Endemism in Middle Miocene Caribbean Molluscan Faunas

Abstract. *The term "middle Miocene Caribbean province" is used for a faunal province that embraced both western Atlantic and eastern Pacific waters. The percentage of endemic species in 13 local faunas in that province is tabulated. In general the largest faunas have the highest percentage of endemic species, but notable exceptions to that generalization are apparent. Many examples of discontinuous distribution of species and genera, which are not relicts, support the conclusion that much of the endemisim is apparent rather than real.*

Endemism, be it apparent or real, is a source of constant harassment to paleontologists. It not only impedes a satisfactory appraisal of age relationships from place to place, but also obscures an understanding of the migration and geological history of species and genera.

In this report the percentage of endemic species in 13 molluscan local faunas in the middle Miocene Caribbean province is tabulated. At that time the Caribbean faunal province embraced both western Atlantic and eastern Pacific waters. These faunas include the largest of that time and province and those showing the greatest geographic spread. The selection was made before the endemic species were tabulated and therefore is unbiased so far as endemism is concerned. The location of the 13 faunas is plotted in Fig. 1, and the total number of species and the percentage of endemic species are tabulated in Table 1.

The Dominican Republic and Jamaica have the largest faunas and a remarkably high percentage of endemic species. Both localities are in the northern part of the province, but are 600 km apart, and one faces the Atlantic Ocean, whereas the other is in the Caribbean Sea. Moreover, the faunal facies in Jamaica is only partly duplicated in the Dominican Republic.

The large number of nonendemic and endemic species in the Dominican Republic may partly be artifacts. Many of those fossils were found only by Gabb in 1869–71. They were inadequately described (*1*), and with few exceptions lack locality and stratigraphic data. Some of the species described by him are known to occur in the late early Miocene Baitoa formation, but not in the Cercado and Gurabo formations of Table 1, of early and late middle Miocene age, respectively. Others included in the tabulation may eventually be found to be Baitoa species.

In much current literature, including publications of the Geological Survey Department of Jamaica, the Bowden formation of Jamaica is assigned to the upper Miocene. Olsson (*2*), in his first work on Caribbean faunas, thought it might be intermediate between middle and upper Miocene, but has not considered the matter recently. I formerly thought it to be at the top of the middle Miocene or at the base of the upper Miocene (*3*). Since then, however, correlation with formations of late middle Miocene age in other parts of the Caribbean province and in Florida has become well grounded. If it is held that the Bowden formation is of late Miocene age, then the Gurabo formation of the Dominican Republic and the middle and upper parts of the Gatún formation of the Canal Zone also are late Miocene.

After the Dominican Republic and Jamaica, the next highest percentages of endemic species are shown by faunas at, or near, the southwestern and southeastern borders of the province (Ecuador and Peru, and Trinidad, respectively), and, strangely enough, in the middle of the western part of the province (Costa Rica). On the contrary, low percentages are shown at the northeastern and known northwestern borders (Tehuantepec area and Chiriquí Province, Panamá, respectively). The Tehuantepec area has close links with the adjoining Florida province. Chiriquí, however, is separated by a 4000 km gap from the next occurrence of middle Miocene fossils in Baja California. The low percentage of the small sample from Chiriquí, the lowest of all, surely indicates that the faunal province actually extended much farther northwestward.

The faunas along the south border of the present Caribbean Sea, in Venezuela and Colombia, and in eastern Pacific waters, in Chiriquí, Darién, and southwestern Colombia, have a low or relatively low percentage of endemic species and also a high percentage of identical species. Aside from the few endemic species, practically all the species in southwestern Colombia, Darién, and Chiriquí occur in the Gatún formation or in northeastern Colombia, or in both. The close faunal similarity suggests

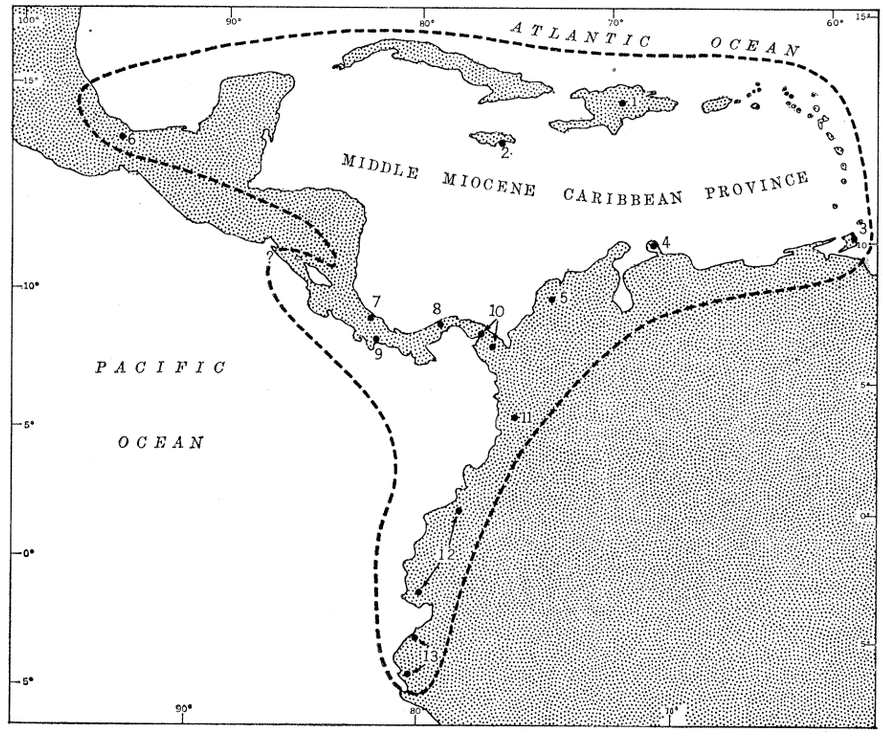

Fig. 1. Map of middle Miocene Caribbean province showing location of the 13 faunas tabulated in Table 1.

Table 1. Middle Miocene local molluscan faunas of 13 localities in Caribbean province (subspecies are treated as species).

No. in Fig. 1	Locality	Geological formation	Approx. outcrop area (km^2)	Species (No.)	Endemic species (%)	References
1	Monte Cristo Prov., Dominican Republic	Cercado and Gurabo*	600	690	60	Maury (*5*); Pilsbry (*6*)
2	St. Thomas Parish, Jamaica	Bowden	<1	630	55	Woodring (*7*)
3	St. Andrew Co., Trinidad	Manzanilla†	5	90	41	Maury (*8*); Rutsch (*9*)
4	Falcón State, Venezuela	Cantaure	5	145	22	Jung (*10*)
5	Atlántico Dept., Colombia	Tubará	100	240	27	Anderson (*11*)
6	Tehuantepec (Vera Cruz and Oaxaca States), México	Agueguexquite	5	90	13	Böse (*12*); Perilliat Montoya (*13*)
7	Limón Prov., Costa Rica	Equivalent of late middle Miocene part of Gatún formation	500	230	42	Olsson (*14*)
8	Canal Zone, Colón and Panamá Prov., Panamá	Middle Miocene part of Gatún formation	350	185‡	38	Woodring (*15*)
9	Chiriquí Prov., Panamá	Equivalent of middle Miocene part of Gatún formation	20	45§	5	
10	Darién Prov., Panamá	Equivalent of middle Miocene part of Gatún formation	450	140§	11	
11	Chocó Dept., Colombia	Equivalent of middle Miocene part of Gatún formation	5	35	17	Oinomikado (*16*)
12	Esmeraldas and Guayas Prov., Ecuador	Angostura, Picaderos, Progreso, and Daule	150	180	52	Marks (*17*); Olsson (*18*)
13	Tumbes and Piura Prov., Perú	Cardilitos and Montera	25	35	50	Olsson (*19*)

* These two alleged formations doubtless are faunal zones in one formation. † Extensive collections from the middle Miocene part of the Brasso formation (*Globorotalia fohsi* zone, underlying the Manzanilla formation, deposited by H. G. Kugler in the U.S. National Museum, have not yet been identified. ‡ Only the gastropods so far described, including 40 species in manuscript. Estimated total fauna, 350 species. § Based on preliminary identification of collections in U.S. National Museum.

westward transportation of planktonic larvae by the Miocene North Equatorial Current along the south border of the Caribbean Sea and through Central American straits into eastern Pacific waters. The relatively high percentage of endemic species in the Gatún formation is due to the large number of small species, many of which doubtless lived in association with endemic species of other phyla.

In attempting to answer the question of whether the endemism is apparent or real, the following items may be considered. The endemism may be apparent because of age disparity, insufficient sampling elsewhere, vagaries of burial and preservation, or because the faunal facies is not represented elsewhere. On the contrary, the endemism may be real because of insufficient time for dispersal, or because of unqualified endemism.

There is no assurance that the 13 samples are of the same age within a range of a few hundred thousand years. It is probable that the time span of the two faunas in the Dominican Republic and the three in the Canal Zone (lower, middle, and upper parts of Gatún formation) is comparable and longer than in the other areas. Nevertheless, on the basis of present correlations, disparity in age is not thought to be a major factor.

Every major contribution to middle Miocene Caribbean molluscan paleontology extends the geographic range of some species, thereby eliminating endemic species. Every major contribution, however, adds endemic species, but the net result is a loss of such species. It will be a long time before every potential locality in the areas under consideration is thoroughly sampled. The Dominican Republic, Jamaica, and the limited area in Venezuela (the Paraguaná Peninsula) have been well sampled, but not the other areas.

No matter how widely distributed a species may be, it survives in the fossil record only wherever it is successfully buried and preserved. If burial and preservation happen to take place only in one area, the species is evaluated as endemic, although the endemism may be apparent rather than real.

If an exceptional faunal facies is not represented elsewhere in the depositional record, the percentage of endemism for the area of the exceptional facies is high, but may partly be only apparent. With one exception, the 13 samples consist of inner-shelf faunas, made up of species that lived at depths ranging from a few tens of meters to about 200 m. The exception is the sample from the Bowden formation of Jamaica, which has the smallest outcrop area, not more than 200 m^2. The Bowden fauna represents not a particular faunal facies, but a whole series of faunal facies, ranging from leaf litter on the forest floor (six species of land snails), through brackish-water courses of streams and mangrove swamps (*Neritina, Mytilopsis*, mangrove oyster), beach vegetation (*Tralia, Planaxis*), sand flats (*Olivella*, approximately 1000 specimens of *Oliva*), inner and outer shelf (the bulk of the fauna), to a depth greater than 200 m, possibly as great as 500 m. It is as though these land, brackish-water (beach, shallow-water), and moderate-depth shells were swept together by a giant broom and dumped down a steep slope to be successfully buried and preserved in granule-gravel along with autochthonous deep-water and planktonic species. The deep-water species include the only American fossil species of *Cocculina* and *Seguenzia*. Of 38 genera and subgenera and 70 species of turrids in this fauna, 34 percent of the genera and subgenera and 74 percent of the species are endemic, so far as known. Though both modern and Tertiary turrids everywhere show a high percentage of endemism, the percentage for the Bowden fauna is exceptionally high.

According to recent estimates, based on K-Ar dating, the duration of the Miocene epoch is about 15 million years. The duration of middle Miocene

time then is about 5 million years, if equal duration of early, middle, and late Miocene be assumed. Should a species, which had a brief larval planktonic stage, have arisen and become extinct during Miocene time, its geographic range may be restricted. The necessary dating ordinarily cannot be fixed within narrow enough limits to evaluate this factor.

There is bound to be a hard core of unqualified endemism, just as in modern faunas.

Owing chiefly to insufficient sampling and the vagaries of burial and preservation, much of the endemism is apparent rather than real. Many examples of widely discontinuous distribution of species and genera, which are not relicts, support that conclusion. *Murex textilis*, the sole species of the subgenus *Subterynotus*, is found in the middle Miocene of the Dominican Republic and Venezuela, and then appears in the Pliocene of Florida, although there are no Miocene records in Florida. Two unrelated species of *Gemmula (G. vaningeni* and *G. machapoorensis)* occur in Trinidad, the Canal Zone, and Florida, but nowhere between those three areas. The occurrence of a mangrove ark (*Anadara tuberculosa*), now living in eastern Pacific waters, in deposits of late Pliocene age in Florida (*4*) is a striking example of missing records. The only rational explanation for that occurrence is that this species migrated through the western Atlantic part of the Miocene Caribbean province. Yet neither the species nor its predecessor has so far been found there.

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20. The nonendemic and endemic species were tabulated by Barbara A. Bedette, and the illustration was drafted by Elinor Stromberg.

15 December 1964

Lungfish Burrows from the Michigan Coal Basin

Abstract. *Five casts of lungfish burrows have been found in a quarry near Grand Ledge, Michigan, in shale of the Saginaw group, Middle Pennsylvanian. The burrows contain no fish remains, but they closely resemble lungfish burrows from the Lower Permian of Texas which contain remains of the genus* Gnathorhiza.

Of the three living genera of lungfish, two (*Lepidosiren* from South America and *Protopterus* from Africa) are known to aestivate. Both genera burrow into the mud beneath ponds, where they may remain buried without desiccation for over a year. Evidence has been obtained of the occurrence of aestivation among lungfish, from deposits as early as the Lower Permian. Romer and Olson (*1*) described numerous casts of lungfish burrows from the Clear Fork group of the Texas Permian, some containing lungfish of the genus *Gnathorhiza*; however, most of the burrows were empty. Other empty casts of lungfish burrows were recorded from the Lower Permian of Prince Edward Island by Langston (*2*), and from New Mexico by Vaughn (*3*). Judging from the size and shape of the burrows, all may have been made by members of the same genus. The burrows are all of about the same dimensions, 4.5 to 10 cm in diameter and up to 45 cm in length. They are essentially straight, with the base somewhat narrower than the remainder. Unlike living lungfish, which coil themselves up (*4*), *Gnathorhiza* remained straightened out, with its tail at the base of the burrow.

In 1963, while collecting plant fossils from one of the quarries of the Grand Ledge Clay Products Company near Grand Ledge, Michigan, I found five large, erect cylinders embedded in a soft shale. The most complete specimen is shown in Fig. 1. All are similar in appearance to the Permian lungfish burrows, but have a somewhat greater diameter. The burrows are approximately 15 cm in diameter at the upper end. The longest remaining portion is 41 cm in length, but the uppermost portions of all the burrows were damaged during excavation of the quarry. The bases of three are intact, showing a roughly spiral pattern on the surface, presumably made by the fish's tail when digging the burrow. Areas of various portions of the burrows are marked by slickensides, also noted in the Texas burrows by Romer and Olson.

The lower block of each burrow was broken open in the laboratory. No bone was found, but there were fragments of plant material, together with small amounts of iron pyrite and crystalline calcite. The burrows are considerably harder than the surrounding shale and have a higher sand content. As in the casts of burrows described by Vaughn, the central portions of the Michigan casts are a lighter color than the outside, apparently because of differential oxidation of the sediments.

The quarry in which the lungfish burrows were found is situated just west of the Grand River in section 34, Eagle Township, Clinton County,

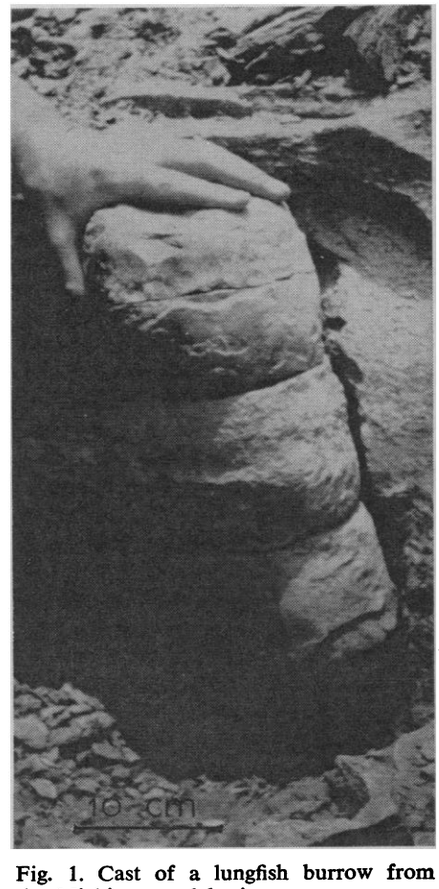

Fig. 1. Cast of a lungfish burrow from the Michigan coal basin.