ON THE OCCURRENCE OF THE GASTROPOD GENUS *CASSIS* IN THE ESMERALDAS FAUNA, NORTHWESTERN ECUADOR

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In his seminal treatment of the Panama Land Bridge as a sea barrier, Woodring (1966) coined the now-familiar term "paciphile" for those molluscan genera and/or species that, during the Tertiary, lived on both sides of the Tropical American landmass, but today are living only on the Pacific side. At that time he listed 43 genera or subgenera classified as paciphiles; predicting, however, that some would be eliminated from the list as living representatives were discovered in the western Atlantic. In contrast, he cited only four "caribphile" genera, those that survive in the Caribbean but are extinct in the eastern Pacific. Time has proved his prediction correct and perhaps five of the formerly paciphile genera have been eliminated from his list, nevertheless the overwhelming number of paciphile genera, in contrast to caribphile genera, remains intact.

In his scant list of caribphile genera he included the gastropod genus *Cassis* Scopoli, 1777, noting that the only eastern Pacific fossil occurrence of the genus is in the Imperial Formation of southern California (1966, p. 430). The Imperial fauna is so like the Caribbean fauna that it barely counts toward documenting an eastern Pacific fossil record for any taxa occurring in it.

Woodring also noted that many of the paciphile genera had no fossil record on the Pacific side due to the smaller area of fossiliferous deposits in the eastern Pacific part. One of the rare occurrences of well-preserved late Tertiary mollusks is found in the Esmeraldas beds, upper Onzole Formation, of Early Pliocene age (Zone N.19) in northwestern Ecuador.

If Woodring is correct in his assessment then there should be a marked similarity between the Pliocene faunas of the Atlantic and Pacific. In an earlier study of the Esmeraldas Muricidae (Vokes, 1988), I was disappointed to discover that the correlation with the Caribbean fauna was much less than hoped for. In the Esmeraldas beds only seven of 21 species of Muricidae also occur in the Pliocene of the western Atlantic, although 12 have unmistakable Atlantic ancestry.

Thus, it was a pleasant surprise to learn of a specimen of the genus *Cassis* in the paleontological collections of the British Museum (Natural History), which was originally collected by C. Roger Bristow, British Geological Survey, at Camarones, Ecuador, from the road-cut that is the equivalent of TU locality 1399. It was tentatively identified as *Cassis sulcifera* Sowerby, 1850, a species originally described from the Dominican Republic.

In the Esmeraldas Muricidae study it was discovered that, in contrast to my expected correlation with the Late Miocene-Early Pliocene Cercado/Gurabo Formation of the Dominican Republic, only one species (*Typhis alatus* Sowerby, 1850) was found to be common to both, but three Esmeraldas muricid species also occur in the the Floridian Pinecrest and Caloosahatchee formations.

Therefore, what species of *Cassis* is this specimen from Ecuador? Various species have been reported from Tertiary localities through the western Atlantic. The most commonly reported is the Dominican *Cassis sulcifera* (pl. 2, fig. 1). This is a relatively small species, the largest specimen seen is that figured by Maury (1917, pl. 18[44], fig. 1), from the Gabb Collection, which measures about 100 mm in length. In our collections from the Dominican Republic the largest example is 95 mm but most examples are 80 mm or less. As Maury noted (1917, p. 110[274]): "This fine shell exhibits such diverse aspects in youth and old age, as to appear, without a connecting series, two different species" (see Abbott, 1968, pl. 29, for four very different individuals in the Gabb Collection at the Academy of Natural Sciences of Philadelphia, no. 2593). Maury reported it from both the Cercado and Gurabo formations, and in our collecting we have taken it at almost every locality in the "middle depths," *i.e.*, the deeper portions of the shallow-water Cercado Formation and the shallower portions of the deep-water Gurabo Formation.

Given the great variability demonstrated by this species, one wonders whether it is possible to separate the Dominican species from that one occurring in the Chipola Formation of northwestern Florida named *Cassis delta* by Parker (1948, p. 91, pl. 6, fig. 1). The major distinguishing criterion seems to be the larger size of *C. delta*. We have numerous examples from the Chipola Formation, and most are about 135 mm in length, comparable to the holotype. In addition, in the adult examples of *C. delta* there is a tendency to lose the lirae on the parietal shield. In young examples the two species are indistinguishable in terms of number of lirae, but in mature examples the parietal area of *C. delta* is nearly smooth.

In the most recent review of *Cassis sulcifera*, Abbott (1968, p. 53) included *C. flintensis* Mansfield, 1940, from the Oligocene Flint River and Chickasawhay formations, Georgia and Mississippi respectively, in the synonymy, but this is clearly incorrect. The Mansfield species is extremely cancellate and appears to be closely related to the European *C. mamillaris* Grateloup, 1827, from correlative beds in France (see Abbott, 1968, pl. 32, for illustrations of several forms of this species). Rutch's reference (*in* Stainforth, 1948, p. 1311) to *Cassis* cf. *sulcifera* from the Morne Diablo Limestone of Trinidad may refer to the Chipolan *C. delta*, which is the same Early Miocene age as the Morne Diablo Limestone (see H. E. Vokes, 1982, p. 51).

The Recent *C. flammea* (Linné, 1758) was reported by Gabb (1881, p. 356) from the Pleistocene Moín Formation of Costa Rica. Gabb's specimen (ANSP 3368) is a large (120+ mm), incomplete shell, far larger than any known examples of *C. sulcifera*, and in overall shape much like *C. flammea;* however, the numerous juveniles in the Tulane collections from the Moín Formation in the vicinity of Puerto Limón (most from TU 954) have the color pattern on the edge of the pareital shield preserved (see pl. 2, fig. 2a) and they possess the strong brown blotches characteristic of *C. tuberosa* (Linné, 1758). The two Recent species, *C. flammea* and *C. tuberosa* are extremely close in morphology and are separated only by the reticulate surface sculpture of *C. tuberosa* and by the presence of the brown markings on the *apertural* side of the outer edge of the parietal shield (both species have blotches on the adapertural side of the outer lip). The specimens from the Early Pleistocene Bowden Formation, Jamaica, identified by Woodring (1928, p. 304, pl. 19, figs. 5, 6) as *C. sulcifera* also have these brown blotches preserved (material in our collection from locality TU 705) and are the same undescribed species as that in the Moín Formation.

However, even extended treatment with sodium hypoclorite bleach (see Vokes and Vokes, 1968, p. 76, for discussion of this treatment to induce fluorescent color patterns) failed to bring out any trace of these blotches on specimens of *C. sulcifera*. Indeed, it would appear that the entire parietal shield was brown. Given the overall morphology of the shell, with the tendency to expand greatly the parietal shield in gerontic individuals, it seems probable that *C. sulcifera* gave rise to the Recent *C. madagascariensis* Lamarck, 1822, which has no brown blotches on the margin of the aperture but only a large colored area in the vicinity of the apertural opening.

In the Florida Pliocene there is another species described as *C. floridensis* by Tucker and Wilson (1932, p. 11[49], pl. 2[6], figs. 2, 5; pl. 5[9], fig. 2). The original holotype specimen came from the Pinecrest Beds at Acline, Florida (= locality

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PLATE 1

Figure

1. *Cassis* sp. cf. *C. subtuberosa* Hanna (X 1)
   BM(NH) Palaeont. Dept. GG 22469; length (incomplete) 53.8 mm, diameter (incomplete) 50.2 mm, height (incomplete) 44.5 mm.
   Locality: CRB 284; 0°59′N, 79°34′W, Punta Camarones, Ecuador. Esmeraldas Beds.
   (Figures 1d-f whitened to show details of ornamentation.)
2. *Cassis delta* Parker (X 1)
   USNM 453851; length (incomplete) 65.2 mm, diameter 51.5 mm.
   Locality: TU 70, Chipola Formation, Florida.
   (Color pattern as shown by ultra-violet light.)

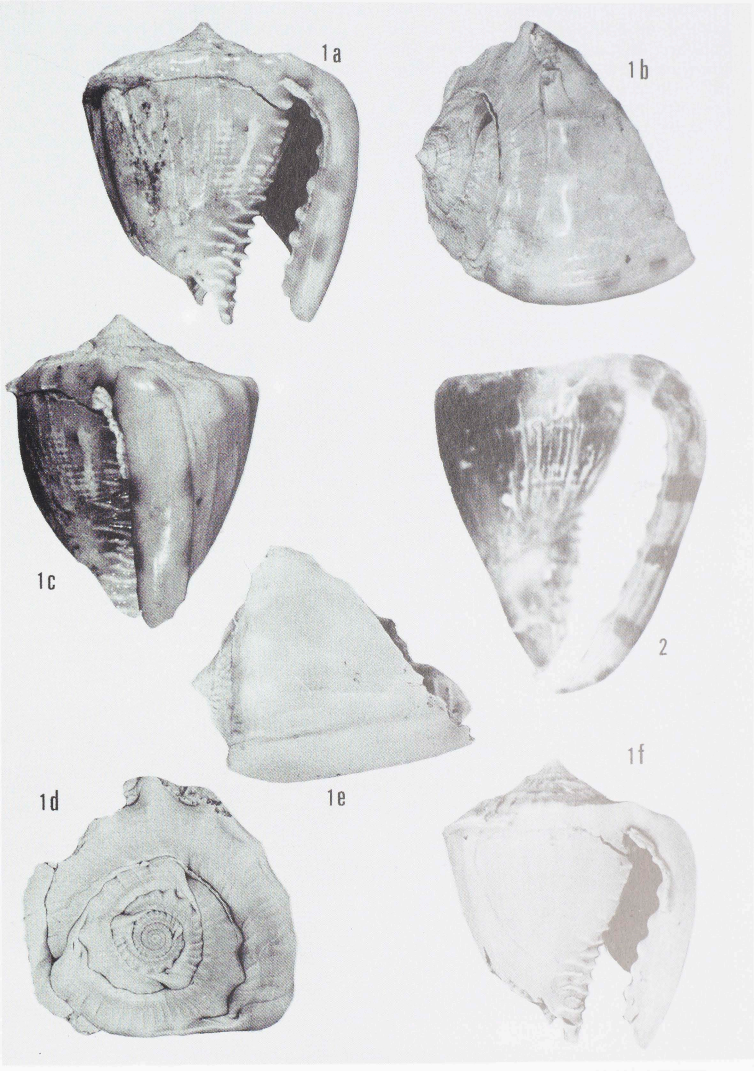

PLATE 1

TU 200), and we have several specimens from other Florida localities, all in the Pinecrest Beds. If, as noted above, the strongest affiliations between the Esmeraldas beds and the western Atlantic fauna are found in Florida, might the Esmeraldas specimen be an example of *C. floridensis*? It is unlikely, as the Florida species is easily recognized by the strongly cancellate surface ornamentation; so strong that it is often visible through the parietal shield (see Petuch, 1988, unnumbered illustration on p. 103). Adults attain a much larger size than *C. sulcifera,* but the juveniles with their cancellate shells are readily separable as well. No specimens of *C. floridensis* show the typical brown markings on the edge of the outer lip and it is probable that *C. floridensis* is the ancestor of the living *C. spinella* Clench, 1944, a species found today in the southern Florida-Yucatan region.

The Imperial Formation species was named *C. subtuberosa* by Hanna (1926, p. 444, pl. 20, fig. 8; pl. 29, figs. 2, 3 – refigured by Abbott, 1968, pl. 25). The material is poorly preserved, as is typical of the Imperial Formation, but the shell shape is closest to the Caribbean *C. flammea*. The Ecuadorian specimen, although badly broken, shows a general shape that is very close to that of *C. subtuberosa*. The color pattern on the Ecuadorian specimen is well-preserved (pl. 1, figs. 1a-c) and shows strong blotches on the apertural side of the outer lip in the manner of *C. tuberosa*. However, the shell is smooth (pl. 1, fig. 1e), lacking the reticulate surface of *C. tuberosa*. With the limited material available, positive identification is not possible but it seems most closely allied with the Imperial species and Hanna apparently was correct in his affiliating the Imperial shell with the living *C. tuberosa*.

In summary, we find that, although *Cassis sulcifera* has been reported from numerous formations throughout the Neogene of the Caribbean, it is confined to the Cercado and Gurabo formations of the Dominican Republic. With its non-colored apertural lip, it is presumed to be ancestral to the living *C. madagascariensis*. In the Floridian Pliocene, *C. floridensis* is the species present and it is presumed to have given rise to the living *C. spinella*. In the Pleistocene Bowden and Moín formations, there is another as-yet undescribed species, presumed to be ancestral to the living *C. tuberosa*.

On the Pacific coast the species of *Cassis* found in the Pliocene of Ecuador cannot be referred to any known Caribbean species and is probably the same as *C. subtuberosa,* described from the Pliocene Imperial Formation of California. The Early Miocene Chipola Formation species *Cassis delta* under ultra-violet light shows marked color bands on the apertural lip (pl. 1, fig. 2), and it is presumed to be the predecessor of this Pacific branch of the *C. tuberosa* lineage, indicating, as noted previously (Vokes, 1988, p. 12), that most of the elements of the Pacific fauna were in place before the Pliocene. The fossil record of the genus *Cassis* in the New World is obviously very incomplete but much richer than has been recognized previously.

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PLATE 2

Figure

1. *Cassis sulcifera* Sowerby (X 1)
   USNM 453852; length 59.0 mm, diameter 44.8 mm, height 43.0 mm.
   Locality: TU 1420, Cercado Formation, Dominican Republic.
2. *Cassis* sp. cf. *C. tuberosa* (Linné) (X 1)
   USNM 453853; length 54.0 mm, diameter 41.3 mm, height 37.6 mm.
   Locality: TU 956, Moín Formation, Costa Rica.

(Figure 2a not whitened to show color pattern; all others whitened to show details of ornamentation.)

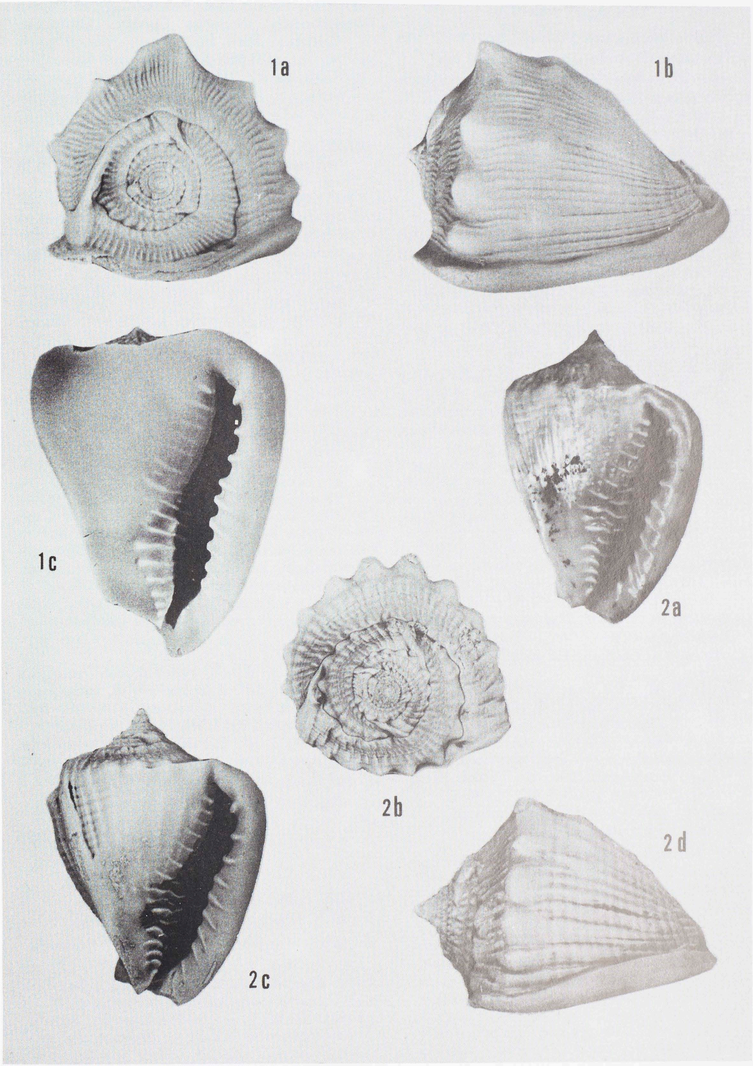

PLATE 2

LOCALITY DATA

The following are Tulane University fossil locality numbers:

70. Chipola Fm., Tenmile Creek, at bridge of Florida Highway 73 (NW 1/4 Sec. 12, T1N, R10W) Calhoun Co., Florida.
200. Pinecrest Beds, borrow pits about one mile southwest of Acline (Sec. 29, T41S, R23E), Charlotte Co., Florida.
705. Bowden Fm., type locality, Bowden, just east of Port Morant, Parish of St. Thomas, Jamaica.
954. Moín Fm., hill cut immediately behind Standard Fruit Company box factory, just west of cemetery at Pueblo Nuevo, about 2 km west of Puerto Limón, Costa Rica.
956. Moín Fm., hillslope behind Baptist church on road from Puerto Limón to Pueblo Nuevo, about .75 km east of Pueblo Nuevo, Costa Rica.
1399. Esmeraldas Beds, roadcut on west side of village of Camarones, which is 20 km (by road) east of bridge over Río Esmeraldas, at Esmeraldas, Prov. of Esmeraldas, Ecuador.
1420. Cercado Fm., Arroyo Bellaco, which is a tributary of the Río Cana from the east; first canyon above the ford at Las Caobas Adentro, 3 km southwest of Las Caobas, Dominican Republic.

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