FAUNAL RESPONSE TO THE INSTABILITY OF REEF HABITATS: PLEISTOCENE MOLLUSCAN ASSEMBLAGES OF ALDABRA ATOLL

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ABSTRACT. Coral ecosystems are considered by many biologists to have been stable over ecological and evolutionary time, yet the Pleistocene history of reefs reveals complex and large-scale habitat changes associated with glacio-eustatic rise and fall of sea-level. Study of the molluscan assemblages from three Pleistocene rock units, together with faunas from Recent habitats on Aldabra Atoll, shows that shallow-water habitats and the associated communities have changed considerably during the period of the late Pleistocene. The communities inhabiting the shallow water of Aldabra today are very different from those of 125 000 years ago, and the latter are in turn different from those of two older Limestones.

Habitat and faunal changes of a similar magnitude are known or can be predicted for many other reefs in the Indo-Pacific province, and it is clear that present-day habitats have been formed and occupied only during approximately the last 3000–5000 years. The high diversity of reef faunas seems to be associated with the long-term survival and stability of the species pool of the Indo-Pacific province and not with the stability of individual reef systems.

CORAL reefs are acknowledged to be amongst the most complex and diverse ecosystems on earth, and hypotheses concerning the high level of tropical diversity stress the stability and predictability of such environments (Pianka 1966; Fischer 1960; Sanders 1968; Pielou 1975). A pervasive view is that coral-reef faunas have evolved in environments that have been stable for considerable periods of time (Newell 1971). Although these ideas are intuitively satisfying there is little information on the relative stability of tropical environments. However, recent studies of the history of individual reef systems have revealed that reef growth does not proceed in an uninterrupted continuous sequence, but that periods of reef accumulation are punctuated by times of non-deposition and erosion (Braithwaite 1973; Mesolella *et al.* 1970; Montaggioni 1974; Purdy 1974; Stoddart 1973, 1976; Ladd *et al.* 1970; Tracey and Ladd 1974). The erosional events occurred during low sea-level stands of the late Pleistocene when reefs were emergent. Successive periods of reef accumulation may be very different in character, reflecting differences in environmental conditions (Braithwaite *et al.* 1973). Furthermore, palaeotemperature analysis of Foraminifera from deep-sea cores has shown that during the Wisconsin glaciation, considerable areas of the tropics which today support prolific reefs would have been too cold for active reef growth (Emiliani 1971; see map in Stoddart 1973).

Clearly, the environmental changes in the tropics induced by the Pleistocene glaciations were not as severe as those of higher latitudes. They nevertheless had profound effects upon the reef environment, although Newell (1971, p. 21) asserts that tropical habitats were scarcely altered during the glaciations. Even though the main outlines of reef history during the late Pleistocene are now beginning to be

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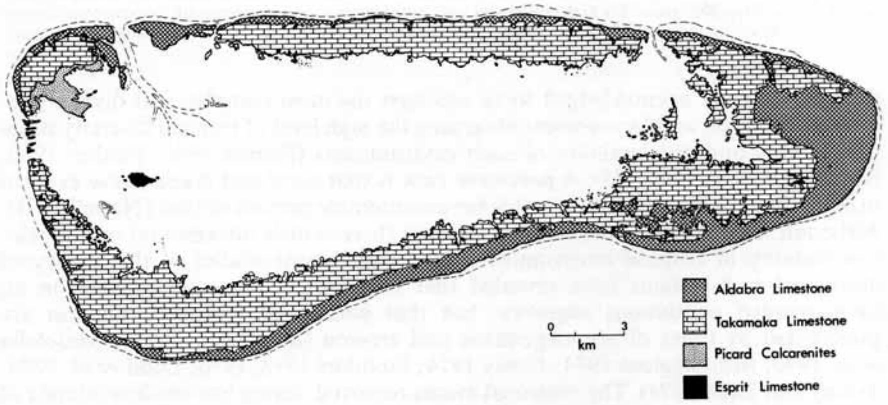
established (Stoddart 1973) we know very little about the faunal response to these environmental changes.

Recent geological studies at Aldabra Atoll in the Indian Ocean revealed a sequence of three late Pleistocene limestones containing abundant fossil molluscs (Braithwaite *et al.* 1973). This paper describes the molluscan assemblages from these three limestones, and, combined with a brief account of the Recent marine molluscan fauna, gives some insight into the evolution of reef faunas and the response of the molluscan faunas to the changing environmental conditions of the late Pleistocene.

GEOLOGICAL SETTING AND HISTORY OF THE ALDABRA ATOLL

The general structural and geomorphological background to Aldabra has been described by Stoddart *et al.* (1971); the atoll is one of a group of slightly elevated coral islands to the north of Madagascar; they are the subaerial tips of individual seamounts which rise 4000 m from the floor of the Somali Basin. The atoll consists of an annular rim surrounding a shallow lagoon (text-fig. 1); four main islands rise about 8 m above sea-level and vary from 0·25 to 5·0 km in width. The total area of the atoll is about 365 km² of which the land occupies 155 km².



TEXT-FIG. 1. Geological map of Aldabra Atoll showing the major marine deposits.

The surface geology (text-fig. 1), described by Braithwaite *et al.* (1973), shows a complex series of Pleistocene depositional and erosional events, consisting of alternating shallow-water marine limestones, with limited terrestrial calcarenites, soils, phosphorites, and cavity-fill deposits. The deposits occur in association with, or alternate with, erosional events which produced solutional dissection of the limestones, or marine planation. In the probable absence of tectonic activity, these events must be interpreted in terms of the independent variable which is the glacio-eustatic rise and fall of sea-level.

The stratigraphic relationships of the main deposits on Aldabra are outlined in text-fig. 2. There are three main marine deposits, namely the Esprit, Takamaka, and Aldabra Limestones; they are separated by erosional events, which in the main left no depositional record. Since the deposition of the Aldabra Limestone 125 000 years ago (Thompson and Walton 1972) there has been a progressive, but oscillating, lowering of sea-level to the glacial minimum about 17 000 years ago when sea-level probably stood at about 130 m below the present (Bloom *et al.* 1974; Chappell 1974*b*). Sea-level rose rapidly in post-glacial times and probably reached approximately its present position at about 3000–5000 years ago. We have no evidence of any extensive marine deposits post-dating the Aldabra Limestone. Present-day conditions at Aldabra may in this context be viewed as an erosional event, and information on the present-day fauna might be extrapolated back to interpret what communities may have been present during the long periods for which we have no depositional record.

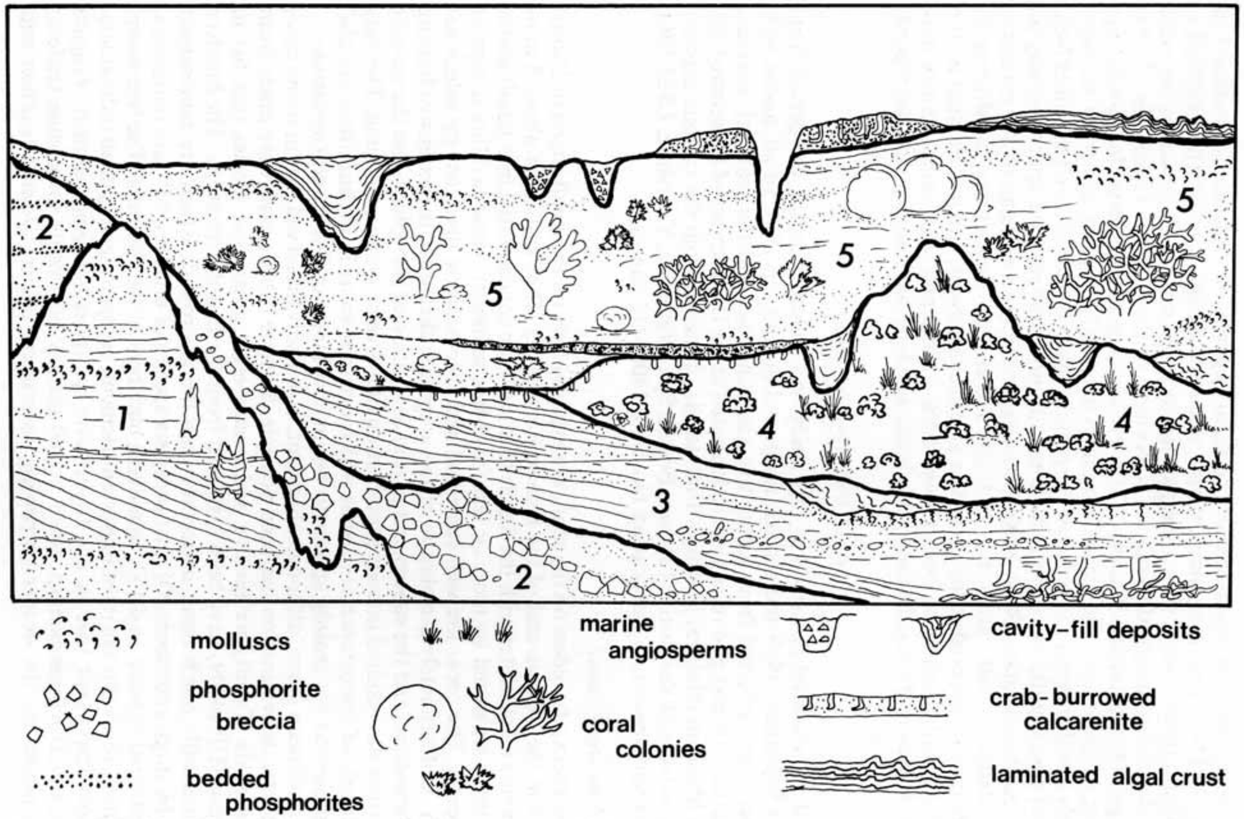
MOLLUSCAN FAUNAS

Most of the material described in this study was collected during the period from June to September 1969 and a small additional quantity in 1973. In all, about 8000 molluscs were collected from eighty-five sampling sites; all the material, together with station lists and grid references is deposited in the Department of Palaeontology, British Museum (Natural History). Full details of species from the various deposits are deposited with the British Library, Boston Spa, Wetherby, Yorkshire, LS23 7BQ, U.K. as Supplementary Publication No. SUP 14009 (12 pages).

Esprit Limestone fauna

These rocks, the oldest on the atoll, are exposed only on the small island of Esprit, situated at the western end of the lagoon (text-fig. 1). They consist of about 8 m of fine-grained calcarenites with the fossils tending to be concentrated into bands about 40 cm thick separated by more or less fossil-free sediment; cross bedding is seen at some levels. The rocks are well cemented and spectacularly dissected by solutional erosion. Unfortunately dissolution of the aragonite skeletons, the extensive fretting of the limestone, and the subsequent partial deposition of phosphate into the moulds and cavities has resulted in poor preservation of a diverse molluscan fauna. The only other fossils of importance are corals which occur at some levels and these are also badly preserved but mainly appear to be small colonies of *Favia* and *Goniastrea*.

The molluscan fauna, although abundant, is so badly preserved that in many cases only generic determination has been possible. Silicone rubber casts were made from many moulds. Twenty-six bivalve and twenty-eight gastropod species (see list in Appendix SUP 14009) have been extracted from the Esprit Limestone. The bivalves are numerically much more important than the gastropods which are represented mostly by single specimens. Of the twenty-six species of bivalves, 65% are burrowers, 20% epifaunal byssate, and 15% free-living members of the epifauna. The burrowers are numerically by far the most important element, comprising 88% of all individuals. The most important species are *Glycymeris* sp. (possibly *tenuicostatus*), *Fragum fragum*, and *Trachycardium* sp. which are all shallow-burrowing suspension feeders; also common are the deeper-burrowing suspension feeders *Dosinia* (*exilium* and



TEXT-FIG. 2. Stratigraphic model for the exposed Pleistocene rocks of Aldabra showing the general relationships of the rock units. 1, Esprit Limestone (marine). 2, Esprit Phosphorites (non-marine). 3, Picard Calcarenites (non-marine). 4, Takamaka Limestone (marine). 5, Aldabra Limestone (marine). The other discontinuous rock units shown, are minor, mainly non-marine deposits. Vertical scale about 9 m, horizontal scale 10 km.

nanus). Only four species of deposit feeders were found, *Tellinella* being the most abundant. The epifaunal species are all uncommon and their presence must have depended upon the availability of suitable attachment sites which, except for the occasional corals, were rare in these deposits. Some of the species found, *Hippopus hippopus* and *Chlamys* species, could live freely upon the sediment surface.

The gastropods are mostly uncommon, and of the twenty-eight species recorded, 71% are normally associated with soft substrates, either as burrowers or surface dwellers, 21% with hard substrates, and 7% parasitic or commensal. In terms of feeding categories 57% of species are algal or detritus feeders, 25% are active carnivores, 7% faunal grazers, and 11% other categories such as suspension feeders, scavengers, or parasites. Various species of *Cerithium*, *Strombus*, and *Terebellum terebellum* are the most common elements; other species are mainly represented by single records.

The assemblage of molluscs is predominantly a soft substrate fauna with only minor contribution from epifaunal hard-substrate species. The fauna inhabited a well-sorted sediment relatively free of organic detritus, but possibly with a surface algal mat and some larger algae, but apparently not *Halimeda* (frequently common in this type of habitat). Several indicator species suggest that for much of the rock sequence the water depth at the time of deposition was probably about 5–20 m; but higher in the rock sequence the presence of abundant *Cerithidea*, a gastropod found living today on the trunks of mangroves, and also the mangrove-associated species *Terebralia palustris* and *Cerithium morum*, indicate a shallowing of the water to intertidal conditions.

The fauna can thus be interpreted as inhabiting a quiet lagoon from 5 to 20 m deep, which in time shallowed, perhaps as a result of sedimentation or falling sea-level and was colonized by mangroves. It must be emphasized that the exposed rocks represent only a tiny fraction of the total area of the atoll, and evidence of the general environmental framework is lacking.

The Takamaka Limestone

This rock unit, characterized by an abundance of calcareous red algae, is about 3 m in thickness and is exposed over wide areas of the atoll (text-fig. 1). There is little facies variation over the entire extent of the atoll, and the rock consists basically of abundant calcareous red algae, the most common genera being *Lithophyllum*, *Mesophyllum*, and *Lithothamnion*.

These occur as profuse papillate heads, foliose masses, and encrusting sheets, which in some places form constructional frameworks. Corals are locally fairly common but only a few species occur of the genera *Tubipora*, *Favia*, *Platygyra*, *Seriatopora*, *Acropora*, *Goniastrea*, *Porites*, and *Millepora*. The rock matrix is usually a white sediment which varies in grain size from a calcareous mud to calcarenite; moulds of *Halimeda* segments and *Seriatopora* branches are abundant in the muds. Facies variations which do occur involve changes in the abundance of the calcareous algae and corals and in the grain size of the matrix. The main area of facies variation is at the eastern end of the present lagoon where the lithothamnoid algae are less common; the matrix varies between a calcilutite and calcarenite and contains mainly branching corals, particularly *Porites nigrescens*.

The Takamaka Limestone is severely dissected by solutional erosion, and the textural relations of the rocks are frequently obscured. There has been a complex post-depositional diagenetic history involving the several phases of solutional erosion and not surprisingly the fossils are generally badly preserved. The corals are usually completely recrystallized, and amongst the molluscs the aragonitic species have been completely dissolved away, leaving moulds. Silicone rubber casts were made from these moulds.

Molluscan fauna. Molluscan diversity and abundance in this deposit is usually rather low. Collections were made at twenty-three sites, but at many localities no mollusca were found. At the western end of the atoll, molluscs are generally rare or uncommon but in the east the fauna is rather more diverse and numerous. The higher diversity in the east may be associated with the facies changes mentioned above.

Twenty-four species of bivalves were found; 58% are epifaunal, either byssate, cemented or free living; 42% are burrowers and well over half of these are suspension feeders. Most of the burrowing species, including *Ctena fibula*, *Pinguitellina robusta*, *Scissulina dispar*, and *Dosinia* occur at one or two sites at the eastern end of the present lagoon where calcarenites are more extensive. The more usual situation over most of the rest of the Takamaka Limestone exposure is the presence of one or two byssate nestling species such as *Cardita variegata* or *Barbatia* or the large *Tridacna maxima* and *T. gigas*.

Gastropods are numerically much more important and thirty-two species have been found of which 65% are epifaunal species normally associated with hard substrates, 18% live epifaunally upon soft substrates, and a further 17% are probably burrowers. In terms of feeding categories, 46% are algal feeders, 31% predators, 15% faunal grazers, and 6% scavengers. Most of the species are uncommon, and the characteristic feature of the fauna is the numerical dominance of Archaeogastropoda which comprise 66% of individuals with *Trochus maculatus*, *T. radiatus*, *Tectus mauritianus*, *Clanculus* cf. *limbatus*, *Phasianella*, *Acmaea*, and *Haliotis varia* particularly common. The only other common gastropods are *Cypraea helvola* and several species of *Cerithium*.

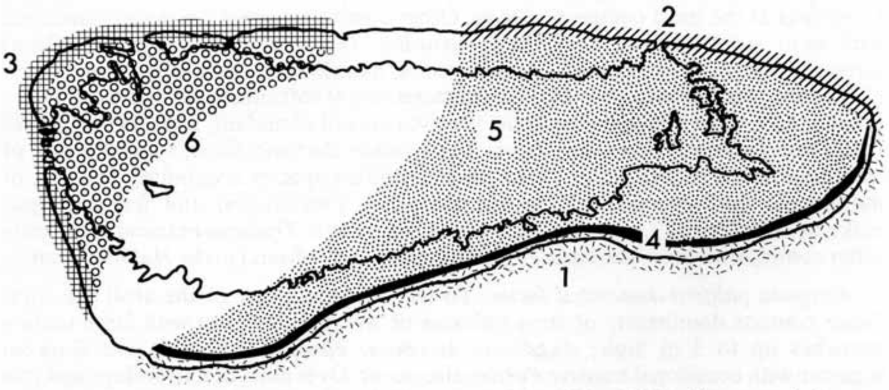
The environmental conditions represented by the Takamaka Limestone are not easily interpreted. On the one hand the abundance of calcareous red algae usually indicates well-circulated, shallow, water; whilst, on the other hand, the abundance of fine-grained sediment indicates a quiet depositional environment. The widespread occurrence of the facies and the low diversity of the fauna are problematic. Braithwaite *et al.* (1973) have interpreted the Takamaka Limestone as representing an environment of meadows of the marine angiosperm *Thalassodendron ciliatum* which frequently colonizes hard substrate areas; calcareous red algae and *Halimeda* are abundant beneath the leaf canopy and fine sediment accumulates in the interstices. Both molluscan and coral diversity are usually fairly low in these habitats. Large stands of *Thalassodendron* growth exist on various shallow banks of the western Indian Ocean and on parts of the east African mainland.

Some of the molluscs from the Takamaka Limestone support this interpretation; for example, *Phasianella*, one of the most abundant gastropods, is today often found living on the leaves of *Thalassodendron*, and other Trochacea are frequently observed around the stem bases and among the underlying calcareous algae. Davies (1970) has described comparable *Posidonia*/calcareous algae communities from Shark Bay, West Australia, in which trochid gastropods, *Phasianella*, *Cerithium*, and a few byssate bivalves such as *Cardita* are common.

The Aldabra Limestone

This extensively exposed limestone (text-fig. 1) is much the best preserved of the marine depositional events; it was formed about 125 000 years ago and consists basically of a 6–8 m thick calcarenite containing abundant corals and molluscs. Limestones of similar age representing a sea-level of up to 10 m above the present, have been recorded from widely separated parts of the tropics (Bloom *et al.* 1974; Chappell 1974*a*).

Braithwaite *et al.* (1973) have shown that the Aldabra Limestone was deposited in shallow water, probably not more than 10 m deep, covering a broad annular platform formed from the erosion of the underlying Takamaka Limestone. The sediment complex which built up on this platform consisted of coral pinnacles and knolls concentrated around the atoll rim and rising from a generally sandy floor. For probably most of the depositional period, there was no land present, and Aldabra consisted of a submerged, shallow, coral-covered bank. Early in the deposition of the limestone a prominent bedding plane and a thin deposit may mark a temporary emergence.



TEXT-FIG. 3. Reconstruction of the distribution of the main facies of the Aldabra Limestone. 1, *Acropora humilis* facies. 2, *Acropora palifera* facies. 3, Faviid-dominated facies. 4, *Goniastrea* facies. 5, *Halimeda* sands facies. 6, *Porites*-coral-knoll facies.

Several distinct biofacies have been recognized on the basis of coral associations and sediments (text-fig. 3) which represent changes in hydrodynamic conditions around and across the atoll. An estimated maximum of about 400 m of Aldabra Limestone has been removed by erosion from around the atoll rim. An abundant and diverse molluscan fauna comprising over 300 species has been recovered from the Aldabra Limestone; the preservation varies from excellent to poor depending upon the local diagenetic history.

The major biofacies recognized by Braithwaite *et al.* (1973) have been used as a framework for the description of the molluscan assemblages, and collection samples have been grouped according to their location within the facies boundaries (full details of species, abundance, and facies deposited in British Library SUP 14009). The relative abundance of the major taxa (text-figs. 3, 4) were obtained by combining all the data from collection sites within each facies. Except for single records, the number of bivalve shells found were halved.

1. *Acropora humilis-dominated facies*. Along 20 km of the southerly and easterly shores of the atoll, the main facies of the Aldabra Limestone consists of a *Halimeda*-rich calcarenite separating patches of more or less abundant coral. The corals are dominantly species of *Acropora*, particularly corymbose *A. humilis* and spray-like branched forms, although the stagshorn form *A. formosa* and *A. palifera* are common. Other corals present include *Pocillopora eydouxi*, *Goniastrea*, *Favia*, *Fungia*, *Galaxea*, *Hydnophora*, *Goniopora*, and sometimes massive *Porites* towards the base of the limestone. Areas of solid constructional frame growth are uncommon, and in some places the corals are tumbled.

Compared with other sites the molluscan fauna is very sparse. The dominant gastropod is the large thick-shelled *Turbo argyrostomus*, which with the other trochaeans *Tectus mauritianus* and *Trochus maculatus*, comprise 55% of the fauna. The Cypraeidae form 16% of the fauna with *Cypraea helvola*, *C. cicercula*, and *C. nucleus* as the most common species. Other common species normally associated with hard substrates are *Columbella turturina*, *Drupella cornus*, *Magilus*, *Conus sponsalis*, and *Neritopsis radula*. A few species, namely *Cerithium echinatum*, *Rhinoclavis asper*, and *Polynices tumida*, are characteristic of soft substrates and would have inhabited the sand between the corals. Bivalves are not abundant, and a rather sparse fauna was extracted from this facies. The byssate *Barbatia fusca*, typical today of *Acropora*-dominated habitats, is the most abundant species accounting for 33% of individuals; the burrowing tellinaceans, *Scissulina*, *Pinguitellina*, and *Scutarcopagia*, make up a further 24% of individuals whilst the byssate *Tridacna maxima* is the only other common bivalve. The large *T. gigas* is occasionally found in the *Halimeda* sands.

2. *Acropora palifera-dominated facies*. To the north and east of the atoll the coral fauna consists dominantly of large colonies of *Acropora palifera* with large clubby branches up to 3 m high; stagshorn *Acropora*, *Favia*, *Goniastrea*, and *Galaxea* together with occasional massive *Porites* also occur. Over most of its development this facies consists of scattered coral colonies in a *Halimeda*-rich calcarenite to calcirudite matrix, and only high in the rock sequence is there any development of constructional frames.

The molluscan fauna is similar but rather more diverse than facies 1, *Turbo argyrostomus* again being the most abundant gastropod with the other trochaceans *Tectus mauritianus* and *Trochus maculatus* also fairly common and together comprising about 56% of the fauna. Cypraeidae are abundant and diverse, and eighteen species account for a further 11% of gastropod numbers. The Conidae (11%), Cerithiacea, mainly *Cerithium echinatum* (7%), and *Strombus* (3%) are the other abundant taxa. Bivalves are uncommon, and again the most abundant species is *Barbatia fusca* (60% of individuals) with *Tridacna maxima* (18%) and a variety of other byssate or cemented bivalves such as *Trapezium*, *Spondylus*, *Chama*, and *Plicatula* making up the rest of the fauna.

3. *Faviid coral-dominated facies*. This biofacies, found around the western and north-western parts of the atoll, consists of pinnacles of often prolific coral growth which are separated by areas of coarse calcarenite made up largely of coral, algal, and molluscan debris. The coral fauna consists dominantly of genera with rounded to massive growth forms such as *Favia*, *Platygyra*, *Leptoria*, *Symphyllia*, or *Porites*. However, branching forms such as *Pocillopora*, *Acropora palifera*, *A. humilis*, *A. formosa*, and *Millepora* are present and sometimes abundant. At some sites there are growths of rigid-frame structures with the faunal composition suggesting shallow-water, high-energy conditions.

This is the richest and most diverse of the atoll-edge facies, containing about twice as many species as facies 1 at the south-eastern end. The molluscan fauna is again overwhelmingly dominated by archaeogastropods of the superfamily Trochacea and in particular by *Turbo argyrostomus*, *Trochus*, and *Clanculus* which make up 70% of gastropods found. The Cypraeacea are represented by fifteen species which make up 10% of the fauna with *Cypraea helvola*, *C. cicercula*, *C. nucleus*, and *C. staphylaea* the most common. The two related families of Muricidae and Coralliophilidae are represented by six species of which *Drupella cornus*, *Coralliophila violacea*, and *Magilus*, which feed upon or are associated closely with living coral (Robertson 1970) are abundant. *Columbella turturina* (Columbellidae 4%) and *Peristernia nassatula* (Fasciolaridae 2%) are other common species normally associated with hard substrates. Some forms, such as *Cerithium echiatum*, *Olivella*, *Harpa*, and *Terebra*, are typical of soft substrates and would have lived in the sediment pockets between the coral knolls.

The bivalve fauna is again dominated by *Barbatia fusca* (Arcacea 41%); other byssate forms include *Chlamys cuneolus* (Pectinacea 6%), *Trapezium* (Arcticacea 7%), and *Tridacna*. Burrowing bivalves present are mainly the opportunistic tellinacean *Scutarcopagia scobinata* which can inhabit small and ephemeral sand pockets between corals.

4. *Goniastrea-dominated facies*. Immediately inside the *Acropora*-dominated outer facies along the south and east sides of the atoll there is a belt about 150 m wide where rounded colonies of *Goniastrea* up to about 1 m in diameter are the dominant coral; other corals are subordinate but include species of *Acropora*, *Millepora*, *Hydnophora*, *Favia*, and *Platygyra*. The sediment between the corals is a *Halimeda*-rich calcarenite. Only a small mollusc fauna has been obtained from this the least diverse of any of the facies; this low abundance is a real feature rather than collection failure. *Turbo argyrostomus* is again the dominant mollusc, comprising about 35% of individuals collected, with several species of *Cypraea*, particularly *C. helvola; Rhinoclavis asper*, *Cerithium echinatum*, *Columbella turturina*, and *Drupella cornus* are the only other common gastropods.

Bivalves are very sparse, the most abundant forms being species of *Chama* (40% of the fauna) with Arcacea, Veneracea, Lucinacea, and Tridacnacea comprising about 10% each of the rest of the sample.

5. *Halimeda sands facies.* A broad area of the south-eastern corner of the atoll consists of fairly open *Halimeda*-rich calcarenites with more or less isolated coral colonies, of a limited number of species, and small, more diverse, coral patches. The main corals present are *Goniastrea*, *Acropora palifera*, *A. formosa*, massive *Porites*, *Goniopora*, and *Millepora*. Other forms such as corymbose *Acropora*, *Hydnophora*, and faviids occur in the small patches.

The dominant element in the gastropod fauna is the Cerithiacea, comprising 36% of individuals; the most abundant species are the sand-living *Rhinoclavis asper* and *Cerithium echinatum*, although seven other species are present. Other gastropods characteristic of soft substrates include *Strombus gibberulus* (7%), *Polynices tumida*, and species of *Nassarius*, *Conus*, and *Terebra*. Gastropods normally associated with hard substrates and probably inhabiting the coral patches include the Cypraeidae, with sixteen species forming 15% of the fauna, the Muricidae, particularly *Drupella cornus*, and *Columbella turturina* of the Columbellidae (9%).

The most abundant bivalves are species of *Tridacna* with *T. crocea* found in excavations eroded into the underlying Takamaka Limestone, and with large *T. gigas* free-living in the *Halimeda* calcarenites and *T. maxima* associated with the coral patches. Most of the other bivalves are burrowing species from the sands and include *Codakia punctata*, *Ctena*, *Jactellina clathrata*, *Scissulina dispar*, *Scutarcopagia scobinata*, and *Timoclea*. Small remanié deposits of Aldabra Limestone on small islets in the south central lagoon have yielded a slightly different fauna and are shown separately in text-fig. 4. Coral colonies of *Acropora*, *Pocillopora*, *Seriatopora*, *Favia*, and *Goniastrea* are separated by a *Halimeda*-rich calcarenite. *Polynices tumidus* is the dominant gastropod (Naticidae 23%), with *Cerithium echinatum* (Cerithiacea 16%), *Strombus gibberulus*, *Trochus maculatus*, *Cypraea helvola*, and *Conus* species also common. The most abundant bivalve is *Fragum fragum* (Cardiacea 30%), and *Chama* species (23%) with *Timoclea marica* (Veneracea 6%), *Ctena*, *Scissulina dispar*, and *Tridacna maxima* also common.

6. *Porites coral-knoll facies.* Occupying a wide area of the north-west quadrant of the atoll there is a facies consisting of coral knolls separated by patches of sand and coral debris. The knolls vary in coral composition; many in the northern part consist basically of *Porites* colonies, but many other corals may occur, particularly branching *P. nigrescens*, large *Acropora palifera*, corymbose *Acropora*, *Favia*, *Platygyra*, and *Galaxea*; *Seriatopora* and *Fungia* are common in the sands around the knolls. One patch at Polymnie consists of broad, flat, cone-shaped colonies of *A. hyacinthus*. The intervening areas between the knolls is uniform sands or coarse rubble and debris; *Halimeda* segments are usually subordinate in these sediments, which at some sites are made up almost entirely of shell debris.

This is by far the most diverse facies in terms of species diversity and numerical abundance of molluscs, and 137 gastropod and 60 bivalve species have been recovered from a sample of 2586 molluscs. The dominant gastropod families represented are the Cerithidae and the Cypraeidae, comprising 25% and 21% of individuals respectively. The ten cerithiid species are all characteristic of soft substrates with *Rhinoclavis asper* and *Cerithium echinatum* the dominant forms. A few other soft substrate gastropods are common, including *Strombus gibberulus*, *Polynices tumidus*, nine species of

Terebra, and seven of *Nassarius*. The Cypraeidae are the most diverse family with twenty-one species recorded from this facies, all of them characteristic of hard substrates; *Cypraea fimbriata*, *C. helvola*, *C. scurra*, *C. isabella*, and *C. caurica* are the most abundant species. Other important gastropods which prefer hard substrate habitats are *Tectus mauritianus*, *Columbella turturina*, *Peristernia nassatula*, *Cantharus undosus*, and the coral-feeding *Drupella cornus* and *Coralliophila violacea*.

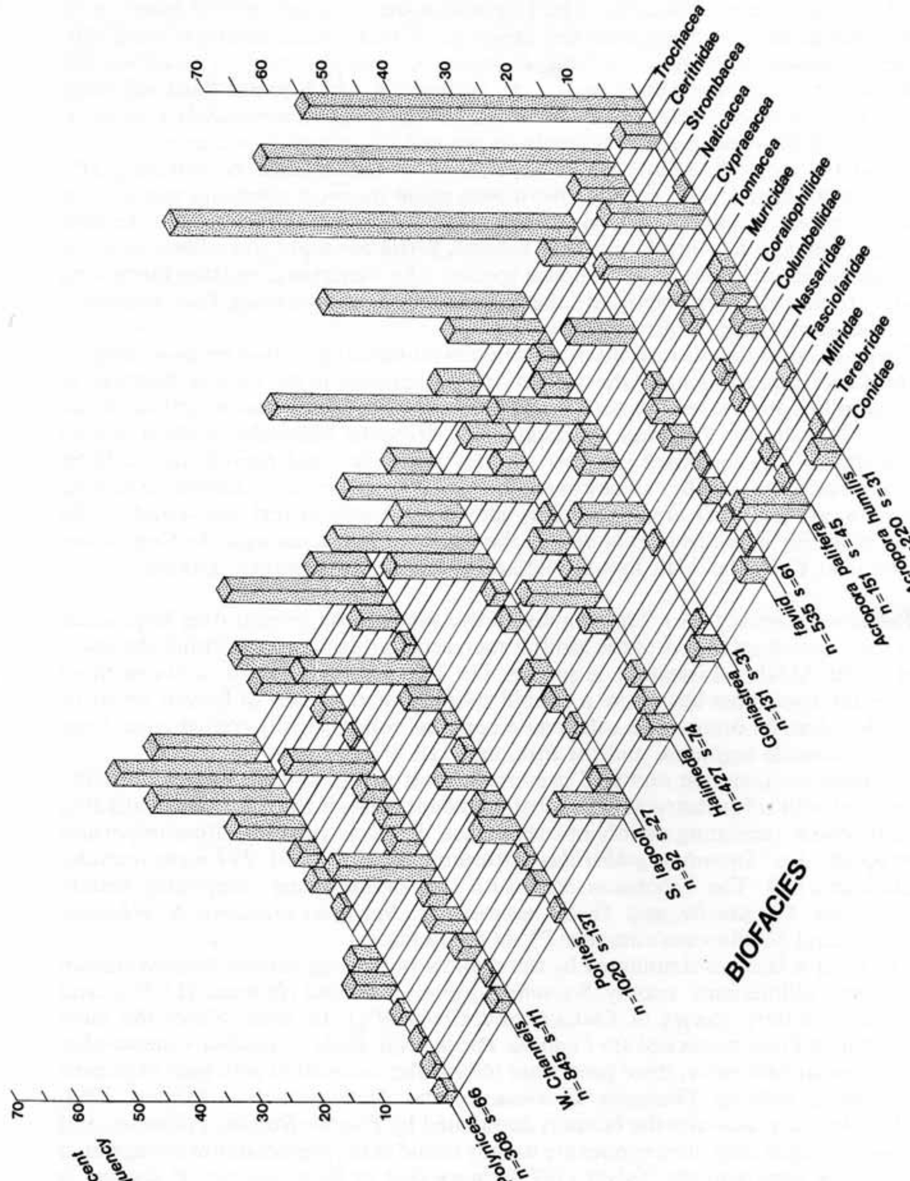
By far the most abundant bivalve superfamily is the Arcacea, constituting 34% of individuals found, with *Barbatia fusca* once again the most abundant species, but *B. helblingi* and *B. tenella* are also common. The burrowing Tellinacea are the next most abundant group with *Pinguitellina robusta*, *Scissulina dispar*, *Jactellina clathrata*, and *Semele jukesi* as the most common species. The Veneracea, another burrowing group, are the next most important, the most abundant species being *Pitar obliquata*, *Timoclea marica*, and *Amiantis grata*.

There is a considerable amount of variation in faunal composition between samples in this facies depending upon the amount of coral present in the habitat. Samples in the Camp Frigate–Passe Gionnet area contained a high proportion of soft substrate species. The site on Polymnie dominated by *Acropora hyacinthus* yielded a high abundance of the cemented bivalves *Chama*, *Spondylus*, and *Ostrea*. In the West Channels area the Aldabra Limestone is extremely fossiliferous; a very large sample was obtained from this area and this is shown separately in text-figs. 4 and 5; the fauna is similar in general to the rest of the *Porites*-knoll facies with the Cerithidae, Cypraeidae, Columbellidae, and Fasciolaridae among the dominant groups.

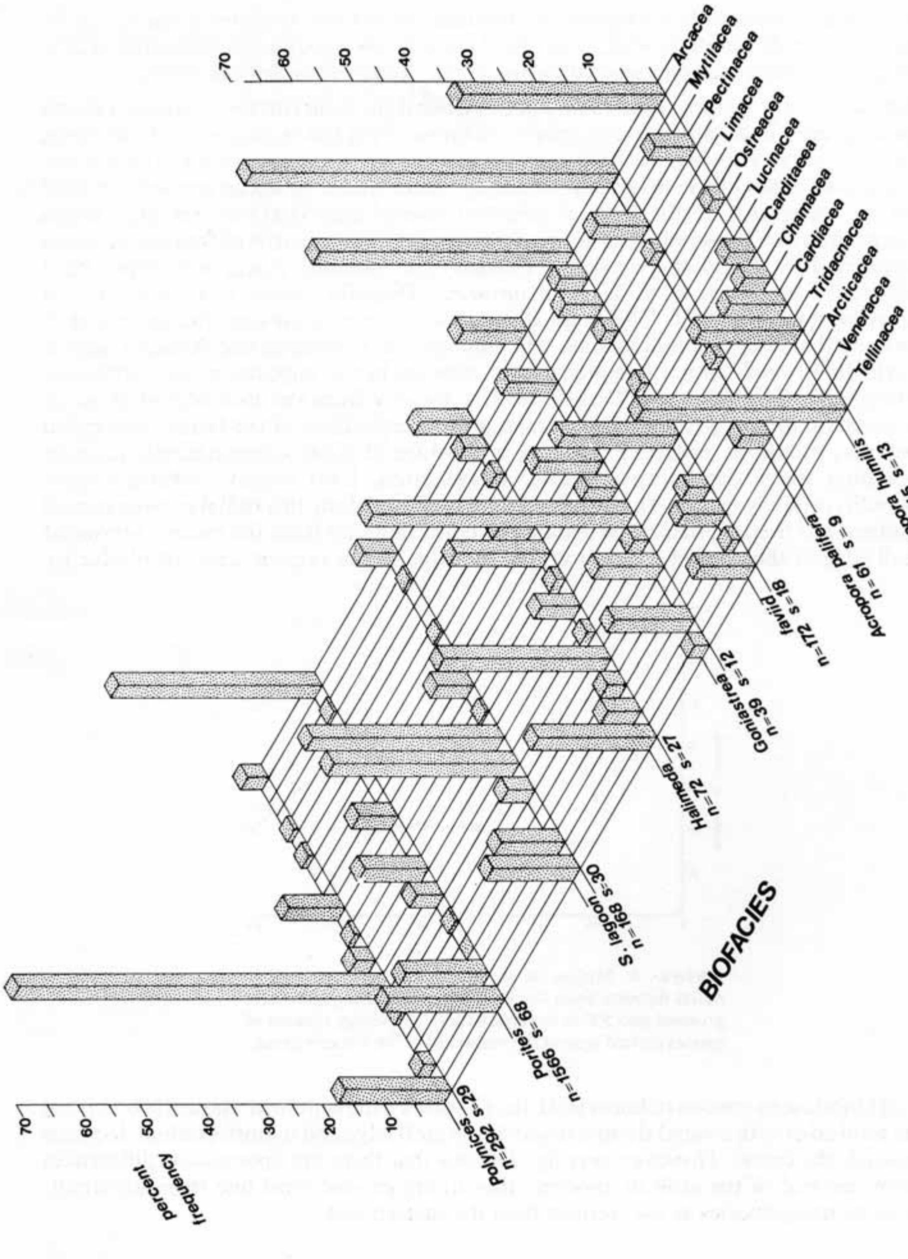
7. *Polynices-Fragum facies*. This is a distinctive thin deposit present over large areas of the south-eastern corner of the atoll; it represents a distinct phase within the lower part of the Aldabra Limestone sequence. The 10–15 cm thick hard, well-cemented calcarenite sometimes lies above a clionid sponge-bored surface of fibrous crusts of possible subaerial origin. The calcarenite contains rolled, algally coated coral fragments, *Halimeda* segments, and the foraminiferan *Marginopora*.

Molluscs are common and well preserved, most of them being species normally associated with soft substrates. The most abundant taxon is the Cerithidae with 26% of individuals, consisting mainly of one species, *Rhinoclavis asper*. Other important gastropods are *Strombus gibberulus* (Strombidae 21%) and *Polynices tumidus* (Naticidae 11%). The Trochacea constitute 17% of the fauna comprising mainly *Cantharidus*, *Phasianella*, and *Tectus mauritianus*. *Nassarius arcularis*, *N. echinata*, *N. pullus*, and *N. albescens* comprise 7% of the fauna.

The bivalve fauna is dominated by the shallow-burrowing cardiid *Fragum fragum* (60%) with tellinaceans, mainly *Scissulina dispar*, *Jactellina clathrata* (17·5%), and Lucinidae, mainly species of *Codakia* and *Ctena* (9%). In some places the most abundant molluscs in this bed are *Codakia*, *Phasianella*, *Bulla*, *Scissulina*, *Cantharidus*, and *Strombus gibberulus*; these genera are today often associated with beds of marine angiosperms such as *Thalassia*, *Cymodacea*, and *Thalassodendron* (Taylor 1968, 1971*a*). At other localities the fauna is dominated by *Fragum fragum*, *Polynices*, and *Rhinoclavis asper*, and these species are usually found at the present day in unvegetated but shallow sand patches. Salvat (1972) shows that in Réao lagoon, *F. fragum* is found only in water less than about 2·5 m deep. The environmental interpretation of



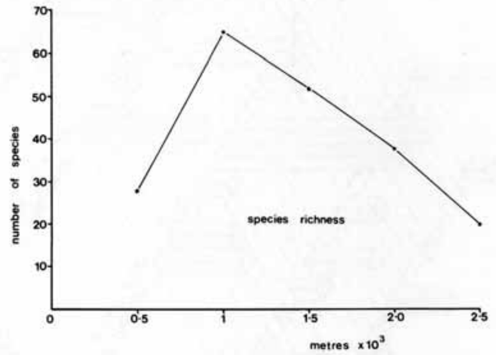
TEXT-FIG. 4. Relative abundance of the major gastropod families and superfamilies in the various facies of the Aldabra Limestone. n = sample size; s = number of species.



TEXT-FIG. 5. Relative abundance of bivalve superfamilies in the various facies of the Aldabra Limestone. n = sample size; s = number of species.

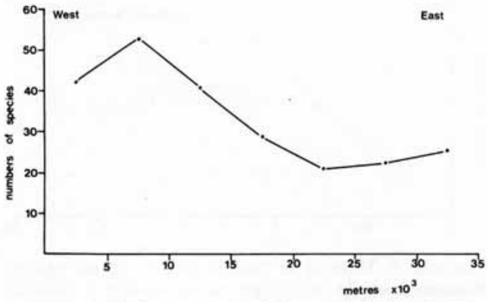
the Aldabra fauna is that it represents intertidal, or shallow sublittoral, marine grass and open sandy habitats, which may have been the first sediments deposited after a temporary emergence represented by the fibrous crusts (Braithwaite 1975).

Summary of the Aldabra Limestone fauna. Around the atoll rim the molluscan fauna varies greatly in abundance and species richness, from the richest area of the *Favia* facies of the north-west to the species-poor areas of the *Acropora* and *Goniastrea*-dominated facies of the south-east. Although three major biofacies around the atoll rim are recognized on the basis of sedimentological and coral features, the species composition of the molluscan fauna is essentially similar around the atoll, being dominated by *Turbo argyrostomus*, *Trochus*, and *Barbatia fusca*, with other hard substrate forms such as *Columbella turturina*, *Drupella cornus*, *Coralliophila*, and *Cypraea* spp. abundant. The main distinctions of the molluscan faunas are seen between the outer and inner facies. The numbers of Trochacea and Arcacea decline markedly inwards with a complementary increase in the importance of Cerithidae, Strombidae, Tellinidae, and Veneridae. The distance from the atoll edge thus seems to be an important parameter determining the composition of the fauna; this radial distance, of course, reflects a complex interaction of many environmental changes including water depth, wave action, oxygenation, food supply, substrate type, turbidity, and insolation. The distribution of molluscs along this radial environmental gradient has been plotted as the distance of collecting sites from the nearest presumed atoll edge at the time of deposition (i.e. the edge of the present seaward platform).



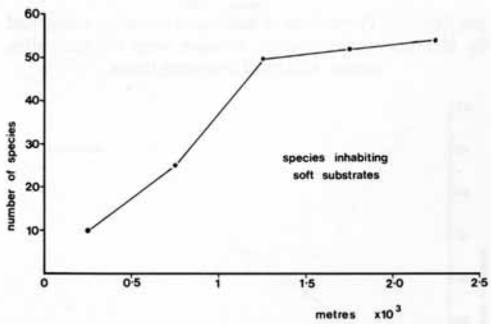
TEXT-FIG. 6. Molluscan species richness plotted against radial distance from the atoll edge. Collecting sites were grouped into 500-m increments and the average number of species plotted against the mid-point of the distance group.

Total molluscan species richness (text-fig. 6) shows a maximum at about 1000 m from the atoll edge with a rapid decline towards the atoll edge and a more gradual decrease towards the centre. However, text-fig. 7 shows that there are appreciable differences from one end of the atoll to another; thus along an east–west line there are about twice as many species at the western than the eastern end.



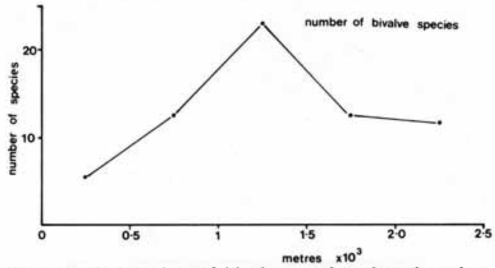
TEXT-FIG. 7. Molluscan species richness plotted against the distance along the west-east axis of the atoll during Aldabra Limestone times.

Text-fig. 8 shows the percentage of numbers of species which normally live on soft substrates; there is a rapid increase from 10 to 50% up to about 1200 m from the edge, the numbers thereafter remaining fairly constant towards the centre of the atoll. In common with the total species richness the greatest number of bivalve species (text-fig. 9) is found 1250 m from the atoll edge, whereas over most of the rest of the distance numbers remain at less than 15% of the total fauna. However, the numerical proportion of bivalve individuals in samples (text-fig. 10) increases from about 25–50% in the distance from the outside to the inside of the atoll.

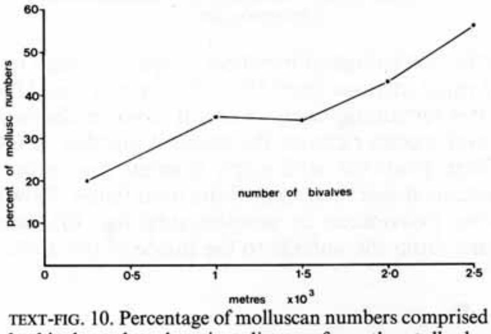


TEXT-FIG. 8. Number of mollusc species normally inhabiting soft substrates plotted against radial distance from the atoll edge during Aldabra Limestone times.

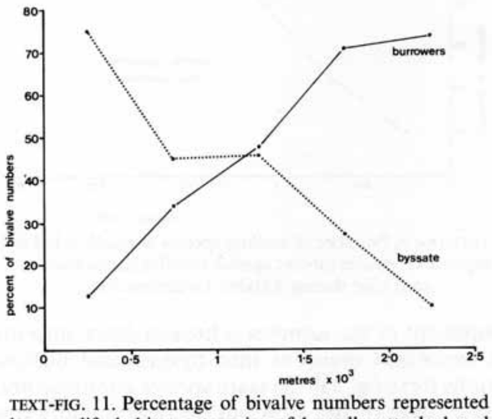
If the bivalve component of the samples is broken down into life-habit categories, then the two most important divisions into byssate and burrowing species show interesting distributions (text-fig. 11). Byssate species comprise about 75% of bivalve individuals at the outer edge of the atoll but decrease rapidly towards the interior. In contrast, burrowing species are poorly represented at the edge but rise to about 75% in the interior.



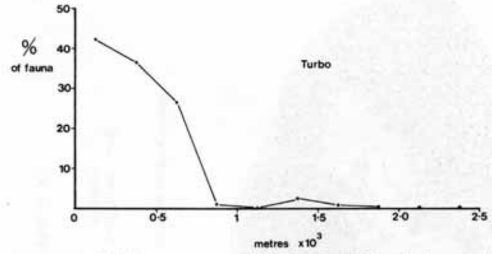
TEXT-FIG. 9. Number of bivalve species plotted against distance from the atoll edge during Aldabra Limestone times.



TEXT-FIG. 10. Percentage of molluscan numbers comprised by bivalves plotted against distance from the atoll edge during Aldabra Limestone times.

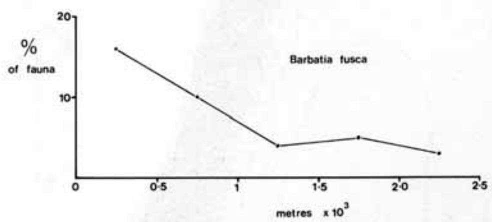


TEXT-FIG. 11. Percentage of bivalve numbers represented by two life habitat categories of byssally attached and burrowing, plotted against radial distance from the atoll edge during Aldabra Limestone times.



TEXT-FIG. 12. Percentage of *Turbo* individuals in total mollusc fauna plotted against distance from the atoll edge during Aldabra Limestone times.

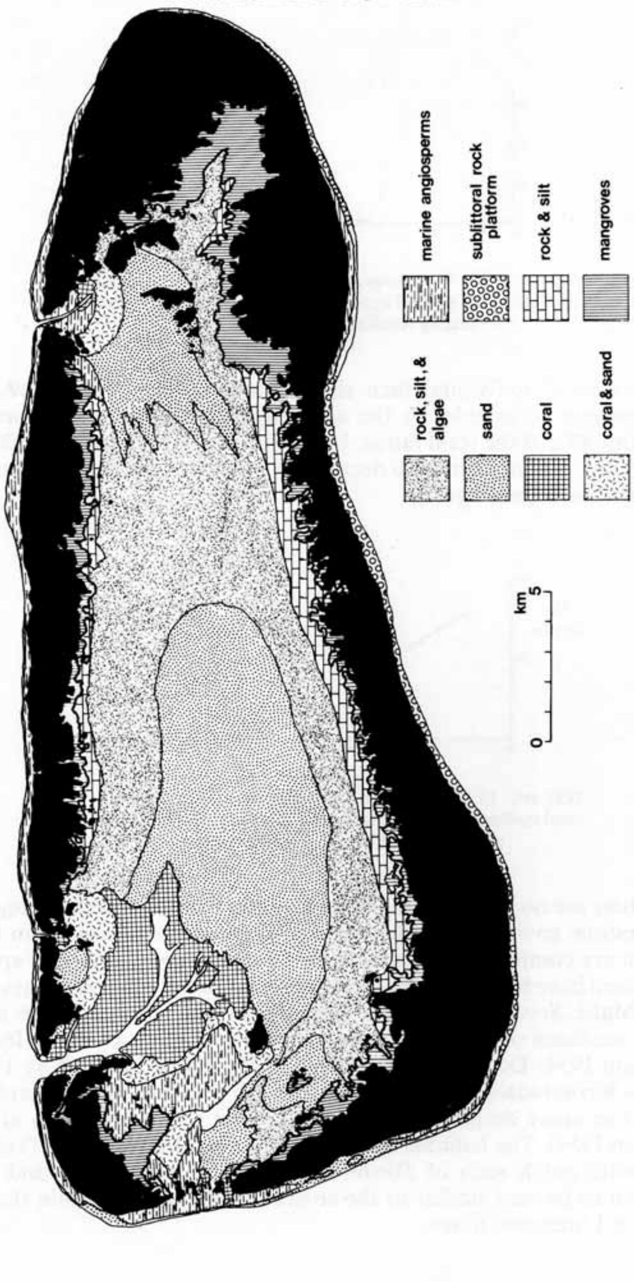
The distribution of individual taxa show similar trends. Thus *Turbo* remains a major component of samples at the atoll edge (text-fig. 12) and comprises an average of about 40% of the total fauna, but is virtually absent by about 900 m from the edge. A similar, but more gradual decrease in importance inwards is shown by the byssate *Barbatia fusca* (text-fig. 13).



TEXT-FIG. 13. Percentage of *Barbatia fusca* individuals in total mollusc fauna plotted against distance from the atoll edge during Aldabra Limestone times.

Although there are no studies of molluscan faunas from complete analogues of the Aldabra Limestone environment, there are descriptions of faunas from individual habitats which are comparable. For instance *T. argyrostomus*, *Trochus* species, and abundant *B. fusca* have been recorded from *Acropora*-dominated reef edges and patch reefs around Mahé, Seychelles (Taylor 1968). *Turbo* and *Trochus* species are among the dominant molluscs on seaward, wave-exposed reef edges of many Indo-Pacific atolls (Morrison 1954; Demond 1957; Salvat 1970; Taylor 1971*a*; Kay 1971).

The families Strombidae, Cerithidae, Naticidae, Tellinidae, and Veneridae are the dominant taxa in many shallow atoll lagoons (Salvat 1967, 1972; Kay and Switzer 1974; Morrison 1954). The habitats and fauna described by Wells (1957) for leeward lagoon reefs with patch reefs of *Porites* separated by sandy areas and abundant *Halimeda*, seem to be very similar to the environments present within the atoll rim during Aldabra Limestone times.



TEXT-FIG. 14. Generalized map of the major shallow-water habitats of Aldabra at the present day.

PRESENT-DAY HABITATS AND FAUNA

In the context of the geological sequence on Aldabra the present day can be considered as an erosional event. It is thought that sea-level has been at approximately the same position since about 3000–5000 years ago, and thus present-day habitats and communities have developed since this time.

Details of the geomorphology have been given by Stoddart *et al.* (1971) and Braithwaite *et al.* (1973) and only the major features are outlined below. A nearly continuous elevated land rim breached at four places by narrow channels surrounds a shallow lagoon. On the seaward side the land is terminated by steep cliffs 4 m high beyond which is an intertidal and shallow subtidal platform up to 400 m wide which ends abruptly at the steep seaward slope of the atoll. The lagoon is almost completely fringed by mangroves which are growing upon rock or silt substrates (Macnae 1971). The rest of the lagoon floor, which rarely exceeds 5 m in depth, is generally rock bottomed but may have a thin cover of fine sand or silt. Near the channels the hydrodynamic situation is much more complex and a mosaic of habitats is developed, with accumulations of sand, beds of marine angiosperms, coral patches, and mixed sand and coral areas (text-fig. 14). Details of the seaward slope of the atoll have been described by Taylor (1971*b*). Along the southerly and easterly coasts the seaward platform consists of algal-covered rock pavement, but at the northerly and westerly ends of the atoll the rather wider platform is covered by beds of marine angiosperms and some mobile sand bodies. Along the seaward edge of the platforms there is usually a zone consisting of loose limestone blocks (the boulder zone) resting upon rock substrate. The seaward slope of the atoll is mainly rocky, with extensive coral growth only at the western end (Barnes *et al.* 1971). More detailed description of the Recent molluscan fauna will be published elsewhere but some idea of the composition and relative abundance of molluscs from some of the major habitats is given below (text-figs. 15, 16) so that comparison may be made with the fossil assemblages.

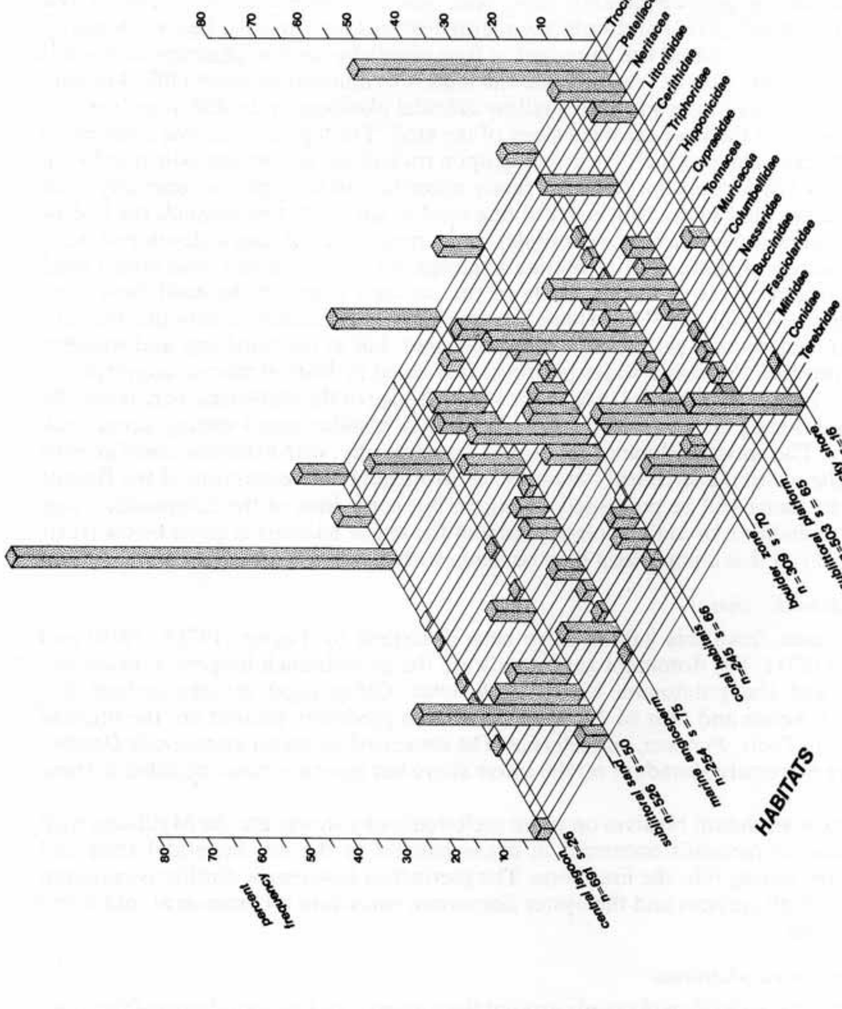
Intertidal rocky shores

The faunas from this habitat have been described by Taylor (1971*b*, 1976) and Hughes (1971). The dominant gastropods are the prosobranch limpets *Acmaea* and *Cellana* and the pulmonate limpet *Siphonaria*. Other algal grazers include five species of *Nerita* and four of *Littorina*. The main predators present are the muricid gastropods *Thais*, *Purpura*, and *Morula*. The cemented vermetid gastropods *Dendropoma* are extremely abundant on the lower shore but have not been included in these counts.

The most abundant bivalves on more sheltered rocky shores are the Mytilacea with *Brachiodontes variabilis* occurring in dense patches in the low intertidal zone and *Lithophaga* boring into the limestone. The pteriacean *Isognomon dentifer* is common byssate in high crevices and the oyster *Saccostrea cuccullata* is common at mid-shore at some sites.

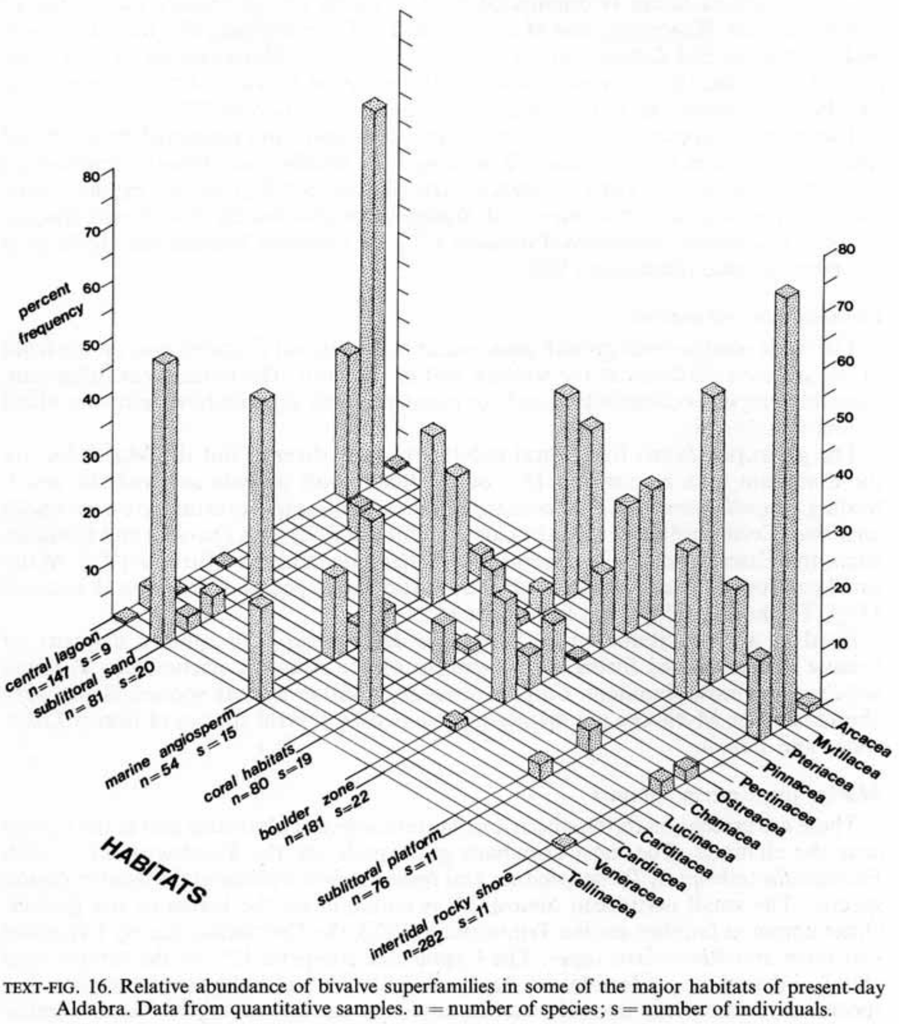
Sublittoral rock platforms

This habitat is developed mainly around the southern and eastern shores of the atoll. Amongst the gastropods the Muricacea (26%) and the Conidae (31%) are the dominant



TEXT-FIG. 15. Relative abundance of families and superfamilies of gastropods in some of the major shallow-water habitats of present-day Aldabra. Data from quantitative samples. n = number of individuals; s = number of species.

taxa, the most abundant forms being species of *Morula*, *Drupa*, and many species of *Conus*, particularly *C. ebraeus*, *C. rattus*, and *C. flavidus*. Other predators are *Engina* and *Peristernia* of the Buccinidae and Fasciolaridae and several species of *Strigatella* (Mitridae). The Cerithidae (9%) comprise mainly small species found in the algal turf. *Cypraea caputserpentis* and *C. histrio* are the most common Cypraeidae and the Tonnacea are represented by *Bursa granularis* (6%).



TEXT-FIG. 16. Relative abundance of bivalve superfamilies in some of the major habitats of present-day Aldabra. Data from quantitative samples. n = number of species; s = number of individuals.

Bivalves are not abundant and are represented by only eleven species. Mytilacea again dominate the fauna with *Modiolus auriculatus* the most common. The Pteriacea with *Isognomon perna*, *I. legumen*, and *Pinctada* are byssate in crevices. Another byssally attached crevice form, *Barbatia helblingi* (Arcacea 15%), is the only other common bivalve.

Platform edge and boulder zone

The gastropod fauna is dominated by Muricacea (41%), mainly by species of *Drupa*, *Morula*, *Mancinella*, and *Maculotriton*. The Fasciolaridae (18%) are abundant, and *Peristernia* and *Leucozonia* are the common forms. Many species of *Conus* are present (Conidae 14%) as well as some small species of Turridae. Other families, the Trochacea, Cypraeacea, and Tonnacea, are all present at about 5%.

This habitat supports quite a diverse fauna of byssate and cemented bivalves and species of Arcacea (23%) include *B. helblingi*, *B. tenella*, and *Arcopsis symmetrica* common beneath blocks and in crevices. The Mytilacea (23%) include byssate forms such as *Modiolus*, *Brachiodontes*, and *Septifer*, but also boring *Lithophaga* species. Small *Pinctada* and *Isognomon* (Pteriacea 13%) are common beneath the blocks as is *Chlamys cuneolus* (Pectinacea 9%).

Coral-dominated habitats

The most prolific coral growth areas occur in the lagoon channels and on the front of the seaward platform at the western end of the atoll. The coral areas differ considerably in species composition and complexity, but all samples have been combined in text-figs. 15, 16.

The gastropod fauna from coral habitats is quite diverse, but the Muricidae are the dominant taxa comprising 15% of the fauna with *Morula uva* and the coral-feeding *Drupella cornus* the most common species. Other important taxa are *Columbella turturina* (Columbellidae 11%), the Coralliophilidae (9%) with *Quoyula* and *Coralliophila*, the Fasciolaridae with *Latirus* and *Peristernia*, and the Mitridae (6%). Many small gastropods occur in these habitats, particularly species of *Rissoina* (Rissoidae 11%), Triphoridae (5%), and Cerithidae (4%).

Bivalves are not abundant, although the habitat supports quite a diversity of byssate and cemented forms with members of the Arcacea, particularly *Barbatia helblingi*, the most abundant. *Cardita variegata*, another byssate species, is also very abundant. The Mytilacea are mainly represented by several species of borers *Lithophaga* and *Botula*.

Marine angiosperm habitats

These are present on the northern and western seaward platforms and in the lagoon near the channels. The most dominant gastropods are the Trochacea (22%) with *Phasianella aethiopica*, *Turbo spinosus*, and *Infundibulum erythraeus* the most common species. The small neritacean *Smaragdia* is common on the leaves of the grasses. Other common families are the Triphoridae (12%), the Cerithidae, mainly *Cerithium rostratum* and *Rhinoclavis asper*. The Cypraeidae comprise 12% of the sample, and mainly inhabit the undersides of dead coral blocks and cobbles, although a few species are found living upon the marine angiosperms. *Strombus gibberulus*, *S. muta-*

bilis, and *Lambis truncata* are often common on the substrate surface, whilst species of *Morula* are found on the blocks and cobbles.

Surprisingly the bivalve fauna is rather sparse, with the most common form, *Chlamys cuneolus* (Pectinacea 35%) being found byssate beneath cobbles. Infaunal suspension feeders *Pinna muricata* and *Atrina vexillum* are locally common. The Tellinacea (16%) are the most abundant burrowing group, and a few Lucinacea occur.

Sublittoral sand habitats

Most of the sublittoral sand habitats are located in the lagoon near the lagoon channels. Amongst the gastropods the numerically dominant taxon is the predatory family Terebridae, represented by twenty-two species and comprising 36% of individuals. Two species of *Conus*, *C. arenatus* and *C. tessulatus*, are also important (Conidae 18%). Other important predatory groups living in the sand are the Mitridae (7%), Vexillidae (5%), and the scavenging Nassaridae (8%). The only other numerically important group is the Cerithidae (16%) mainly represented by *Rhinoclavis asper* and *Cerithium echinatum*.

This habitat supports quite a diverse bivalve fauna dominated by burrowers, particularly the Tellinacea (49%), including species such as *Tellinella crucigera*, *T. staurella*, *Jactellina clathrata*, and *Scissulina dispar*. The other most common group is the Lucinacea, with *Codakia punctata*, *Anodontia edentula*, and *Diplodonta* the more abundant species.

Central lagoon habitats

The turbid central lagoon is the greatest area of shallow-water habitat available at Aldabra and is occupied by an essentially uniform fauna. The fairly shallow more or less silt-covered rock substrate is covered with the algae *Halimeda*, *Hydroclathrus*, *Cystosiera* and *Caulerpa*, and sponges.

The Mollusca inhabiting this habitat are dominated by Cerithiacea, and in particular by two species, *Cerithium morum* and *C. rostratum*, which occur in great abundance. Few other macrogastropod species occur, and these include *Infundibulum erythraeus*, *Peristernia*, and occasional *Cypraea* and *Pyramidella*.

The most common bivalve in the lagoon is the small byssate *Brachiodontes variabilis* attached to rock surfaces, and *Vulsella vulsella* is common commensal among the benthic sponges. Infaunal bivalves are uncommon except near channels where sediment is thicker and *Scissulina dispar* and *Jactellina* may occur.

Mangrove habitats

Mangrove habitats are developed around the margins of the lagoon, and the faunas inhabiting them vary according to the substrate type. At the outer edges the mangrove faunas merge transitionally into lagoon faunas. Cerithiacea are the dominant gastropod super family with *Terebralia palustris* and *Cerithium morum* occurring in immense numbers on the substrate beneath the mangroves. *Littorina scabra* is common on the trunks and leaves of the mangroves and *Nerita undata*, *Siphonaria*, and the large chiton *Acanthopleura* are common on rock outcrops within the mangrove habitats. Bivalves are not common, although *Isognomon dentifer* and *Brachiodontes* may be found on the rocks and *Quidnipagus palatum* in the silt.

CONCLUSIONS

The three successive molluscan faunas described from the Pleistocene rocks of Aldabra Atoll, coupled with the present-day fauna, give some insight into the evolution of the present-day marine faunas of Aldabra. Each of the faunas is very different in character and this is a reflection of the changes in habitat structure of the shallow-water marine environment accompanying each geological event.

The Esprit Limestone fauna, dominated by infaunal bivalves and cerithiid gastropods, lived in sublittoral to intertidal sandy, probably lagoonal, conditions. It must be stressed that the rocks exposed represent only a small fraction of the atoll area at this time.

The Takamaka Limestone fauna, dominated by trochacean gastropods, inhabited a wide shallow bank with abundant crustose coralline algae, corals, possibly the marine angiosperm *Thalassodendron*, and with calcareous muds in quiet water areas. Conditions were apparently fairly uniform over the whole atoll. The Aldabra Limestone fauna inhabited a shallow bank with abundant coral growth around the rim passing inwards into more sandy areas with abundant *Halimeda* and coral patches and knolls. The molluscan fauna was highly diverse and an abundance of *Turbo* and trochacean gastropods, epifaunal byssate, and cemented bivalves inhabited the atoll rim, with many Cerithidae, Strombidae, and burrowing bivalves in the more sandy areas within.

At the present day the large, shallow, turbid lagoon supports abundant cerithiid gastropods, but the more varied coralline, marine angiosperm, and sandy habitats around the channels support a much more diverse fauna. The seaward sides of the atoll are surrounded by limestone cliffs and the more exposed parts of the seaward platform covered by an algal turf with stands of marine angiosperms in the more sheltered parts. Epifaunal gastropods and byssate and cemented bivalves dominate in these seaward habitats.

Similar large-scale changes in the habitat structure of reefs are seen elsewhere; for instance, recent studies of the Pleistocene limestones of the Kenya coast (Crame 1976) have shown that during the last interglacial Kenya was probably bordered by linear patch reefs with a broad back reef area consisting of sands with abundant *Halimeda* and coral knolls. Today, by contrast, the present 'reef' is a broad, shallow, erosional platform cut into elevated Pleistocene limestones. Present-day coral growth is limited in extent and very localized. Assemblages of molluscs very different from those occurring today have been obtained from the Pleistocene limestones. Similarly, Kay and Switzer (1974) report fossil Mollusca in Fanning Island lagoon very different from those living there today.

Although there have been other taxonomic studies of Pleistocene Mollusca from other reef areas in the Indian Ocean (Cox 1927, 1930; Nardini 1934, 1937; Abrard 1942), comparison with the Aldabra sequence has been prevented by the lack of a reliable dating framework. It is apparent, however, that in these areas there has been considerable faunal change. The widely recognized 125 000-year-old limestone, representing sea-level from 2 to 10 m above the present, would make a suitable datum for the comparison of late Pleistocene reef faunas.

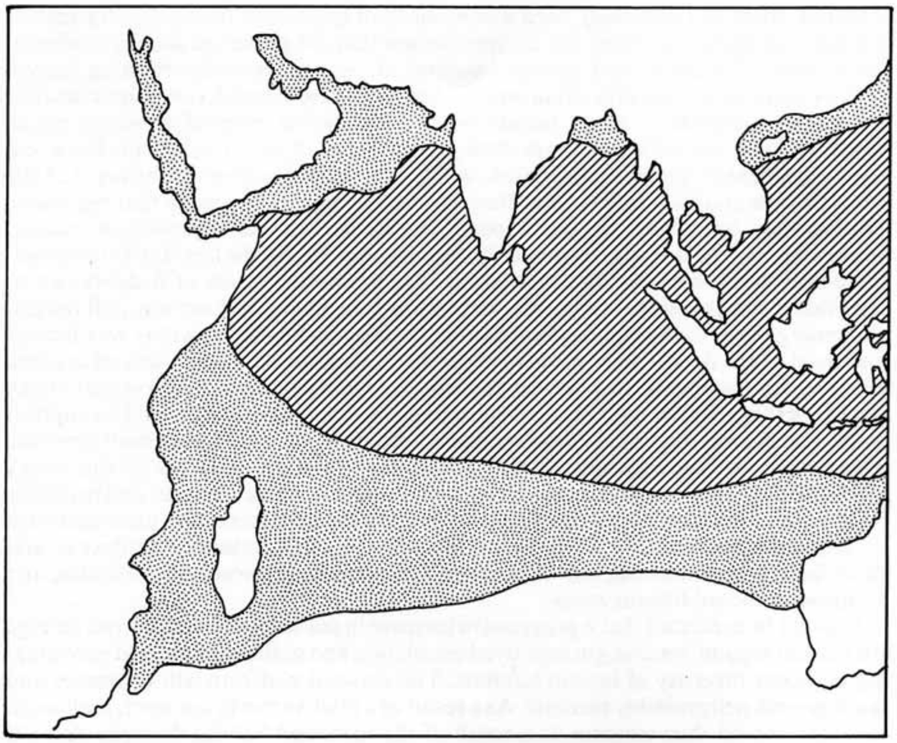
During the times of the late Pleistocene sea-level changes which have affected

Aldabra, there has obviously been a continuity of molluscan occupation of marine habitats but the faunas from the different stages that are preserved are very different in character. The three fossil faunas described all occur in beds representing depositional events associated with rising, and higher than present, sea-levels. Unfortunately there is no information about faunas which lived during times of erosional events when sea-level was falling or lower than present, or of depositional events from sea-levels significantly lower than present, which may have occurred in the last 125 000 years (Bloom *et al.* 1974). Evidence from the surface geology suggests that periods of erosion may have been of much longer duration than the depositional phases; Mesolella *et al.* (1970) suggests that only during about 35% of the last 600 000 years has there been active reef growth at Barbados. The present-day state of Aldabra can be considered as an erosional event, marked by lowering of the land surface, cliff retreat, and enlargement of the lagoon. Sediment deposition and coral growth is very limited and most of the deposits are probably ephemeral in nature. During times of lowered sea-level, for instance during the last glaciation, Aldabra stood as a steep-sided, rocky island, perhaps 130 m high. The surrounding sea was probably too cold to support active reef growth (text-fig. 17) and sediment accumulation would have been minimal. The molluscan fauna inhabiting the limited shallow-water habitats of this rocky island would have been dominated by epifaunal and endolithic animals, and probably fairly similar in character to that fauna inhabiting the sublittoral and intertidal hard substrate habitats today. That is, an abundance of Patellacea, Neritacea, and Muricidae in the intertidal, and Trochacea, Cypraeidae, Muricacea, Buccinidae, and Conidae in the sublittoral zones.

It might be predicted that a progressive increase in sea-level will deepen and enlarge the present lagoon, resulting in improved circulation and sedimentation and encouraging a greater diversity of lagoon habitats. The seaward platform will be deeper and coral growth will probably increase. As a result of a relative rise in sea-level, molluscan diversity should thus increase as a result of the increased habitat diversity and the greater area available for colonization. As a result of increased and more stable sedimentation, the numbers of soft substrate-associated and burrowing species should also rise. By contrast, a lowering of sea-level will cause the emersion of the lagoon and seaward platforms, thus diminishing habitat space and faunal diversity. The fauna resulting from these changes will be predominantly epifaunal in character.

As well as the dramatic changes which affected the shallow-water benthos around Aldabra itself there were broad-scale habitat changes in other shallow-water areas of the western Indian Ocean that may well have affected the distribution of organisms. Thus, at the time of the maximum depression of sea-level during the last glaciation, most of the coral islands, atolls, and shallow banks of the area would have been emergent. The slopes of all these submarine features are steep and rocky, and the over-all area of soft substrates would have been considerably reduced, which should have affected the diversity of infaunal animals present in the area. Conversely the habitats available for rocky-shore and hard-substrate species were considerably increased, and diversity may have been higher.

It is apparent that relatively small changes in sea-level will cause large habitat changes on reefs, resulting in the destruction or formation of new habitats and causing either extinctions or opportunities for new colonizations. This might be exemplified



TEXT-FIG. 17. Possible extent of the contraction of the coral reef seas (i.e. within the 20° C. isotherm) of the Indian Ocean during times of glacial advance. Redrawn from Stoddart (1973), original data from palaeotemperature analyses. Cross hatching = water warmer than 20° C. during last glacial advance; stippling = water warmer than 20° C. at present day.

by the present shallow lagoon at Aldabra; a major event during the post glacial sea-level rise was the breaching of the land rim to form the present lagoon, an event which at once enormously increased the area of shallow-water habitat available for colonization by marine faunas. Because of the drastic effects resulting from small sea-level changes there has probably been more continuity of habitats and communities on continental margins and high islands than on atolls and low oceanic islands. The higher environmental and topographic complexity on continental margins must improve the chances of particular habitats surviving through rapid sea-level changes; whereas comparable changes on atolls would result in the complete elimination of habitats.

Most differences in the composition of successive faunas at Aldabra are obviously related to the different habitats available for colonization. However, as Diamond (1975) has discussed, the final species composition of the community may partly be determined by random factors such as the order in which colonists arrive, which may affect the admission of later arrivals into the community. Thus alternate stable communities can be assembled. The great variation seen in closed lagoon faunas of Pacific atolls may result from such random factors (Salvat 1967, 1972; Kay and Switzer 1974). However, the similarity of seaward reef faunas at various localities around the Indian Ocean suggests that upon seaward reefs such factors are unimportant (Taylor 1977).

It is also probable that during the late Pleistocene there have been changes in the tropical Indian Ocean species pool from which the Aldabra marine fauna has been recruited. Although our knowledge is incomplete, we are aware that the present-day species pool is not uniform; for instance, some species are restricted to continental margins and large islands whilst others are found only in parts of the region. Unfortunately few Pleistocene faunas have been investigated in sufficient detail for comparisons to be made. However, that such changes have occurred is evidenced by the bivalve family Tridacnidae which are taxonomically and zoogeographically well known (Rosewater 1965). At Aldabra, five species are found in Pleistocene rocks, *Tridacna maxima*, *T. squamosa*, *T. crocea*, *T. gigas*, and *Hippopus hippopus*, whilst only two, *T. maxima* and *T. squamosa*, are found at the present day. *Hippopus* occurs in the Esprit and Takamaka Limestones, *T. gigas* and *T. maxima* in both the Takamaka and Aldabra Limestones and *T. crocea* and *T. squamosa* in the Aldabra Limestone. *Hippopus*, *T. gigas*, and *T. crocea* are at the present day restricted in distribution to the Indonesian–W. Pacific area, and are absent from the Indian Ocean west of Sumatra. *T. gigas* and *T. crocea* have been similarly recorded from Pleistocene rocks of the Kenya coast (Crame 1976). There have thus been major changes in the distribution of *Tridacna* species since the last interglacial period 125 000 years ago. Similar changes are known in other groups, for instance the mangrove-associated gastropod *Cerithidea*, now restricted to continental margins in the Indian Ocean, was present in the Esprit Limestone of Aldabra.

Implicit in many hypotheses concerning the high diversity of tropical areas compared with high latitudes is the idea of the stability of the tropical environment over long periods of both ecological and evolutionary time (Pianka 1966; Pielou 1975; Sanders 1968, 1969). Along with tropical rain forests, coral reefs are usually cited as the most diverse and complex ecosystems to have evolved.

We know from the studies at Aldabra and from many other reef systems in the Indo-Pacific area that during the late Pleistocene, reef systems have certainly not been stable, and periods of active reef growth have alternated with emergence and erosion (Tracey and Ladd 1974; Purdy 1974; Brousse *et al.* 1974; Stoddart 1976). Moreover, many reefs on tectonically active shores have been either elevated high above sea-level or submerged too deeply for coral growth to proceed (Bloom *et al.* 1974; Chappell 1974*a*; Mesolella *et al.* 1970). Following the high sea-level stand of the last interglacial about 125 000 years ago there was a progressive but oscillating decrease in sea-level to about 17 000 years ago, at the height of the last glaciation when sea-level stood about 130 m below the present (Chappell 1974*b*). This would have exposed all the present shallow-water habitats of coral islands and atolls of the Indian Ocean high above sea-level. The subsequent and rapid (*c.* 1 m/100 yrs) post-glacial rise in sea-level reached approximately the present position about 5000 years ago. It follows, therefore, that most reef habitats and the communities inhabiting them have developed during this time. Thus in talking about the evolution and survival of reef faunas we are referring to the stability of the faunal province and species pool in general, and not to the stability of individual reef systems which are clearly unstable over evolutionary time.

The Indo-West Pacific marine province forms a more or less stable species pool from which the faunas of individual reef systems are recruited. The uniform thermal conditions over much of the area, the broad latitudinal extent, and the great variation in tectonic style and hence habitat diversity, has ensured the long-term continuity of the faunal province. The dimensions of the whole province, however, must have changed considerably during the cooling and warming periods of glacial advance and retreat. Reference to text-fig. 17 shows that the area occupied by the tropical species pool in the Indian Ocean was probably reduced by about 50% during the last glacial maximum. The highest diversities of the Indo-Pacific province are found in the Indonesian area (Stehli 1968; Valentine 1971, 1973) which is also the tectonically, and hence environmentally, most complex; an extensive subduction zone is marked by east–west chains of trenches, mountains, and island arcs bordering the continental margins of Asia and Australia. The Indo-Pacific species pool has thus been able to survive the climatic disturbance of the glacial advances which resulted in provincial retraction and widespread habitat changes. With some exceptions, species have been able to recolonize into areas from which they were probably excluded during periods of global cooling, even though reef habitats have drastically changed.

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