bahía Formation; Gulf of California; Pleistocene)
  5. (R) POLINICES (POLINICES) OTIS (Esmeraldas beds)
  6. (R) POLINICES (POLINICES) PANAMAENSIS (Esmeraldas beds; Charco Azul Formation)
  7. (R)\* NEVERITA (GLOSSAULAX) RECLUSIANA (Angostura and Gatun formations; Charco Azul Formation?; numerous Eocene to Pleistocene deposits from Washington to the Gulf of California)
  8. (R) SINUM cf. CYMBA (Esmeraldas beds; Galápagos Islands)
- II. Caribbean
1. NATICA (STIGMAULAX) GUPPIANA (Angostura, Cachabí, Shoal River, La Vela, Río Banano, and Gatun formations; Tubará Group)
  2. POLINICES (POLINICES) CAROLINIANUS (Esmeraldas beds; Duplin, Jackson Bluff, Fruitville, and Mare formations)
  3. (r) POLINICES (POLINICES) HEPATICUS (Angostura, Cachabí, Progreso, Zorritos, Springvale, Gurabo, Gatun, Río Banano, and Bowden formations; Tubará Group)
  4. POLINICES (POLINICES) STANISLASMEUNIERI (Angostura, Progreso, La Vela, Springvale, Gurabo, Gatun, and Río Banano formations; Tubará Group)
  5. POLINICES (POLINICES) LAVELANA (Esmeraldas beds; La Vela and Bowden formations)
- III. California – Northern Pacific
1. NEVERITA (GLOSSAULAX) PABLOENSIS (Angostura and Gatun formations; numerous Miocene localities from central to southern California)
- IV. Endemic
1. NATICA (STIGMAULAX) LANDESIANA
  2. POLINICES (EUSPIRA) ELLA
  3. SINUM LACONDAMINI

17 species total

R – living in eastern Pacific; \*no longer on the Ecuadorian coast

r – living in Atlantic

diversity and number of specimens, and together with the localities in and around Palestina, are the only Angostura Formation localities that are easily accessible.

Exposures of the Esmeraldas beds of the Onzole Formation include: the intertidal exposures at Punta Gorda, which appear to be gone, although we did obtain a few specimens, and with a very low Spring tide, parts may remain; Quebrada Camarones, which at one time was a fine collecting locality, with material from the talus slope, but has been poor more recently; and the road cut south of Camarones,

another fine locality now overgrown with vegetation.

Exposures of the Cachabí Formation along the Río Santiago are best collected in the Fall when the river level is usually low, as most of the outcrops are in the river bank.

The Bahía Formation in the cliff-section south of Bahía needs a low tide to be readily accessible and fossils are sparse.

The excellent section along the coastal cliffs north of the village of Río Verde, according to Whittaker (1988, p. 10), contains an exposed Miocene (N.12) section of the

Viche Formation, which is overlain by the presumably Late Miocene Angostura Formation (N.16). The age is uncertain as these shallow-water deposits contain only a few, poorly preserved benthic foraminifers. The Angostura Formation is overlain by the Late Miocene, Lower Onzole Formation (latest N.16; Whittaker, 1988, p. 11).

Olsson (1964, p. 8) noted that many species from the Angostura Formation are very closely related to Gatun species and differ only in minor details. These minor differences may be more a difference in facies than in time, or *vice versa*.

### III. ACKNOWLEDGMENTS

We want to thank Harold and Emily Vokes of Tulane University for their encouragement, help in the field, and use of the University collections. We especially want to thank Emily Vokes without whose help this manuscript would not have been possible. We also thank the following persons for making museum collections available: Peter Hoover, Paleontological Research Institution; James McLean, Gale Sphon, and Lindsey Groves, Natural History Museum of Los Angeles County; Thomas Waller and Warren Blow, United States National Museum of Natural History. Thanks also go to Roger Bristow, British Geological Survey, Exeter, England and John Whittaker, Department of Palaeontology, British Museum (Natural History), for making available their unpublished information and locality data from Ecuador, as well as making the museum collections available. We are grateful to Allan McMakin for the photography and Wayne Barnett for the original ultra-violet light photograph of *Natica guppiana* from the Gatun Formation. Finally for reviewing this manuscript and offering their helpful criticism we want to thank Alan Kabat of the United States National Museum; Louie Marincovich of the United States Geological Survey, Menlo Park, California; Ryuichi Majima of Yokohama National University, Japan.

### ABBREVIATIONS FOR REPOSITORY INSTITUTIONS

ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania  
 BM(NH) – British Museum (Natural History)

CAS – California Academy of Sciences, San Francisco, California

LACM – Museum of Natural History, Los Angeles County, Los Angeles, California

PRI – Paleontological Research Institution, Ithaca, New York

TU – Tulane University, New Orleans, Louisiana

UCMP – Museum of Paleontology, University of California, Berkeley

USNM – United States National Museum of Natural History

SU – Stanford University, collections now at California Academy of Sciences

### IV. SYSTEMATIC PALEONTOLOGY

Class GASTROPODA

Order MESOGASTROPODA

Superfamily NATICACEA

Family NATICIDAE Forbes, 1838

Subfamily POLINICINAE

Finlay and Marwick, 1937

Genus POLINICES Montfort, 1810

*Polinices* MONTFORT, 1810, Conchyliologie Systematique, v. 2, p. 223, pl. 56.

*Type species: Polinices albus* Montfort, 1810 by original desig. (– *Nerita mammilla* Linnaeus, 1758).

Subgenus POLINICES s.s.

POLINICES (POLINICES) CAROLINIANUS

(Conrad)

Plate 1, figures 1-4

*Natica caroliniana* CONRAD, 1841, Amer. Jour. Sci., (ser. 1) v. 41, p. 347, pl. 2, fig. 18; CONRAD, 1868, Amer. Jour. Conchology, v. 4, p. 65, pl. 6, fig. 3.

*Polinices (Mammillaria?) caroliniana* (Conrad). MANSFIELD, 1930, Florida State Geol. Surv., Bull. 3, p. 127, pl. 19, fig. 1.

*Polinices (Polinices) caroliniana* (Conrad). OLSSON and HARBISON, 1953, Acad. Nat. Sci. Phila., Mon. 8, p. 268, pl. 57, fig. 6.

*Polinices subclausus* (Sowerby). WEISBORD, 1962, Bulls. Amer. Paleontology, v. 42, no. 193, p. 241 [in part], pl. 22, fig. 13, 14 [not figs. 11, 12, 15, 16, *P. hepaticus* (Röding, 1798)].

*Description:* Shell of medium size, globose; spire evenly tapered; suture appressed; parietal callus heavy; columella with large funicular rib, bordered by a deep sulcus extending from the columella wall, anteriorly, around the funicular rib to the parietal callus, and reaching the columellar wall.

*Holotype*: ANSP 15149.

*Type locality*: Natural Well, North Carolina.

*Occurrence*: Esmeraldas beds, Ecuador. Duplin Formation, North Carolina; Jackson Bluff and Fruitville formations (= "Pinecrest Beds"), Florida; Pliocene. Mare Formation, Venezuela; Pleistocene.

*Discussion*: Specimens of *Polinices carolinianus* (Conrad) (USNM 114425-topotypes) examined vary in that some specimens have a depression below the suture, on the body whorl, also a slight hook on the columellar wall, posterior to the funicular rib; however, these features are variable. Specimens of *P. carolinianus* (Conrad) from the Esmeraldas beds, also have a slight depression just below the suture making the body whorl appear slightly shouldered. Ecuadorian specimens do not have the sulcus ending as close to the columellar wall posteriorly as do specimens from the type locality; in specimens examined from Florida this appears to be a variable feature throughout the range. *Polinices boutakoffi* Rutsch (1942, p. 139, pl. 6, figs. 7a, 7b) is a close ally that differs in having a deeper groove on the parietal callus, is more inflated, and is not as appressed at the suture.

*Polinices carolinianus* probably originated in the Caribbean with the specimens from the Esmeraldas beds representing the western extreme for this species, now extinct in the Tropical East Pacific.

POLINICES (POLINICES) HEPATICUS  
(Röding)

Plate 1, figures 5-10

*Albula hepatica* RÖDING, 1798, Mus. Bolten., pt. 2, p. 21.

*Natica subclausa* SOWERBY, 1850, Geol. Soc. London, Quart. Jour., v. 6, p. 51.

*Polinices (Polinices) subangulata* NELSON, 1870, Connecticut Acad. Arts and Sci., Trans., v. 2, art. 5, p. 195 [in part], pl. 6, fig. 4 [not figs. 12, 13].

*Polinices subclausa* (Sowerby). BROWN and PILSBRY, 1911, Acad. Nat. Sci. Phila., Proc., v. 63, p. 360; MAURY, 1917, Bulls. Amer. Paleontology, v. 5, no. 29, p. 300(136), pl. 23, fig. 14; OLSSON, 1922, *ibid.*, v. 9, no. 39, p. 329(157), pl. 13, figs. 16, 17; HODSON, HODSON, and HARRIS, 1927, *ibid.*, v. 13, no. 49, p. 69, pl. 36, fig. 5; ANDERSON, 1929, Calif. Acad. Sci., Proc., (ser. 4) v. 18, no. 4, p. 124.

*Polinices brunnea subclausa* (Sowerby). WOODRING, 1928, Carnegie Inst. Washing-

ton, Publ. 385, p. 385, pl. 30, fig. 13.

*Polinices (Mammilla) cf. brunnea* (Link). WEISBORD, 1929, Bulls. Amer. Paleontology, v. 14, no. 54, p. 261(29), pl. 9, fig. 12.

*Polinices (Polinices) nelsoni* OLSSON, 1932, Bulls. Amer. Paleontology, v. 19, no. 68, p. 208, pl. 24, figs. 8, 10.

*Polinices brunneus subclausus* (Sowerby). WOODRING, 1957, U.S. Geol. Surv., Prof. Paper 306-A, p. 89, pl. 20, fig. 9.

*Polinices subclausus* (Sowerby). WEISBORD, 1962, Bulls. Amer. Paleontology, v. 42, no. 193, p. 241 [in part], pl. 22, figs. 11, 12, 15, 16 [not figs. 13, 14; = *P. carolinianus* (Conrad, 1841)].

*Description*: Shell of medium size; spire height medium to high, evenly tapered; suture appressed; parietal callus heavy, with a transverse groove posteriorly, junction of parietal and columellar callus posterior to center of aperture opening, at which point a narrow columellar callus tapers to a point anteriorly; umbilicus open with funicular rib indistinct to lacking.

*Type material*: Chemnitz, 1781, pl. 189, figs. 1932, 1933; no certain type material can be traced today (Zoologisk Museum, Copenhagen, Denmark; written comm.).

*Type locality*: Uncertain, possibly West Indies.

*Occurrence*: Angostura, Cachabí and Progreso formations, Esmeraldas beds, Ecuador. Zorritos Formation, Peru; Springvale Formation, Trinidad; Miocene. Gurabo Formation, Dominican Republic; Mio-Pliocene. Gatun Formation, Panamá; Río Banano Formation, Costa Rica; Pliocene. Tubará Group, Colombia; Plio-Pleistocene. Bowden Formation, Jamaica; Pleistocene. Recent, Texas, West Indies to Brazil.

*Discussion*: Although the spire is fairly consistent in height, the shell is globose to rather slender and the width of the umbilical opening varies from narrow to wide. Recent examples of *P. hepaticus* differ in having a lower spire than most specimens studied in this report, otherwise the two are morphologically equal.

Maury (1917, p. 300(136)) noted that some specimens of *P. subclausus*, a synonym of *P. hepaticus*, retain a color pattern of gray stripes and for this reason she felt that *P. subclausus* was distinct from its Recent analogue. One of her specimens of *P. subclausus* (PRI 33113) examined does have gray axial streaks, as do several specimens of *P. hepaticus* from locality TU 1358 (see pl. 1, fig. 6). Some Recent specimens examined at Tulane and USNM also have these axial streaks. Most specimens of *P.*

*hepaticus* are of a solid color, and this color pattern of axial streaks on some specimens (fossil and Recent) does not warrant treating these as a distinct species as believed by Maury.

*Polinices subclausus*, as figured by Weisbord (1962, pl. 22, figs. 11-16), represents two species: figures 11, 12, 15, 16 represent *P. subclausus*; figures 13, 14 represent *P. carolinianus* (Conrad).

In his remarks when describing *P. nelsoni*, a synonym of *P. hepaticus*, Olsson (1932, p. 209) noted that *P. subangulata* Nelson (1870 [in part], pl. 6, fig. 4 [not figs. 12, 13] is probably this species, as the young shells of *P. subangulata* do not differ greatly from adult shells in form.

*Polinices prolactea* Anderson (1929, p. 124, pl. 14, figs. 8, 9) differs in having a lower spire, a smaller umbilical opening, and has the junction of the columellar callus and the parietal callus at the center of the aperture opening. This species may prove to be a synonym of the Recent *P. lacteus* (Guilding, 1834).

In the Tropical East Pacific *P. hepaticus* is closely allied in form to the group of white *Polinices* discussed under *P. stanislasmeyneri*, the closest species morphologically being *P. panamaensis* (Récluz, 1844), which differs mainly in lacking the

transverse groove on the parietal callus and having a much narrower umbilical opening.

*Polinices hepaticus* has a living relative in *P. lacteus* (Guilding) in the Atlantic, as well as the white *Polinices* group in the Tropical East Pacific. *Polinices hepaticus* is widespread in the Caribbean Neogene and it is not surprising to find it in the Neogene of the Tropical East Pacific, as a number of species that occur in the Caribbean Neogene also occur in the Peruvian Miocene, including *Turritella abrupta* Spieker, which was described from Peru. Since *P. hepaticus* is widespread in the Caribbean Neogene and Recent, but only sparingly in the Tropical East Pacific Neogene, it probably arose in the Caribbean.

POLINICES (POLINICES) INTEMERATUS  
(Philippi)

Plate 2, figure 1

*Natica intemerata* PHILIPPI, 1851, Systematisches Conchylien-Cabinet, v. 2, pt. 1, p. 129, pl. 18, fig. 10; PHILIPPI, 1853, *ibid.*, p. 233, 234; TRYON, 1886, Manual Conchology, v. 8, p. 46, pl. 18, fig. 83, pl. 19, fig. 93.

*Polinices uber* var. *intemeratus* (Philippi). DALL, 1908, Harvard Mus. Comp. Zool., Bull., v. 43, no. 6, p. 334. *Natica alabaster* REEVE, 1855, Conch. Icon., v. 9, *Natica*, pl. 9, figs. 33a, 33b. KEEN, 1971, Sea Shells

PLATE 1

Figures

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| 7. CASG 66571; height 26.1 mm, diameter 20.8 mm (X 1.9).<br>Locality: P-100, Ecuador; Esmeraldas beds.                |     |
| 8. CASG 66572; height 22.0 mm, diameter 18.9 mm (X 1.8).<br>Locality: P-103, Ecuador; Angostura Formation.            |     |
| 9. LACM 147856; height 32.0 mm, diameter 26.0 mm (X 1.4).<br>Locality: LACM A-2777, Veracruz, Mexico; Recent.         |     |
| 10. CASG 66573; height 24.9 mm, diameter 19.9 mm (X 1.5).<br>Locality: P-101, Ecuador; Esmeraldas beds.               |     |



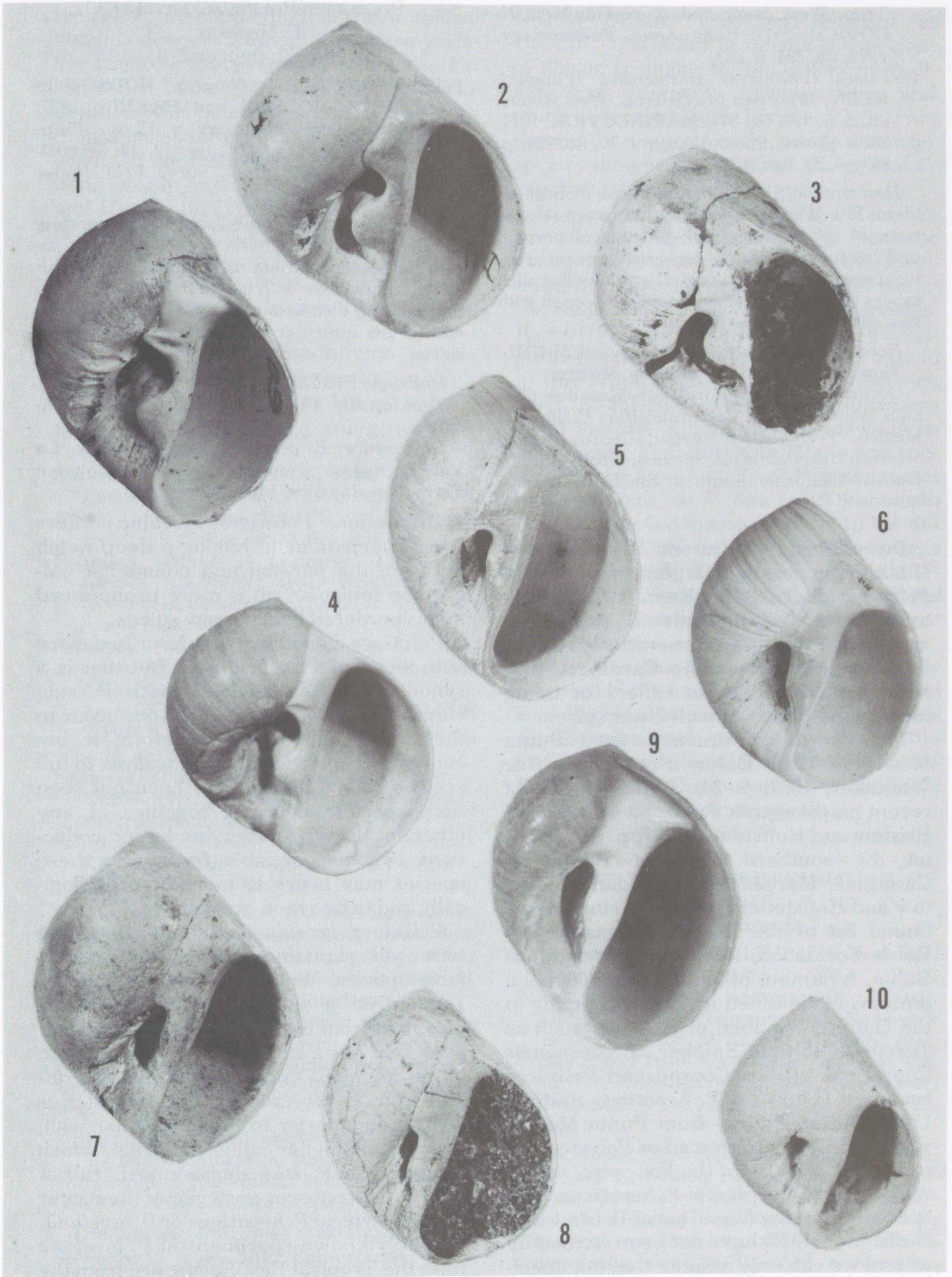


PLATE 1

Trop. West Amer., ed. 2, p. 478; MARINCOVICH, 1977, *Bulls. Amer. Paleontology*, v. 70, no. 294, p. 253.

*Polinices (Polinices) intemeratus* (Philippi). KEEN, 1971, *Sea Shells Trop. West Amer.*, ed. 2, p. 478, fig. 877; MARINCOVICH, 1977, *Bulls. Amer. Paleontology*, v. 70, no. 294, p. 253, pl. 22, figs. 8, 9.

*Description:* Shell of medium size; globose, of about four whorls; spire low, suture appressed; parietal callus heavy with junction of parietal and columellar callus posterior to center of apertural opening at which point the columella callus tapers to a point anteriorly; umbilicus open with an indistinct funicular rib.

*Holotype:* Unknown, presumably at BM(NH).

*Type locality:* Gulf of California, Mexico.

*Occurrence:* Bahía Formation, Ecuador. Carmen Island, Gulf of California, Baja California, Mexico; Pleistocene. Recent, Cedros Island, western Baja California, Mexico, throughout the Gulf of California, south to the Galápagos Islands and Peru.

*Discussion:* *Polinices intemeratus* (Philippi) is part of a large group of white *Polinices* discussed by Keen (1971, p. 480) and in this paper under *P. stanislasmeunieri*. *Polinices intemeratus* is related to *P. hepaticus* from the Caribbean and Peruvian Miocene, but differs in being more globose with a much lower spire.

The figured specimen is from Punta Mesita (P-126), Bahía Formation (*vide* Whittaker, 1988, p. 24). Punta Mesita (of recent maps) equals Punta La Colorada of Bristow and Hoffstetter (1977, p. 59), and is on the southern edge of Bahía de Caráquez, Manabí Prov., Ecuador. Bristow and Hoffstetter (1977, p. 59) included a faunal list of the Borbón Formation (= Bahía Formation) from the cliffs south of Bahía. A number of the species have been tentatively identified as those occurring in the Gatun Formation of Panamá, such as *Turritella abrupta* Spieker, *T. gatunensis* Conrad, *T. altilira* Conrad and *Polinices brunneus* (Link) (= *P. hepaticus* Röding, 1798). Our specimens from Punta Mesita, south of Bahía, are treated as *Polinices intemeratus* because of the low spire, which we have not observed in *P. hepaticus*. The specimens on the faunal list of Bristow and Hoffstetter (1977) have not been studied by us and we can only assume that our specimens are probably the same as those of Bristow and Hoffstetter.

POLINICES (POLINICES) LAVELANA

F. Hodson

Plate 2, figures 2, 3

*Polinices subclausa lavelana* F. HODSON in HODSON, HODSON and HARRIS, 1927, *Bulls. Amer. Paleontology*, v. 13, no. 49, p. 69, pl. 36, fig. 8, pl. 37, figs. 12, 14; WOODRING, 1957, *U.S. Geol. Surv., Prof. Paper* 306-A, p. 90.

*Description:* Shell of medium size, moderately slender to inflated; whorls evenly tapering; suture impressed; parietal callus heavy, columellar callus narrow with a deep notch between parietal and columellar callus; umbilicus deep, with a low funicular rib, bordered by narrow sulcus.

*Holotype:* PRI 22870.

*Type locality:* PRI locality 1033; La Vela, Venezuela.

*Occurrence:* Esmeraldas beds, Ecuador. La Vela Formation, Venezuela; Miocene. Bowden Formation, Jamaica; Pleistocene.

*Discussion:* *Polinices lavelana* differs from *P. hepaticus* in having a deep notch between the parietal and columellar callus; the funicular rib is more pronounced and is bordered by a narrow sulcus.

*Polinices lavelana* was described as a subspecies of *P. subclausus*, but that is a synonym of *P. hepaticus*. Both *P. subclausus lavelana* and *P. hepaticus* occur in the Esmeraldas beds; therefore, it becomes necessary to raise *P. lavelana* to full species rank. The authors have not seen both species occurring together at any other locality. However, as larger collections become available for study, these species may prove to merge morphologically and to be synonymous.

*Polinices lavelana* is similar to some forms of *P. stanislasmeunieri*, a highly variable species. Woodring (1957, pl. 21, fig. 14) figured a specimen of *P. stanislasmeunieri* from the Gatun Formation, Panamá, that has a small notch at the junction of the columella and parietal callus but differs from *P. lavelana* in that the notch is central or anterior to the columellar wall, and the columellar callus is narrow, which is typical in *P. stanislasmeunieri*, rather than at the center or posterior of the center as in the typical *P. hepaticus* or *P. lavelana*. The only known specimens of *P. lavelana* from the Tropical East Pacific are from the Esmeraldas beds (P-101). The specimens from the Esmeraldas beds differ from the

typical *P. lavelana* in that the umbilical notch is deeper, although there are variations among the specimens from the Esmeraldas beds. The difference in the depth of the notch is probably no more than a facies difference. Since *P. lavelana* occurs in the Pleistocene, Bowden Formation, of Jamaica (*vide* Hodson, Hodson, and Harris, 1927, p. 69) it is not surprising to find it in the Pliocene Esmeraldas beds. *Polinices lavelana* is more widespread in the Caribbean than in the Pacific and probably originated in the Caribbean.

POLINICES (POLINICES) OTIS  
(Broderip and Sowerby)  
Plate 2, figures 4, 5

*Natica otis* BRODERIP and SOWERBY, 1829,  
Zool. Jour., London, v. 4, p. 372.

*Natica galapagosa* RÉCLUZ, 1844, Zool. Soc.  
London, Proc., (1843), v. 11, p. 213.

*Natica unimaculata* REEVE, 1855, Conch.  
Icon., v. 9, *Natica*, pl. 19, figs. 85a, 85b.

*Polinices (Polinices) brunneus* (Link) sub-  
species. OLSSON, 1964, Neogene Moll.  
Northwest. Ecuador, p. 179, pl. 32, figs. 6, 6a,  
[not of Link, 1807].

*Polinices (Polinices) otis* (Broderip and Sower-  
by). KEEN, 1971, Sea Shells Trop. West  
Amer., ed. 2, p. 478, fig. 879; ABBOTT, 1974,  
Amer. Sea Shells, p. 155, no. 1686; MARIN-  
COVICH, 1977, Bulls. Amer. Paleontology,  
v. 70, no. 294, p. 255, pl. 22, figs. 10, 11.

*Polinices (Polinices) unimaculatus* (Reeve).  
KEEN, 1971, Sea Shells Trop. West Amer.,  
ed. 2, p. 480, fig. 883.

*Polinices (Polinices) galapagosus* (Récluz).  
KEEN, 1971, Sea Shells Trop. West Amer.,  
ed. 2, p. 478, fig. 875.

*Description:* Spire low to moderately elevated; suture distinct to appressed; body whorl globose; umbilical callus heavy, partially filling umbilicus posteriorly, at which point a transverse groove separates the anterior and posterior lobes, anterior lobe flattened, overhanging umbilicus and becoming slender anteriorly; umbilicus broadly open with wide sulcus; low wide funicular rib originating about center of anterior lobe.

*Holotype:* Unknown, presumably in BM(NH).

*Type locality:* Mazatlan, Mexico.

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

*Discussion:* *Polinices otis* (Broderip and Sowerby), from the Esmeraldas beds, compares favorably to "*P. brunneus* (Link) subspecies" Olsson (1964, p. 179, pl. 32, fig. 6, USNM 645444; the specimen in fig. 6a,

USNM 643892, was not received at USNM). "*Polinices brunneus* subspecies" of Olsson is similar to, but differs from, *P. hepaticus* in having a lower spire and much wider umbilicus, bordered by a wide flattened area posteriorly, and is a smaller species (height 20 mm) than the typical *P. hepaticus* (height about 40 mm).

In comparing *P. otis* from the Esmeraldas beds to Recent specimens from the Panamic Province we find that the specimens from the Esmeraldas beds fall within the range of variability for Recent species. Keen (1971, p. 478) noted that *P. galapagosus* (Récluz) is the lowest-spined naticid in the Tropical East Pacific. Marinovich (1977, p. 257) synonymized *P. galapagosus* (type locality, Albemarle Island, Galápagos Islands, Ecuador) with *P. otis* and considered the type locality of *P. galapagosus* to be in error, as *P. otis* is not known to occur in the Galápagos Islands. In his description of *P. otis* he noted that the spire is moderately high. The average height of *P. otis* is about 35 mm, larger than specimens from the Esmeraldas beds, which are about 20 mm.

*Polinices otis* has not been previously reported in the fossil record of the Tropical East Pacific. *Polinices hepaticus*, a similar species goes back to the Miocene in the Caribbean and Ecuador and occurs in the Recent in the Caribbean. It is probable that *P. otis* arose from this stock.

POLINICES (POLINICES) PANAMAENSIS  
(Récluz)

Plate 2, figures 6, 7

*Natica panamaensis* RÉCLUZ, 1844, Zool. Soc.  
London, Proc., (1843), v. 11, p. 208.

*Polinices (Polinices) panamaensis* (Récluz).  
OLSSON, 1964, Neogene Moll. Northwest  
Ecuador, p. 180, pl. 32, fig. 4; KEEN, 1971,  
Sea Shells Trop. West Amer., ed. 2, p. 478,  
fig. 880; MARINCOVICH, 1977, Bulls. Amer.  
Paleontology, v. 70, no. 294, p. 252, pl. 22,  
figs. 5-7.

*Description:* Shell globose to moderately elongate; spire moderately elevated; three and one-half smooth nuclear whorls; post-nuclear whorls four; suture slightly impressed; body whorl inflated with rounded angulation below suture, giving body whorl a flat-sided appearance; parietal callus heavy; umbilicus slightly to moderately open; columellar callus narrow, coming to a point anteriorly.

*Syntypes*: Three syntypes, BM(NH) no. 1964446.

*Type locality*: Panamá [Pacific Coast].

*Occurrence*: Esmeraldas beds, Ecuador. Charco Azul Formation, Panamá; Pleistocene. Recent, Mexico to Peru.

*Discussion*: Olsson (1964, p. 180, pl. 32, fig. 4) based his determination of *P. panamaensis* on a single specimen from the Esmeraldas beds at Punta Gorda. This determination will be accepted here allowing for the variability within the species and the fact that there is only one specimen upon which to base a judgment.

In comparing *P. panamaensis* (Récluz) to other species, it has some similarity to *P. hepaticus* (Röding) but differs in being more globose, somewhat flat-sided and lacks the transverse groove on the parietal callus; *P. stanislasmeyneri* Maury differs in having a higher spire, is not as globose and also lacks a transverse groove on the parietal callus. *Polinices panamaensis* is

most similar to *P. subangulata* Nelson, 1870 (see pl. 2, fig. 8) from the Peruvian Miocene, which also is flat-sided and lacks a transverse groove on the parietal callus, but differs in being higher spired and less globose. *Polinices panamaensis* possibly arose in the Tropical East Pacific from *P. subangulata*. It may even prove to be a synonym.

POLINICES (POLINICES) STANISLASMEUNIERI  
Maury

Plate 2, figures 9-12; Plate 3, figures 1-4

*Polinices stanislasmeyneri* MAURY, 1917, *Bulls. Amer. Paleontology*, v. 5, no. 29, p. 300(136), pl. 23, figs. 15, 16; OLSSON, 1922, *ibid.*, v. 9, no. 39, p. 329(157), pl. 13, fig. 7; MAURY, 1925, *ibid.*, v. 10, no. 42, p. 392(240), pl. 40, fig. 7; ANDERSON, 1929, *Calif. Acad. Sci., Proc.*, (ser. 4) v. 18, no. 4, p. 124; WOODRING, 1957, *U.S. Geol. Surv., Prof. Paper 306-A*, p. 90, pl. 21, figs. 11-14; JUNG, 1969, *Bulls. Amer. Paleontology*, v. 55, no. 247, p. 483, pl. 48, figs. 16-18.

PLATE 2

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CASG 66574; height 23.1 mm, diameter 22.0 mm (X 1.9).	
Locality: P-126, Ecuador; Bahía Formation.	
2-3. <i>Polinices (Polinices) levalana</i> F. Hodson . . . . .	118
2. PRI 22870 (holotype); height 32.0 mm, diameter 24.0 mm (X 1.3).	
Locality: Venezuela; La Vela Formation.	
3. CASG 66575; height 30.9 mm, diameter 25.0 mm (X 1.4).	
Locality: P-101, Ecuador; Esmeraldas beds.	
4-5. <i>Polinices (Polinices) otis</i> (Broderip and Sowerby) . . . . .	119
4. CASG 66576; height 33.4 mm, diameter 31.5 mm (X 1.2).	
Locality: TU R-185, Panamá; Recent.	
5. CASG 66577; height 21.0 mm, diameter 18.5 mm (X 2).	
Locality: P-100, Ecuador; Esmeraldas beds.	
6-7. <i>Polinices (Polinices) panamaensis</i> (Récluz) . . . . .	119
6. CASG 66578; height 41.2 mm, diameter 35.0 mm (X 0.9).	
Locality: Panamá; Recent.	
7. USNM 643893; height 31.0 mm, diameter 25.3 mm (X 1.2).	
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8. <i>Polinices (Polinices) subangulata</i> Nelson . . . . .	120
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9-12. <i>Polinices (Polinices) stanislasmeyneri</i> Maury . . . . .	120
9. PRI 28836 (holotype); height 36.0 mm, diameter 28.0 mm (X 1.3).	
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Locality: P-102, Ecuador; Angostura Formation.	
11. CASG 66580; height 28.6 mm, diameter 22.7 mm (X 1.4).	
Locality: P-95, Panamá; Gatun Formation.	
12. CASG 66581; height 26.4 mm, diameter 21.7 mm (X 1.9).	
Locality: TU 1377, Dominican Republic; Cercado Formation.	

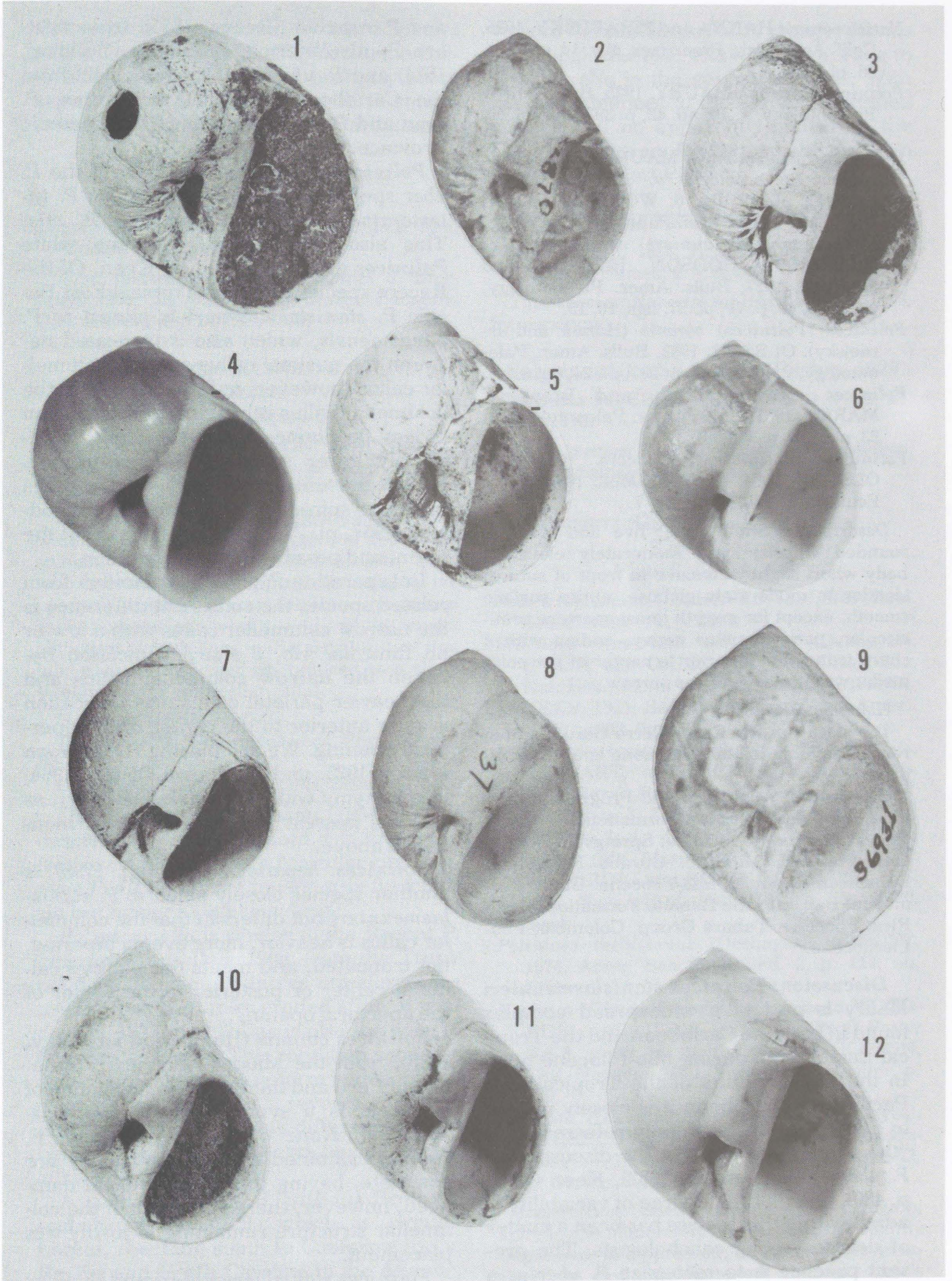


PLATE 2

*Natica coronis* HANNA and ISRAELSKY, 1925, Calif. Acad. Sci., Proc., (ser. 4) v. 14, no. 2, p. 46, pl. 8, fig. 4.

*Polinices caparona* MAURY, 1925, Bulls. Amer. Paleontology, v. 10, no. 42, p. 392(240), pl. 40, fig. 5.

*Polinices springvalensis* MAURY, 1925, Bulls. Amer. Paleontology, v. 10, no. 42, p. 393(241), pl. 40, fig. 6; WOODRING, 1957, U.S. Geol. Surv., Prof. Paper 306-A, p. 90.

*Polinices stanislasmeunieri venezuelana* F. HODSON in HODSON, HODSON, and HARRIS, 1927, Bulls. Amer. Paleontology, v. 13, no. 49, p. 70, pl. 37, figs. 10, 15.

*Polinices (Polinices) coronis* (Hanna and Israelsky). OLSSON, 1932, Bulls. Amer. Paleontology, v. 19, no. 68, p. 207, pl. 24, fig. 9.

*Polinices coronis* (Hanna and Israelsky). MARKS, 1951, Bulls. Amer. Paleontology, v. 33, no. 139, p. 368(98).

*Polinices (Polinices) cf. cora* (Orbigny). OLSSON, 1964, Neogene Moll. Northwest Ecuador, p. 180, pl. 32, fig. 7.

**Description:** Shell ovate; five and one-half rounded whorls; spire moderately elevated; body whorl slightly concave in front of suture, slender to moderately globose, entire surface smooth, except for growth lines; aperture semi-circular; parietal callus heavy, ending with a sharp truncation anterior to center of the columellar wall, anterior callus narrow.

**Holotype:** PRI 28836.

**Type locality:** Río Cana, Cerro Gordo to Mao road (Guayubin to Mao telephone line), Dominican Republic.

**Occurrence:** Angostura and Progreso formations, Ecuador. Zorritos Formation, Peru; La Vela Formation, Venezuela; Springvale Formation, Trinidad; Miocene. Gurabo Formation, Dominican Republic; Mio-Pliocene. Gatun Formation, Panamá; Río Banano Formation, Costa Rica; Pliocene. Tubará Group, Colombia; Plio-Pleistocene.

**Discussion:** *Polinices stanislasmeunieri* Maury is part of a widespread complex found in both the Caribbean and the Tropical East Pacific during Mio-Pliocene time. In the Recent fauna of the Tropical East Pacific and Caribbean it is closely related to a large group commonly referred to as "the white *Polinices*." In the discussion of *P. uber* (Valenciennes, 1832), Keen (1971, p. 480), noted: "The degree of variability to admit within this species has been a matter of debate among conchologists. The present practice is to recognize *P. uber* as a central form among a number of related species of white *Polinices*, namely, *P. cora* (Orbigny, 1840), *P. dubius* (Récluz, 1844),

and *P. rapulum* (Reeve, 1855), from western South America; *P. lacteus* (Guilding, 1834) and *P. uberina* (Orbigny, 1842) from the Caribbean area; *P. intemeratus*, *P. lima* and *P. unimaculatus* of the Panamic Province."

*Polinices panamaensis* is part of the *P. uber* species-group, which includes *P. intemeratus*, *P. panamaensis* and *P. otis*. This also places it in with the white *Polinices* group as noted by Keen. Of the Recent species from the Tropical East Pacific *P. stanislasmeunieri* is closest to *P. panamaensis*, which also is truncated between the parietal callus and the columellar callus, however, in *P. panamaensis* the columellar callus is heavier, the truncation is less pronounced and the shell is uniformly lower spired and more robust. *Polinices stanislasmeunieri* can at times be a low spired, robust form (*vide* Woodring, 1957, pl. 21, fig. 12) but this is not the norm, and possibly just an aberration.

In separating *P. stanislasmeunieri* from related species the consistent difference is the narrow columellar callus with a low or no funicular rib, a sharp truncation between the narrow columellar callus and the heavier parietal callus; the truncation is at or anterior to the center of the apertural opening. We are placing *P. caparona* Maury, 1925, and *P. cf. cora* Olsson, 1964, in synonymy with *P. stanislasmeunieri*, as they all possess the basic features mentioned above.

*Polinices hepaticus* (Röding, 1798) is another species closely allied to *P. stanislasmeunieri* but differs in that the columellar callus is heavier, more evenly tapering, not truncated, and meets the parietal callus at center or posterior to the center of the apertural opening.

*Polinices coronis* (Hanna and Israelsky, 1925), from the Miocene Zorritos Formation of Peru and the Progreso Formation of Ecuador, is a synonym of *P. stanislasmeunieri*. None of the specimens of *P. coronis* examined from either locality are complete, having the anterior canal damaged, however, there is enough of the columellar structure remaining to justify this placement.

*Polinices stanislasmeunieri* and its allies in the Caribbean and the Tropical East Pacific were widespread during Mio-Pliocene time. Although the group of white

*Polinices* is represented by more species in the Tropical East Pacific than in the Caribbean; individual species probably arose separately in both regions with *P. stanislasmeyneri* originating in the Caribbean.

Subgenus EUSPIRA Agassiz  
in J. Sowerby, 1838

*Euspira* AGASSIZ in J. SOWERBY, 1838, Min. Conch. Grossbritt., p. 14.

*Type species*: *Natica glaucinoides* J. Sowerby, 1812, by subsequent desig., Bucquoy, Dautzenberg and Dollfus, 1883.

POLINICES (EUSPIRA) ELLA  
(Olsson)

Plate 3, figure 5

*Natica (Natica) ella* OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 177, pl. 37, figs. 5, 5a.

*Description*: Shell small; slightly higher than wide; spire moderately elevated, of about four smooth, somewhat shouldered whorls, early whorls eroded; suture appressed to slightly impressed; sculpture of short retractive grooves on early post-nuclear whorls; body whorl convex with faint growth lines; parietal callus thin; umbilicus open, funicular rib reduced to a slight swelling on the columellar callus.

*Holotype*: USNM 643884.

*Type locality*: Esmeraldas beds, Punta Gorda, Ecuador.

*Occurrence*: Esmeraldas beds, Ecuador.

*Discussion*: When Olsson (1964, p. 177) described *P. ella* he placed it in the genus *Natica* on the basis of a funicular rib, however *P. ella* does not have a true funicular rib but rather a slight swelling.

*Polinices ella* is similar to the Recent *P. crawfordianus* Dall, 1908, from the Tropical East Pacific. *Polinices crawfordianus* usually has the apex eroded (*fide* Marinovich, 1977, p. 292), as is also the case in the apex of *P. ella*. This condition probably occurs only in the adult form and is a common occurrence in several species. *Polinices crawfordianus* differs mainly in being not as globose, and having an arcuate columella.

A similar species, *P. pallidus* Broderip and Sowerby, 1829, which is circum-boreal, reaching south to California in the Pacific and North Carolina in the Atlantic, is variable in outline. The spire is moderately elevated, the whorls are slightly flattened below the suture, and the axial sculpture is of incremental growth lines. In

view of the similarities of *P. crawfordianus* and *P. pallidus* to *P. ella* it is appropriate to place *P. ella* in the genus *Polinices*. With the resemblances to the above mentioned species and no apparent relatives in the Caribbean region; *P. ella* probably arose in the Tropical East Pacific.

Genus NEVERITA Risso, 1826

*Neverita* Risso, 1826, Hist. Natur. Nice et des Alpes Maritimes, v. 4, p. 149.

*Type species*: *Neverita josephina* Risso, 1826, by monotypy.

Subgenus GLOSSAULAX Pilsbry, 1929

*Glossaulax* PILSBRY, 1929, Nautilus, v. 42, no. 4, p. 113.

*Type species*: *Natica reclusiana* Deshayes, 1839, by original desig.

NEVERITA (GLOSSAULAX) RECLUSIANA  
(Deshayes)

Plate 3, figures 6-8

*Natica reclusiana* DESHAYES, 1839, Rev. Zool. Soc. Cuvier, v. 2, p. 361.

*Polinices (Neverita) reclusianus* (Deshayes). GRANT and GALE, 1931, San Diego Soc. Nat. Hist., Mem. 1, p. 800, text-figs. 13a-13c; KEEN, 1971, Sea Shells Trop. West Amer., ed. 2, p. 482, fig. 888.

*Neverita reclusiana* (Deshayes). WOODRING, STEWART, and RICHARDS, 1940, U.S. Geol. Surv., Prof. Paper 195, p. 86 [in part], pl. 20, figs. 1, 3, 5 [not pl. 15, figs. 19, 20, pl. 20, figs. 2, 4, = *N. (G.) andersoni* (Clark, 1918), *fide* Marinovich (1977, p. 317)]; WOODRING and BRAMLETTE, 1950, U.S. Geol. Surv., Prof. Paper 222, p. 73, pl. 20, fig. 4.

*Polinices reclusianus* (Deshayes). ABBOTT, 1974, Amer. Sea Shells, ed. 2, p. 154, no. 1679.

*Neverita (Glossaulax) reclusiana xena* WOODRING, 1957, U.S. Geol. Surv., Prof. Paper 306-A, p. 92, pl. 21, figs. 5, 8, 9; OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 179.

*Neverita (Glossaulax) reclusiana* (Deshayes). MARINOVICH, 1977, Bulls. Amer. Paleontology, v. 70, no. 294, p. 317, pl. 29, figs. 4-12, pl. 30, figs. 1-4, text-fig. 13.

*Description*: Shell subglobose to elongate; spire low to moderately elevated; suture slightly impressed to appressed; shoulder evenly tapered to distinctly flattened; nuclear whorls smooth, two and one-half turns; post-nuclear whorls about four; sculpture of axial incremental growth lines and microscopic, closely spaced wavy costellae; parietal callus heavy, umbilical

callus moderately open to closed, divided into two lobes by a transverse groove, posterior lobe always largest.

*Type material:* Three syntypes, Muséum National d'Histoire Naturelle, Paris, France.

*Type locality:* "Mers de California."

*Occurrence:* Angostura Formation, Ecuador. Gatun Formation, Panamá; Pliocene. Numerous Eocene to Pleistocene localities from Washington to the Gulf of California. Recent, from northern California and south throughout the Gulf of California.

*Discussion:* *Neverita reclusiana* (Deshayes) is an extremely variable species, which in the Recent occurs from northern California to the southern Gulf of California. It apparently arose in the Eocene and at that time was widespread in the eastern Pacific, as well as appearing sparingly in the Caribbean Pliocene. For an extensive discussion of geographic occurrences see Marinovich (1977, p. 319).

In comparing Recent specimens of *N. reclusiana* to *N. reclusiana xena* Woodring (1957, p. 92) noted: "It is remarkably similar to a small form of *N. reclusiana* (Deshayes) found along the outer coast of Baja

California and along the Gulf of California. The Gatun neverite in general has a narrower space between the umbilical wall and the anterior callus lobe. Some small Recent shells, however are practically indistinguishable from the fossils. . . . Inasmuch as *N. reclusiana* has a long history in the eastern Pacific going back to the Miocene if not earlier, *N. reclusiana xena* evidently is a migrant from the Pacific." In comparing specimens from the Angostura Formation of Ecuador, the Gatun Formation of Panamá and paratypes of *N. reclusiana xena* (SU 8711, from Woodring, 1957, locality 137, now at CASG 66586) we find that they are indistinguishable from the many forms of Recent specimens. Therefore we place *N. reclusiana xena* Woodring in synonymy with *N. reclusiana* (Deshayes). It is noteworthy that we have not found *N. reclusiana* in the Pliocene Esmeraldas beds, which indicates that it became extinct in the Caribbean region and the southern end of its range in the Pacific by Pliocene time.

Olsson (1942a, p. 21) in his faunal list from Río Blanco, Charco Azul Formation,

### PLATE 3

Figures	Page
1-4. <i>Polinices (Polinices) stanislasmeunieri</i> Maury . . . . .	120
1. CASG 66582; height 39.2 mm, diameter 31.7 mm (X 1). Locality: TU 589, Costa Rica; Río Banano Formation.	
2. CASG 1716 (holotype- <i>P. coronis</i> Hanna and Israelsky); height 31.3 mm, diameter 24.6 mm (X 1.3). Locality: CAS 328, Peru; Zorritos Formation.	
3. PRI 33122; height 24.7 mm, diameter 17.1 mm (X 1.6). Locality: IPC 508, Ecuador; Progreso Formation.	
4. CASG 66583; height 22.6 mm, diameter 17.8 mm (X 1.8). Locality: CAS 339, Peru; Zorritos Formation.	
5. <i>Polinices (Euspira) ella</i> (Olsson) . . . . .	123
CASG 66584 (topotype); height 12.4 mm, diameter 11.4 mm (X 3). Locality: P-99, Ecuador; Esmeraldas beds.	
6-8. <i>Neverita (Glossaulax) reclusiana</i> (Deshayes) . . . . .	123
6. CASG 66585; height 30.0 mm, diameter 29.8 mm (X 1.4). Locality: P-105, Ecuador; Angostura Formation.	
7. CASG 66586; height 27.4 mm, diameter 30.1 mm (X 1.5). Locality: P-97, Panamá; Gatun Formation.	
8. CASG 66587 (paratype- <i>Neverita (Glossaulax) reclusiana xena</i> Woodring); height 27.9 mm, diameter 18.8 mm (X 1.9). Locality: Panamá; Gatun Formation.	
9-10. <i>Neverita (Glossaulax) pabloensis</i> (Clark) . . . . .	126
9. CASG 66588; height 27.2 mm, diameter 28.3 mm (X 1.4). Locality: CAS 65, California; Round Mountain Silt.	
10. CASG 66589; height 25.4 mm, diameter 25.8 mm (X 1.8). Locality: P-103, Ecuador; Angostura Formation.	



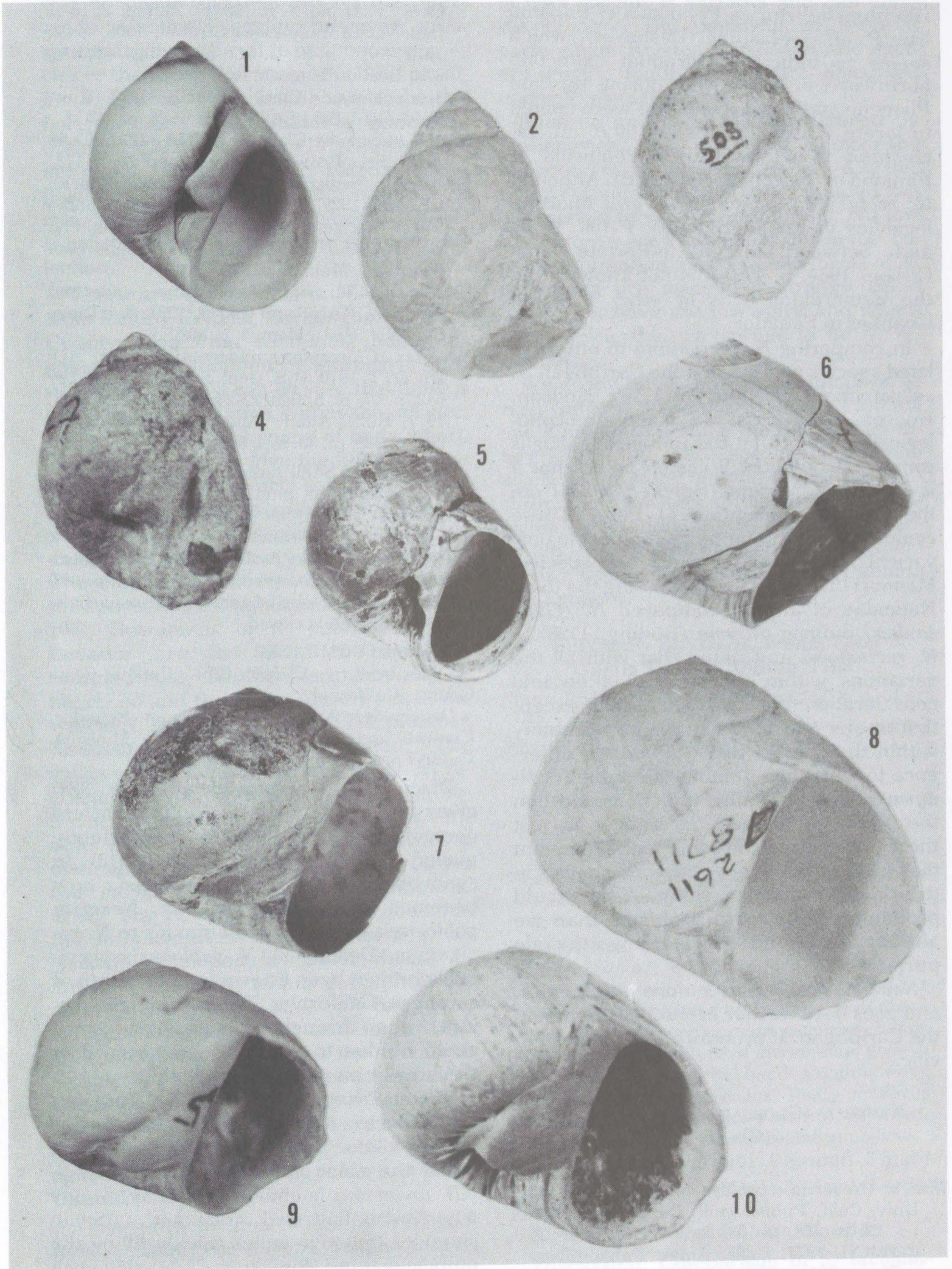


PLATE 3

(Pleistocene) Burica Peninsula of Panamá lists *P. aff. reclusiana* (Deshayes), which seems to indicate a gradual extinction northward in the Pacific during the late Pliocene and Pleistocene. We were unable to locate Olsson's specimen of *P. aff. reclusiana* from the Burica Peninsula of Panamá in the collections at PRI. Although *N. reclusiana* occurs in several Miocene localities in Ecuador (P-105, P-106, P-107 and between Mompiche-Portete, *vide* Olsson, 1964, p. 179) it is not known from the Esmeraldas beds or other Pliocene localities in Ecuador.

In comparing *N. reclusiana* to other related species we find that the Caribbean *N. subporcana* (Williston, 1927, *ex* Hodson, Hodson, and Harris, MS) is close morphologically except that the umbilical callus is somewhat bulbous. Williston noted that it is close to *N. porcana* (Spieker, 1922) from the Zorritos Formation of Peru. These could prove to be no more than ecological variants of a highly variable species. Majima (1989, p. 53), in discussing the fossil Naticidae of Japan, compared *N. (Glossaulax) didyma didyma* (Röding, 1798) to *N. reclusiana* and noted that with all the variations within the species taken into consideration the two are equal except that at one end of the range of variability within the species there is enough difference to warrant retaining the name *N. didyma didyma*. Taking into consideration the above mentioned differences in just these few species one could make the point that there is but one world-wide species in this highly variable group. This would probably create more problems than we already have and serve no worthwhile purpose.

*Neverita reclusiana* is more widespread, and goes back farther in the Pacific than in the Caribbean. It probably arose in the Pacific.

NEVERITA (GLOSSAULAX) PABLOENSIS  
(Clark)

Plate 3, figures 9, 10; Plate 4, figures 1, 2

*Natica (Neverita) pabloensis* CLARK, 1915, Univ. Calif. Publs., Bull. Dept. Geol., v. 8, no. 22, p. 488, pl. 68, figs. 12, 14; MARINCOVICH, 1977, Bulls. Amer. Paleontology, v. 70, no. 294, p. 329.

*Natica (Neverita) reclusiana andersoni* CLARK, 1918, Univ. Calif. Publs., Bull. Dept.

Geol., v. 11, no. 2, p. 168, pl. 20, figs. 3, 10-12 [not *Natica anderssoni* Strebel, 1906, Zool. Jahrb. Syst., v. 24, p. 142, pl. 11, figs. 67, 67a, 67b; Recent, Magellanic region].

*Natica pabloensis* Clark. TRASK, 1922, Univ. Calif. Geol. Sci., Bull., v. 13, no. 5, p. 143.

*Natica andersoni* Clark. HANNA, 1924, Calif. Acad. Sci., Proc., (ser. 4) v. 13, no. 10, p. 173.

*Polinices reclusianus pabloensis* (Clark). CLARK, 1929, Strat. and faunal horiz. of the Coast Range, California, pl. 34, fig. 12; GRANT and GALE, 1931, San Diego Soc. Nat. Hist., Mem. 1, p. 802.

*Polinices (Neverita) reclusiana andersoni* (Clark). GRANT and GALE, 1931, San Diego Soc. Nat. Hist., Mem. 1, p. 802.

*Neverita (Glossaulax) andersoni* (Clark). ADDICOTT, 1970, U.S. Geol. Surv., Prof. Paper 642, p. 67, pl. 5, figs. 22-24; MARINCOVICH, 1977, Bulls. Amer. Paleontology, v. 70, no. 294, p. 328, pl. 30, figs. 5-8.

*Description:* Shell large; slightly wider than high; whorls three, plus protoconch; spire low, body whorl large, inflated, sides somewhat flattened giving appearance of being shouldered; aperture semi-lunar; parietal callus heavy; umbilical callus large, divided by a transverse groove, posterior lobe larger, umbilicus partially open to completely closed.

*Holotype:* UCMP 11592.

*Type locality:* UCMP 1227, Contra Costa County, California.

*Occurrence:* Angostura Formation, Ecuador. Central and southern California; Miocene. Gatun Formation, Panamá; Pliocene.

*Discussion:* Marincovich (1977, p. 328) gives full species rank to *N. Neverita andersoni* (Clark, 1918) and inadvertently placed *N. pabloensis* (Clark, 1915) in synonymy; therefore, *N. pabloensis* now becomes the taxon of priority. *Neverita pabloensis* (Clark) is most similar to *N. reclusiana* (Deshayes); *N. pabloensis* previously has not been known to occur south of southern California. This seemingly disjunct range throughout its geologic history could be due to a lack of fossil record in this area or an artifact of collecting.

In comparing *N. reclusiana* to *N. andersoni* (Clark), it is noted by Marincovich (1977, p. 331): "When typically developed, as are the great majority of specimens, *N. (G.) andersoni* is characterized by a body whorl with flattened sides and tabulate shoulder, massive callus thickly filling the umbilicus, and low spire." Marincovich also noted that, although there are consistent morphologic differences, the two spe-

cies do occur together but do not intergrade at a single locality, however, some specimens are difficult to assign to one species or the other. Marinovich (1977, pl. 30, fig. 5) figured what is supposed to be the holotype of *N. reclusiana andersoni* (UCMP 11212, loc. no. 1131; height 15.3 mm), but Clark (1918, P. 168) cited the height of the type specimen as about 32 mm. The holotype, as described by Clark, is not the specimen placed in the type collection.

There are several lots of *N. pabloensis* from locality CAS 65, Barker Ranch, Kern County, California containing numerous specimens, indentified by Marinovich. In examining these it can be seen that there is considerable variation within the species, in spire height, and shape of body whorl. The spire is always low; the body whorl is straight sided, or nearly so. The size and shape of the umbilical callus, the degree to which it covers the umbilicus is highly variable, as is also the case with *N. reclusiana*. These specimens compare favorably with the specimens from Palestina, Ecuador (P-105). Specimens of *N. pabloensis* from Ecuador are flat sided to somewhat rounded; the shoulders are tabulate, or nearly so and the spires are low, as in the typical *N. pabloensis*. Clark (1918, p. 168) in discussing his *N. andersoni* noted: "The callus is very similar to that seen on *N. reclusiana* Petit, of which this form is described as a subspecies, and is just as variable; on some specimens the umbilicus is open anterior to the callus, while on others the callus covers the entire umbilical area." Marinovich (1977, p. 331) adds that the umbilical callus in *N. andersoni*, when typically developed, is massive, thickly filling the umbilicus, with a deep pit at the anterior margin. We have only one specimen that truly meets this criterion (P-105). One specimen (P-129) has the umbilicus slightly open. Of a dozen specimens identified as *N. reclusiana* from the Gatun Formation, Panamá (P-97) there are a few that have the straight sides and somewhat flat spires, enough to place *N. pabloensis* in the Gatun Formation.

*Neverita reclusiana* differs from *N. pabloensis* mainly in a spire height that is highly variable rather than consistently low and somewhat flattened. The body is more evenly rounded. The umbilical callus

of both species is variable and can completely cover the umbilicus or leave it partly open. Related Caribbean and eastern Pacific fossil species are discussed under *N. reclusiana*.

*Neverita andersoni* (Clark) (figured by Marinovich, 1977, pl. 30, fig. 8) from the Miocene Topanga Formation, Los Angeles County, California, is a straight sided but high spired form of *N. pabloensis*. No low spired forms are known to occur in the Topanga Formation and, as some forms of *N. reclusiana* are somewhat straight sided but do not have the low spire and shouldered spire, this may prove to be *N. reclusiana*.

We do not have enough specimens of *N. reclusiana* or *N. pabloensis* from Panamá and Ecuador to verify if the two species intergrade. Until more specimens become available for study we will accept the conclusions of previous studies done in California (*vide* Addicott, 1970, p. 67; Marinovich, 1977, p. 328) and report *N. pabloensis* as a valid species occurring in Panamá and Ecuador.

#### Subfamily SININAE Wenz, 1941

#### Genus SINUM Röding, 1798

*Sinum* Röding, 1798, Mus. Bolten., pt. 2, p. 14.

*Type species: Helix haliotoidea* Linnaeus, 1758, by subsequent desig., Dall, 1915.

#### SINUM LACONDAMINI

Olsson

Plate 4, figure 3

*Sinum lacondamini* OLSSON, 1964, Neogene Moll. Northwest Ecuador, p. 183, pl. 37, figs. 4, 4a.

*Description:* Shell globose; spire low to moderately elevated; whorls rounded; suture distinct to slightly impressed; spiral sculpture of flat topped bands separated by interspaces of about equal width, with one or more secondary bands between; axial sculpture of incremental growth lines, at times giving spiral bands a slightly wavy appearance; parietal callus thin; umbilicus open, slitlike; umbilical callus narrow, flattened, overlapping and partially concealing umbilicus.

*Holotype:* USNM 644120.

*Type locality:* Esmeraldas beds, Punta Gorda, Ecuador.

*Occurrence:* Esmeraldas beds, Ecuador.

*Discussion:* Comparison of *S. lacondamini* Olsson to Caribbean fossil specimens of *S. gabbi* (Brown and Pilsbry, 1913),

shows the latter is very close in most morphological details, except that the aperture is larger and flares outwardly to a much greater degree. Olsson (1964, p. 183) compared *S. lacondamini* to *S. imperforatum* Dall, 1915, but Dall's species is taller, the aperture is nearly round, and the spiral threads are minutely zigzagged by incremental growth lines. In another related species, *S. waltonense* Gardner (1947), the surface is covered by fine and crowded lirae, minutely crinkled by the incrementals, equal to the zigzag spirals of *S. imperforatum*. These two species are similar in general morphology and are the closest species morphologically.

In the Recent fauna of the Tropical East Pacific *S. grayi* (Deshayes, 1843) is similar to *S. lacondamini* in that the apertures are about the same shape, except that the anterior portion from the columella to the outer portion in *S. lacondamini* is straight, rather than curved, which leaves the outermost part almost truncated.

All of the above mentioned species are part of a closely allied group and most probably arose from the same stock. Woodring (1957, p. 94), in his discussion of *S. gabbi*, noted that no similar species are living today in the Caribbean. The fossil record of this group in the Tropical East Pacific is not known to go as far back as it does in the Caribbean, leaving the probability that these related species arose in the Caribbean.

SINUM sp. cf. *S. CYMBA* (Menke)  
Plate 4, figure 4

*Sigaretus cymba* MENKE, 1828, Synopsis Methodica Molluscorum Museo Menkeano, p. 88.

*Sigaretus concavus* Lamarck. BURCH and BURCH, 1964, Nautilus, v. 77, no. 4, p. 109, pl. 5, figs. 2, 4, [not *S. concavus* (Lamarck, 1822)].

*Sinum cymba* (Menke). KEEN, 1971, Sea Shells Trop. West Amer., ed. 2, p. 482, fig. 889; MARINCOVICH, 1977, Bulls, Amer. Paleontology, v. 70, no. 294, p. 343, pl. 32, figs. 1-6,

PLATE 4

Figures

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1-2. <i>Neverita (Glossaulax) pabloensis</i> (Clark) . . . . .	126
1. CASG 66590; height 29.3 mm, diameter 30.8 mm (X 1.3). Locality: P-105, Ecuador; Angostura Formation.	
2. CASG 66591; height 28.7 mm, diameter 31.1 mm (X 1.4). Locality: P-97, Panamá; Gatun Formation.	
3. <i>Sinum lacondamini</i> Olsson . . . . .	127
CASG 66593; height 18.7 mm, diameter 17.2 mm (X 2.4). Locality: P-101, Ecuador; Esmeraldas beds.	
4. <i>Sinum</i> sp. cf. <i>S. cymba</i> (Menke) . . . . .	128
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5-7. <i>Natica (Natica) inexpectans</i> Olsson . . . . .	130
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6. CASG 66553; height 15.2 mm, diameter 15.6 mm (X 2.3). Locality: P-100, Ecuador; Esmeraldas beds. (Color pattern as shown by ultra-violet light).	
7. USNM 701161 (holotype); height 23.1 mm, diameter 22.6 mm (X 1.6) (from Olsson, 1971). 7a, operculum; length 15 mm; width 10.4 mm (X 1.7). Locality: Panamá Bay, Panamá; Recent.	
8-10. <i>Natica (Naticarius) scethra</i> Dall . . . . .	130
8. CASG 66554; height 23.7 mm, diameter 20.8 mm (X 1.8). Locality: P-101, Ecuador; Esmeraldas beds.	
9. CASG 66555; height 29.0 mm, diameter 27.1 mm (X 1.4). Locality: P-101, Ecuador; Esmeraldas beds.	
10. LACM 66-130.3; height 27.2 mm, diameter 26.0 mm (X 1.4). Locality: Paíta, Peru; Recent.	

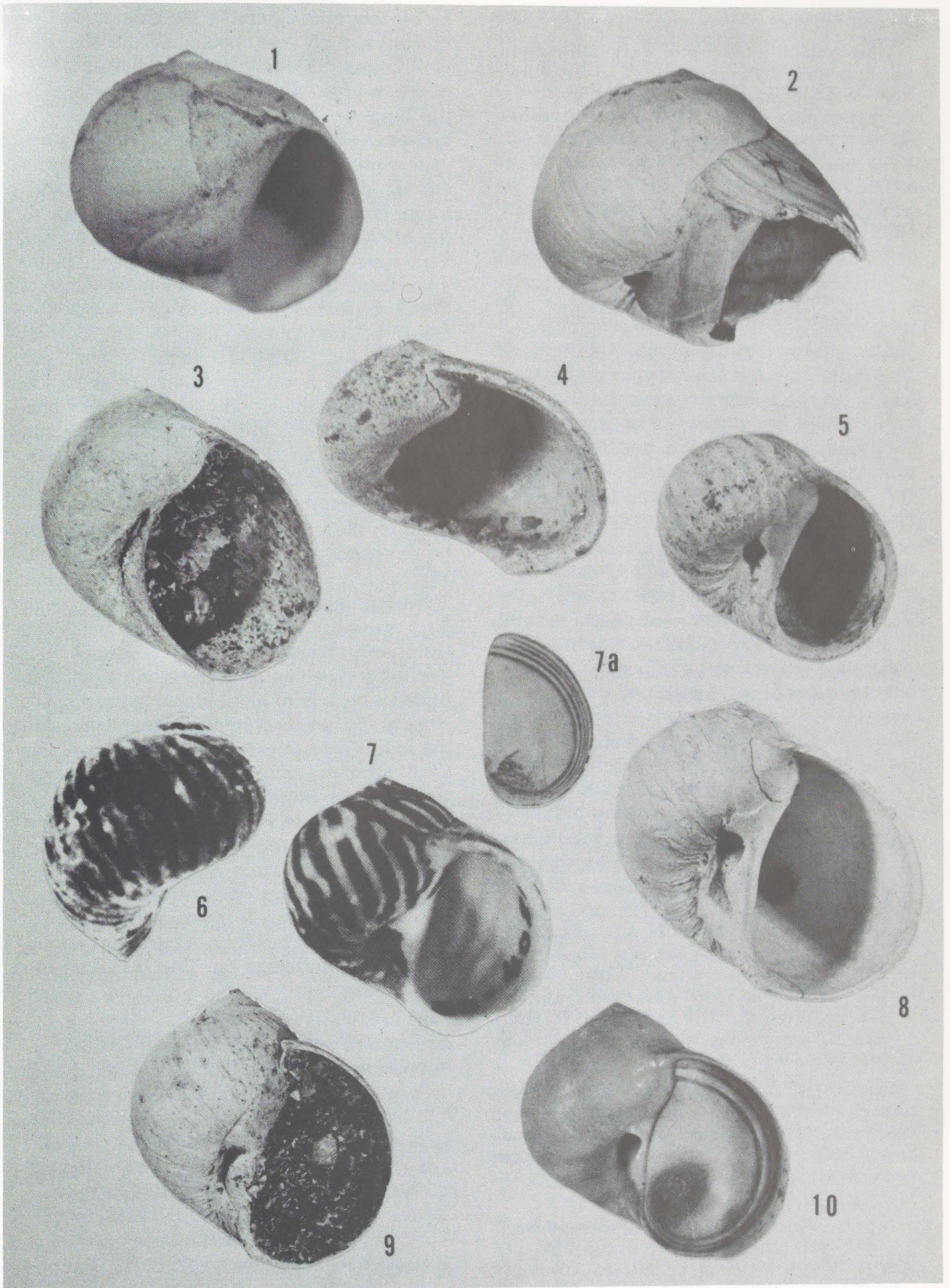


PLATE 4

text-fig. 11d.

*Description:* Spire low to moderately elevated; suture slightly impressed; spiral sculpture of fine, flat-topped bands with narrower interspaces; axial sculpture of incremental growth lines, disrupting the spirals and giving them a wavy appearance; aperture ovate, flaring, oblique, pointed anteriorly; parietal callus thin; umbilicus open, slitlike; umbilical callus flattened, partially concealing umbilicus.

*Type material:* Unknown, presumably sold to a dealer and lost (Zilch, 1958, p. 53).

*Type locality:* "Oceano Peruviana."

*Occurrence:* Esmeraldas beds, Ecuador.

*Discussion:* *Sinum cymba* (Menke) differs from *S. grayi* (Deshayes) by having a lower spire, a more widely flaring aperture, and a body whorl that is somewhat flattened anteriorly. We hesitate to refer our specimen to *S. cymba* except with "cf.," as our single specimen has all of the columella missing.

#### Subfamily NATICINAE Forbes, 1838

##### Genus NATICA Scopoli, 1777

*Natica* SCOPOLI, 1777, *Introductio ad Historiam Naturalem*, p. 392.

*Type species:* *Nerita vitellus* Linnaeus, 1758, by subsequent desig., Anton, 1839.

##### Subgenus NATICA s.s.

##### NATICA (NATICA) INEXPECTANS

Olsson

Plate 4, figures 5-7

*Natica (Naticarius) cf. scethra* DALL, OLSSON, 1964, *Neogene Moll. Northwest. Ecuador*, p. 178, pl. 32, figs. 9-9c [not *Natica (Cochlis) scethra* DALL, 1908].

*Natica inexpectans* OLSSON, 1971, *Bull. Mar. Sci.*, v. 21, no. 1, p. 69, figs. 31a, 31b, 32.

*Natica (Natica) inexpectans* OLSSON, KEEN, 1971, *Sea Shells Trop. West Amer.*, ed. 2, p. 475, no. 864a; MARINCOVICH, 1977, *Bull. Amer. Paleontology*, v. 70, no. 294, p. 370, pl. 36, figs. 6, 7.

*Description:* Shell small, of about four whorls; suture distinct; spire low or of medium height; whorls smooth except for incremental growth lines; body whorl large, globose; umbilicus open, deep; funicular rib small or lacking.

*Holotype:* USNM 701161.

*Type locality:* R/V *John Elliot Pillsbury* locality P-513, Gulf of Panamá ENE of Cabo Mala (7° 39.5' N, 79° 40.7' W, depth 117 meters).

*Occurrence:* Esmeraldas beds, Ecuador. Recent, Gulf of Panamá.

*Discussion:* In comparing specimens of

*N. inexpectans* Olsson, from Quebrada Camarones, to *N. inexpectans* from the Recent fauna, as described by Olsson (1971, p. 69), we find that the only difference is in the height of the spire, which is generally higher in specimens from Quebrada Camarones, otherwise they are morphologically equal. Under ultra-violet light the specimens from Quebrada Camarones (pl. 4, fig. 6) show the same color pattern as Recent specimens, with widely spaced axial lines from the suture to the base. Specimens of *Natica cf. scethra* Dall of Olsson (1964, p. 178, pl. 32, figs. 9, 9a, USNM 645250; 9b, USNM 643887) do not fluoresce. Not all specimens of a single species from one locality will fluoresce and we were not able to treat the specimens at the USNM with sodium hypochlorite, which is often necessary to bring out the color pattern. In view of these data we consider *N. cf. scethra* Dall of Olsson, 1964, to be a synonym of *N. inexpectans* Olsson, 1971.

*Natica inexpectans* Olsson is similar to *N. brunneolinea* McLean, 1970, from the Galápagos Islands, Ecuador, except that the latter species is generally larger; the color pattern is of axial lines that are more closely spaced than in *N. inexpectans*, and the axials do not extend to the base of the shell. Marincovich (1977, p. 385), discussing *N. brunneolinea*, noted: "This species is most similar to *N. scethra* Dall, 1908 and the opercula of the two species are indistinguishable." *Natica scethra* is morphologically similar but lacks the axial stripes of *N. brunneolinea*. It is probable that all of these species came from a common ancestor and originated in the Tropical East Pacific.

##### Subgenus NATICARIUS Duméril, 1806

*Naticarius* DUMÉRIL, 1806, *Zoologie Analytique*, p. 164.

*Type species:* *Natica canrena* Linnaeus, 1758, by subsequent desig., Froriep, 1806.

##### NATICA (NATICARIUS) SCETHRA

Dall

Plate 4, figures 8-10

*Natica (Natica) scethra* DALL, 1908, *Harvard Mus. Comp. Zool., Bull.*, v. 43, no. 6, p. 333, pl. 11, fig. 5.

*Natica (Naticarius) othella burica* OLSSON, 1964, *Neogene Moll. Northwest. Ecuador*, p.

178, pl. 32, figs. 5-5c.

*Natica (Natica) scethra* Dall. KEEN, 1971, Sea Shells Trop. West Amer., ed. 2, p. 475, fig. 866.

*Natica (Naticarius) scethra* Dall. MARINCOVICH, 1977, Bulls. Amer. Paleontology, v. 70, no. 294, p. 382, pl. 37, figs. 7, 8.

*Description:* Shell of medium size, thin, spire moderately elevated; suture distinct; axial sculpture of retractive grooves from suture to about one-half distance to periphery, weaker on later whorls; body whorl inflated, evenly rounded; aperture ovate to semicircular; parietal callus thin, ending with a small notch posteriorly; umbilicus narrowly open, with small, flat funicular rib fused to columellar callus.

*Holotype:* USNM 123048.

*Type locality:* R/V Albatross station 3391, Gulf of Panamá, 153 fms [280 meters].

*Occurrence:* Esmeraldas beds, Ecuador. Burica Peninsula, Panamá; Pleistocene. Recent, Mexico to Ecuador and the Galápagos Islands.

*Discussion:* *Natica scethra* Dall, resembles the Tropical East Pacific species *N. othello* Dall, which has a higher spire, and is not as globose; the umbilical sulcus is not as narrow and the posterior notch on the umbilical callus is deeper. The Recent *N. caneloensis* Hertlein and Strong (1955) is very close in form, differing mainly in having a wider umbilical sulcus, and a different color pattern. In discussing differences between *N. scethra* and *N. caneloensis*, Marincovich (1977, p. 383) noted that these species probably could not be separated if preserved as fossils, lacking color pattern and opercula. Numerous lots of *N. scethra* examined at LACM show considerable variation within the species.

In comparing specimens of *N. othella burica* Olsson (1964, p. 178) to *N. othello* Dall (1908, p. 332) and *N. scethra* Dall (1908, p. 333) we find that specimens from the Esmeraldas beds are not as high spired, they are more globose and have a more narrow umbilical opening than the typical *N. othello*. Most specimens do have a small sulcal notch as in *N. othello* (Marincovich, 1977, pl. 37, fig. 1). *Natica scethra* (*ibid.*, pl. 37, fig. 8) shows the typical *N. scethra* with the narrow umbilical opening, but pl. 37, fig. 7 shows a specimen with a slight notch in the umbilical callus. *Natica othello* (Marincovich, 1977, pl. 35, fig. 11) is morphologically equal to *N. scethra*. The color

pattern of the two species is slightly different and they are most difficult to separate in the fossil record.

Olsson (1942a, p. 231), in discussing *N. scethra burica* (pl. 5, figs. 1, 1a), noted that the operculum of this subspecies has two marginal ribs with the outer one being smaller, whereas Dall's figure of *N. scethra* shows the ribs being of nearly equal size. From Recent specimens examined we find that the ribs are not always of equal size. Olsson (1964, p. 178) placed his subspecies *N. scethra burica* Olsson, 1942, in synonymy with his new subspecies *N. othella burica* Olsson, 1964. The holotype of *N. scethra burica* Olsson (1942a, p. 231(79), pl. 10, figs. 2, 7) has a more open umbilicus than the typical *N. scethra* and is more like *N. othello* Dall; however, *N. othello* has an operculum with two narrow marginal ribs, both being pustulate. The operculum of *N. scethra burica* is the same as the operculum of *N. scethra*. *Natica scethra burica* has a raised rib just posterior to the umbilicus. *Natica othella burica* Olsson, 1964, does not have the raised rib adjacent to the umbilicus and we have not seen an operculum equal to the operculum of *N. scethra burica* in the Esmeraldas beds. For the above reasons we consider *N. othella burica* a synonym of *N. scethra* and reinstate *N. scethra burica* as a valid subspecies of *N. scethra*.

*Natica scethra* does not appear to have any close relatives in the Caribbean region and probably arose in the Pacific.

#### Subgenus STIGMAULAX Mörch, 1852

*Stigmaulax* Mörch, 1852, Cat. Conch. Yoldi, fasc. 1, p. 133.

*Type species:* *Nerita sulcata* Born, 1778, by subsequent desig., Harris, 1897.

#### NATICA (STIGMAULAX) BRODERIPIANA

Récluz

Plate 5, figures 2, 3

*Natica broderipiana* RÉCLUZ, 1844, Zool. Soc. London, Proc. (1843), v. 11, p. 205; DALL, 1909, U.S. Natl. Mus. Proc., v. 37, no. 1704, p. 235; PILSBRY and OLSSON, 1941, Acad. Nat. Sci. Phila., Proc., v. 93, p. 8, 45; OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, p. 163(11), 169(17), 170(18), 173(21).

*Natica (Stigmaulax) broderipiana* Récluz. KEEN, 1971, Sea Shells Trop. West Amer.,

ed. 2, p. 477, fig. 870; MARINCOVICH, 1977, *Bulls. Amer. Paleontology*, v. 70, no. 294, p. 399, pl. 40, figs. 6, 7.

*Stigmaulax broderipiana* (Récluz). OLSSON, 1964, *Neogene Moll. Northwest. Ecuador*, p. 181, pl. 32, figs. 1-1b; ABBOTT, 1974, *Amer. Sea Shells*, ed. 2, p. 160, no. 1728.

*Description:* Medium size; spire moderately high to high; whorls about five; suture impressed; body whorl inflated, evenly rounded; sculpture of fine axial grooves from suture to umbilicus, strongest from suture to periphery of body whorl where they become indistinct; aperture large, parietal callus fairly heavy; columellar wall curved; umbilicus opening large, bordered anteriorly by a sulcus; umbilical callus large, broad, semicircular, with concave anterior portion; funicular rib large, filling anterior half of umbilicus.

*Holotype:* No. 1350/51, Muséum d'Histoire Naturelle, Geneva, Switzerland.

*Type locality:* "Xipixapi, West Colombia" [Jipijapa, Ecuador], 29 meters, sandy mud (Récluz, 1844).

*Occurrence:* Esmeraldas beds, Canoa Formation, Ecuador. Magdalena Bay, Baja California and the Tres María Islands, Mexico; Burica Peninsula, Panamá; Pleistocene. Recent from Cabo San Lucas, Baja California, Mexico, throughout the Gulf of California and south to Ecuador.

*Discussion:* In comparing *N. broderipiana* from the Esmeraldas beds to *N. guppiana* Toula, 1909, it may be seen that *N. guppiana* differs in having axial grooves in adult shells that do not generally extend below the periphery; the suture is more deeply impressed; there is a small secondary rib adjacent to the funicular rib. Some specimens of *N. broderipiana* show indications of swelling on the columella where the secondary rib of *N. guppiana* occurs. The opercula are similar except that the central rib is wider in *N. guppiana*. The color pattern is similar, but in *N. broderipiana* the markings are square

#### PLATE 5

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1. <i>Natica (Naticarius) scethra burica</i> Olsson . . . . .	131
PRI 4068 (holotype); height 27.5 mm, diameter 27.0 mm (X 1.3).	
1a, operculum; height 21.0 mm, diameter 12.0 mm (X 1.3).	
Locality: Panamá; Charco Azul Formation.	
2-3. <i>Natica (Stigmaulax) broderipiana</i> Récluz . . . . .	131
2. CASG 66556; height 36.0 mm, diameter 34.8 mm (X 1.3).	
Locality: P-101, Ecuador; Esmeraldas beds.	
3. CASG 66557; height 42.2 mm, diameter 40.9 mm (X 1).	
Locality: P-101, Ecuador; Esmeraldas beds.	
(Color pattern as shown by ultra-violet light).	
4-9. <i>Natica (Stigmaulax) guppiana</i> Toula . . . . .	134
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Locality: TU 1429, Panamá; Gatun Formation.	
5. CASG 66559; height 18.1 mm, diameter 16.2 mm (X 2).	
Locality: P-95, Panamá; Gatun Formation.	
(Color pattern as shown by ultra-violet light).	
6. CASG 66560; height 24.0 mm, diameter 23.7 mm (X 1.9).	
Locality: P-95, Panamá; Gatun Formation.	
7. CASG 66561; height 16.5 mm, diameter 15.1 mm (X 2.3).	
Locality: P-103, Ecuador; Angostura Formation.	
8. CASG 66562; height 13.7 mm, diameter 13.4 mm (X 2.5).	
8a, Color pattern as shown by ultra-violet light (X 2.7).	
Locality: P-125, Ecuador; Cachabí Formation.	
9. CASG 66563; height 19.7 mm, diameter 17.1 mm (X 2).	
Locality: P-102, Ecuador; Angostura Formation.	
10. <i>Natica (Stigmaulax) landesiana</i> Olsson . . . . .	135
CASG 66564 (topotype); height 11.7 mm, diameter 11.7 mm (X 3.3).	
Locality: P-100, Ecuador; Esmeraldas beds.	
11. <i>Naticid operculum</i> . . . . .	136
CASG 66592; length 9.3 mm, width 5.9 mm (X 3.9).	
Locality: P-101, Ecuador; Esmeraldas beds.	



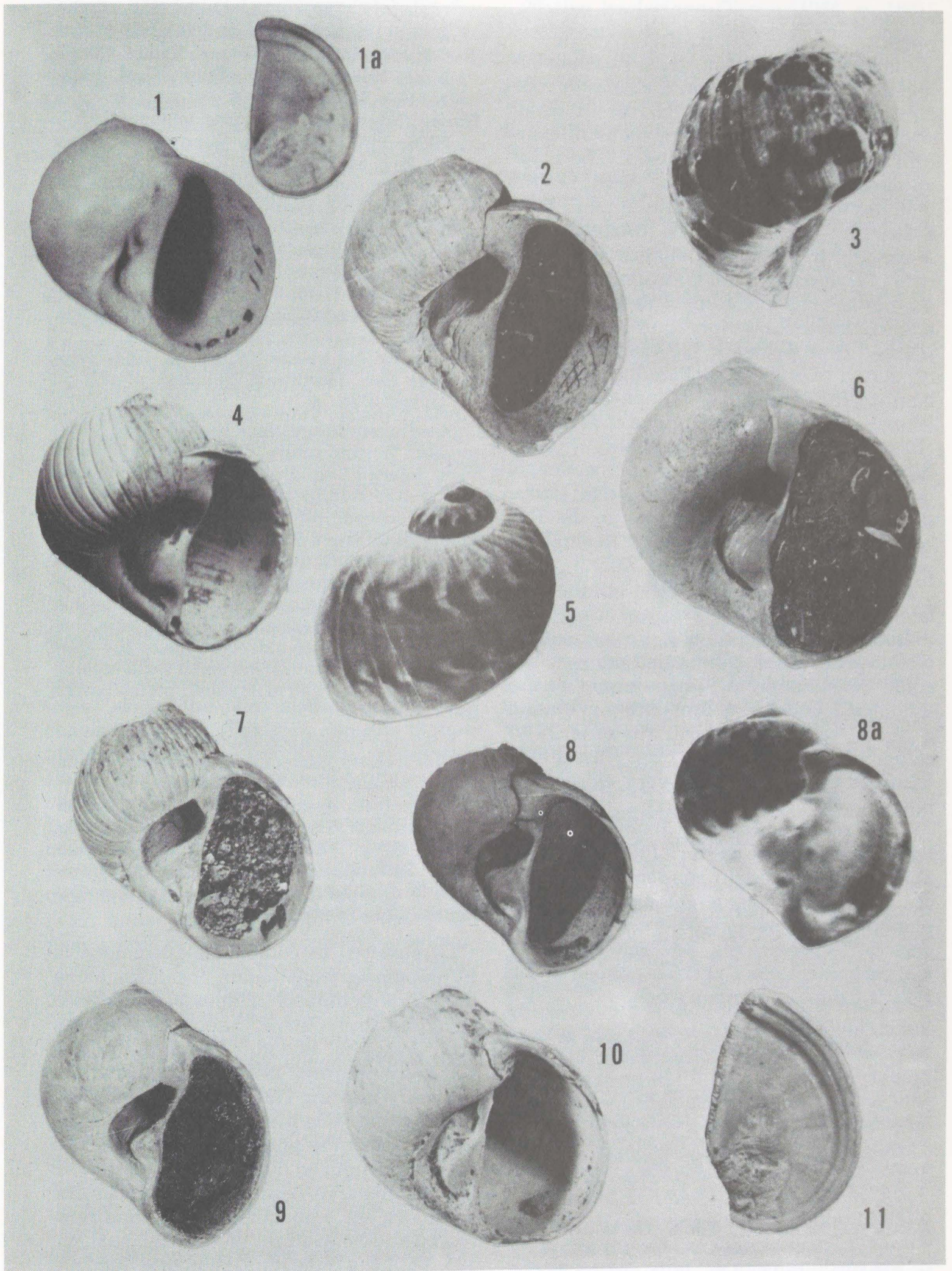


PLATE 5

rather than chevron shaped as in *N. guppiana*.

*Natica sulcata* Born, 1778, another related Recent species from the Atlantic, differs in having the axial grooves of equal strength from suture to umbilicus; the suture is more deeply impressed. The color pattern varies from white with brown blotches to pure white and is smaller than either *N. guppiana* or *N. broderipiana*. Marinovich (1977 p. 400) noted that the suture of *N. broderipiana* is strongly impressed; however, some Recent specimens examined have the suture only slightly impressed or appressed. Woodring (1957, p. 87) noted: "Forms of *Stigmaulax* closely related to the Recent Caribbean *S. sulcata* (Born) are found in formations of Jamaica, Haiti, the Dominican Republic, Puerto Rico, and Brazil. *S. guppiana*, however, is not one of them. It lacks gross spiral sculpture and is more closely allied to the Recent Panamic *S. broderipiana* (Récluz), as pointed out by Olsson (1932, p. 207)."

*Natica elenae* Récluz, 1844, another related species, from the Tropical East Pacific Recent, differs in having a color pattern of fine axial lines. The axial grooves become indistinct from the periphery to the umbilicus. The operculum differs in having a heavy secondary spiral rib anteriorly, rather than several low spiral ribs; otherwise the two species are very close morphologically.

The oldest known record of *N. broderipiana* in the eastern Pacific is in the Esmeraldas beds of Ecuador. The difference between *N. broderipiana* and *N. guppiana* lies in the color pattern and the secondary funicular rib, or lack of same. *Natica broderipiana* probably arose in the Pacific from *N. guppiana* stock.

NATICA (STIGMAULAX) GUPPIANA  
Toula

Plate 5, figures 4-9

- Natica guppiana* TOULA, 1909, Geol. Reichs. Jahrb., v. 58, p. 696, pl. 25, fig. 6; HODSON, HODSON, and HARRIS, 1927, Bulls. Amer. Paleontology, v. 13, no. 49, p. 67, pl. 36, figs. 1, 4.  
*Natica guppyana* [sic] Toula. OLSSON, 1922, Bulls. Amer. Paleontology, v. 9, no. 39, p. 328(156), pl. 13, figs. 13-15; ANDERSON, 1929, Calif. Acad. Sci., Proc., (ser 4) v. 18, no. 4, p. 123.  
*Natica* (*Naticarius*) *guppyana* [sic] Toula.

OINOMIKADO, 1939, Geol. Soc. Japan, Jour., v. 46, p. 621(107), pl. 29(15), fig. 18.

*Natica* (*Stigmaulax*) *guppiana* Toula. GARDNER, 1947, U.S. Geol. Surv., Prof. Paper 142-H, p. 546, pl. 59, fig. 9.

*Natica* (*Stigmaulax*) *guppiana toulana* GARDNER, 1947, U.S. Geol. Surv., Prof. Paper 142-H, p. 547, pl. 59, figs. 7, 8.

*Natica* (*Stigmaulax*) *guppyana* [sic] Toula. MARKS, 1951, Bulls. Amer. Paleontology, v. 33, no. 139, p. 368(98).

*Stigmaulax guppiana* Toula. WOODRING, 1957, U.S. Geol. Surv., Prof. Paper 306-A, p. 86, pl. 20, figs. 11-16; OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 181, pl. 37, figs. 2, 2a.

*Stigmaulax kugleriana* OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 181, pl. 37, figs. 3, 3a.

*Description*: Large; thick shelled; spire low to medium height; suture distinct; whorls about four, inflated, rapidly enlarging; body whorl with well rounded profile; sculpture of relatively widely spaced, retractive grooves, generally ending at or above periphery of body whorl, extending to umbilicus in some shells but not on last half of body whorl on large shells; umbilicus wide with large funicular rib, rapidly enlarging, ending with a moderately wide callus lobe, concave anteriorly, with a deep sulcus on the anterior side of the funicular rib and a small secondary rib posteriorly on most shells; parietal callus thick.

*Holotype*: Tech. Hochschule, Vienna.

*Type locality*: Gatun Locks excavation, Canal Zone, Panamá.

*Occurrence*: Angostura and Cachabí formations, Ecuador. La Vela Formation, Venezuela; Shoal River Formation, Florida; Miocene. Gatun Formation, Panamá; Río Banano Formation, Costa Rica; Pliocene. Tubará Group, Colombia; Plio-Pleistocene.

*Discussion*: In comparing specimens of *N. guppiana* from Gatun localities along the Transisthmian Highway, between Sabanita and Cativá, San Judas Todeo, and Payardi Island, Panamá (Lower Gatun, Woodring, 1957, p. 125) to the figures of Woodring (1957, pl. 20, figs. 11-18) we find that Woodring's figures show axial grooves over the entire body surface. The specimens figured by Woodring come from the eastern area near the Gatun locks, the third lock cut, and along the Panamá Railroad (Middle Gatun, Woodring, 1957, p. 125, 126). We have more than one hundred specimens from Lower Gatun localities, and find only a few specimens, mostly small, having axial grooves over the entire

surface. The figured specimen (pl. 5, fig. 4, locality TU 1429) is from near Woodring's locality 178 (Upper Gatun) and does have axial grooves over the entire body surface as do Woodring's figured specimens from the Upper Gatun. Olsson (1964, p. 181, pl. 37, figs. 2, USNM 645256, fig. 2a, USNM 643895) figured small poorly preserved specimens of *N. guppiana* from between Mompiche and Portete, Manabí Prov., Ecuador. He also noted that the smaller specimens have axial grooves over the entire body surface.

Comparing *N. guppiana* Toula from the Angostura Formation of Ecuador to specimens from the Gatun Formation of Panamá shows that specimens from Ecuador have the axial grooves more closely spaced and the secondary funicular rib less pronounced than in most Gatun specimens. One specimen from Ecuador has a wide shallow sulcus and a flat face on the umbilical callus lobe rather than the typical deep sulcus and concave face on the callus lobe.

Specimens of *N. guppiana* from localities (P-103, P-129) south of Punta Verde have grooves over the entire body surface with four or five faint axial striations on the axial ribs. Upon close examination of specimens from along the Transistmian Highway (Lower Gatun), Panamá, we find that under the surface glaze of well preserved shells the faint striations on the ribs can be seen.

Barro Colorado, Cachabí Formation, (locality P-125) Río Santiago, Esmeraldas Prov., Ecuador, is morphologically equal to other specimens of *N. guppiana*, however, under ultra-violet light the color pattern is similar to that of typical *N. guppiana* except that it has a central row of arrow shaped marks. This is probably an ecological variant rather than a different species. One specimen is hardly enough evidence to justify a new species based on color pattern, as color patterns can vary from locality to locality in some species.

Weisbord (1962, p. 247) mentioned *N. guppiana* from the Mare Formation, Venezuela, but noted that it was incomplete and he was unable to make a positive identification. Since the Mare Formation is Pleistocene and the specimen is incomplete it is appropriate to disregard this reported possible occurrence.

*Natica kugleriana* Olsson (1964, p. 182) was described as differing from *N. guppiana* "by its thinner shell; in having the penultimate whorl with a less pronounced bulge and more important in that the axial groovings are restricted to the sutural area at all stages of growth, even the smallest specimens, less than 8 mm in diameter, are sculptured similar to the large ones." Upon examining specimens of *N. guppiana* from Panamá it is noted that USNM 561343 is a thin shelled specimen, USNM 561342 does not have the penultimate whorl as bulbous as most specimens of *N. guppiana*. In view of all the variations in *N. guppiana* we find no reason to retain the name *N. kugleriana* and place this species in synonymy with *N. guppiana*.

NATICA (STIGMAULAX) LANDESIANA  
(Olsson)

Plate 5, figure 10

*Stigmaulax landesiana* OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 182, pl. 32, figs. 8, 8a.

*Description:* Shell small; globose; spire low, of about four whorls; body whorl large, profile well rounded, surface smooth except for fine growth lines and a series of retractive grooves extending from the suture to the shoulder of the whorl; umbilicus open with a large funicular rib, wide at base, bounded by a deep sulcus; aperture semi-ovate; outer lip thin.

*Holotype:* USNM 643898.

*Type locality:* Esmeraldas beds, Quebrada Camarones, Ecuador.

*Occurrence:* Esmeraldas beds, Ecuador.

*Discussion:* Comparing *N. landesiana* (Olsson) to *N. guppiana* Toula shows that the outline of both species is similar, but *N. guppiana* differs in having the axial grooves more widely spaced; the umbilical area is more open; the columellar callus lobe has a depression anteriorly, whereas in *N. landesiana* the callus lobe is flat, and there is a distinct band bordering the umbilicus, which is lacking in *N. guppiana*. Also, *N. guppiana* has a small secondary rib on the posterior side of the funicular rib, which is totally lacking in *N. landesiana*. Upon close examination of the axial ribs there is an indication of faint striations on the ribs, as can be observed in well-preserved specimens of *N. guppiana*.

Several East Pacific species, including *N. landesiana*, are apparently derived from *N. guppiana* and represent the last appearance of the *N. guppiana* complex in the Tropical East Pacific.

NATICID operculum  
Plate 5, figure 11

*Description:* Calcereous; flat; semicircular; outer edge bordered by four smooth, narrow, raised ribs with narrow grooves between, except that the inner groove is wide.

*Occurrence:* Esmeraldas beds, Ecuador.

*Discussion:* Olsson (1964, p. 178), in discussing *N. cf. scethra* Dall noted that the operculum is unknown, but figured an operculum with no explanation (1964, pl. 32, fig. 9c).

In describing the operculum of *N. scethra*, Marincovich (1977, p. 382) stated "outer surface smooth except for two deep, sharply incised grooves near outer margin that form two undercut ribs, one between the grooves and one along the outer opercular margin. Outermost margin with one minute, weakly pustulate costella."

Olsson (1971, p. 69), noted that the operculum of *N. inexpectans* is bordered by four ribs. We collected one specimen from the Esmeraldas beds (P-100), which has two ribs but shows sign of wear along the outer margin and may have had another rib. The operculum figured by Olsson (1964, pl. 32, fig. 9c) has only two ribs but has a wide groove inside the innermost rib, the same as the operculum that we have, which leaves these belonging to an unknown species, possibly *N. landesiana*, a small species with an unknown operculum.

## V. LOCALITY DATA

The following are Pitt localities:

- P-95. Gatun Fm., south side of Boyd-Roosevelt Highway, San Judas Todeo housing project, about 2 km north of Cativá, Colón Prov., Panamá.
- P-97. Gatun Fm., north side of Boyd-Roosevelt Highway, about 1 km east of junction with road to Puerto Pilon, Sabanita, Colón Prov., Panamá.
- P-99. Esmeraldas beds, Punta Gorda (intertidal), about 8 km west of Las Palmas, Esmeraldas Prov., Ecuador.
- P-100. Esmeraldas Beds, east bank of Estero Camarones, east of the village of Camarones, about 10 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-101. Esmeraldas Beds, road cut (south side), immediately west of the village of Camarones, about 10 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-102. Angostura Fm., Punta Verde (intertidal), about 2 1/2 km east of the mouth of Río Verde and about 22 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-103. Angostura Fm., sea cliffs about 300 m west of Punta Verde, about 2 1/4 km east of the mouth of the Río Verde and about 22 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-105. Angostura Fm., road cut (south side), at junction of road from Esmeraldas to Río Verde, with road to El Alto in village of Palestina, Esmeraldas Prov., Ecuador.
- P-106. Angostura Fm., road cut (west side), about 0.6 km south of Palestina on road to El Alto, about 20 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-107. Angostura Fm., road cut (west side), about 1.5 km south of Palestina, on road to El Alto, about 20 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.
- P-125. Cachabí Fm., blocks in river and on the river bank on the outside of the first turn downstream from Barro Colorado, Río Santiago, Esmeraldas Prov., Ecuador.
- P-126. Bahía Fm., Punta Mesita, (of recent maps, equals Punta La Colorada of older literature) sea cliffs about 5 km southwest of Bahía de Caráquez, Manabí Prov., Ecuador.
- P-129. Angostura Fm., cliff face about 50 m east of P-103, about 2 1/4 km east of the mouth of Río Verde and about 22 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.

The following are Tulane University localities:

60. Jackson Bluff Fm., borrow pits at Jackson Bluff, Ochlockonee River (NW 1/4 Sec. 21, T1S, R4W), Leon Co., Florida.
376. Duplin Fm., "Natural Well," sinkhole on Matthews' farm, on North Carolina Highway 11, 2 miles west of Magnolia, Duplin Co., North Carolina.
589. Río Banano Fm., Río Banano, north bank, about 0.6 to 0.8 km above the railroad bridge at La Bomba, Limón Province, Costa Rica.
1000. "Pinecrest Beds" [now Fruitville Fm.], APAC pits at east end of 17th street about 8 miles east of U.S. Highway 301 [now northwest of Fruitville Rd. exit, I-75] at Sarasota, (T36S, R19E), Sarasota Co., Florida.

1358. Cercado Fm., Río Gurabo, west side and downstream from mouth of Arroyo La Cabra, or about 5.75 km to 6.0 km (airline), above the bridge on the Los Quemados-Sabaneta Road, Dominican Republic.
1377. Cercado Fm., Río Gurabo, west side, about 0.5 km above the mouth of Arroyo La Cabra, or approximately 6.4 km (airline) above the ford on Los Quemados-Sabaneta road, Dominican Republic.
1429. Gatun Fm., 1 km southeast of Boyd-Roosevelt Highway, just south of Coco Solo Hospital, Panamá.
- R-185. Farfan Beach, south side of Panamá Canal on road to Palo Seco, Panamá.

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