

Caribbean molluscs and plate tectonics

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Abstract — The non-marine mollusc fauna of Jamaica, like that of most Caribbean islands, is highly endemic at specific levels, but families and some genera are more widespread in the region. Their biogeography may reveal the sequence of colonization of major islands and thus the plate tectonic history of the region. However, homeomorphy of shells requires cautious interpretation of modern faunal lists and fossil records. For example, snails referred to the subfamily Urocopinae are recorded from Cuba and Jamaica, but some of the Cuban forms have significantly different anatomy and are not closely related to any Jamaican taxa. Nevertheless, a few shell morphologies are so distinctive as to reduce significantly the possibility of convergent evolution. Two examples are (a) the genus *Proserpina*, a prosobranch without an operculum, but with apertural lamellae and resorbed inner whorls, currently confined to the Caribbean and Neotropics and a known fossil in Britain over 40 million years ago, and (b) species of the genus *Brachypodella* s.l. with a unique perforate protoconch, the modern distribution of which follows very closely the northern and eastern boundaries of the Caribbean plate.

INTRODUCTION

VIEWED FROM a European standpoint, three things strike one immediately about the non-marine molluscan fauna of Jamaica. First, the fauna is very diverse. Jamaica has an area about one thirtieth of that of the British Isles but over two and a half times as many species of non-marine molluscs. Indeed, with approximately one species per 25 km², Jamaica must have one of the densest molluscan faunas of any part of the world. This diversity is very largely due to the land snails; of the 500 or more non-marine species known (Vendryes, 1899) only about 10 per cent are fresh- or brackish-water forms. In Britain over a third of the fauna consists of freshwater species (Waldén, 1976; Kerney, 1976).

Second, roughly half the Jamaican land snails are prosobranchs, whereas Britain boasts just two species out of 130-odd terrestrial slugs and snails, and the whole of northwest Europe has only 16 species of prosobranchs out of nearly 300 (Kerney and Cameron, 1979). To some extent this is a reflection of the climate and not unique to the Caribbean. Terrestrial prosobranchs lack a pneumostome and are particularly susceptible to desiccation during activity (although the operculum greatly reduces water loss when they are inactive). As a result, terrestrial prosobranchs thrive in warm, humid climates.

Third, a very high proportion (over 90 per cent) of the species are endemic to Jamaica. In this case, comparison with Britain is inappropriate. The British fauna recolonized the islands after the retreat of the ice at the end of the last glaciation, or has been introduced by man, over the last 12,000 years, and hence could not be expected to include any endemic taxa. These comments apply equally to other large Caribbean islands. The combination of high diversity and high endemism has led to considerable interest in the biogeography of the Caribbean fauna going back at least to Adams (1849).

ENDEMISM

THE ENDEMISM of the Jamaican molluscan fauna becomes even more marked when one considers the precise taxa which do occur elsewhere. Some are known to be recent human introductions. *Strophocheilus* (*Megalobulimus*) *oblongus* was introduced from South America before World War II and possibly again since. Others, like *Bulimulus guadaloupensis*, are possibly human introductions, while *Subulina octona*, if it is native, has become established widely elsewhere. It now has a circumtropical range, is common in heated greenhouses in Britain and Europe, and we will probably never establish its precise

original provenance. Individuals are self-fertile and adults always carry numerous developing eggs. Introduction of single individuals into a suitable habitat usually results in the establishment of a viable colony. Those non-endemic species that appear to have natural distributions (as opposed to human introductions) are all small, thus tending to confirm Vagvolgyi's (1975) arguments about aerial dispersal of island molluscs. Some species of *Pupisoma*, *Bothryopupa*, *Guppya*, *Cecilioides*, and *Gastrocopta* occur in Jamaica and Puerto Rico, for example (See Van der Schalie, 1948), while others may be very widespread. If *G. pellucida* is correctly identified throughout its range, it occurs as far north as Indiana and New Jersey in mainland North America. However, examples I have from Indiana are twice the size of those from Jamaica, and Pilsbry (1948) accepted the mainland forms as a distinct subspecies, *hordeacella*.

The endemism of the Jamaican fauna suggests a prolonged period of isolation or very rapid speciation. Nevertheless, endemism is not always the result of evolution in an isolated habitat, but may also represent a relict distribution. There is unequivocal evidence that the prosobranch *Tudorella ferruginea*, which is currently confined to the Mediterranean islands of Mallorca and Menorca, formerly inhabited Ibiza (Paul, 1982), Sardinia (Esu, 1978) and possibly mainland France (Michaud, 1862). Its present distribution results from reduction in range to a last refuge, not to evolution in isolation. Some Caribbean taxa have also suffered reductions in range through the Tertiary (see below). However, with so many endemic species, it is reasonable to assume that a considerable amount of both the diversity and endemism of the Jamaican fauna results from radiation in isolation from other Caribbean islands or the mainland of adjacent continents.

When one considers higher taxa, genera and families, the proportion of endemics declines. Indeed, not one family is confined to Jamaica and several families represented in the Jamaican fauna have a very broad, even worldwide distribution (e.g., Hydrobiidae, Planorbidae, Camaenidae, Helicinidae, Cyclophoridae). Others are confined to the Central American/Caribbean region or even to the Greater Antilles (e.g., Annulariidae, Proserpinidae, Urocoptidae, Sagdidae). Most of the families have known fossil records extending back to the lower Tertiary or Mesozoic (50-100 million years) — e.g., Helicinidae, Proserpinidae, Cyclophoridae, Hydrobiidae, Ellobiidae, Planorbidae, Vertiginidae, Urocoptidae, Subulinidae, Camaenidae. The possibility exists, therefore, that analysis of distribution of taxa within the Caribbean may reveal something of the geological evolution of the region. This idea is now new: Hunter discussed precisely this point with respect to the endemism of the Jamaican molluscs in 1955, although of course in the con-

text of the prevailing concept of land bridges, not plate tectonics. Before that Simpson (1894), Bland (1861) and C.B. Adams (1849), among others, have discussed the molluscan biogeography of the Antilles. More recently, Rosen (1975) has proposed a vicariance model of Caribbean biogeography, based largely on distribution data for non-marine vertebrates. Although Rosen's paper has been criticized by Pregill (1981), it remains a pioneering work that first raised the possibility of tracing the connection between the plate tectonic history and the biogeography of the Caribbean. MacFadden (1981) and Hedges (1982) have supported Rosen's basic arguments, while Durham (1985) has stressed the importance of recent plate tectonic history to Caribbean biogeography. In this article I want to present some evidence that may also be relevant to plate movements and the evolution of the Caribbean, as well as to draw attention to the difficulties of interpretation due to our current poor knowledge of the taxonomy and distribution of Caribbean land snails.

PATTERNS OF DISTRIBUTION AND COLONIZATION

TWO EXTREME biogeographic models have been proposed to account for the present-day distribution of terrestrial organisms. The first is the traditional view that taxa arise at a centre and spread outwards through time. The alternative, the vicariance model, suggests that widespread distributions are fragmented by 'island' formation and thereafter evolve independently. This view relies heavily on the allopatric speciation model (i.e., the origin of new species in geographically isolated areas) and argues firstly that higher taxa should be the most widespread and secondly that the relative dates of separation may be reflected in a hierarchical classification of monophyletic taxa. Both ideas have some merit. After all, widespread distributions, the starting point of the vicariance model, do not arise instantaneously but must follow an initial period of expansion of range. Add to these a third possibility, that the positions of the 'islands' may have shifted relative to one another in a complex pattern — i.e., not just drifting apart with the opening of the Atlantic — and the possibilities become even more varied. What I wish to do here is to discuss the third possibility, which, incidentally, was central to Rosen's (1975) original vicariance model.

When considering the present-day geography of any group of islands in the context of natural means of dispersal of terrestrial fauna and flora (i.e., the traditional view of biogeography), the simplest hypothesis is that the shortest sea passages will be the easiest to cross. Clearly, however, one needs to take into account local factors such as prevailing wind direction or storm track, prevailing cur-

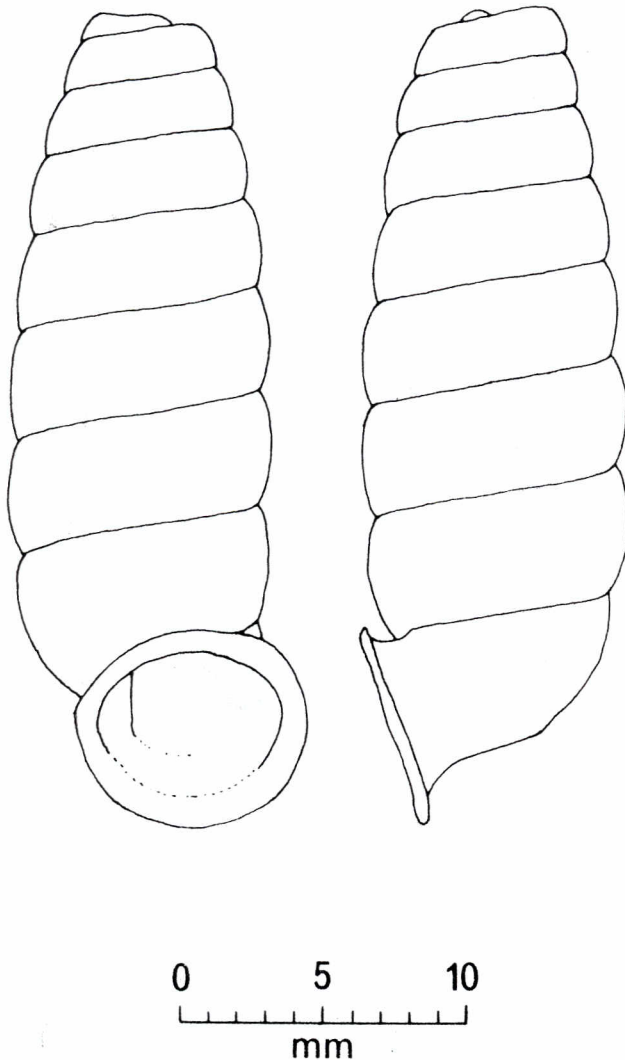


Figure 1. Basic shell morphology of *Urocoptis cylindrus*.

rent direction, routes of migrating birds, etc., as these may make colonization in certain directions more easy than in others. Colonization downcurrent or downwind will be easier, and therefore more likely, than across or against winds or currents. Depth of the intervening sea is obviously also relevant, since Pleistocene falls in sea level undoubtedly did establish land bridges across shallow seas during glacial maxima. Britain was connected with Europe and Mallorca with Menorca, to mention just two examples. However, in the present context the oceans between Jamaica and both Cuba and Hispaniola are far too deep to have even been narrowed by Pleistocene falls in sea level. The Cayman Trench between Cuba and Jamaica is particularly deep, so the chances of pre-Pleistocene land

bridges having existed across that particular stretch of sea are virtually zero.

Even so, the nearest points of both Cuba and Hispaniola are only about 150 km from Jamaica, and one would expect that some terrestrial organisms might have crossed these barriers. Indeed, anoline lizards of the genus *Xiphocercus* are only known from Jamaica and the southwest peninsula of Haiti (Underwood and Williams, 1959), and this is possibly also true of the tree snail genus *Anoma*. However, considerable problems exist in interpreting land snail data since a high proportion of Antillean species are known only from their shells and shells may come to resemble each other closely by convergence. These days we rely mostly on anatomy to determine relationships between molluscs. For example, both the Cuban and Jamaican faunas contain many species of the family Urocoptidae. Recently, Paul (1983) has described the anatomy and relationships of the Jamaican urocoptids, while Jaume and de la Torre (1976) revised those of Cuba. The type species of *Urocoptis* s.s. is a Jamaican form, *U. cylindrus* (Chemnitz). It has a tall (up to 50 mm high), cylindrical shell which loses the apical whorls when mature (i.e., is decollate) and uncoils very briefly before forming a slightly flared lip to the aperture (Fig. 1). *U. cylindrus* and all other species of *Urocoptis* from Jamaica have a radula in which the teeth are arranged in V-shaped rows. The central tooth is very narrow and is flanked by laterals which decrease in size very gradually and imperceptibly away from the centre of the radula towards the edge, so that it is impossible to distinguish marginal teeth. All the laterals have enlarged ectocones arranged in a separate row behind the mesocones and both ectocones and mesocones have smooth rounded edges. Urocoptids with similar large, cylindrical shells occur in Cuba, and Jaume and de la Torre (1976) attributed them to the same subfamily as *Urocoptis* s.s. However, their descriptions of the radular teeth of these Cuban snails (they give no figures, regrettably) include statements like 'lateral teeth well differentiated from marginal' (key to subfamilies, p. 5) and 'the two lateral teeth on each side [of the central] are very large. The marginal teeth are few and much smaller than the lateral' (characters of the subfamily Urocoptinae, p. 40). No Jamaican *Urocoptis* has a radula which fits these descriptions, although the four Jamaican genera in the subfamily Apominae do. As a result, I think that a large number of Cuban genera attributed to the subfamily Urocoptinae by Jaume and de la Torre (1976) represent a distinct radiation from a different stock to true urocoptines from Jamaica. However, the situation is not entirely clear, as Pilsbry (1902-4, pl. 61) figured several Cuban urocoptids with a typical urocoptine radula.

Snails with shells like Jamaican *Urocoptis* and *Anoma* also occur in Hispaniola. Thompson and Franz (1976)

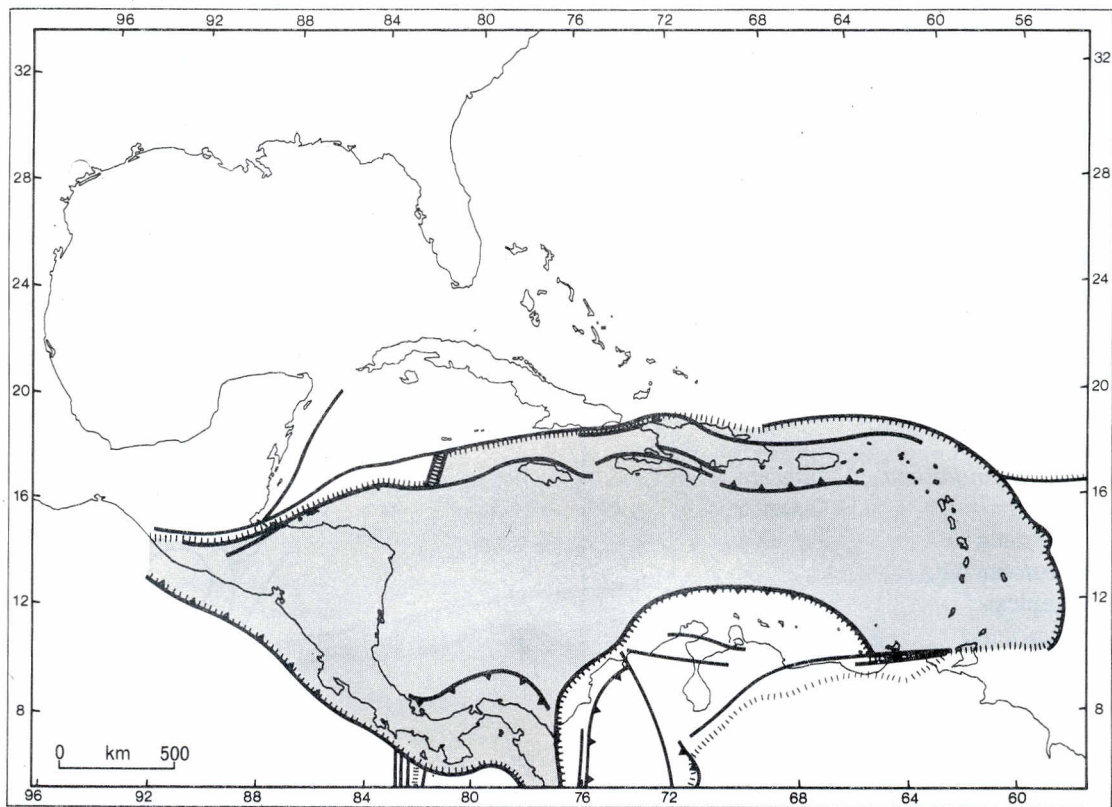


Figure 2. Principal structural features of the Caribbean region. Outline of the Caribbean Plate shaded. Hatched lines indicate approximate plate boundaries; solid lines indicate faults, with triangles indicating relative motions on destructive plate boundaries. (Adapted from Mattson, 1984, Fig. 1.)

have described the radulae of four species of urocoptid from Santo Domingo which have teeth very similar to true *Urocoptis*. They have V-shaped rows of teeth, laterals with smooth round mesocones and ectocones in separate rows, and marginals which cannot be distinguished. There are also some differences. The central is proportionately larger than in Jamaican *Urocoptis*, and the ectocone of the laterals is slightly larger than the mesocone, whereas the reverse is true of Jamaican *Urocoptis*. Clearly, relying on shell characters alone is likely to suggest some spurious similarities between faunas and possibly spurious differences too. Nevertheless, the little information on the anatomy of Hispaniolan urocoptids suggests that they may be more closely related to the Jamaican than many Cuban species are. It would be particularly interesting to know more about the fauna of the southwest peninsula of Haiti.

The same difficulty arises when considering fossil snails. Thus, while the distribution of molluscs in the Caribbean region offers considerable potential for confirming details of plate movements, at the current state of anatomical knowledge the potential will remain unrealized. However, the situation is not entirely hopeless. Ex-

remely unusual shell morphologies are less likely to arise more than once by convergence and may be better indicators of true affinities than more generalized shell forms. Two examples are discussed below which, I believe, are sufficiently distinctive to accept affinities and which demonstrate very interesting distributions. A third case of taxa with a more generalized shell shape is also presented because there is sufficient anatomical information to explain the apparent anomaly in distribution. Altogether, despite being limited, these examples are sufficient to illustrate the potential of land snail biogeography to the study of Caribbean plate tectonics, though clearly very much more remains to be done.

PLATE BOUNDARIES AND MOVEMENTS

THE CURRENTLY accepted plate boundaries and other principal structural features of the region are shown in Fig. 2. Burke *et al.* (1984) and Mattson (1984) have presented two slightly different reconstructions of plate movements in the Caribbean Region over the last 100 mil-

Table 1. Species of *Brachypodella* with the 'Jamaican apex'

	Species	Localities
1.	' <i>B.</i> ' <i>subtilis</i>	Livingston, Guatemala
2.	<i>Geoscala seminuda</i>	Jamaica
3.	<i>G. costulata</i>	Jamaica
4.	<i>G. robertsi</i>	Jamaica
5.	<i>Simplicervix inornata</i>	Jamaica
6.	<i>S. simplex</i>	Jamaica
7.	<i>S. humilis</i>	Jamaica
8.	<i>Apoma chemnitziana</i>	Jamaica
9.	<i>A. gracilis</i>	Jamaica
10.	<i>A. agnesiana</i>	Jamaica
11.	<i>Mychostoma alba</i> complex	Jamaica
12.	' <i>B.</i> ' <i>truncatula</i>	Haiti
13.	' <i>B.</i> ' <i>benettai</i>	Santo Domingo
14.	' <i>B.</i> ' <i>riisei</i>	Puerto Rico
15.	' <i>B.</i> ' <i>collaris</i>	Puerto Rico
16.	' <i>B.</i> ' <i>pallida</i>	Puerto Rico, St Thomas, St John's, Tortola
17.	' <i>B.</i> ' <i>chordata</i>	St Croix
18.	' <i>B.</i> ' <i>antiperversa</i>	Guadeloupe, Martinique, St Vincent
19.	' <i>B.</i> ' <i>costata</i>	St Vincent, Barbados

lion years or more. In both reconstructions the northern boundary of the Caribbean Plate is accepted as passing along the northern margin of the Cayman Trench between Cuba and Haiti and thence north of Santo Domingo and Puerto Rico. It then swings round east of the Lesser Antilles Arc to become the eastern margin of this plate. Again, both reconstructions propose sinistral displacements along this margin, with the Caribbean Plate moving eastwards with respect to the North American Plate. This movement is complicated by parallel faults to the south of the Cayman Trench and offshoots from them through the island of Hispaniola. According to these interpretations, Hispaniola has reached its present state by the docking of several originally distinct terranes. As far as the present subject is concerned, both reconstructions show Jamaica and the southwest peninsula of Haiti maintaining their respective positions back through the last 40 to 50 million years, but moving progressively eastwards. Thus, Jamaica is depicted as being south of the Yucatan Peninsula 50

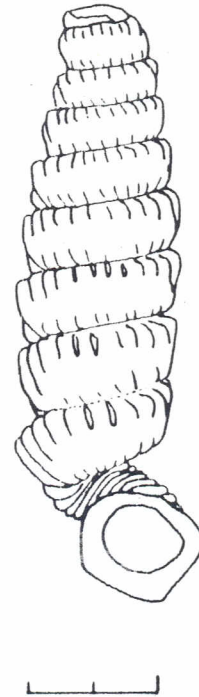


Figure 3. Typical shell morphology of *Brachypodella*. Scale in mm.

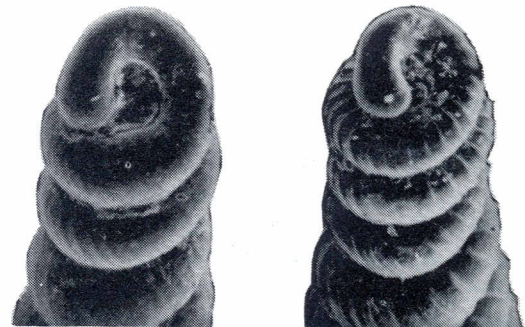


Figure 4. The 'Jamaican apex' in *Geoscala* species. Note the hollow about which the initial whorl is coiled. Scanning electron micrograph. Specimens coated with gold/palladium. Both $\times 55$.

million years ago, with central Hispaniola and Puerto Rico south of eastern Cuba in approximately the position Jamaica now occupies. If these reconstructions are correct, one could predict that the faunas of Jamaica and southwestern Haiti should be closely comparable (as the occurrence of *Xiphocercus* seems to confirm), because these

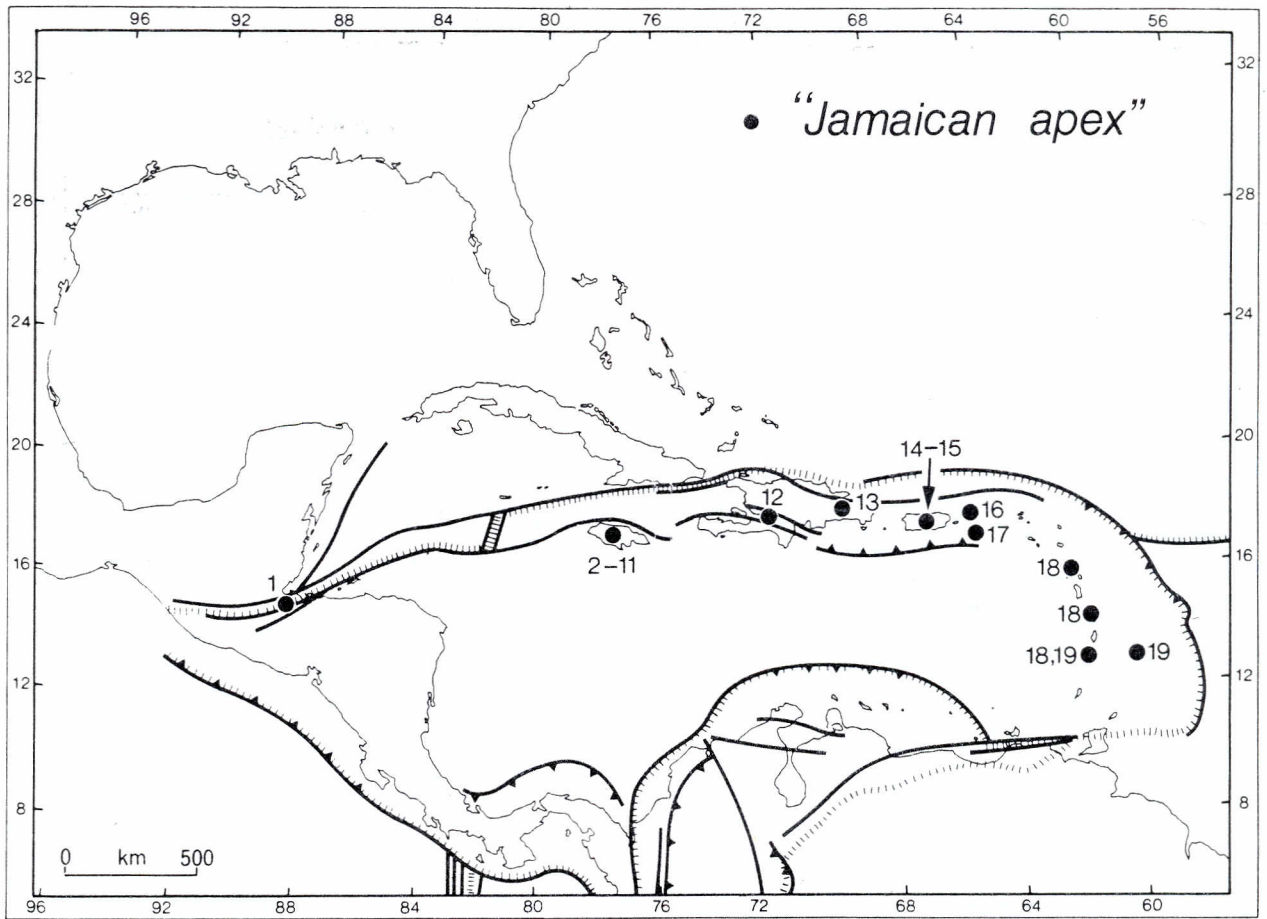


Figure 5. Distribution of the 'Jamaican apex' in the Caribbean region. Numbers refer to the species listed in Table 1. Structural symbols as in Fig. 2.

islands have been about as far apart as they are now for the last 50 million years or more — ample time for chance introductions to cross 150 km of ocean. Equally, one could predict a distinct difference between the faunas of Jamaica and Cuba because only recently have they come into close proximity. Fifty million years ago they were more than 1,000 km apart. Furthermore, under these reconstructions the fauna of Santo Domingo and Puerto Rico ought to be similar because these islands have always been close to each other. Thompson (1982) presents some reliable evidence to support this idea. In short, plate reconstructions based on geophysical evidence inevitably carry some testable predictions about the biogeography of terrestrial biota (provided, of course, the plate reconstructions are not themselves based on biogeographic data).

Even this simple idea cannot be applied without caution. The widespread occurrence of Miocene marine carbonates over much of Jamaica has been taken to imply that the whole island was submerged at that time (Eva and McFarlane, 1985; but see conflicting view of Robinson, 1971). If true, it follows that the present-day fauna has colonized Jamaica and radiated throughout the island since the Miocene — an extremely rapid diversification. Furthermore, the position of Jamaica with respect to other islands in the Caribbean 50 million years ago becomes irrelevant if the present-day fauna dates only from the Miocene. This is, of course, also true of adjacent islands. Personally I am doubtful about the complete submergence of Jamaica in the Miocene and it would negate much of Rosen's (1975) argument about vertebrate distribution. However, the possibility cannot be ignored in

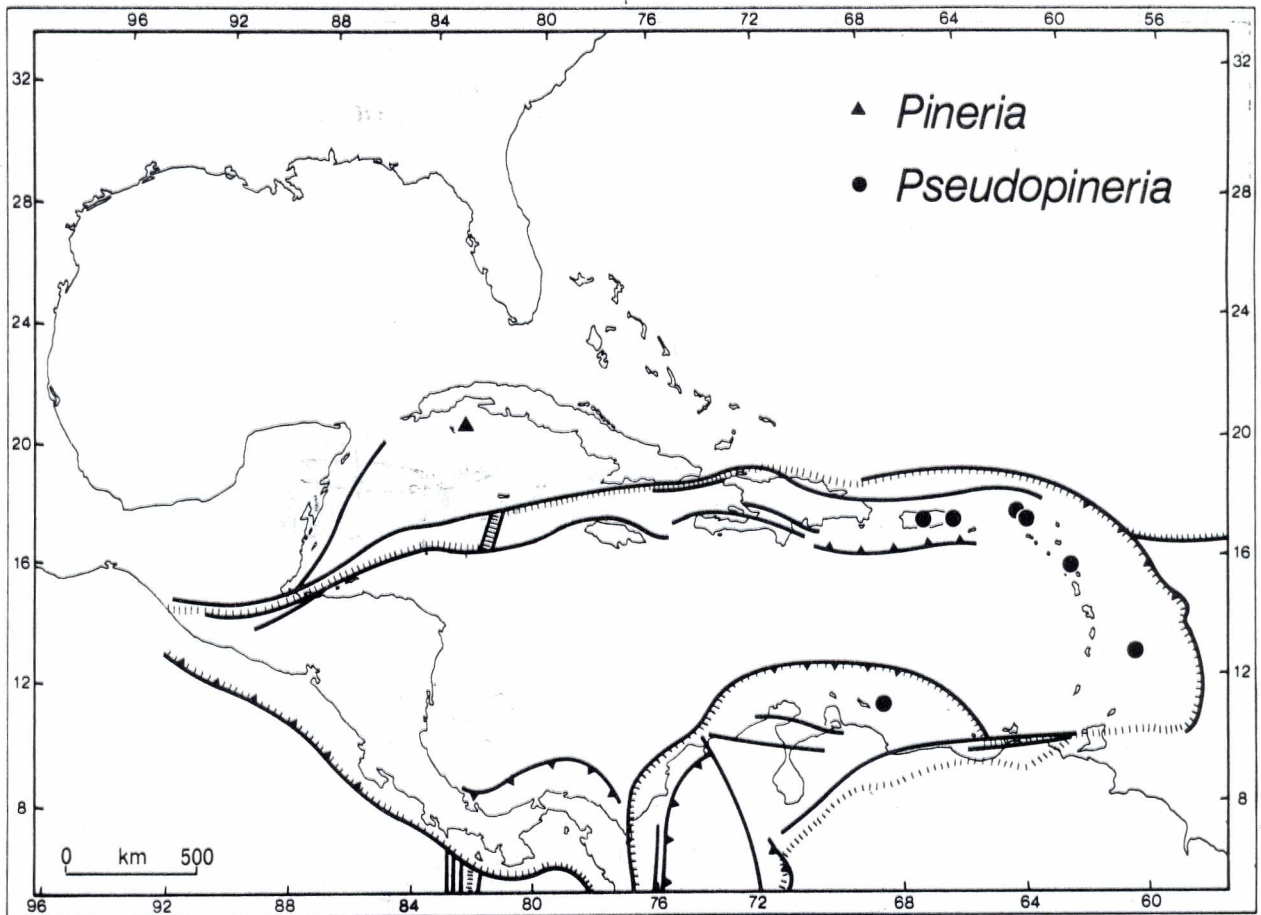


Figure 6. Distribution of *Pineria* and *Pseudopineria* in the Caribbean region. Structural symbols as in Fig. 2.

the present context. Under current plate tectonic schemes Jamaica was approximately as close to Cuba as it was to southwest Hispaniola 10 to 15 million years ago, during the Miocene.

DISTRIBUTIONS

The 'Jamaican apex'

Small, cylindrical to fusiform urocoptid shells of the type shown in Fig. 3 are usually referred to the genus *Brachypodella*. In common with the majority of urocoptids they lose their juvenile whorls and are decollate as adults. Since many shell collectors kept only prime specimens, knowledge of the detached larval and juvenile portions of the shell has grown more slowly than that of the adult. The morphology of these parts of the shell can help

reveal relationships (e.g., Thompson, 1982). In Jamaica there are four genera (formerly subgenera) of urocoptids with shells like those of typical *Brachypodella*. All species of all four genera have a very distinctive protoconch in which the initial whorl is very high-sided and coils about a perforation in the apex (Fig. 4), which I have christened an 'apical umbilicus', for want of a better term (Paul, 1982). I also refer to this type of protoconch as the 'Jamaican apex' because it is typical of all Jamaican species of *Brachypodella s.l.* The Jamaican apex is not confined to Jamaica. Its known distribution is shown in Fig. 5, while Table 1 lists the species in which it is found. Urocoptids with shells like those of *Brachypodella*, but with normal apical whorls, occur throughout the region shown in Fig. 5 (except the southern United States) and beyond into Mexico northwards and Colombia and Ecuador southwards, but so far as is known the Jamaican apex is con-

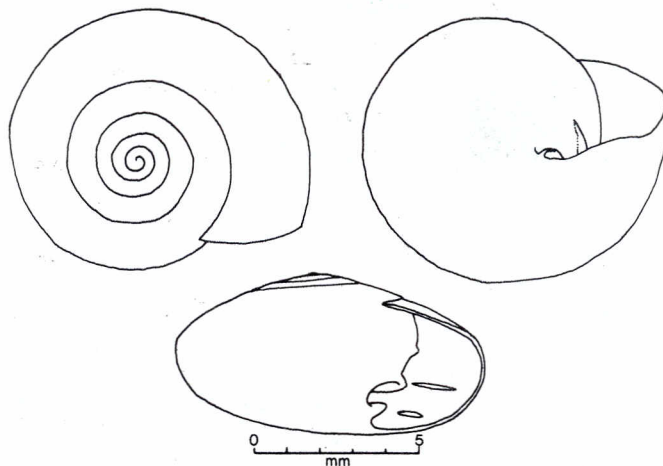


Figure 7. The shell of *Proserpina*. Note the lamellae in the aperture.

fined to the northern and eastern boundaries of the Caribbean Plate. *B. trinitaria* from Trinidad has a high-sided initial whorl, but it is not perforate apically and therefore not considered to have a true Jamaican apex. *B. benettai*, *B. riisei* and *B. chordata* (species 13, 14 and 16 in Fig. 5) all have a distinctly striate apex and form a small subgroup within the Jamaican apex which has a fairly compact geographic distribution from Santo Domingo through Puerto Rico to St Croix. As far as I am aware, the anatomy of none of the non-Jamaican species with the Jamaican apex is known. However, radulae of Jamaican species of *Brachypodella* and all other species with normal apices are very similar, having a narrow central, two enormously enlarged laterals with reduced or absent ectocones, and a small number of tiny marginals in straight rows. Thus, the basic brachypodelline stock seems to have spread throughout Central America and the Caribbean, but those forms with the Jamaican apex are confined to the Caribbean Plate, while among the latter a distinctly striate apex only occurs in a small region of the eastern Greater Antilles. Both geographic and taxonomic distribution seem to reflect the timing of the evolution of the features concerned. The brachypodelline radula evolved before the Jamaican apex, which preceded the striate Jamaican apex. In this case, the earliest forms to evolve have spread the farthest, which tends to support the traditional view of biogeography.

Pineria and *Pseudopineria*

The distribution of the genus *Pineria*, as understood by Pilsbry (1902-4) in his review of the entire family Urocopitidae, appears to contradict my suggestion that plate movements may have controlled mollusc distributions. *Pineria* was originally described from the Isle of Pines, south of western Cuba, but is also known from Puerto Rico

east and south through the Lesser Antilles to the island of Bonaire off the northern coast of South America, thus apparently crossing the Caribbean-North American plate boundary. Once again, however, anatomical details show that the original *Pineria* is quite distinct (not even in the same subfamily, according to Aguayo, 1938) from what Aguayo called *Pseudopineria*, and the distributions of the two genera (Fig. 6) become much more in line with plate reconstructions.

Proserpina

This genus not only has extremely unusual anatomy and behaviour, but also an interesting fossil record. Typical terrestrial prosobranchs have an operculum which fits tightly into the aperture. As a result, the aperture is usually simple, often circular, and in particular the inner margin lacks any processes such as apertural denticles or lamellae which might obstruct the operculum when the snails withdraw into the shell. *Proserpina* is remarkable in having no operculum and several spiral lamellae which modify the inner margin of the aperture considerably (Fig. 7). The shell is even more distinctive because, in common with other neritacean prosobranchs, *Proserpina* resorbs the inner shell walls to produce a single large internal cavity.

The lobes of the mantle collar of *P. nitida* and *P. bidentata* are cryptic against the rocks and tree trunks on which they crawl; that of *P. pisum* is bright green and prickly, like a minute horse chestnut seed casing. All species have a very long, thin muscular foot. In keeping with this peculiar morphology and anatomy, Jamaican species of *Proserpina* also have unusual behaviour. When disturbed they have a dramatic dymantic reaction, which involves first withdrawing the mantle, thus changing shape, size and colour and, if further disturbed, waving the foot from side

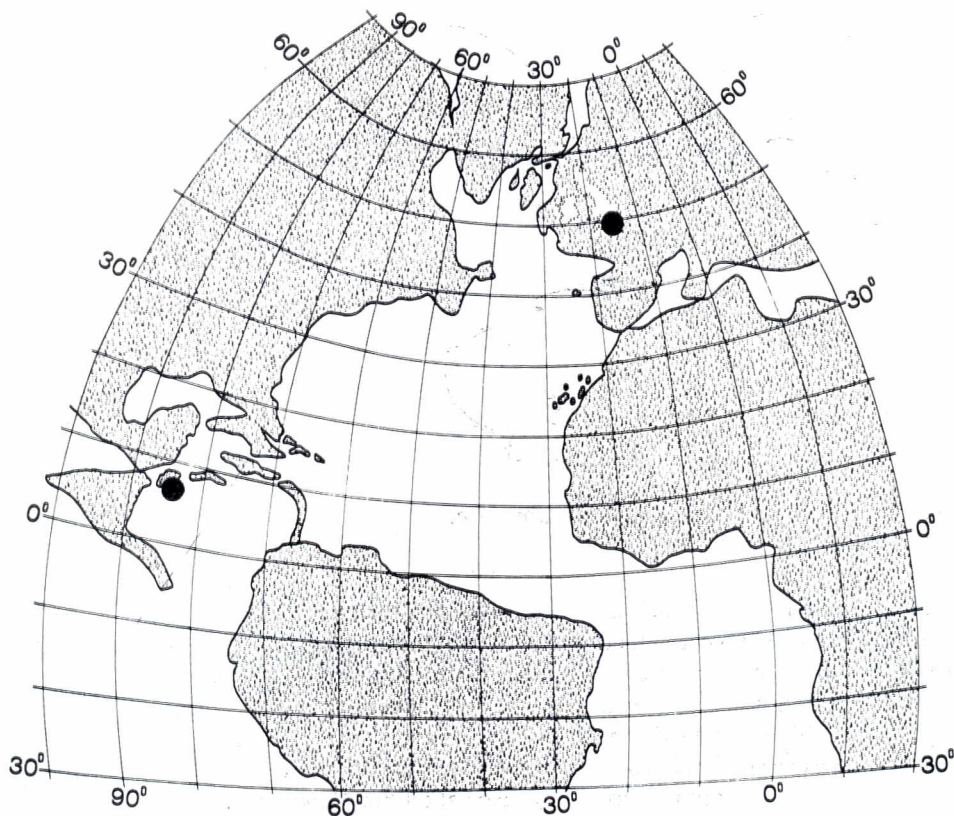


Figure 8. Fossil and recent occurrences of *Proserpina* plotted on Eocene palaeogeography. After Owen, 1983, map 17, modified to include details of intra-Caribbean plate movements.

to side vigorously. *P. bidentata*, in particular, wriggles like a small fish caught in a net.

With such distinctive shell morphology it is reasonably easy to recognize proserpine snails from shells or as fossils. At present they occur in the Greater Antilles (Jamaica, Hispaniola and Cuba), Mexico and northeast South America (Peru, Venezuela, Bolivia and Ecuador) (Boss and Jacobson, 1975b). The genus *Proserpina* occurs in Jamaica and Hispaniola (Boss and Jacobson, 1975a), and undoubted fossil examples of this genus occur in the Upper Eocene of Britain (Preece, 1981). Their present distribution represents a remarkable reduction in range over the last 45 million years or so, even allowing for the narrower Atlantic Ocean in the Eocene (Fig. 8).

Bishop (1979) has documented another major reduction in range for the camaenid genus *Caracolus*. He described an undoubted example of the genus from the Oligocene of Nebraska, whereas the present-day distribution is confined to the Greater Antilles (from Cuba through Hispaniola, Puerto Rico and Vieques to St Croix). Goodfriend (personal communication) has reminded me that species of another camaenid genus,

Pleurodonte, have an unusual disjunct distribution, occurring in Jamaica and the Lesser Antilles. In both these latter cases at least, the modern distributions are confirmed by anatomical information (Wurtz, 1955).

Finally, Houbrick (1987) presents a distribution map for a marine snail, *Varicopeza crystallina* (Dall). This snail occurs along the northern margin of the Caribbean Plate and northwards in the Bahamas and Gulf of Mexico. Its distribution is not quite restricted to one plate, but it does not penetrate far onto the Caribbean Plate. However, it is extremely puzzling to find the distribution of marine snails apparently controlled by past plate movements and one presumes some other explanation, such as current flow or salinity, affects this particular pattern. Since the only other known species of *Varicopeza* is a Pacific Ocean form, the occurrence of *V. crystallina* on the Caribbean Plate, not the North American Plate, would fit better with plate motions if they really controlled its distribution.

CONCLUSIONS

- (1) The present-day distribution of non-marine molluscs in the Caribbean Region offers potential for confirming plate tectonic interpretations of the history of the area.
- (2) Preliminary results suggest that the fauna of Jamaica may be more closely similar to that of Hispaniola than to that of Cuba, despite both islands being equidistant from Jamaica.
- (3) Such a relationship would be in agreement with current plate tectonic models, which suggest that the south-west peninsula of Haiti may have remained close to Jamaica over the last 50 million years or more, whereas Cuba was formerly much further from Jamaica and may well be at its closest approach now.
- (4) Much more information is needed on the distribution of molluscs, and particularly their anatomy, before these preliminary suggestions can be confirmed.
- (5) If Jamaica was indeed submerged completely during the Miocene, then only post-Miocene plate movements need be considered. This idea implies dramatic rates of colonization and diversification and would suggest that Cuban and Hispaniolan non-marine molluscs ought to be equally closely related to the Jamaican forms.
- (6) Two cases of dramatic restriction in range over the last 50 million years involve the genera *Proserpina* and *Caracolus*. The former is a known fossil in the Upper Eocene of Britain, the latter from the Oligocene of Nebraska. Currently both genera are confined to the Greater Antilles.

ACKNOWLEDGEMENTS — The paper was significantly improved following discussions with Dr Glenn Goodfriend, and I am also grateful to Dr S.K. Donovan for drawing my attention to the paper by Houbriek on *Varicopeza*.

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