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Terrestrial faunas and habitats of Aldabra during the late Pleistocene

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[Plate 1]

Far from being fixed and unchanging, the islands and land areas of the western Indian Ocean are in a dynamic state; the most important variable, apart from tectonic activity, has been the rise and fall of sea level as a consequence of late Pleistocene glacial advances and retreats. Geological studies at Aldabra show that there have been great variations in the land area of the atoll, the topography, and the height above sea level. Moreover, the land has been completely submerged on at least two occasions. Fossil tortoises, crocodiles, lizards, birds and snails illustrate, if fragmentarily, the pattern of colonization and extinction on the Atoll. Although the earliest terrestrial deposits represent vegetated sandy cay habitats colonized by crocodiles, iguanas, petrels, tortoises and snails, the later deposits indicate dissected rocky substrates with meagre soil formation and scrub vegetation more similar to present day Aldabra. However, both the lizard and snail faunas indicate that considerable faunal change has occurred.

Introduction

The faunas and floras of oceanic islands have long excited biologists interested in both evolution and biogeography. The publication of MacArthur & Wilson's *The theory of island biogeography* (1967) emphasized the growing interest in the dynamic nature of island biotas, with both short-term studies and the examination of historical records revealing patterns of colonization and extinction on islands which conform, more or less closely, with their models. However, with few exceptions, it is rare to find any evidence of the long-term history of the fauna on an oceanic island. Atolls in particular, by virtue of their mode of formation by subsidence, rarely reveal any of their previous history from a study of the surface deposits, and what fragmentary evidence is available concerning the history of the land biota of atolls has come from a few boreholes (Ladd 1958; Leopold 1969). It was therefore of some interest when, during the geological survey of the slightly elevated atoll of Aldabra in the western Indian Ocean, Braithwaite, Taylor & Kennedy (1973) discovered a series of fossiliferous terrestrial deposits within a dominantly marine, late Pleistocene rock sequence.† The importance of these deposits to the understanding of the present day fauna of the Atoll was underlined when it was demonstrated that the giant tortoises must have colonized the atoll on at least three separate occasions. It is the purpose of this paper to show that this pattern of colonization and extinction extends to a number of other fossil groups.

In this paper we describe the fossils and sediments from a variety of fragmentary deposits distributed throughout the Aldabran rock sequence. We attempt to reconstruct the palaeo-

† Incidentally, Sir John Fryer collected a sample of these rocks from Bassin Cabri in 1908 which he clearly recognized as of terrestrial origin. The fossils were reported upon by Dr Bullen-Newton of the British Museum (Natural History), but the information was not incorporated into Fryer's (1911) report on the geology of the atoll.

environments which these represent and discuss the significance of the fossils in relation to the faunal history of Aldabra and the biogeography of the area in general. The field work upon which this study is based was carried out by J. D. Taylor in 1969 and 1973, and by C. J. R. Braithwaite in 1969.

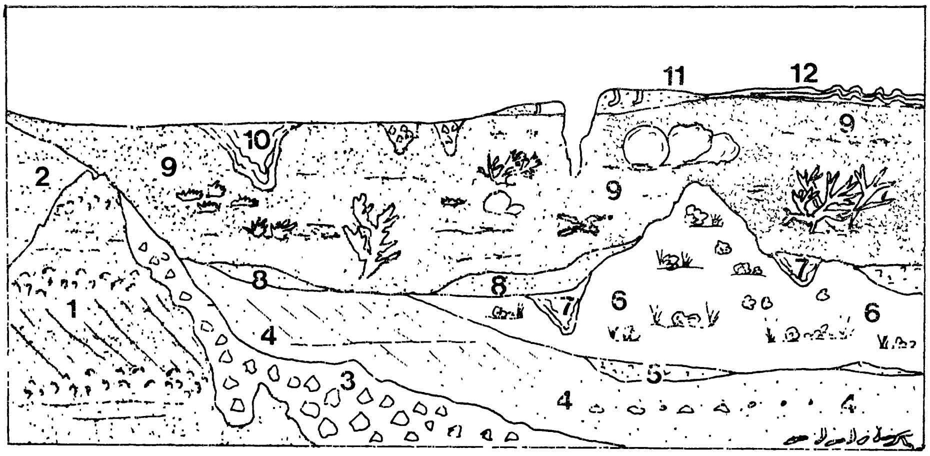

Figure 1. Stratigraphic model for Aldabra showing the general relations of terrestrial and marine rock units. Lateral scale approximately 10 km, vertical scale 9 m. Bed thickness not to scale. 1, Esprit Limestones; 2, 3, Esprit Phosphorites; 4, Picard Calcarenites; 5, Post-Picard Calcarenite 'soils'; 6, Takamaka Limestone; 7, post-Takamaka Limestone 'soils'; 8, hard marine calcarenites; 9, Aldabra Limestone; 10, post-Aldabra Limestone solution pits and fillings; 11, crab burrowed calcarenites; 12, stromatolites.

Geological history and physical setting of Aldabra

Aldabra Atoll (lat. 9° 24′ S, long. 46° 20′ E) is 34 km long and 14.5 km wide, with islands 0.25–5 km wide and 155 km^2 in area. It is one of a group of slightly elevated coralline islands lying to the north of Madagascar which form the subaerial tips of individual sea-mounts rising 4000–4500 m from the abyssal floor of the Somali Basin.

The Pleistocene surface geology has been described by Braithwaite *et al.* (1973), and the geomorphology by Stoddart, Taylor, Fosberg & Farrow (1971); only the essential features are outlined below. The exposed rocks reveal a complex series of erosional and depositional events which consist of shallow-water marine limestones, limited terrestrial calcarenites, calcareous soils and cavity-fills, and phosphorites. These deposits occur in association with, or are separated by, erosional surfaces which were produced by subaerial solution–dissection or by marine planation of the limestones. The nature of the geological events recognized and of the depositional processes is such that no single deposit is found over the entire area of Aldabra. Some deposits are, and perhaps were, merely a few centimetres thick, and occupy areas of only a few square metres.

The major sedimentary units and the events affecting Aldabra are shown diagrammatically in figure 1. The oldest sediments exposed are marine calcarenites (1), the Esprit Limestones. The deposition of these was followed by a period of emergence with subaerial erosion and the subsequent accumulation of the Esprit Phosphorites (2, 3). The next recorded event was a marine regression, culminating in the deposition of terrestrial calcarenites and soils, the Picard Calcarenites (4, 5). These were covered by a transgression represented by the Takamaka Limestone (6), which is a marine calcarenite/calcilutite containing abundant calcareous algae.

A period of emergence followed, resulting in solutional erosion and the deposition of cavity-fill and other terrestrial deposits (7, 8). This regression may also be related to the deposition of beach sediments in the Passe Houareau area. Submergence about 125 ka B.P. (Thompson & Walton 1972) formed an extensive thick calcarenite, the Aldabra Limestone (9) containing abundant corals. Following this important marine interval there was emergence and erosion of the limestones, perhaps with the deposition of cavity-fill deposits. Submergence cut the +8 m and +4 m terraces interpreted by Braithwaite *et al.* (1973) as being produced by simple still-

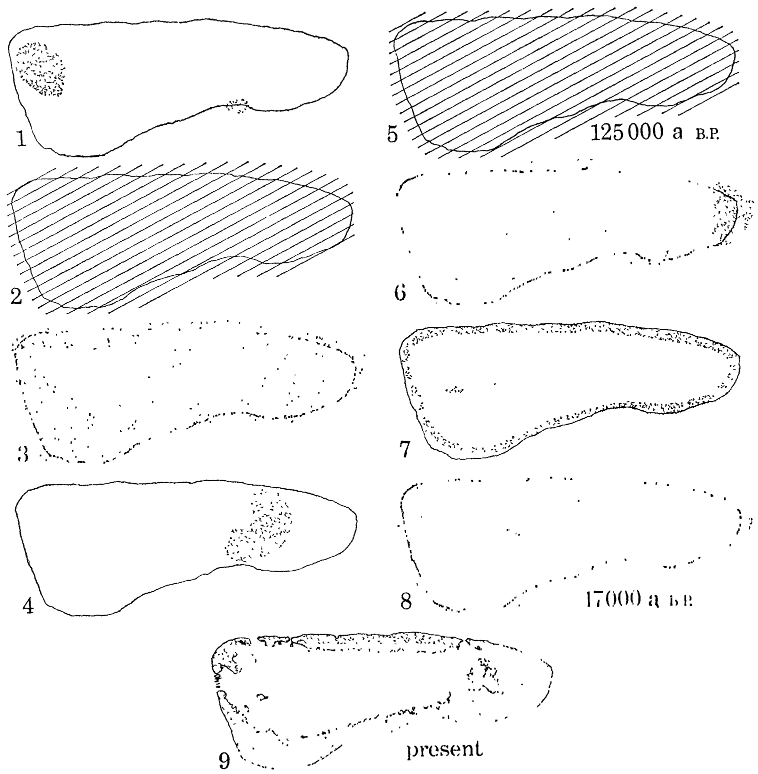

FIGURE 2. Diagrammatic representation of the sequence of possible land areas at various times in the history of Aldabra. Stippled areas, land; cross-hatched areas, complete marine inundation. Key events: 1, Picard Calcarenites; 2, Takamaka Limestone; 5, Aldabra Limestone; 7, The +4 m terrace; 8, The Wisconsin glacial minimum sea level.

stands of a sea level falling progressively from the last interglacial to the Wisconsin glacial maximum about 17 ka B.P. Evidence from other parts of the world shows, however, that this is a very poor record of this interval. Steinen, Harrison & Matthews (1973), and Bloom *et al.* (1974), describe 'reef terraces' on the emergent coasts of Barbados and New Guinea respectively. At the New Guinea site, as many as five depositional terraces were recorded, dated between 125 and 15 ka B.P., and apparently separated by erosion surfaces produced by periods of lowered sea level. There is no evidence on Aldabra of deposits of comparable ages, although the +8 and +4 m terraces are probably partly time-equivalent. However, both the peaks and the troughs of the oscillations in New Guinea and Barbados are thought to represent sea levels well below the present. Braithwaite *et al.* (1973) postulated that Aldabra had been tectonically stable in the late Pleistocene, but if the New Guinea and Barbados estimates of eustatic sea levels are correct, then Aldabra may well be emergent and the planation surfaces elevated.

Whatever the interpretation, it is clear that, after the deposition of the Aldabra Limestone, sea level fell, probably exposing a land area as large as the whole atoll (400 km²). A subsequent rise in sea level inundated the land with marine erosion, forming the +8 m terrace. A further fall in sea level, represented by the +4 m terrace, exposed a narrow fringe of low rocky islands of about 50 km² area encircling a large shallow rock-bottomed lagoon (at the end of the stand). Sea level then dropped again, with probable oscillations, down to about −120 m at the Wisconsin glacial maximum about 15 ka B.P. Aldabra would have stood at this time as a steep-sided, flat-topped rocky island about 120 m high and again about 400 km² in area. Extensive solutional erosion took place, probably accompanied by cavity-fill deposition. The subsequent post-glacial sea level rise reached its present level 3–5 ka B.P. (Stoddart 1976). The most significant result of this rise was the breaching of the present lagoon which would have reduced the land area by about 60%. The present situation is simply the latest event in this series; it is again notable for the extensive marine and terrestrial erosion taking place without significant deposition (Trudgill 1976*a*, *b*). As one might expect, this appears to be true for all of the terrestrial or regressive intervals.

Regional context of Aldabra

Far from being fixed and unchanging, the islands and land areas in the western Indian Ocean are in a dynamic state. The most important variable, apart from tectonic activity, has been the rise and fall of sea level as a consequence of late Pleistocene glacial advances and retreats.

Most of the islands close to Aldabra, such as Cosmoledo, Astove, Assumption, Farquhar and Glorioso, are low coralline islands which would have been inundated during the last interglacial when sea level stood about 10 m higher than at present. However, the volcanic Comores, the granitic Seychelles and Madagascar are high islands, and would have been present as land during this period with relatively little change in area. By contrast during the last glacial maximum when sea level was considerably lower than at present, large areas of land now submerged as shallow platforms would have been emersed. These include the Seychelles, Amirantes, Nazareth, Farquhar and Zelee Banks, and Saya de Malha. This emergence would have produced a series of large islands with a total area of approximately 140000 km². Individual banks were quite large, the Seychelles Bank would have been about 43000 km² and Saya de Malha about 40000 km². These banks are largely uninvestigated at present, but coring may be expected to reveal terrestrial sediments or subaerial erosion surfaces produced during these emergent periods. Sea level changes have thus been of critical importance in determining the land areas available for colonization and continuing habitation by a terrestrial biota.

In addition to variations in the habitat and its area there have been significant changes in climatic conditions. The $^{16}O/^{18}O$ palaeotemperature records indicate a drop in the surface water temperatures of the Indian Ocean of about 8 °C (Emiliani 1971). This would have placed the islands of the Aldabra group outside the region of active coral growth. Rainfall and cloud cover were possibly also higher, and would have had direct effects upon vegetation and terrestrial habitats.

The terrestrial deposits and their faunas

Although some of the terrestrial sediments are bedded, most are in the form of irregular cavity-fill deposits. These are usually small in extent, isloated from one another, and thus difficult to correlate, or to place satisfactorily into a stratigraphic time sequence. Braithwaite

(1975) has described in detail the structure, petrology and mineralogy of the sediments, and Arnold (1976), van Bruggen (1975), and Harrison & Walker (1978) have described some of the terrestrial fossils.

Although the cavity-fill deposits are very common on Aldabra, those containing fossils are comparatively rare. In the case of vertebrate material, this is not surprising, but the patchy occurrence of terrestrial snails, which are more likely to be widely distributed, seems anomalous.

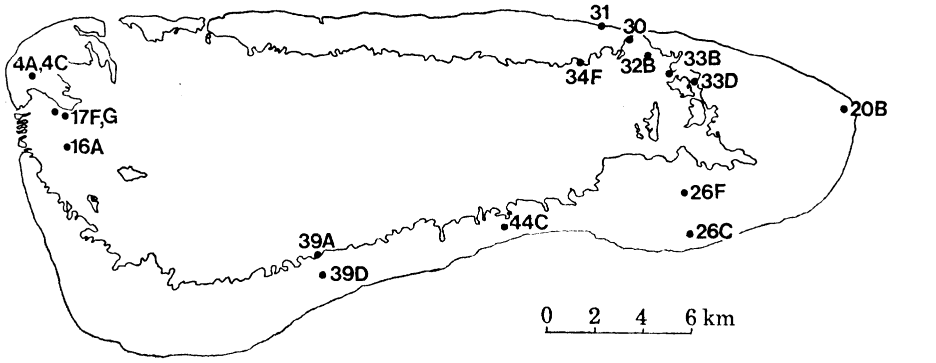

Figure 3. Location on Aldabra of the terrestrial rock sample sites mentioned in the text.

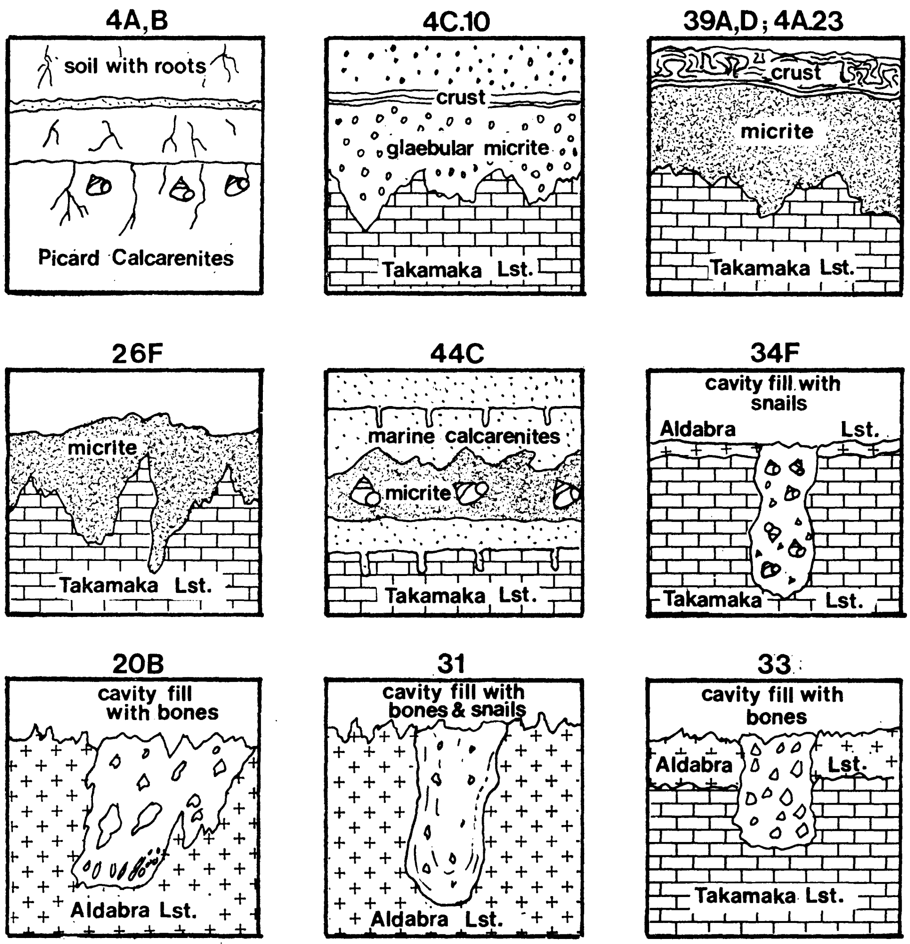

Figure 4. Diagrammatic representation of the stratigraphic positions of the various terrestrial deposits discussed in the text.

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It may conceivably be attributed to preservational loss, but if this is the case there is no direct diagenetic evidence and it must have taken place before lithification. The nature of each terrestrial deposit, its sediment and contained fossils, and an environmental interpretation is outlined below in an approximate time sequence. The localities and stratigraphic positions of each deposit discussed are shown in figures 3 and 4 respectively. In the text, each deposit is referred to by grid reference and sample collection number. The present account is concerned only with those deposits for which there is substantive evidence (in the form of diagnostic fossils) of a terrestrial origin. The degree of refinement in the identification of the fossils varies considerably according to both the state of preservation and the morphological complexity of the animal group concerned.

The Picard Calcarenites

0635.0990, samples 4A1, 2; 4B4, 6, 12, 13, 20, 21, 22; 4C1, 2.

These deposits post-date the Esprit Limestones and Phosphorites, and are overlain by the Takamaka Limestone. The present exposures occupy an area of about 20 km^2 at the southern end of Picard (Bassin Cabri) extending to Iles Châlen. Evidence for a second island in the Point Lion area is given by Braithwaite *et al.* (1973) and there may have been others. The surface upon which the deposits rest is not seen, but probably included rocky pinnacles such as that now formed by Esprit.

Sediment

In the Bassin Cabri area, two sets of beds have been recognized, representing parts of the same major depositional cycle, but separated by an erosional break. The lower, thicker, and more extensive unit consists of about 3 m of cross-bedded calcarenites in which the laminae dip gently (5–7°) in a general westerly to southwesterly direction. The top of this rock unit consists of a more massive bed, 0.5–1 m thick, of a coarse calcarenite containing abundant moulds of rootlets with oxidized plant remains, moulds of terrestrial snails, and partly articulated bones. The sediment was originally of marine origin but, apart from the post-depositional solution or alteration of aragonite bioclasts, has been little modified. The micritic matrix

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Description of plate 1

Some fossil terrestrial snails from the Aldabra deposits.

Figure 1. Silicone rubber cast of *Tropidophora* sp. from the Picard Calcarenites. Actual height 14.4 mm

Figure 2. *Tropidophora* sp. from site 44C. Height 21.6 mm.

Figure 3. *Tropidophora* sp. from site 44C. Height 15.9 mm.

Figure 4. *Otopoma flexilabris* from site 31. Height 16.2 mm.

Figure 5. *Tropidophora* sp. from site 44C. Height 21.9 mm.

Figure 6. *Tropidophora* cf. *aspera* from site 34F. Height 31.8 mm.

Figure 7. *Cyathopoma* cf. *pauliani* from site 26F. Height 5.1 mm.

Figure 8. *Rachis aldabrae* from site 4A. Height 19.7 mm.

Figure 9. *Neritina* sp. from site 44C. Height 12.6 mm.

Figure 10. Silicone rubber internal cast of '*Succinea*' from the Picard Calcarenites. Height 6.0 mm.

Figure 11. *Melampus* sp. from site 44C. Height 12.3 mm.

Figure 12. Ellobiid from site 44C. Height 3.9 mm.

Figure 13. *Truncatella* cf. *guerini* from site 26F. Height 6.9 mm.

Figure 14. Moulds of *Tropidophora* and rootlets in the Picard Calcarenites.

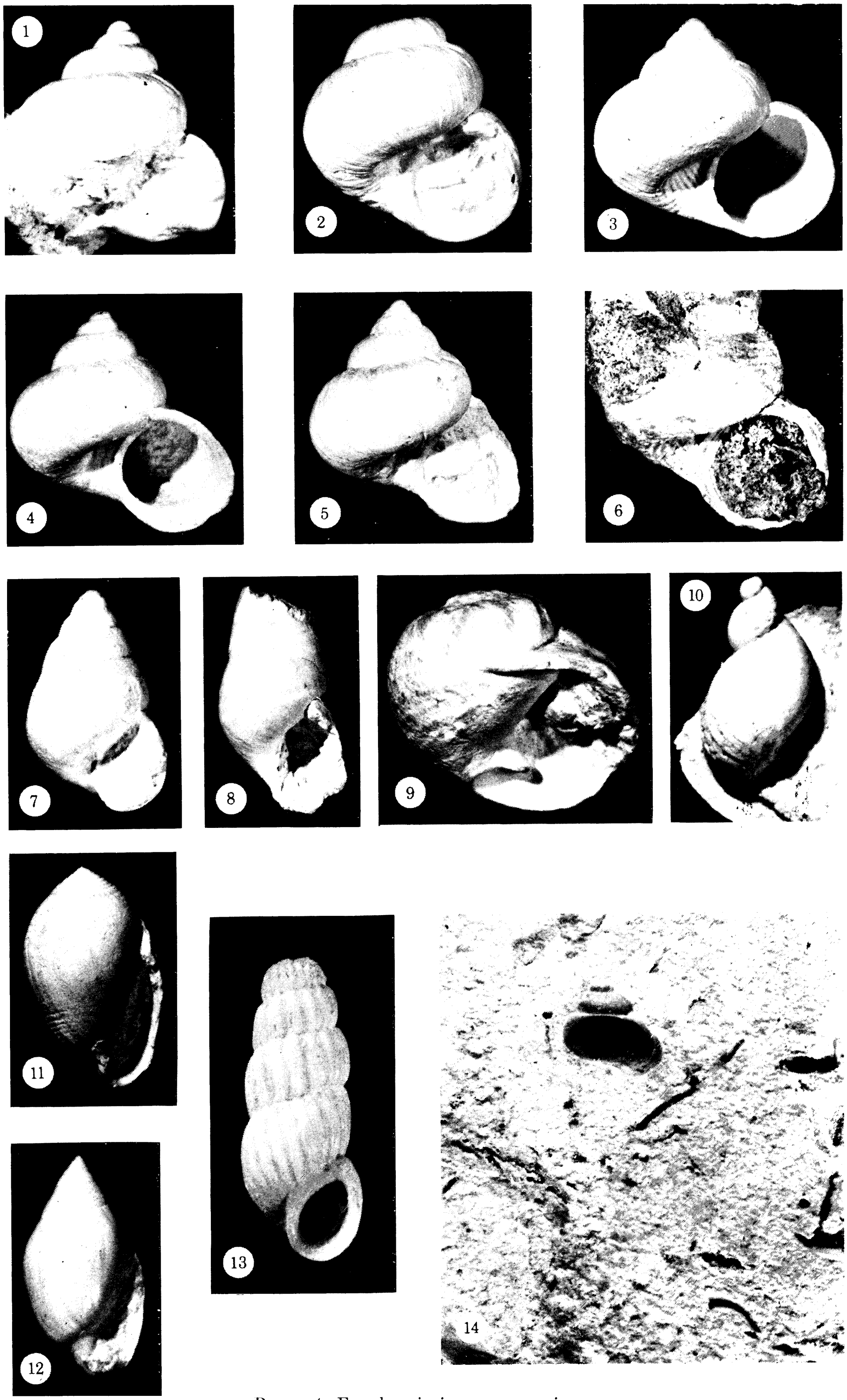

PLATE 1. For description see opposite.

(*Facing p.* 52)

present in some areas may have been introduced by infiltration (by rainwash) or by mixing by animal activity.

These lower calcarenites were cemented and subjected to solutional erosion for an unknown period before the deposition of a group of soils now restricted in occurrence to a small area at Bassin Cabri. The sediments in these are 10–15 cm thick and occur in three distinct layers. The lowest layer is a fairly homogenous biomicrite packed with ostracods and, towards the top, Foraminifera. It is burrowed and penetrated by rootlet tubules, but filled cavities suggest that it may have been lithified before deposition of the unit above. This is a thin (5–15 mm) white calcarenite and rests upon a well defined erosion surface. It contains fragments of calcareous algae, mollusc shells, Foraminifera and echinoderms, but also includes some chips of bone. There is again evidence of lithification before deposition of the uppermost sediment, a dense brown–white micrite with an anastomosing network of tapering fractures and a crude lamination. This contains abundant ostracods, Foraminifera and moulds of terrestrial snails, together with occasional burrows. The lower part also contains numerous, possibly faecal, pellets.

The fauna

Mollusca. The uppermost bed of the lower calcarenite unit contains abundant moulds of a terrestrial prosobranch snail belonging to the genus *Tropidophora* (plate 1, figure 1) but impossible to identify with certainty to species level.

In the thin soils from the upper sequence, moulds of the small pulmonate snail '*Succinea*' were abundant. Patterson (1975) has demonstrated the impossibility of making specific identifications of this family from shell material alone, but extrapolating from her work it might be expected that the species here belongs to the genus *Quickia*, which is represented by endemic species on Indian Ocean islands.

Vertebrata. All of the vertebrate material recovered came from the lower calcarenite unit.

(1) Tortoise bones are abundant in the upper part of the calcarenite and occur as individual disarticulated bones or, in the Bassin Cabri area, as eroded but probably once complete articulated skeletons. In addition, a lower horizon of the calcarenites in the La Gigi area, about 30 cm above low water level, contained large numbers of shell fragments and other bones which appeared on the outcrop as slot-like moulds. The tortoise bones are indistinguishable from those of *Geochelone gigantea* (Schweigger).

(2) Two teeth thought to belong to *Crocodylus niloticus* (Laurenti) were found in the upper part of the calcarenite in the Bassin Cabri area.

(3) Three pieces of maxilla, two pieces of dentary and a single tooth found at Bassin Cabri were identified as derived from an iguanid lizard *Oplurus*, resembling *O. cuvieri* (Gray). The animals had an estimated body size from snout to vent of about 170 mm.

(4) Many disarticulated bird bones were found at Bassin Cabri. Of these, 15 were identifiable and were ascribed to a species of *Pterodroma*, a gadfly petrel.

(5) A single bone, the distal end of a humerus of a duck described as a new genus *Aldabranas* (Harrison & Walker 1978) and resembling a shelduck.

Environmental interpretation

The sedimentological evidence shows that this deposit represents a prograding sand-cay rising to probably not more than 2 m above sea-level. This was probably extensively vegetated, but the component sediment was not modified and a true soil was not developed. The cay was colonized by tortoises, iguanas and crocodiles with the ground-nesting gadfly petrel probably seasonally abundant (figure 5). The large prosobranch snail *Tropidophora* was extremely abundant, but the heavy shells are resistant to erosion and large numbers could have accumulated over a considerable period. It belongs to a group of species which are characteristic of open dry habitats, such as might develop upon the upper parts of sand cays.

The estimated area of present outcrops (20 km^2) was probably inadequate to support the terrestrial vertebrate fauna described. The evidence for a second land area which may have been continuous with the Bassin Cabri islet has been noted, and perhaps the proto-Aldabra platform bore one or two large, or a number of smaller, sand-cays.

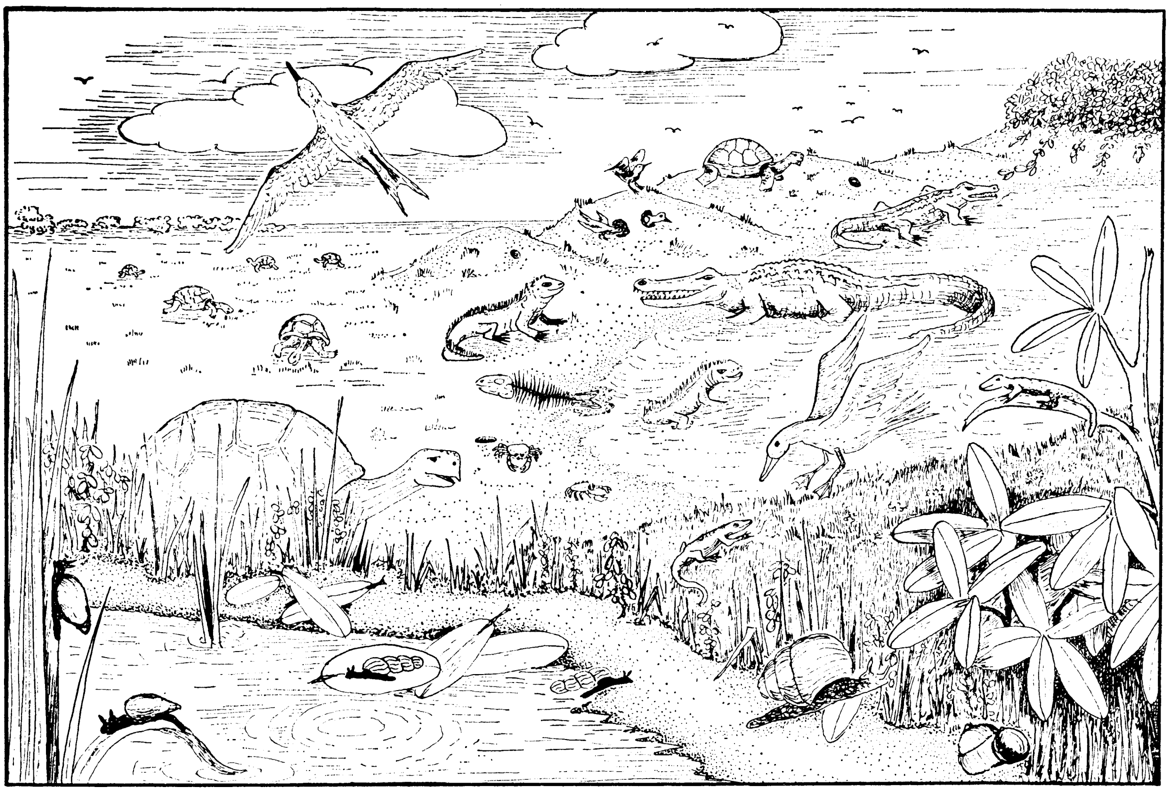

FIGURE 5. Sketch impression of the general habitat during the formation of the Picard Calcarenites.

The abundant ostracods and '*Succinea*' in the upper soil sequence indicate at least seasonal flooding of a moist, low, grassy habitat, the desiccation cracks suggest perhaps periodic drying of the sediment. The thin marine intercalation may have resulted from a storm influx. Such an environment is not inconsistant with the continuing existence of beach ridges and dune sands similar to those described above, and analogous facies mosaics may be seen in present-day Andros and parts of the Florida Everglades.

The Takamaka deposits

The next group of deposits all post-date the deposition and cementation of the Takamaka Limestone and are believed to pre-date the accumulation of the Aldabra Limestone. However, within these time limits the deposits are not necessarily contemporaneous.

0635.0990, samples 4C10, 11.

This deposit is exposed in a mound in the Bassin Cabri area approximately 20 m long and rising 1.5 m above the general erosion surface. The base of this outcrop is made up of Takamaka Limestone which has a solution-fretted upper surface, with the cavities filled with a fine-grained friable terrestrial sediment.

Sediment

The fine-grained grey–orange sediment consists of amorphous micritic glaebules 0.03–0.3 mm in diameter, with occasional lithoclasts. Glaebules are oval or subspherical in shape, and areas in which they are well-defined grade laterally into dense micrite. Burrows and rootlet moulds are common. This sediment is overlain by a yellow–brown laminated crust which passes gradationally into a paler unlaminated sediment containing large (up to 1 mm) concentrically zoned glaebules bound by a sparry calcite cement. A 'bird's-eye' fabric of spar-filled spaces is common.

Fauna

The lower glaebular soil has yielded an abundant fauna of terrestrial snails: *Truncatella* cf. *guerini*; *Streptostele nevilli*; *Cyathopoma* sp.; and four other unidentified pulmonates.

Environmental interpretation

The sediment gives little information about environmental conditions, other than that the land was rocky with an irregular topography with soils accumulating in cavities. The possible climatic implications of the concentric glaebules have been discussed elsewhere (Braithwaite 1975). The precise mechanism of formation of these bodies is not fully understood, but it may be linked to a marked seasonal variation in rainfall. The gastropod fauna is composed entirely of small species. *Streptostele* and *Cyathopoma* are forms which are associated with an accumulation of leaf litter and insulation from high temperatures. Such conditions are found in high scrub with a dense canopy which has been established long enough to develop a litter layer. *Truncatella* is a group which now has a wide distribution on the Atoll, but is typically found close to the sea; however, shells can be passively transported considerable distances.

3368.0545, sample 26F.

At this site, cavities in the irregular, fretted upper surface of the Takamaka Limestone contain an earthy brown filling.

Sediment

The sediment is poorly sorted and texturally disorganized, with cavities formed by differential compaction. Some parts consist of amorphous or concentrically zoned glaebules (0.1–0.5 mm) set in a sparry cement, others of apparently amorphous micrite. Burrows 1 mm in diameter are present containing ovoid faecal pellets.

Fauna

The site contains abundant terrestrial gastropods including: *Truncatella guerini*; *Tropidophora* sp.; *Assiminea* sp.; *Rachis aldabrae*; '*Succinea*' sp.; *Gulella peakei*; and one unidentified pulmonate.

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Environmental interpretation

The habitat at this site was an irregular rocky surface with soil accumulating in pockets. The diverse gastropod fauna suggests a wider range of habitats than in 4C10. The presence of *Succinea, Tropidophora* and *Rachis aldabrae* suggests open habitats varying from low vegetation with periodic flooding to drier habitats with open scrub. *Rachis aldabrae* is an arboreal species now frequently associated with *Euphorbia pyrifolia*, a shrub typical of 'edge' habitats. *Assiminea*, like *Truncatella*, is now found close to the sea. Thus there is again indirect evidence of transport of material from a number of different habitats. The presence of ovoid faecal pellets and burrows could indicate the presence of an organism associated with the breakdown of litter, similar to the millipede *Spirobolus* recorded from the Atoll today (Spaull 1976).

1858.1288 and 1858.0238, samples 39A, D.

At localities north of Dune d'Messe, the irregular fretted surface of the Takamaka Limestone is overlain by small patches of buff, friable, terrestrial sediments.

Sediment

Individual outcrops are quite variable. Some sediments contain uncompressed but poorly preserved rootlets and others abundant ovoid faecal pellets and burrows. In some cases they are overlain by up to 5 cm of a dense micritic laminated crust with discrete mamillated or pisolitic horizons. Numerous filaments are present within some sediments, which may be borings. Crusts and 'soils' contain terrestrial snails. In some cavities these early sediments are overlain by a fine-grained calcarenite with well preserved marine molluscs.

Fauna

The terrestrial sediments have yielded an extensive snail fauna, of which the most common members are *Tropidophora* and *Cyathopoma*, but it includes: *Tropidophora* sp.; *Otopoma flexilabris*; *Assiminea* sp.; *Cyathopoma* cf. *pauliani*; *Cyathopoma* sp.; *Rachis aldabrae*; *Gulella gwendolinae*; and *Gulella peakei*.

Environmental interpretation

The snail fauna from these samples is less restricted that for site 26F. The presence of *Tropidophora* and *Rachis* suggest patchy scrub or edge zone habitats, although van Bruggen (1975) comments that species similar to *Gulella peakei* are restricted to forest habitats in Africa.

0635.0990, sample 4A23.

A small outcrop in the Bassin Cabri area contained a sediment similar to 39A, D, and rested upon an irregular surface of Takamaka Limestone. It contained the following terrestrial molluscs: *Truncatella guerini*; *Tropidophora* sp.; *Otopoma flexilabris*; *Cyathopoma* cf. *pauliani*; *Cyathopoma* sp.; *Rachis aldabrae*; and *Gulella* sp. This is a similar fauna to 39A, D, although the presence of *Truncatella* indicates close proximity to the sea.

2633.0418, sample 44C.

This is a complex bedded deposit (figure 4) found in a small area immediately to the north of Dune Jean-Louis. It clearly overlies the Takamaka Limestone, but underlies, at least in part, the Aldabra Limestone.

Sediment

Borings in the planated Takamaka Limestone surface are filled by a hard fine-grained calcarenite containing *Halimeda*, lithothamnioid algae and some molluscan shell fragments. Overlying this is a soft light brown friable sediment which is basically micritic but which contains some indistinctly pelleted areas. In addition to abundant terrestrial molluscs there are rock fragments, and some areas are penetrated by laminated pedotubules, probably rootlets. The terrestrial sediment is overlain by a second hard, well cemented erosion surface, bored by *Cliona* and polychaetes, and encrusted by algae and Foraminifera.

Evidence from other sites around the atoll suggests that this deposit represents a brief terrestrial interlude during the deposition of the lowest part of the Aldabra Limestone. Unfossiliferous calcarenites in the Bras Takamaka area and beach deposits at Passe Houareau may be contemporaneous.

Fauna

The fauna recovered from the chalky soil consists of abundant terrestrial molluscs with *Tropidophora*, *Truncatella* and *Melampus* prominent: *Truncatella guerini*; *Tropidophora* sp; *Cyathopoma* sp.; *Neritina* sp.; and *Melampus* sp.

Environmental interpretation

The presence of abundant *Melampus* and *Truncatella* in this deposit indicates a close proximity to the sea. The abundant *Tropidophora* suggest a low dry scrub vegetation, with *Cyathopoma* suggesting patches of denser scrub, while the occurrence of *Neritina* means the presence of standing bodies of fresh water.

3143.1193, sample 30A; 3195.1173, sample 32B; 3318.1058, sample 33B.

At these three sites, deposits fill small cavities which cut the Takamaka Limestone, but are overlain by Aldabra Limestone. They yielded fragmentary bones of *Geochelone*. The sediments are dense and micritic with local crumb-like aggregates. Some areas contain well-preserved roots, and the sediment clearly functioned as a soil. Elsewhere, however, (32B4), there is evidence of extensive reworking during an intermittant deposition.

Post-Aldabra Limestone deposits

This series of deposits post-dates the Aldabra Limestone but probably includes sediments of widely differing ages within the 125 ka interval.

2928.1090, sample 34F.

This outcrop consists of the deposit filling a single cavity about 1 m deep and 1.5 m in diameter. This cuts both the Takamaka Limestone and about 30 cm of hard calcarenite believed to be a lower facies of the Aldabra Limestone.

Sediment

Large, commonly broken, shells of *Tropidophora* cf. *aspera* are the dominant element in this sediment. They are contained within a dark brown micritic sediment with micropellets and scattered larger grains. Rootlets preserved in calcite are common.

Fauna

The fauna extracted from this deposit consists of an abundant and diverse association of terrestrial molluscs. The large ribbed shells of *Tropidophora aspera* are the most conspicuous elements, but some of these shells were packed with hundreds of smaller shells, which also occurred, less commonly, in the matrix. Species found were: *Truncatella guerini*; *Tropidophora* cf. *aspera*; *Cyathopoma* cf. *pauliani*; *Cyathopoma* sp.; *Assiminea* sp.; *Rachis aldabrae*; *Gulella gwendolinae*; *Gulella peakei*; *Gulella insulicola*; *Gulella* sp.; and five other unidentified pulmonates.

Environmental interpretation

The occurrence of the large *Tropidophora* in this sediment in closely packed masses could represent accumulation over a number of years, or an aestivating group which died within a particular solution cavity. Similarly, the smaller species, by virtue of their high density and unbroken appearance, may have used the larger dead shells as refuges. Their general paucity in the matrix sediment suggests that this may have been added at a slightly later date, possibly by rainwash, but clearly the loosely aggregated mass became colonized by higher plants and penetrated by their roots. The fauna in general indicates a wide range of habitats from well developed, open wood and scrub with litter formation and insulation, while the presence of *Rachis aldabrae* indicates open or 'edge' habitats, and *Truncatella* the proximity of the sea.

3005.1225, sample 31.

This deposit fills a solution pipe 2 m deep and 0.5 m in width, penetrating the Aldabra Limestone and exposed on the 3.5–4 m high cliffs. The sediment can be seen to be crudely bedded with laminae draped against pit margins.

Sediment

The sediment is a pale, friable, highly porous calcarenite with visible rootlet moulds. It has a poorly sorted heterogeneous texture, the smaller fraction consisting of 0.15 mm diameter round or irregular glaebules, probably of faecal origin, with a few which are concentric. The coarser fraction consists of lithoclasts and bioclasts which include abundant coral and *Halimeda* fragments and bones. Rootlets are not common, but algal filaments are abundant between the grains. There is no obvious precipitated cement.

Fauna

This deposit has yielded a single bone of *Geochelone* as well as abundant but mostly fragmentary terrestrial snails, *Otopoma* being the most common. They include: *Truncatella guerini*; *Otopoma flexilabris*; *Cyathopoma* cf. *pauliani*; '*Succinea*' sp.; *Rachis aldabrae*; *Streptostele nevilli*; and *Gulella gwendolinae*.

Environmental interpretation

At least some of the elements in this fauna indicate open habitats with at least seasonal moist conditions; *Streptostele* and *Cyathopoma* are, however, associated with denser scrub and litter development. Periodic, perhaps seasonal, sediment increments are also indicated by the crudely bedded nature of the deposit. The wetter periods were probably characterized by the growth of filamentous algae and the activity of the organisms producing pellets.

4025.0930, sample 20B, Point Hodoul.

In the Point Hodoul area there is an unusually large number of pipe-fill deposits. These can be seen in the cliff line penetrating the Aldabra Limestone, but about 200 m inland in an area of land-enclosed tidal pools, many such deposits have been exposed as residual pinnacles, and bones derived from them litter the present pool floors.

Sediments

The pipe-fill deposits consist of brown earthy sediment containing abundant, but largely comminuted, bones and limestone fragments. The matrix has an open friable texture and consists in general of pellets (0.1 mm diam.), sometimes grouped into crumb-like aggregates, and structureless micritic areas cut by tapering shrinkage fractures. Intraclasts similar to the host soil are common and indicate more than one cycle of deposition. Tubules of rootlets and small burrows are common. The bones range in size from tiny fragments 8–10 mm in diameter to unbroken limb elements, but they often occur as densely packed aggregates of small splinters. The cement in general is a clear granular calcite but local inclusions suggest that an early stalagmite-like cement may have been present. In a few samples small areas of a late dahllite cement are present.

Fauna

A large and diverse vertebrate fauna is present within these deposits:

(1) Abundant tortoise bones similar to *Geochelone gigantea*.

(2) Many bones of crocodiles identical with *Crocodylus niloticus* are present; these include pre-maxillae, maxillae, jugals, frontals, parietals, teeth, vertebrae and osteodermal scutes. The bones seem to have been derived from animals 2.33–2.4 m in length, smaller in general than adults in normal mainland populations but dwarf assemblages are known (Cott 1961). The sample may, of course, be biased.

(3) Lizard bones are common in some of the deposits and six species have been recognized. These are reported upon in more detail by Arnold (1976) and are summarized below.

Iguanidae:

Oplurus cf. *O. cuvieri* (Gray)

7 bones, total length of animal estimated at 570–680 mm.

Gekkonidae:

Geckolepis cf. *G. maculata* Peters

54 bones, general estimated size 90–100 mm from snout to vent.

Paroedura cf. *P. stumpfii* group

598 bones, animals estimated snout to vent length 90–100 mm.

Phelsuma sp.

4 fragments, distinct from *P. abbotti* (Stejneger) present on Aldabra today. Estimated size of animal from snout to vent 50 mm.

Scincidae:

'*Scelotes*' sp.

437 bones similar to those of *S. johannae* Gunther and *S. valhallae* Boulenger from Glorioso.

Mabuya maculabris (Gray)

18 bones from animals with an estimated snout to vent length of 80–95 mm.

(4) A single bone was found, the distal end of a right metatarsus 17–7 mm long, typical of *Dryolimnas cuvieri*, the rail (Harrison & Walker 1978).

(5) In addition to these vertebrate remains occasional broken fragments of the snails *Tropidophora* and two specimens of *Cyathopoma* were recovered from the matrix.

Figure 6. Sketch impression of the general habitat at the time of the formation of the Point Hodoul cavity-fill deposits (20B).

Environmental interpretation

It is clear that at the time of formation of these deposits, the Point Hodoul area was rocky, intensely pot-holed, and close to the sea (figure 6). The densely packed aggregations of bones are suggestive of winnowing and concentration by flowing water, indicating a high rainfall. However, fragments are angular and unworn, and this indicates that transport was minimal. Both tortoises and crocodiles could have fallen into open pits and been trapped. This is a frequent occurrence with the tortoises on Aldabra today, but does not account for the very high concentration of bone fragments nor for the level of breakage and lack of even partial articulation. The lizard bones appear to be concentrated in particular cavities and are unlikely to have accumulated by pit-fall trapping. It is possible that they represent the food residue of some predator; such situations are known from the West Indies where accumulations of small vertebrate fossils have been attributed to the activities of owls (Etheridge 1965). No owl bones or the remains of any other comparable predator have been found at Point Hodoul or elsewhere on Aldabra, but both very small and very large bones are rare, and it may be significant that a

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high proportion of the individuals represent nocturnal species. No owls are present on Aldabra today, but the Barn owl *Tyto alba* (Scopoli) has become extinct there since 1906 (Benson & Penny 1971).

The presence of crocodiles suggest a sea level close to or slightly higher than at present, with subaerial solution producing a few relatively large pits rather than the highly irregular, delicately fretted, surface characteristic of coastal areas today. A higher rainfall may be indicated.

3380.1028, sample 33D.

Scattered around the atoll are a fairly large number of small resistant pinnacles of cavity deposits which are distinguished by their pinkish red–brown colour. The pipes containing these deposits cut both the Takamaka Limestone and the Aldabra Limestone. Ilot Rose (33D) is a typical example of such deposits.

Sediment

The rock is a breccia with a light brown to pinkish red–brown earthy matrix enclosing bone fragments, limestone blocks, travertine fragments and other lithoclasts. In section the matrix is micritic, but it is almost entirely pelleted. A few areas have a crudely laminated structure which may be algal.

Fauna

These deposits contain abundant fragments of bone, all the identifiable pieces of which seem to be *Geochelone gigantea*.

Environmental interpretation

These sediments may be compared with those forming on the atoll at the present day in solution pits inhabited by the crab *Cardisoma carnifex* (Herbst). In these pits tortoise bones may be derived from animals which fall in accidentally, and tufa and limestone blocks may become detached from pit margins. However, in the Ilot Rose deposits, bones are disarticulated and broken to a degree which the activities of the crustacean scavengers does not adequately explain. There is further the important point that modern *Cardisoma* pits commonly contain few bones. The sediments are unbedded and, if incremental, have been subject to a re-working which obscures increment boundaries.

Present day environments

Aldabra today is a series of rocky islands surrounding a large central lagoon. The limestones are intensely dissected and soil accumulation is generally limited to cavities and depressions within the rock surface. Sand dunes and perched beach deposits are small in extent and are only significant along the south coast. The Atoll is generally covered by a low scrub vegetation with varying density of cover, open areas of coastal turf being present along the southern and easterly shores. The lagoon shores are fringed with dense mangroves.

The terrestrial flora comprises 190 species, of which 44 are believed to have been introduced by man and 18 are endemic. Most plants are coastal bush or supralittoral forms, many of them widespread palaeo- and pantropical varieties. A small but significant proportion are derived specifically from the Afro-Oriental and Madagascar regions.

Among the land fauna those forms which are potentially fossilizable include the giant tortoise

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Geochelone gigantea and three species of lizards. The latter comprise two geckos, *Phelsuma abbotti* Stejneger and *Hemidactylus mercatorius* Gray, and a skink, *Cryptoblepharus boutonii* (Desjardins). The bird fauna includes 14 species of breeding land birds with two endemic species (Benson & Penny 1971), 14 regular migrant waders, and 10 species of breeding sea birds. The terrestrial snail fauna consists of 14 species, most of which are rather small.

Table 1. Distribution of fossil reptiles and birds in the Aldabra terrestrial deposits

	4C1, 2	4C10	26F	39A, D	4A23	44C	30A	20B	33D	34F	31	present
reptiles												
Geochelone gigantea (Schweigger)	*						*	*	*		*	*
Crocodylus niloticus Laurenti	*							*				
Oplurus cf. *cuvieri* (Gray)	*							*				
Paroedura sp.								*				
Geckolepis cf. *maculata* Peters								*				
Mabuya cf. *maculabris* (Gray)								*				
Scelotes sp.								*				
Phelsuma sp.								*				
Phelsuma abbotti (Stejneger)												*
Hemidactylus mercatorius (Gray)												*
Cryptoblepharus boutoni (Desjardins)												*
Birds												
Pterodroma sp.	*											
Aldabranas sp.	*											
Dryolimnas cuvieri (Pucheran)								*				*

marine incursion (between 4C1, 2 and 4C10) — marine incursion (between 30A and 20B)

Discussion

Although the position of the sea relative to the land, and hence the land area, of Aldabra has been constantly changing with time, the major events affecting the terrestrial biota were the complete inundations of the Atoll by the sea. These occurred during Takamaka Limestone times, later during the deposition of the Aldabra Limestone (125 ka B.P.) and possibly in post-Aldabra Limestone times (100–80 ka B.P.) during the formation of the + 8 m terrace. On each of these occasions the terrestrial biota must have been completely eliminated. The data on the fossil terrestrial fauna are summarized in tables 1 and 2 and arranged in an approximate time sequence. The fossil terrestrial gastropods provide the best evidence of habitat type and they divide into four clear groups:

(1) Maritime habitats in close proximity to the sea with snails just above storm levels: *Truncatella* and *Assiminea*.

(2) Open habitats, with freshwater flooding and standing fresh water: '*Succinea*' and *Neritina*.

(3) Open habitats, consisting of thick grass, open scrub or edge habitats: *Tropidophora*, *Rachis aldabrae*, *Otopoma flexilabris* and *Gulella gwendolinae aldabrae*.

(4) Denser scrub, providing insulation, tending towards a closed canopy with some soil development and moist conditions: *Cyathopoma*, *Streptostele nevilli*, *Gulella peakei*, Ereptinae.

The Picard Calcarenites, interpreted as originating on a low sand cay, represent a habitat of small importance on Aldabra today, and were probably similar to some existing low atolls. By contrast, all of the other deposits indicate dissected rocky substrates, meagre soil formation perhaps concentrated by rain-wash, and scrub vegetation, features which probably differed very little from Aldabra today. Evidence of cave systems, groove and buttress structures and other erosional features (Braithwaite *et al.* 1973; Barnes *et al.* 1971) indicates that at times the rainfall was probably higher than that of the present day.

The present biota of the atoll has colonized Aldabra since 80–100 ka B.P., previous terrestrial faunas having been eliminated by marine inundation. During this period, since the last high sea level stand, the land area of Aldabra has undergone quite drastic changes in size, the most

TABLE 2. DISTRIBUTION OF FOSSIL MOLLUSCA IN THE ALDABRA TERRESTRIAL DEPOSITS

	4C1, 2	4C10	26F	39A, D	4A23	44C	30A	20B	33D	34F	31	present
terrestrial												
Truncatella guerini A. & J. B. Villa		*	*		*	*		*		*	*	*
Tropidophora – small	*		*	*				*				*
Tropidophora – medium						*						
T. cf. *aspera* (large) Potiez & Michaud										*		
Otopoma flexilabris Sowerby					*						*	
Cyathopoma cf. *pauliani* F. Salvat				*	*			*		*	*	*
Cyathopoma sp.		*		*	*	*				*		
Assiminea spp.			*	*						*		*
Rachis aldabrae Martens			*	*	*					*		*
‘*Succinea*’ cf. *Quickia*	*		*								*	*
Streptostele nevilli H. Adams		*									*	*
Gulella gwendolinae aldabrae van Bruggen			*	*							*	*
Gulella peakei van Bruggen			*	*						*		
Gulella insulicola van Bruggen										*		
Gulella sp.					*					*		
Pulmonate sp. A		*								*		
Pulmonate sp. B			*									
Pulmonate sp. C										*		
Unidentified species		3	2	1	1					3	1	
Gastrocopta microscopica Nevill												*
Lamellaxis gracilis Hutton												*
Kaliella sp.												*
freshwater												
Neritina sp.						*						
Bulinus bavayi (Dautzenberg)												*
littoral fringe												
Ellobiacea						*				*		*

marine incursion (between 4C1, 2 and 4C10) — marine incursion (between 30A and 20B) recent being the breaching of the lagoon perhaps 5 ka ago. Aldabra, in common with low atolls but in contrast to the higher igneous islands of the Indian Ocean (which have not been submerged since their formation), exhibits a low degree of endemism, with a vegetation consisting largely of maritime lowland species. Faunal size is about what might be expected for an atoll the size of Aldabra, and Peake (1971, fig. 9) has shown for terrestrial molluscs a clear distinction in faunal size that exists between the high and low islands of the western Indian Ocean.

The main point to emerge from this study is that in the history of Aldabra there has been considerable faunal turnover, with periods of extinction followed by recolonization, the most spectacular of the colonists being the giant tortoise. Two problems emerge: first the origin of the faunal propagules and secondly the method of dispersal.

The data from Aldabra provide a salutary warning of interpreting past distributions from the present, but it is possible that faunal turnover on higher islands is not as great as on small remote atolls. Within the fossil fauna of Aldabra it is possible to see affinities with Madagascar (in birds, reptiles and some terrestrial molluscs) and with other islands such as the Comores (reptiles and molluscs); some forms have widespread island distributions while others have African mainland affinities. It is interesting that the Atoll is not completely dominated by present day African and Madagascan taxa. This may be attributable to the presence during some of Pleistocene time of other land areas of considerable size. There is a considerable literature concerning methods of dispersal, but many accounts appear to reflect subjective judgements regarding the probability of successful dispersal by a particular method. Nevertheless, whatever methods are employed, they are obviously successful. As Peake (1969) has emphasized, no particular method must be considered exclusive to any taxon. In the case of island faunas, much attention has been paid to methods of dispersal in the Pacific region, where there is a wide variety of island types with varying degrees of isolation and a range of taxa which have successfully colonized islands. Three methods of dispersal, namely by wind, birds and sea, have received the most attention.

Peake (1969) and later Vagvolgyi (1975) have analysed terrestrial molluscan faunas from the Pacific and found that a large proportion of island snails are small in size, and that the more isolated islands are colonized by the smaller species. The basic conclusion of these observations is that aerial dispersal by wind is a major mechanism. The molluscan fauna of Aldabra is predominantly small and therefore, extrapolating from the Pacific, many species probably arrived by wind dispersal. Constant wind movements are not required. The main problem could be that of becoming airborne in strong winds and storms, with then a very slow rate of descent, even in light winds. Dispersal by birds is often cited, but its importance is very difficult to assess; species which are frequently found upon birds' feathers have sticky mucus, for example *Vitrina pellucida* (see review by Rees 1965). Marine dispersal of molluscs by rafting can be considered for those species which are frequently found in littoral habitats, and are thus resistant to seawater. In the operculate taxa, the operculum isolates the snail from the surrounding medium, and it is possible to consider these and even the large thick shelled *Tropidophora aspera* as perhaps being dispersed by sea. In the case of the reptile fauna, seaborne dispersal is the only obvious mechanism.

The giant tortoise has had an almost continuous presence in the terrestrial deposits, and has obviously managed to colonize the Atoll on at least three occasions. In historical times the tortoise was present in vast numbers on other western Indian Ocean islands (Rothschild 1915), but was extinct everywhere except on Aldabra by about 1830 (Stoddart & Peake 1979, this

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volume). Recolonization from higher islands such as the Seychelles, Comores, or northern Madagascar would have been feasible, but ocean current considerations suggest that Madagascar would have been the most likely origin (see Arnold 1979, this volume). Tortoises are extremely buoyant, and on Aldabra today they frequently make excursions on to the shore to feed upon intertidal debris. It is not unusual at high spring tides in mangrove areas to see tortoises floating around. Grubb (1971) has pointed out that the distribution of tortoises of the *Geochelone* group on isolated islands in the Indian Ocean, Galápagos, Celebes and West Indies clearly indicates that they are able to survive trans-oceanic crossings better than any other large tetrapod. The remains of *Crocodylus niloticus* present in the Picard and Point Hodoul deposits represent two successful colonizations of Aldabra. Crocodiles were probably eliminated either by the higher sea level stand which cut the +8 m terrace, or by the restriction of habitat consequent upon the depressed sea level of the last glacial maximum. Crocodiles are present today on the East African coast and in Madagascar, and were once found upon both the Comores and the Seychelles. They became extinct in the Seychelles only at the end of the eighteenth century and, according to Lionnet (1970), early visitors to the islands found them abundant, some occurring far out to sea. Marine transport of crocodiles is well known. Wood-Jones (1909) for example, records two *Crocodylus porosus* which had made a trans-oceanic journey of 965 km (600 miles).

The iguana *Oplurus* was present during deposition of the Picard Calcarenites and the Point Hodoul terrestrial sediments and had obviously made more than one colonization. However, apart from this species, we have no record of lizards other than those in the extensive Point Hodoul fauna. Here, at least six species of lizard of Comoran or Madagascan affinities had managed to colonize the Atoll after the high sea level stand of the Aldabra Limestone. The pipe-fill deposits in which they are contained are truncated, possibly by the +8 m but certainly by the +4 m terraces, and these high sea level stands were probably responsible for the extinction of the lizards. None of the six species named is present on the Atoll today. By contrast, Williams (1969), considers that the four species of *Anolis* lizards found now on the small island north of Bimini (Bahamas) represent a residual concentration from their former extent over the now submerged Great Bahamas Bank during the last glaciation. As has been mentioned before, tortoises and crocodiles can make trans-oceanic voyages by virtue of their natural buoyancy. Lizards, on the other hand, although they appear able to disperse relatively easily, obviously require some form of rafting. Successful colonization of oceanic islands by lizards must necessarily be rare events (Williams 1969).

At present, large rafts of floating vegetation, consisting mainly of bamboo, are fairly frequent arrivals at Aldabra. Their provenance is unknown, but northern Madagascar could be considered a likely source. The distance from northern Madagascar to Aldabra is approximately 420 km and, with surface currents running in a fairly constant northwesterly direction at 0.5–1.0 m/s, the journey time to Aldabra could be as short as 3–9 days. Although no vertebrates have yet been found on such rafts, the number examined before or upon arrival is small.

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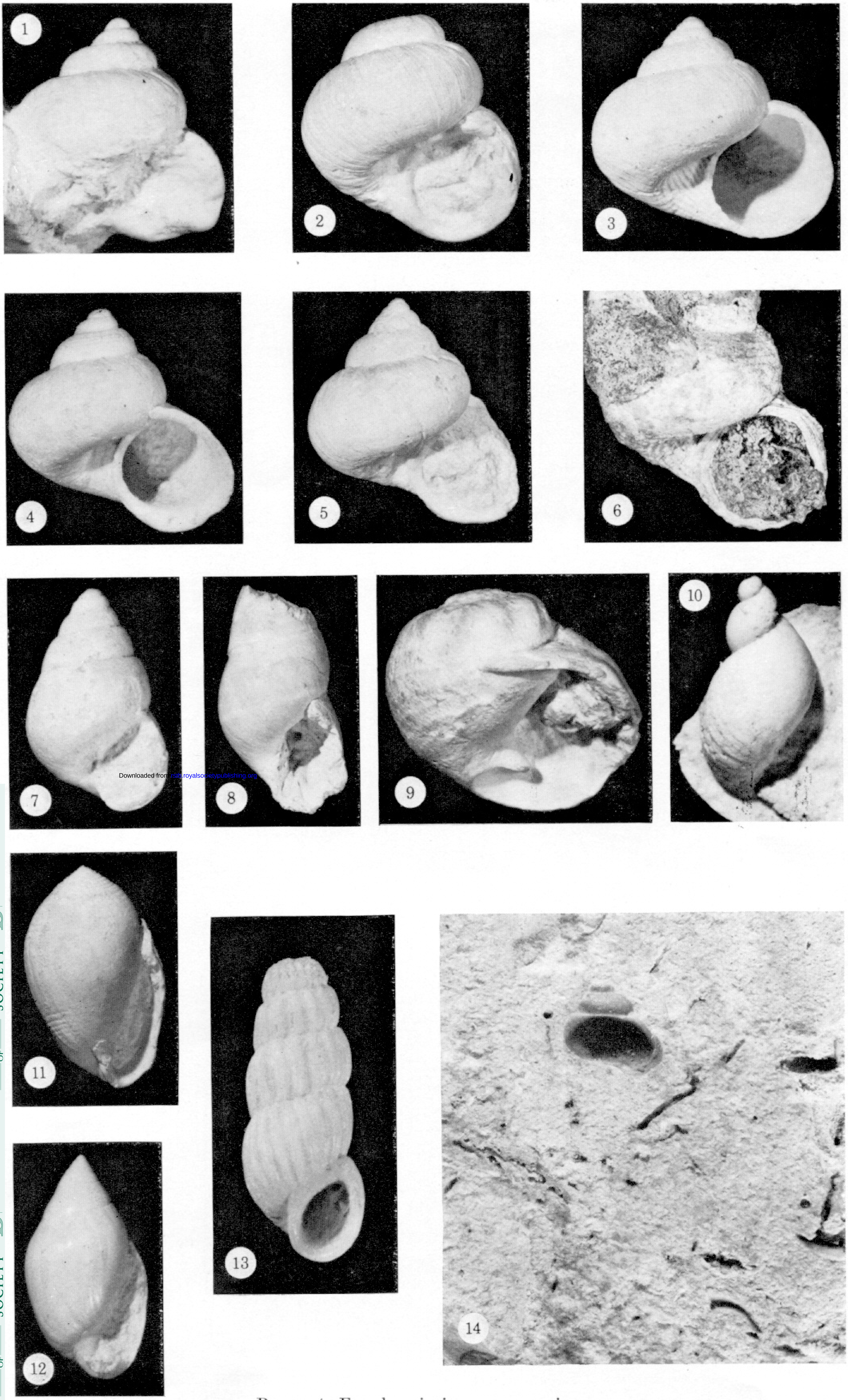

PLATE 1. For description see opposite.