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NO. 223

D'ARROS AND ST. JOSEPH, AMIRANTE ISLANDS

by D. R. Stoddart, M. J. Coe and F. R. Fosberg

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D'ARROS AND ST. JOSEPH, AMIRANTE ISLANDS

INTRODUCTION

D.R. Stoddart

This report results from a request by the then Governor of the former Colony of Seychelles, H.E. Mr. C.H. Allan, for advice on the ecology of D'Arros Island and St. Joseph Atoll in the Amirantes, recently acquired by H.I.H. Prince Chahram Pahlavi. Stoddart and Coe visited the islands on 5-8 April 1976. In addition to making specific recommendations, the following accounts of D'Arros and St. Joseph were prepared as summary papers incorporating scientific information on the islands previously obtained, mainly by the *Alert* and *Sealark* (Percy Sladen Trust) Expeditions, together with our own observations.

There is surprisingly little information available on most of the Amirante Islands, and the value of much of the published data is reduced by the lack of detailed locality records. This applies to early studies, such as that of Dufo (1840) on the marine molluscs, as well as to the reports of the Percy Sladen Trust Expedition. There are few recent accounts of the fauna and flora of islands in the group. This paper completes the coverage of the northern Amirantes - African Banks, Remire, Desroches - initiated in 1968 (Stoddart and Poore 1970a, 1970b, 1970c; Fosberg and Renvoize 1970a, 1970b, 1970c). The southern islands of the group - Poivre, Etoile, Boudeuse, Marie-Louise, Desnoeufs, Alphonse, St. François, and Bijoutier - have yet to be visited.

The present investigation was made possible through the assistance of William A. Pomeroy of Mahé. We are particularly grateful to Miss Jenny Furneau for hospitality and help on the islands, and to Capt. Marsh for the opportunity to see them from the air. C.W. Benson, Department of Zoology, Cambridge University, kindly commented on the sections on birds, and also made available his notes on Parker's collection of birds now in the National Museum of Kenya, Nairobi. G.E. Watson of the National Museum of Natural History, Washington,

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kindly supplied details of the St. Joseph pelican. We are grateful to the following in the British Museum (Natural History) for determinations of collections: P. Freeman (insects), D. MacFarland (millipedes), F.R. Wanless (spiders), R.W. Ingle (crabs), and E.N. Arnold (reptiles); J.F. Peake assisted in many ways. F.R. Fosberg and M.-H. Sachet, National Museum of Natural History, Smithsonian Institution, Washington, D.C., undertook the work on the plant collections as part of their general project on the floras of western Indian Ocean coral islands. J.E. Böhlke, Academy of Natural Sciences, Philadelphia, supplied information on ichthyological work at both D'Arros and St. Joseph in March 1964.

We are grateful to H.I.H. Prince Chahram Pahlavi, through Mr. William A. Pomeroy, for contributing to the cost of publication of this report.

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Figure 2. D'Arros Island and St Joseph Atoll. Produced from part of British Admiralty Chart No 721 with the sanction of the Controller, H.M. Stationery Office and of the Hydrographer of the Navy

GEOGRAPHY AND ECOLOGY OF D'ARROS ISLAND

D.R. Stoddart and M.J. Coe

Introduction

D'Arros Island is situated in latitude 5°24½'S, longitude 53°18'E, in the Amirante Islands, western Indian Ocean, immediately to the west of the small atoll of St. Joseph. It is an oval-shaped sand cay (Plate 1), oriented NE-SW, with its major axis 1.9 km long and minor axis 1.0 km long. The island stands on a patch reef similarly orientated, with maximum dimensions of 2.8 and 1.4 km. The island stands on the northern sector of the reef; there are drying reef flats 250-400 m wide on its south side, but only a narrow fringing reef about 75 m wide on its north side. The total reef area at low water is about 270 ha; of this the island occupies 170 ha or 62 per cent; and of the island area (measured from the foot of the beaches) 160 ha are vegetated.

Previous work

Table 1 lists previous scientific visits to D'Arros. The island was discovered in 1771 by M. de la Biolière, during a voyage of exploration from Mauritius, and was named after Baron d'Arros, Commandant de la Marine at the Ile de France in 1770-71 (Froberville 1848, 111). The first hydrographic survey was carried out in 1822 by Lt. Russell under the direction of Capt. Fairfax Moresby and was mainly concerned with the establishment of accurate co-ordinates (Moresby 1842). The island was charted and the first scientific visit carried out during the visit of H.M.S. *Alert* during 20-23 March 1882. The chart by Capt. J.P. Maclear, though much corrected, is still the basis of the published chart (Admiralty Chart 724). R.W. Coppinger contributed a general description of the island and also collected marine invertebrates. The Percy Sladen Trust Expedition, with J. Stanley Gardiner and C. Forster Cooper, on board H.M.S. *Sealark*,

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spent 10-11 October 1905 on D'Arros, contributing general descriptions and collecting birds, reptiles and arthropods, especially insects.

Table 1. Previous work at D'Arros

Year	Investigator	Field of study	Main publication
1771	M. de la Biolière	Discovery	
1822	F. Moresby	Survey	Moresby 1842
1882	R.W. Coppinger J.P. Maclear H.M.S. *Alert*	Marine zoology Survey	Coppinger 1883
1892	W.L. Abbott	Birds	Ridgway 1895
1905	J.S. Gardiner C. Forster Cooper H.M.S. *Sealark*	Land and marine animals	Gardiner and Cooper 1907
1950s	J.L.B. Smith	Marine fish	Smith 1955, 1956
1960	C.J. Piggott B.H. Baker	Soils, coconuts Geology	Piggott 1968, 1969 Baker 1963
1964	J.E. Böhlke and others	Marine fish	Starck 1969, Tyler 1967, McCosker and Randall 1977.
1967	I.S.C. Parker M.D. Gwynne D. Wood M.F.R.V. *Manihine*	Birds, plants	Parker 1970 Gwynne and Wood 1969
1975	R.J. Campbell H.M.S. *Hydra*	Survey	
1976	D.R. Stoddart M.J. Coe	Fauna and flora	

Apart from occasional visits by Government economic entomologists and a visit by the ichthyologist J.L.B. Smith, no further information was collected until a survey in 1960, when C.J. Piggott described the soils and coconut plantation and B.H. Baker the geology; both were able, for the first time, to use an accurate map derived from aerial photographs at an approximate scale of 1:12,800 flown in June 1960 (Piggott 1968, 55; 1969, 33-34; Baker 1963, 54-56). Subsequently M.F.R.V. *Manihine* visited the island on 22-24 September 1967, when I.S.C. Parker (1970) studied birds and M.D. Gwynne and D. Wood (1969) collected vascular plants. H.M.S. *Hydra*, Cdr. R.J. Campbell, charted the island and adjacent waters, especially to the north, during a visit on 20-23 October 1975. Our own visit took place on 5-8 April 1976.

Geomorphology

The Amirantes (Figure 1) comprise a chain of small reef islands extending from African Banks in the north to Desnoeufs in the south, located on a bank 180 km long and 8-40 km wide; in addition to the main chain there are also islands on banks separated from the main bank, notably Desroches and Alphonse. Depths on the bank itself are mostly less than 40 m, with parts of the rim rising to 10-25 m, with occasional surface reefs. Immediately to the west of the bank the Amirantes Trench reaches depths of 5 km. The bank probably consists of a coral cap overlying volcanic rocks. Matthews and Davies (1966) suggested a basaltic foundation at a depth of 1 km or less from geophysical evidence, while near Alphonse basalts dredged from depths of 2430-3000 and 2400-2700 m have yielded a radiometric age of 82 ± 16 m yr, i.e. mid-late Cretaceous (Fisher, Engel and Hilde 1968).

The D'Arros reef itself (Figure 2) rises from the main bank surface at 30-60 m, near its eastern edge. The reef slopes are fairly gentle to the west and south, where the 30 m isobath lies 1-1.4 km from the reef edge, but they are more abrupt in the north and especially the east, where this contour is 100-300 m from the reef edge. The channel between D'Arros and St. Joseph is about 1100 m wide and 60 m deep. An un-named bank slightly smaller than the D'Arros reef is located 5 km due north of it, and has least depths of 2.7 m.

The windward reef flats are rocky pavements veneered with mobile sand and gravel, and with no living coral. There are no reef blocks on the reef edge, and no well-marked algal rim. Near the west point there is an accumulation of slightly lithified storm rubble, mostly composed of small whole *Acropora* colonies, forming a transverse tongue on the reef flat, and there are signs elsewhere on the reef flat of similar tongues now eroded. The leeward reef is irregular, with sea-grass swards and coral colonies.

The beaches of the island are all sandy (Plates 3 and 4). They are highest between Pavé Matin and Bois Blanc, where low coastal dunes are at present being eroded, leaving several lines of beachrock on the reef flat close inshore (Plate 5). No elevations were measured on the island, but the greatest height is probably not more than 7 m and much of the surface probably stands at about 2-3 m above sea-level. The interior of the island is flat and featureless; except for areas of phosphate rock the entire island is composed of carbonate sand. Piggott (1968, 55) describes the main soil as a well developed Shioya Series with an organic layer 45 cm deep; the phosphate rock he describes as a truncated Jemo Series soil with the superficial guano removed. The approximate area of the phosphate rock as mapped by Baker (1963) is shown in Figure 3. Most of the local surface irregularity on the island results from the excavation of holes through the rock during the planting of coconuts. The outcrop is either a pavement with an irregular surface, or consists of angular irregular blocks; the extent to which the broken character of the blocks results from human activity is unknown. The thickness of the rock is usually about 1 m.

Climate

D'Arros is under the influence of the northwest monsoon from December to March, and of the southeast trades from April to November. During the trades the weather is dry, and months completely without rain are not infrequent. Most rainfall occurs during December and January (Figure 4). The mean annual rainfall for the period 1951-62 was 1497 mm; the highest annual total was 2486 mm in 1961, and the lowest 804 mm in 1958 (Table 2). The mean of 1497 mm compares with 1350 mm for Poivre (1949-62) 43 km to the south, which is the only other Amirantes station with a comparable record.

No other meteorological records are available for D'Arros. Temperatures probably vary from 25 to 30°C. Humidity is probably high, being greatest during the period of the northwest monsoon.

Marine fauna

The only collections of marine invertebrates from D'Arros are those of the *Alert* expedition in 1882. Smith (1884) lists 25 species of molluscs, mainly gastropods, Bell (1884) 18 species of echinoderms, including echinoids, ophiuroids and holothurians, Miers (1884) 16 species of crustaceans, mainly crabs, Ridley (1884a, 1884b) 7 species of sponges and a single alcyonarian. Monro (1924, 1926) also listed three species of polychaete from *Alert* material. Subsequently J.L.B. Smith (1955, 1956) listed three species of marine fish, and more species have been cited from J.E. Böhlke's collections in 1964 (Tyler 1967, Starck 1969, McCosker and Randall 1977). From these very patchy records the shallow water marine fauna appears characteristic of that of western Indian Ocean reefs generally, and of other islands in the Amirantes. According to Rosen (1971) 31 genera of reef-building corals have been recorded from the Amirantes as a whole but he predicts that the fauna probably comprises 57 genera.

Vegetation

D'Arros is presently covered with coconut woodland, but this is of comparatively recent origin. Coconut oil was being produced on at least some of the Amirantes early in the nineteenth century (Prior 1820, 59), but plantations came at a much later date. In 1882 Coppinger (1885, 221) on D'Arros noted "a large plantation of young cocoa-nuts, which in five or six years will doubtless be productive". As late as 1905, however, Gardiner and Cooper (1907, 153) gave a clear impression

Table 2. Monthly rainfall at D'Arros, 1950-1962

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
1950	217	280	161	126	-	43	69	-	16	18	72	199	-
1951	157	57	97	170	97	0	17	58	88	290	159	288	1476
1952	212	252	84	236	111	149	0	22	0	8	13	135	1218
1953	410	71	193	111	196	0	11	12	22	244	130	348	1747
1954	194	107	196	84	125	0	0	109	25	0	0	211	1050
1955	422	245	23	70	203	0	0	0	51	74	89	365	1541
1956	193	175	259	117	180	36	51	15	0	53	188	267	1534
1957	366	173	163	164	79	39	49	19	0	167	158	299	1674
1958	28	118	46	166	112	90	85	15	0	19	64	61	804
1959	363	159	79	97	179	56	36	33	208	239	97	64	1610
1960	194	221	159	194	64	39	10	7	57	203	0	275	1423
1961	300	348	382	77	30	83	64	159	191	221	296	338	2486
1962	132	213	127	137	120	98	51	37	232	52	96	103	1398
Mean	245	186	151	134	124	49	34	40	68	122	105	227	1497

Original data in inches; converted to mm and rounded to nearest mm.

of rather sparse coconut growth: "Against the sea was a thick belt of the usual scrub with a few small coconuts behind; inside it had evidently been burnt. 'A thirsty and dry land where no water is'." On the other hand figures of nut production at this time (see below), which probably derive jointly from both D'Arros and St. Joseph, suggest a total planted area (assuming a yield of 2000 nuts/ha) of not less than 200 ha, or two-thirds of the combined land area of the two islands. It seems likely from this evidence that the present dense plantations are the product of the last 70-100 years. Both vegetation and flora have thus been greatly influenced by man.

The following vegetation units may be distinguished:

Coastal scrub

Most of the island is surrounded, especially on the south and west sides, by a monospecific hedge of *Scaevola taccada* about 50 m wide, 5-8 m tall, and almost impenetrable (Plates 2-4). This reaches the upper part of the beach, and consequently there is very little pioneer herbaceous vegetation on the beach crest. One or two small patches of *Lepturus repens* and clumps of *Cyperus ligularis* were seen. In addition to *Scaevola*, there are very occasional shrubs of *Suriana maritima* and *Tournefortia argentea*. *Pemphis acidula* has not been recorded from D'Arros.

Casuarina woodland

Casuarina litorea is extensive on the beach crest along much of the north and northeast shore, extending round the east end of the island to Pavé Matin (Plates 4 and 11). Coppinger noted "a handsome grove" of trees 25 m tall at the present settlement in 1882; they were then said to be nineteen years old and to have been introduced by a Frenchman named Hoyaeux (Coppinger 1885, 221, 226). Many of the present trees are very large, often more than 30 m tall (Plate 5); a few are being undermined by beach retreat, and others are being felled for timber.

Neisosperma groves

Medium-sized trees of *Neisosperma* (= *Ochrosia*) *oppositifolia* form a narrow but extensive belt between the road and the coastal *Scaevola* scrub in the southeastern part of the island east of Pavé Matin (Plate 8). Here, as well as elsewhere on the inland side of the *Scaevola*, there are mature trees of *Guettarda speciosa*.

Calophyllum groves

Between Dardanelle and Takamaka there are several discrete groves of tall *Calophyllum inophyllum* trees (Plate 7), presumably a relict of the indigenous woodland of the island. These form a dense canopy, and no other plants are found in the heavily shaded area beneath. The trees are about 25 m tall.

Other broadleaf groves

In the western part of the island there are occasional small groves, often of 2-3 trees, of *Cordia subcordata, Barringtonia asiatica* (Plate 6), *Guettarda speciosa* and *Pisonia grandis*. The *Cordia* and *Barringtonia* trees are particularly large; the latter is introduced.

Coconut woodland

Over most of the island the woodland canopy is formed by tall *Cocos nucifera* (Plate 9), interspersed with frequent tall but isolated trees of *Casuarina litorea*. An intermediate tree storey comprises trees 5-15 m tall of juvenile *Casuarina, Morinda citrifolia, Pipturus argenteus,* and *Leucaena leucocephala,* though these are largely replaced in the areas of phosphate rock by *Carica papaya*.

The ground layer of herbs and grasses is luxuriant and variable (Plate 10). *Kalanchoe pinnata* is the dominant tall herb, forming extensive dense stands up to 2 m tall. There are also frequent clumps of the fern *Nephrolepis biserrata* 1-2 m tall. The most common herbs are those typical of Indian Ocean coconut plantations: *Turnera ulmifolia, Passiflora suberosa, Euphorbia cyathophora, Phyllanthus maderaspatensis,* *Bidens pilosa, Asystasia bojeri, Boerhavia repens, Stachytarpheta jamaicensis, Striga asiatica* and *Tridax procumbens*, with the sedges *Fimbristylis cymosa* and *Cyperus dubius* and the grasses *Cenchrus echinatus, Dactyloctenium aegyptium, Digitaria ciliaris* and *Eragrostis tenella*. There is one small area with clumps of *Panicum maximum* 3-4 m tall and of *Pennisetum polystachyon* reaching 2½m. *Achyranthes aspera* was curiously not recorded in 1976, nor has it been collected on D'Arros in earlier years, but it is almost certainly present.

Other cultivated and decorative plants

It will be apparent that most of the herbs of the coconut woodland are introduced weedy species. Much of the vegetation near the main settlements is also dominated by introduced species of more restricted distribution. These include massive trees at the main settlement of *Terminalia catappa* and *Hernandia sonora*, as well as *Casuarina litorea*, together with decorative plants (*Catharanthus roseus, Bougainvillea, Canna, Crinum, Hymenocallis*) and food plants (*Musa sapientum, Solanum nigrum, Moringa oleifera, Ricinus communis, Carica papaya, Vanilla mexicana, Cucurbita pepo, Capsicum frutescens*). Coppinger (1885, 221) noted that "many introduced plants - such as papaws, cotton, pumpkin, etc. - were growing in a neglected state over the island".

Flora

Gwynne and Wood (1969) in the only previously reported collection of plants from D'Arros record 42 species, based on the 53 numbers collected in 1967 (these included *Cynodon dactylon* L., not listed in their publication). 50 numbers were collected in 1976 and determinations are listed by F.R. Fosberg in the following section of this report. With sight records, the recorded flora of D'Arros is now 69 species, including two sea-grasses; this compares with 60 species for Desroches and 58 for Remire, the only other islands of a similar nature and with comparable information in the Amirantes.

Terrestrial fauna

Birds

Birds form the most conspicuous element in the land fauna of D'Arros. They are listed here in systematic order, and some effort has been made to incorporate all previously published records in this account.

Wedge-tailed Shearwater *Puffinus pacificus*

Noted as numerous by Parker (1970), though as a result of the level of human activities it is unlikely that any still breed on the island.

Audubon's Shearwater *Puffinus lherminieri*

Seen at sea 1.6 km north of D'Arros by Parker (1970); not recorded on either D'Arros or St. Joseph.

White-tailed Tropicbird *Phaethon lepturus*

Two birds seen flying round the crown of a coconut palm on 6 April 1976.

Brown Booby *Sula leucogaster*

Listed by Ridgway (1895) on the basis of three specimens collected by Abbott on 30 August 1892; no subsequent record.

Red-footed Booby *Sula sula*

Listed as *S. piscator* by Ridgway (1895); there is no subsequent record.

Greater and Lesser Frigatebirds *Fregata minor, F. ariel*

Frigates are recorded in sightings by Parker (1970). Up to 500 birds were seen over the north end of D'Arros on 7 April 1976. These are undoubtedly non-breeding birds which range widely from their main nesting site on Aldabra between November and July (Penny 1974). The lack of suitable nesting sites and the pressure of human activities make it unlikely that frigates breed on D'Arros.

Little Green Heron *Butorides striatus*

Seen by Parker (1970) and common on D'Arros in 1976. See the comments under this species on St. Joseph Atoll. Ridgway (1895) lists *B. atricapilla*.

Grey Heron *Ardea cinerea*

Seen roosting along the shoreline of D'Arros in 1976.

Cattle Egret *Bubulcus ibis*

Reported by Watson et al. (1963), and listed as *B. bubulcus* by Ridgway (1895).

Grey Francolin *Francolinus pondicerianus*

Coppinger (1885, 225) mentions in his account of Desroches Island a "partridge ... identical with that already seen at Eagle and Darros Islands"; this "small red-legged partridge", still common at Desroches, must be this species, introduced on several of the Amirantes. It was listed without identification by Ridgway (1895), but there is no other record of its occurrence on D'Arros.

Turnstone *Arenaria interpres*

Listed by Ridgway (1895). Common on D'Arros along the shoreline and in coconut plantations in April 1976, birds spending the night in small parties in the coastal scrub. In the early morning these small groups of up to 20 birds moved about together in a closed flock, but during the morning they broke up into small groups of up to 6 birds, regrouping again at sunset. One male and two females collected by Parker on 22 September 1967 are in the National Museum of Kenya, register numbers 20924-20926.

Greater Sand Plover *Charadrius leschenaultii*

Sight record by Parker (1970).

Grey Plover *Squatarola squatarola*

Sight record by Parker (1970).

Whimbrel *Numenius phaeopus*

Listed by Ridgway (1895) and by Watson et al. (1963). Very common on the shoreline and in coconut plantations in 1976, calling almost continuously.

Sanderling *Crocethia alba*

Sight record by Parker (1970).

Bridled Tern *Sterna anaethetus*

This species, seen by Parker (1970), is not recorded for the Amirantes by Watson et al. (1963). Penny (1974) records it as occurring in the Amirantes, and quotes Vesey-FitzGerald as finding nesting birds on Recif and Cosmoledo. This may be the species collected on D'Arros by Gardiner in 1905 and named *Sterna bernsteini* (Gadow and Gardiner 1907).

Common Noddy *Anous stolidus*

Sight record by Parker (1970). Two birds were seen off the northern end of D'Arros on 7 April 1976.

White Tern *Gygis alba*

Recorded as very common by Parker (1970). Very common in 1976 along the shore, but no nesting birds seen.

Turtledove *Streptopelia picturata*

Collected by Parker (1970). Two birds were observed on D'Arros, 7 April 1976; see the discussion under this species in the account of St. Joseph Atoll.

House Sparrow *Passer domesticus*

Recorded for D'Arros by Ridgway (1895), as *P. indicus*, and listed by Watson et al. (1963); recorded as a breeding species by Penny (1974). Parker found it very common (Parker 1970). Very common in 1976, and breeding freely. It is not clear when this species arrived in the Amirantes, but it was probably introduced from the African mainland (Penny 1974).

Madagascar Fody *Foudia madagascariensis*

This species has been introduced into many of the islands of the Amirantes, after an original introduction to the Seychelles about 1800. Parker (1970) found it numerous. Present on D'Arros in 1976, but numbers apparently reduced by the presence of the House Sparrow.

Seychelles Fody *Foudia sechellarum*

This species was introduced into D'Arros by the Bristol Seychelles Expedition in 1965, and it was recorded again there in 1968 (Penny 1974). Not seen in 1976.

Reptiles

Only two reptiles are recorded from D'Arros: the Green Gecko *Phelsuma madagascariensis* and the skink *Mabuia sechellensis* (Boulenger 1909). The skink was common on houses on D'Arros in 1976.

Insects

Only a very small number of insects has been recorded from D'Arros, mostly collected by the Percy Sladen Trust Expedition in 1905 (Table 3). Lepidoptera (8 species) and Coleoptera (6 species) are best represented. The mosquito *Aedes aegypti* (L.), recorded as *Stegomyia fasciata* by Theobald (1912), is very abundant; it has also been collected on the island by Mattingly and Brown (1955). These insects occur in large numbers in areas of overgrown plantation, but recent clearing operations have reduced their abundance in some parts. Piggott (1969, 34) also noted the Long-tailed Mealy Bug *Pseudococcus adonidum* and the Rhinoceros beetle *Oryctes rhinoceros* as pests of coconuts. We collected the pantropical cockroach *Pycnoscelus surinamensis* (L.) at the settlement.

Table 3. Insects collected on D'Arros

Orthoptera	Bolivar 1912, 1924	3 species
Dermaptera	Burr 1910	1 species
Neuroptera	Needham 1913	1 species
Lepidoptera	Fletcher 1910	8 species
Coleoptera	Arrow 1922 Champion 1914 Gebien 1922	6 species
Hymenoptera	Cameron 1907 Forel 1907	3 species
Diptera	Theobald 1912 Lamb 1922 Stein 1910	3 species

Other invertebrates

One species of spider was recorded by Hirst (1913).

Settlement and development

Very little is known of the history of the island. At the time of the *Alert* visit in 1882 the population of D'Arros was 11 (Coppinger 1885, 221). Magistrates' reports in 1905-6 put the total at 24 in September 1905, 35 in November 1905, and 42 in July 1906 (A. Tonnet, ms.). Census reports give totals of 56 in 1931, 57 in 1947, and 105 in 1960, with males exceeding females on each occasion.

Piggott (1969, 33) states that guano has been dug from the surface of the phosphate rock, though no details have been found of this activity. Baker (1963, 120) puts the amount of guano remaining at 2200 tons, and suggests it is only of value for local use.

As already stated, planting of coconuts began about 1880 on a commercial basis. In September 1905 the yield of the plantations on D'Arros and St. Joseph was 30,000 nuts per month, and in July 1906 it was 43,000 nuts per month (A. Tonnet, ms.). Both copra and oil (the latter 500 veltes, or 3400 litres) were exported at this time. Piggott (1969) took an optimistic view of the present state of the plantations.

In 1975 the lease of the island was taken over by H.I.H. Prince Chahram Pahlavi, and it is now managed by W. Pomeroy and Co. of Mahe. In 1976 an airstrip was constructed across the centre of the island

(Plate 11). There is a good anchorage immediately opposite the Settlement on the north shore (Plates 12-19), and during the northwest monsoon pirogues can be launched from a boathouse on the south shore.

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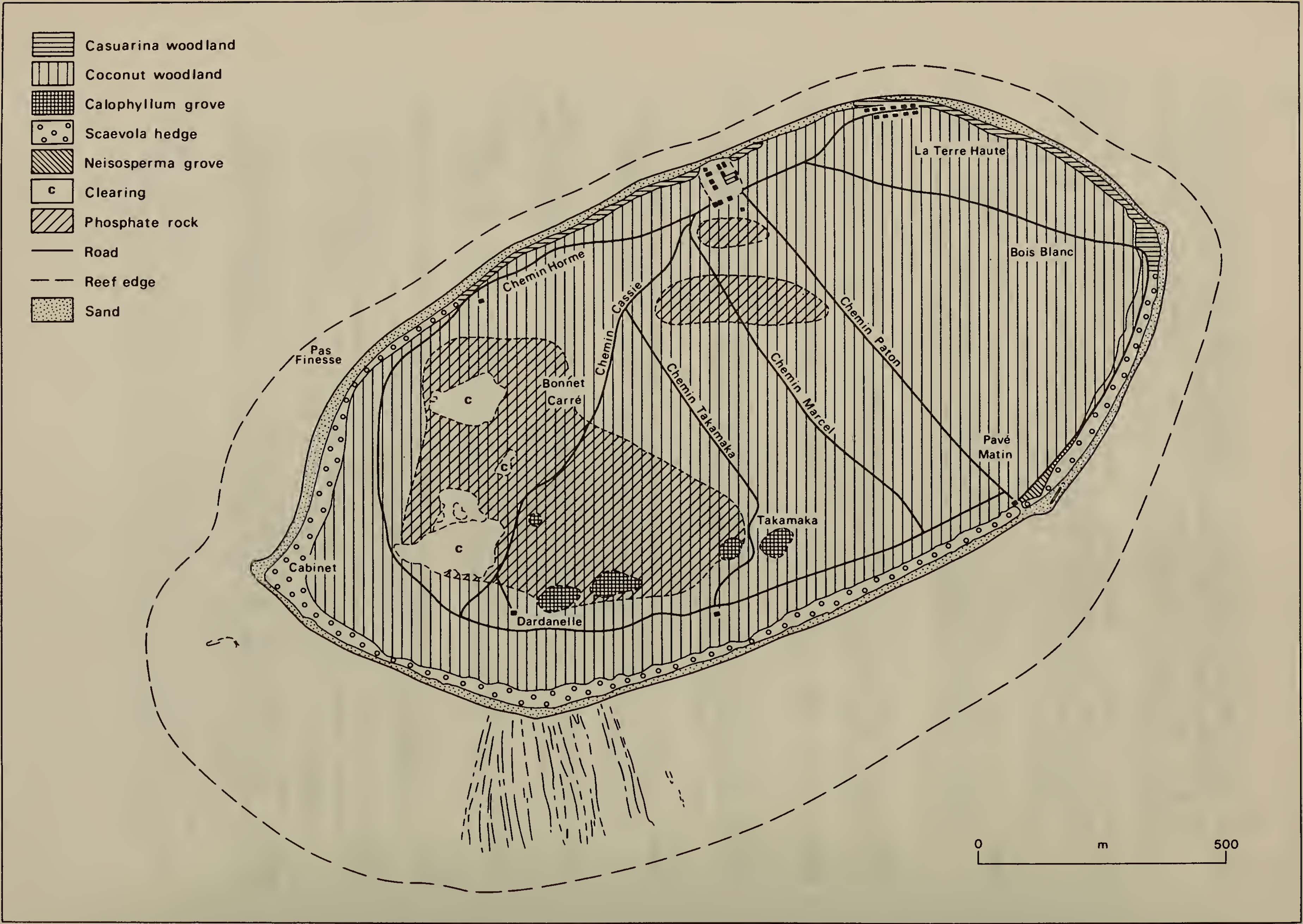

Figure 3. D'Arros Island. Based on aerial photographs with detail added from Baker (1963) and Piggott (1968)

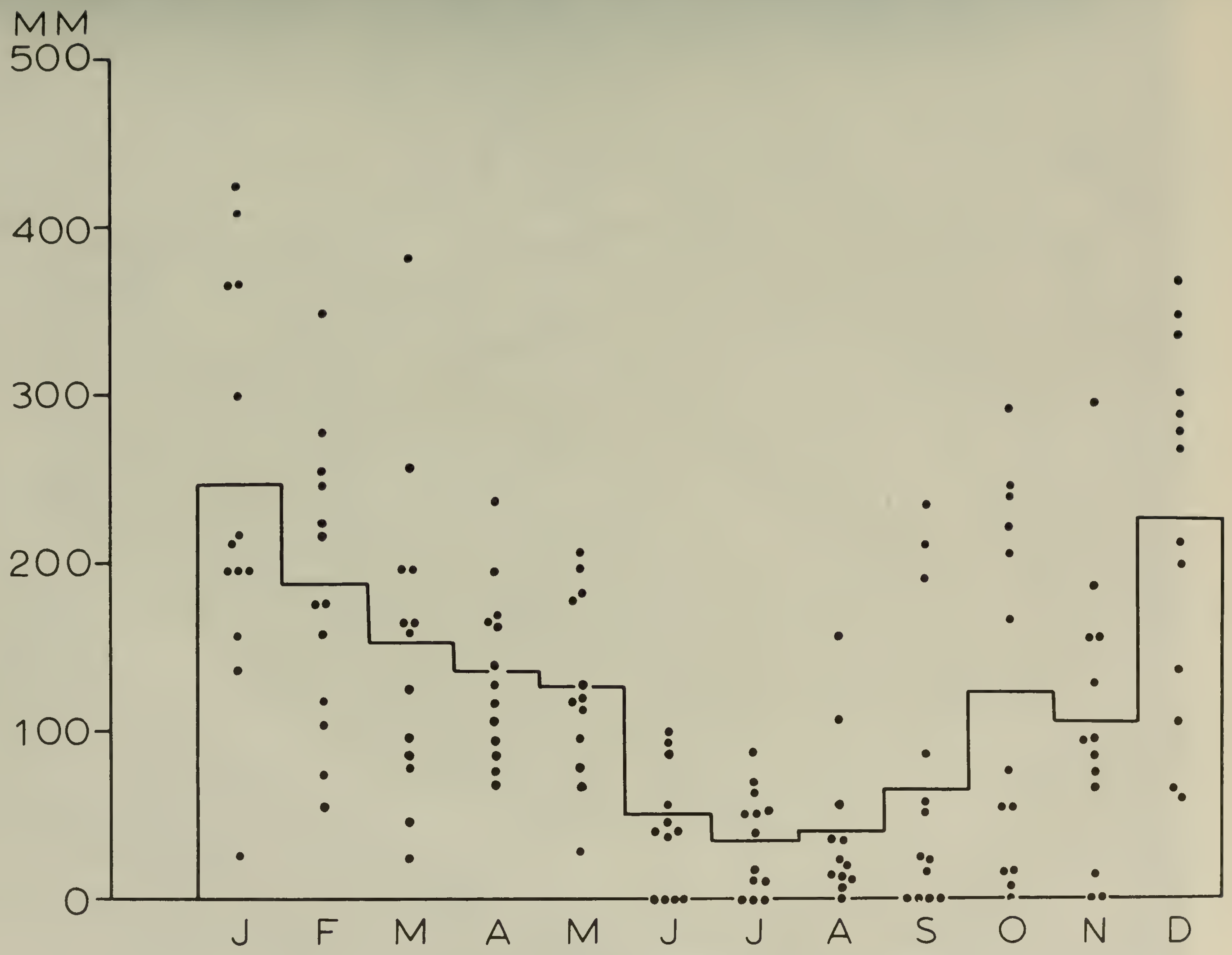

Figure 4. Monthly rainfall at D'Arros Island, 1950-62

Plate 1. D'Arros Island aerial photograph. Reproduced by permission of the Chief Surveyor, Survey and Lands Department, Republic of Seychelles

Plate 2. Southwest coast of D'Arros, showing *Scaevola* fringe, coconut woodland, and broadleaf groves

Plate 3. *Scaevola* and *Casuarina* at the southwest point of D'Arros

Plate 4. *Scaevola* and *Casuarina* at the northeast point of D'Arros

Plate 5. Tall *Casuarina* on the south coast of D'Arros Island

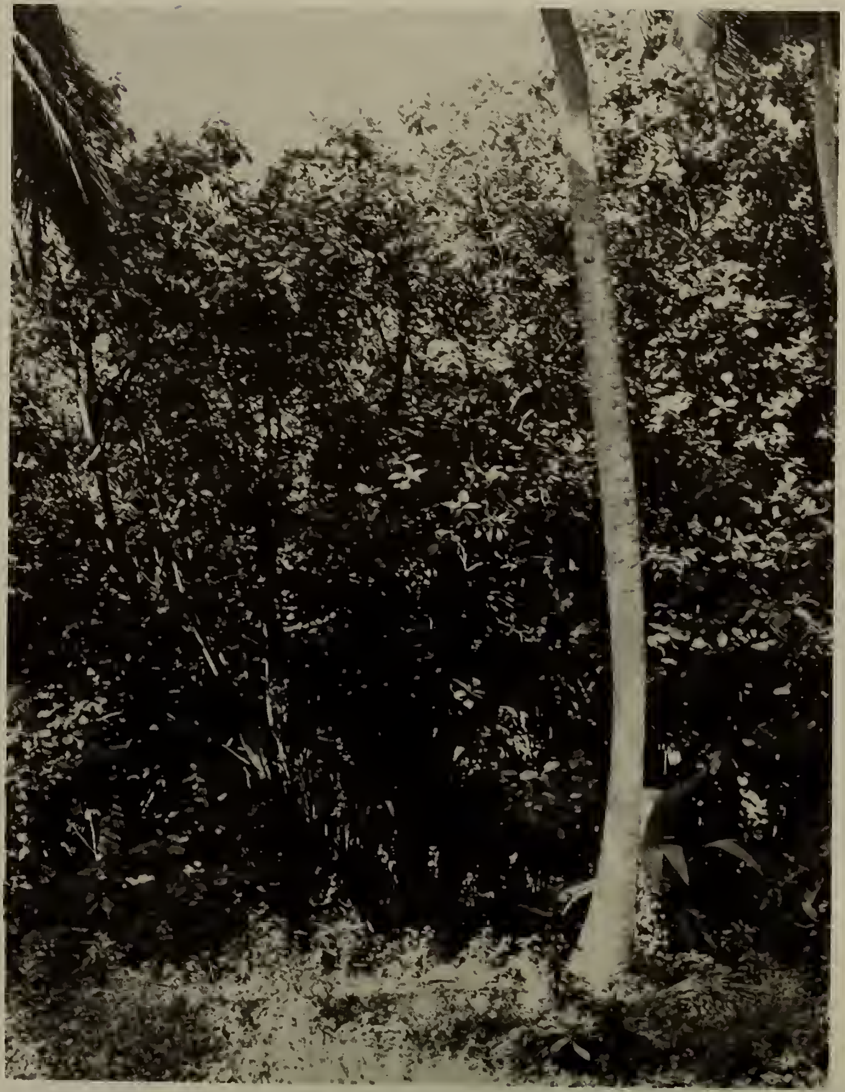

Plate 6. Mature *Barringtonia* within coconut woodland at D'Arros Island

Plate 7. Tall *Calophyllum* of inland groves at D'Arros Island

Plate 8. *Neisosperma* groves near the south coast of D'Arros Island

Plate 9. Coconut plantation near the north coast of D'Arros Island

Plate 10. Coconuts with undergrowth of *Kalanchoe*, northwestern part of D'Arros Island

Plate 11. New airstrip, western part of D'Arros Island

Plate 12. North shore of D'Arros Island showing tall *Casuarina* and the settlement

Plate 13. Centre of the settlement at D'Arros Island

Plate 14. Labourers' quarters at D'Arros Island

Plate 15. Manager's house at D'Arros Island

Plate 16. Copra works at D'Arros Island

Plate 17. Rainwater reservoir at D'Arros Island

Plate 18. Vegetable garden at D'Arros Island

Plate 19. Cemetery near the southeast shore at D'Arros Island

PLANTS OF D'ARROS ISLAND

F.R. Fosberg

POLYPODIACEAE

Nephrolepis biserrata (Sw.) Schott
    Stoddart 7215 (US)

POTAMOGETONACEAE

Syringodium isoetifolium (Aschers.) Dandy
    Gwynne and Wood 1007 (EA)

Thalassodendron ciliatum (Forsk.) den Hartog
  Cymodocea ciliata (Forsk.) Ehrenb. ex Aschers
    Gwynne and Wood 940 (EA)

GRAMINEAE

Cenchrus echinatus L.
    Gwynne and Wood 936 (EA); Stoddart 7157 (US)

Cynodon dactylon (L.) Pers.
    Gwynne and Wood 1011 (EA)

Dactyloctenium aegyptium (L.) Willd.
    Gwynne and Wood 934 (EA); Stoddart 7161 (US)

Digitaria ciliaris (Retz.) Koel.
    Stoddart 7162 (US), 7203 (US)

Digitaria horizontalis Willd.
    Gwynne and Wood 946 (EA), 1025 (EA)

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Eleusine indica (L.) Gaertn.
Gwynne and Wood 925 B (EA), 1024 (EA)

Eragrostis tenella var. *insularis* Hubb.
Gwynne and Wood 925 A (EA), 928 (EA)

Lepturus repens R. Br.
Gwynne and Wood 926 (EA)

Lepturus repens R. Br. var. *subulatus* Fosb.?
Stoddart 7188 (US)

Panicum maximum Jacq.
Stoddart 7223 (US)

Pennisetum polystachion (L.) Schult.
Stoddart 7222 (US)

CYPERACEAE

Cyperus dubius Rottb.
Mariscus dubius (Rottb.) Fischer
Gwynne and Wood 1013 (EA); Stoddart 7158 (US)

Cyperus ligularis L.
Mariscus ligularis (L.) Urb.
Gwynne and Wood 960 (EA); Stoddart 7191 (US)

Fimbristylis cymosa R. Br. (s.l.)
Fimbristylis obtusifolia sensu auct.
Gwynne and Wood 924, 1004, 1008, 1009, 1010 (all EA);
Stoddart 7226 (US), 7163 (US)

PALMAE

Cocos nucifera L.
Gwynne and Wood, sight; Stoddart, sight

ARACEAE

Alocasia macrorrhiza (L.) Schott
Stoddart 7206 (US)

AMARYLLIDACEAE

Crinum sp.
Stoddart 7190 (US)

MUSACEAE

Musa sapientum L.
Stoddart, sight

ORCHIDACEAE

Vanilla mexicana Mill.
Vanilla planifolia Andr.
Gwynne and Wood 945 (EA); Stoddart, sight

CASUARINACEAE

Casuarina litorea L.
Casuarina equisetifolia L.
Gwynne and Wood 1026 (EA)

URTICACEAE

Laportea aestuans (L.) Chew
Fleurya aestuans (L.) Miq.
Gwynne and Wood 942 (EA); Stoddart 7220 (US)

Pipturus argenteus (Forst.) Wedd.
Stoddart 7197 (US)

NYCTAGINACEAE

Boerhavia repens L. var.
Stoddart 7219 (US); Gwynne and Wood, sight

Mirabilis jalapa L.
Gwynne and Wood 944A (EA), 1029 (EA); Stoddart 7208 (US)

Pisonia grandis R. Br.
Gwynne and Wood 931 (EA), 941 (EA), 947B (EA)

PORTULACACEAE

Portulaca oleracea L.
Stoddart 7200 (US)

LAURACEAE

Cassytha filiformis L.
Gwynne and Wood 943 (EA), 948 (EA)

HERNANDIACEAE

Hernandia sonora L.
Gwynne and Wood 922 (EA); Stoddart 7195 (US)

MORINGACEAE

Moringa oleifera Lam.
Stoddart 7224 (US)

CRASSULACEAE

Kalanchoe pinnata (Lam.) Pers.
Bryophyllum pinnatum Lam.
Gwynne and Wood 1014 (EA); Stoddart 7187 (US)

LEGUMINOSAE

Adenanthera pavonina L.
Gwynne and Wood 1031 (EA)

Leucaena leucocephala (Lam.) deWit
Leucaena glauca sensu auct.
Gwynne and Wood 919 (EA), 1016 (EA); Stoddart 7210 (US)

Sesbania sericea (Willd.) Link
Gwynne and Wood 1002 (EA)

SURIANACEAE

Suriana maritima L.
Gwynne and Wood 937 (EA); Stoddart 7186 (US)

EUPHORBIACEAE

Euphorbia cyathophora Murr.
Gwynne and Wood 1022 (EA); Stoddart 7209 (US)

Euphorbia hirta L.
Gwynne and Wood 1023 (EA)

Euphorbia prostrata Ait.
Stoddart 7207 (US)

Phyllanthus maderaspatensis L.
Gwynne and Wood 1030 (EA)

Ricinus communis L.
Stoddart 7212 (US); Gwynne and Wood, sight

TILIACEAE

Triumfetta procumbens R. Br.
Stoddart 7194 (US)

MALVACEAE

Gossypium hirsutum L.
Gwynne and Wood 935 (EA); Stoddart 7202 (US)

Sida parviflora DC.
Stoddart 7192 (US)

Sida rhombifolia L.
Gwynne and Wood 1027 (EA)

GUTTIFERAE

Calophyllum inophyllum L. var. *takamaka* Fosb.
Stoddart 7221 (US)

TURNERACEAE

Turnera ulmifolia L.
Gwynne and Wood 927 (EA), 950 (EA), 961 (EA); Stoddart 7213 (US)

PASSIFLORAE

Passiflora suberosa L.
Gwynne and Wood 962 (EA); Stoddart 7216 (US)

CARICACEAE

Carica papaya L.
Stoddart 7214 (US)

CUCURBITACEAE

Cucurbita pepo L.
Stoddart 7201 (US)

COMBRETACEAE

Terminalia catappa L.
Stoddart, sight

LECYTHIDACEAE

Barringtonia asiatica (L.) Kurz
Gwynne and Wood 920 (EA); Stoddart 7198 (US)

APOCYNACEAE

Catharanthus roseus (L.) G. Don
Vinca rosea L.
Gwynne and Wood 1028 (EA); Stoddart 7204 (US)

Neisosperma oppositifolia (Lam.) Fosb. and Sachet
Ochrosia oppositifolia Lam.
Gwynne and Wood 923 (EA); Stoddart 7193 (US)

CONVOLVULACEAE

Ipomoea macrantha R. & S.
Ipomoea tuba (Don) Schlecht.
Gwynne and Wood 929 (EA), 932 (EA)

BORAGINACEAE

Cordia subcordata Lam.
Gwynne and Wood 921 (EA), 947A (EA); Stoddart 7199 (US)

Tournefortia argentea L. f.
Messerschmidia argentea (L. f.) Johnst.
Gwynne and Wood 1019 (EA); Stoddart 7189 (US)

VERBENACEAE

Lippia nodiflora L.
Gwynne and Wood 1003 (EA); Stoddart 7159 (US)

Stachytarpheta jamaicensis (L.) Vahl
Stoddart 7160 (US); Gwynne and Wood, sight

SOLANACEAE

Capsicum frutescens L.
Stoddart 7225 (US)

Solanum nigrum L. (sensu lato)
Gwynne and Wood 1018 (EA)

SCROPHULARIACEAE

Striga asiatica (L.) O. Ktze.
Gwynne and Wood 939 (EA); Stoddart 7217 (US)

ACANTHACEAE

Asystasia bojeri Nees
Gwynne and Wood 1021 (EA); Stoddart 7205 (US)

RUBIACEAE

Guettarda speciosa L.
Gwynne and Wood 930 (EA), 944B (EA); Stoddart 7196 (US)

Morinda citrifolia L.
Gwynne and Wood 1020 (EA); Stoddart 7218 (US)

GOODENIACEAE

Scaevola taccada (Gaertn.) Roxb.
Scaevola sericea Vahl
Scaevola frutescens sensu auct.
Stoddart 7165 (US)

COMPOSITAE

Bidens pilosa L.
Gwynne and Wood 1005 (EA); Stoddart 7211 (US)

Tagetes patula L.
Stoddart, sight

Tridax procumbens L.
Stoddart 7164 (US)

GEOGRAPHY AND ECOLOGY OF ST. JOSEPH ATOLL

D.R. Stoddart and M.J. Coe

INTRODUCTION

St. Joseph is an atoll located in latitude 5°25'S, longitude 53°20'E, in the Amirante Islands, immediately to the east of D'Arros Island (Figure 2). The atoll is roughly oval-shaped, and measures 7 km in longer and 4.4 km in shorter dimensions (Plate 20, Figure 5). The windward (eastern) reef flat is exceptionally wide, reaching 2.8 km at the eastern point; the northern reef flat is 1-1.5 km wide, the southern 1 km, and the western 600-800 m. The main island, at the eastern end, is St. Joseph; Fouquet and Ressource are larger islets on the northern rim; and there are several small islets in the south. There is some confusion over the names of these islets, and Table 4 gives the names recorded on recently published maps.

Previous work

Table 5 lists the main investigations carried out at St. Joseph. It was discovered by M. de la Biolière, aboard the *Etoile du Matin*, in 1771, and named St. Joseph. Moresby (1842) fixed its position in 1822. Though charted by Capt. J.P. Maclear of H.M.S. *Alert* in 1882, it was by-passed by the scientists of that expedition. Abbott collected birds in 1892, but the first general scientific studies were those of J. Stanley Gardiner and C. Forster Cooper of the Percy Sladen Trust Expedition on 10-11 October 1905. Later Vesey-Fitzgerald worked there, and more recently it has been visited by C.J. Piggott and B.H. Baker in 1960, and by the *Manihine* expedition (with I.S.C. Parker, M.D. Gwynne and D. Wood) in 1967. The present chart (Admiralty Chart 724) is based on the 1882 survey by the *Alert*, but it was again charted by H.M.S. *Hydra* in October 1975. It was visited by the present authors on 5-8 April 1976. Air photograph cover at a scale of 1: 12,800 was flown in 1960.

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Table 4. Names of islets on St. Joseph Atoll

Alert 1882	Hydra 1885	Baker 1963
St. Joseph	St. Joseph	St. Joseph
Cascassaye	Cascassaye	-
-	-	Banc Ferrari
Benjamen	Benjamen	Chien
Pelican	Pelican	Benjamin
Chien	Chien	Paul, Pelican
-	Sand bar	Banc Sable
Poule	Poule	Banc Coco
Ressource	Ressource	Ressource
Fouquet	Fouquet	Fouquet

Geomorphology

St. Joseph lies on the eastern edge of the Amirantes Bank (Figure 1). To the west, on the bank surface, bottom depths are less than 50 m, except in the narrow channel between the atoll and D'Arros, where they reach 60-62 m. To the east depths of 500 m are found 1.5 km from the reef edge, and of 1000 m about 2.5 km from the reef.

The total area of the atoll is 2253 ha. Of this, 79 per cent or 1774 ha comprises peripheral reef flat, and 21 per cent or 480 ha the interior lagoon. Islets occupy 8 per cent of the peripheral reef flats, or 139 ha. The lagoon is completely enclosed by the surrounding reef; at low water it drains over a narrow sill, Passe Lerein Fin, at its western end. The greatest depth sounded by H.M.S. *Alert* within the lagoon was 6.4 m; other soundings ranged from 2.1 to 3.7 m.

The peripheral reefs, in addition to being exceptionally wide, are covered (except on the west side) with mobile sand. Intertidal sand sheets are encroaching on the margins of the lagoon on its windward side, which is marked for much of its extent by a discontinuous linear sandbar. There are no flourishing reefs in the lagoon. Transverse reef ridges, especially in the centre and west, mark the location of former flourishing reefs; but these are now sediment-capped ridges topped with sea-grasses, with massive poritid and faviid corals on their sides. At least at the time of our visit in 1976 the lagoon water was turbid and visibility poor, in marked contrast to the sea outside the atoll reefs.

Table 5. Previous work at St. Joseph Atoll

Year	Investigator	Field of study	Main publication
1771	M. de la Biolière	Discovery	
(1882)	F. Moresby	Survey	Moresby 1842
1892	W.L. Abbott	Birds	Ridgway 1895
1905	J.S. Gardiner C. Forster Cooper H.M.S. *Sealark*	Land & marine animals	Gardiner and Cooper 1907
ca 1940	L.D.E.F. Vesey-FitzGerald	Birds	Vesey-FitzGerald 1941
1960	C.J. Piggott B.H. Baker	Soils, coconuts Geology	Piggott 1968, 1969 Baker 1963
1964	A.J. Bruce R.V. *Anton Bruun*	Marine fauna	Bruce 1971
1964	J.E. Böhlke and others	Marine fish	Tyler 1966, 1967; McCosker and Randall 1977
1967	I.S.C. Parker M.D. Gwynne D. Wood M.F.R.V. *Manihine*	Birds, plants	Parker 1970 Gwynne and Wood 1969
1975	R.J. Campbell H.M.S. *Hydra*	Survey	
1976	D.R. Stoddart M.J. Coe	Fauna and flora	

The reef islets are of two types: longitudinal and transverse (Plates 21-24). The longitudinal islets are aligned parallel to the reef edge, e.g. St. Joseph and Fouquet. They are sandy islands, and because of the amount of sediment on the reef flats it is often difficult clearly to delimit the foot of the island beaches. These islands probably do not rise more than 2.5 m above the level of the reef flats. The transverse islands have a foundation of transverse rubble bars, as at Ile Poule and Ile Chien (Plates 25-27). These comprise narrow tongues of storm debris standing about 1 m above the level of the flats, and often widening seawards. Such bars are very common on the southern reef, and not all of them have sand spits or vegetated islets on them. They appear to be of similar age, and may represent a single phase of storminess.

There is some indication of considerable topographic change over the last century in the form of some of the smaller islets. Thus in 1882 Chien was charted as much larger than at present; Benjamen has apparently similarly decreased from a single large islet to a group of small ones; Cascassaye, the southernmost section of St. Joseph, was then a separate islet. These interpretations rely on the accuracy of the survey during the brief visit by the *Alert*, but they are not inconsistent with the impression of considerable mobility of large amounts of sediment on the reef flats. Gardiner (1906, 457, 461; Gardiner and Cooper 1907, 154) gives photographs of beaches and beach rock on the eastern side of the atoll, and also speculates on topographic change.

Piggott (1968, 1969) emphasised the apparent recency of the islands, indicated by the absence of phosphatic Jemo Series soils and the dominance of immature sandy and gravelly Shioya Series soils. Baker (1963, 17), however, noted the existence of an area of phosphatic sandstone near Mare Frégate in the southern part of St. Joseph, but this area was not visited by us.

Marine fauna

There appear to be no records in the literature of marine animals from St. Joseph atoll, other than single species of pontoniinid shrimp recorded by Bruce (1971), and some species of fish collected by J.E. Böhlke in 1964 (Tyler 1966, 1967; McCosker and Randall 1977).

Vegetation

The larger islands of St. Joseph, notably St. Joseph itself, Fouquet and Ressource, are covered with coconut plantations which are at least as old as those of D'Arros. Probably because of the more isolated state of the atoll, resulting from the absence of a passage into the lagoon, the introduced weed flora is much more restricted than on D'Arros, and the whole aspect of the vegetation in the plantations is therefore very different. This paucity in the herb and grass flora also extends, however, to pioneer habitats, which are characteristically occupied by shrubs, and where much ground remains bare. Athough there can be little climatic difference between D'Arros and St. Joseph, the former therefore gives an impression of damp luxuriance, and the latter in many areas of much greater aridity; these differences undoubtedly reflect the differences in the nature and level of human activity on the two places.

Pioneer shrub community

A mixed community of shrubs on the sand islet of Poule includes *Pemphis acidula* up to 5 m tall (Plate 28), *Suriana maritima*, *Tournefortia argentea* (Plate 29) and *Scaevola taccada*. The ground surface is completely bare, except for a single tussock of *Lepturus repens*, one small patch of *Boerhavia*, and a pair of germinating coconuts. Similar areas of low shrubs with bare ground beneath are found on the islands south of St. Joseph.

Coastal scrub

Scaevola taccada is the typical shrub species of seaward beaches on the larger islands, as on D'Arros, together with occasional shrubs of *Tournefortia argentea* (Plates 30-33).

Coastal woodland

Guettarda speciosa is a very common beach crest tree, especially on lagoon shores (Plates 34-35), as on Fouquet and Chien. Both islands, and also Ressource, have coastal *Casuarina litorea* (Plate 36), both as individual trees and as groves. There is a single coastal tree of *Hernandia sonora* on Ressource.

Pemphis thicket

Most of the larger islands have extensive beach-foot thickets of *Pemphis acidula* on their lagoon shores, occupying locations where mangroves might be expected; these thickets are particularly extensive in the area of mud and sand flats at Cascassaye (Plates 28 and 37). A single tree of *Rhizophora mucronata*, fruiting abundantly, was found on the lagoon shore of Pelican (Plate 38), and it is not clear why mangroves are not much more common along lagoon shores.

Suriana thicket

A small pool at the eastern end of Fouquet is surrounded by a low scrub of *Suriana maritima* (Plate 39).

Coconut plantations

The coconut plantations are intensively managed on St. Joseph (Plate 40), but on the other islands they form a thicket with tall herbs and juvenile palms (Plate 41). *Kalanchoe pinnata* up to 1 m tall is common in these latter situations. Other common herbs in the plantations include *Achyranthes aspera, Boerhavia repens, Cassytha filiformis, Euphorbia hirta, Ipomoea macrantha, Passiflora suberosa, Phyllanthus maderaspatensis, Portulaca oleracea, Sida parvifolia, Stachytarpheta jamaicensis, Striga asiatica, Tridax procumbens, Turnera ulmifolia* and *Vernonia cinerea*; the grasses *Lepturus repens, Eragrostis ciliaris, Stenotaphrum micranthum, Sporobolus virginicus,* and *Dactyloctenium aegyptium;* and the sedges *Cyperus ligularis* and *Fimbristylis cymosa*.

Settlement vegetation

The small settlement at the western end of St. Joseph has a cluster of introduced trees: *Barringtonia asiatica* and *Terminalia catappa* 15 m tall, *Hernandia sonora* 10 m tall, and *Leucaena leucocephala*. There are cultivated trees of *Moringa oleifera, Carica papaya,* shrubs of *Capsicum frutescens,* and decorative *Hymenocallis, Crinum* and *Catharanthus*.

Flora

The first collection of vascular plants from St. Joseph was that made by Gwynne and Wood (1969). Their 40 numbers comprised 28 species (including *Pithecellobium unguis-cati*, omitted from their published list). The 44 numbers collected in 1976 comprise 39 species, bring the total number of plants recorded to 47 species, including two sea-grasses, listed in the following paper by F.R. Fosberg. The flora is noteworthy in comparison with that of neighbouring D'Arros by the presence of *Pemphis* and *Rhizophora*, and the absence of *Cordia* and of many of the common introduced weedy species of D'Arros.

Terrestrial fauna

Birds

Wedge-tailed Shearwater *Puffinus pacificus*

Recorded as *P. tenuirostris*, breeding in large numbers, by Gadow and Gardiner (1907). Gardiner and Cooper (1907, 153) also mention a "vast number" on Fouquet, as well as burrows on Pelican (ibid., p.154). It was recorded as breeding by Vesey-FitzGerald (1941), and as numerous, and breeding on Fouquet, by Parker (1970). One male and two females collected by Parker are in the National Museum of Kenya, registered numbers 20937-20940. Fouquet was still covered with large numbers of burrows in 1976, and local workers assured us that the birds were still common. No burrows were seen on Ressource, but they were said to be still found at the southern end of St. Joseph. They were also found on the southern end of Pelican. The restriction of clearing on Fouquet would doubtless ensure the survival of the nesting area on that island.

White-tailed Tropicbird *Phaethon lepturus*

Six were seen at Ressource by Parker (1970).

Pink-backed Pelican *Pelecanus rufescens*

W.L. Abbott collected a specimen of this species on 29 August 1892 and it was listed by Ridgway (1895, 516), with a note by Abbott referring to "a small colony - perhaps one hundred individuals ... the only colony of pelicans in these seas". The colony was again seen by Gardiner in 1905. "These large birds were found breeding in a colony in the coconut and other large trees of the eastern island of St. Joseph Atoll, Amirante Group. Young birds were seen in October 1905" (Gadow and Gardiner 1907, 110). No specimens were taken but the birds were identified as Dalmatian Pelican *Pelecanus crispus*. Gardiner and Cooper (1907, 154) state: "St. Joseph is covered with tall coconuts, some of which were weighted down and killed by the large nests of

Pelecanus crispus, of which there was a numerous colony. How far this bird is a wanderer we do not know". Both Betts (1940, 504) and Watson et al. (1963, 180) follow Gardiner in listing the species as the Dalmation Pelican, even though this is a ground-nesting species. *P. crispus* does not breed closer to the Amirantes than the Persian Gulf. Dr. G.E. Watson has located Abbott's original specimen and has confirmed its overlooked identification by Ridgway as *P. rufescens* (Stoddart 1977); the specimen is in the National Museum of Natural History, Washington. There are several records of this species from Madagascar and one from the Dahlak Archipelago, Red Sea, but otherwise none outside mainland Africa; its occurrence on St. Joseph is thus of some interest. Loustau-Lalanne (1963, 23) gives a hearsay report of two individuals of *P. crispus* on Bijoutier, Alphonse, southern Amirantes; if the presence of these birds is confirmed they may also be *P. rufescens*. The colony was not seen by Vesey-FitzGerald in the 1930s, has not been subsequently reported, and was not present in 1976. The fact that one of the islets on St. Joseph was charted as 'Pelican' by H.M.S. *Alert* in 1882 may indicate either that the species was present then, or that it had nested there sufficiently recently for the name to be recognised.

Brown Booby *Sula leucogaster*

Listed by Ridgway (1895) on the basis of Abbott's report. A nest with two eggs was recorded in November by Vesey-FitzGerald (1941). This species was not seen in 1976.

Red-footed Booby *Sula sula*

Abbott collected a single specimen of this species in 1892 (Ridgway 1895). Gardiner and Cooper (1907, 153-154) refer to "another common bird, likewise breeding, - the booby (*Sula piscator*), found so abundantly before at St. Pierre, and wandering daily from St. Joseph over every reef in the group". There is no later record of this species on the atoll.

Great Frigatebird *Fregata minor*

One immature was collected by Parker (1970). Up to 500 birds, either Great or Lesser Frigates, were seen over Fouquet on 6 April 1976. As on D'Arros, it is unlikely that they breed because of the lack of suitable nesting sites.

Lesser Frigatebird *Fregata ariel*

Sight record by Parker (1970). A male was taken by Abbott in August 1892 (USNM 128775) (Ridgway 1895).

Grey Heron *Ardea cinerea*

Recorded by Watson et al. (1963). Fifteen were seen by Parker (1970). Common on all the islands and the reef flats.

Little Green Heron *Butorides striatus*

Listed as *B. atricapilla* by Ridgway (1895). Noted as resident by Watson et al. (1963), and as common on all the islets by Parker (1970). The National Museum of Kenya has a female collected on the "reef between D'Arros and St. Joseph", 23 September 1967, by Parker, registered number 20931. Abundant in 1976 on all the islands. During the heat of the day and evening the birds commonly roost on palm fronds, landing and creeping close to the shelter of the crown with the body held horizontal. This bird is the subspecies *B. s. crawfordi* which is common from Aldabra to the Amirantes, being replaced in the Seychelles by *B. s. degens*. Although the latter subspecies may occur in the Amirantes (Penny, 1974), it was the former which was observed on the islands visited in 1976.

Cattle Egret *Bubulcus ibis*

Recorded by Ridgway (1895) (as *B. bubulcus*) and by Watson et al. (1963, 180).

Turnstone *Arenaria interpres*

Listed by Ridgway (1895) and as a non-breeding migrant by Watson et al. (1963); seen by Parker (1970). Common in 1976 along shorelines and in plantations.

Grey Plover *Squatarola squatarola*

Seen by Parker (1970). A single bird was seen on the reef flat on 7 April 1976.

Greater Sand Plover *Charadrius leschenaultii*

Seen by Parker (1970).

Whimbrel *Numenius phaeopus*

Listed by Ridgway (1895) and as a non-breeding migrant by Watson et al. (1963). Very common on the shoreline and in plantations in 1976.

Greenshank *Tringa nebularia*

Six seen by Parker (1970).

Common Sand Piper *Tringa hypoleucos*

Seen on the shorelines of St. Joseph and Ressource, 6-7 April 1976.

Sanderling *Crocethia alba*

One male collected on Ressource, 23 September 1967, by Parker, and now in the National Museum of Kenya, registered number 20923.

Crab Plover *Dromas ardeola*

Twelve seen by Parker (1970), who collected one female and two juveniles on 23 September 1967, now in the National Museum of Kenya, registered numbers 20932-20934. Three birds observed on St. Joseph and two on Ressource, 7 April 1976.

Black-naped Tern *Sterna sumatrana*

Recorded as nesting, without precise locality, by Vesey-FitzGerald (1941, 256), and noted as breeding in September-November by Watson et al. (1963, 181). One seen by Parker (1970) on Ressource. Several seen over the reef flats off Ressource and St. Joseph on 7 April 1976. Both Ressource and several of the small islets south of St. Joseph would seem to have suitable beaches for terns to nest.

Bridled Tern *Sterna anaethetus*

This species, seen by Parker (1970), is not recorded from the Amirantes by Watson et al. (1963). Penny (1974) records it as occurring in the group.

Sooty Tern *Sterna fuscata*

There is no previous record of this species from St. Joseph Atoll. A group of a dozen was seen on Ressource, 7 April 1976, settling on vegetation on the beach crest and fishing over the reef flat margin.

Crested Tern *Thalasseus bergii*

Two birds seen on the reef flat off Ressource, 7 April 1976.

Common Noddy *Anous stolidus*

Seen by Parker (1970). A small group flying with Sooty Terns seen on Ressource, 7 April 1976.

White Tern *Gygis alba*

Recorded as breeding by Vesey-FitzGerald (1941, 529-530), and noted as very common by Parker (1970). Very common along the shores of all islands in 1976, but no nesting birds seen.

Turtledove *Streptopelia picturata*

The endemic subspecies of the Madagascar Turtledove in the Amirantes is the vinous-headed *S. p. saturata*. Parker collected two grey-headed females on 23 September 1967 on St. Joseph Island, and these are in the National Museum of Kenya, registered numbers 20927-20928. Benson (1970) has suggested that these specimens are hybrids resulting from an introduction of *S. p. picturata* from the Seychelles. Two birds were observed on D'Arros, 7 April 1976, and one on St. Joseph, 7 April 1976; all had typical grey heads and deep purple mantles.

House Sparrow *Passer domesticus*

First recorded as introduced by Abbott in 1892 (Ridgway 1895). Noted as very common on Ressource and St. Joseph by Parker (1970). He collected one female on Ressource on 23 September 1967, now in the National Museum of Kenya, registered number 20901. Very common in 1976 on St. Joseph Island, but not seen on Fouquet or Ressource.

Madagascar Fody *Foudia madagascariensis*

Noted as numerous on Ressource and St. Joseph by Parker (1970). One male collected on Ressource on 23 September 1967, now in the National Museum of Kenya, registered number 20900. Present on all the larger islands of the atoll, but the presence of the House Sparrow on St. Joseph Island seems to reduce its numbers there. Only seen in large parties on Ressource where the House Sparrow is apparently absent.

Reptiles

Madagascar Green Gecko *Phelsuma madagascariensis*

This species was common on all four main islands of the atoll. The presence of palm trees seems to favour their presence, and up to four animals were commonly seen on their trunks. Aggressive displays were observed in which the combatants faced each other and the bright red tongue was flashed across the face, having the appearance of a small red balloon momentarily inflated. This display was initiated usually by one of a pair after which the other gave way and retreated. Previously recorded from the atoll by the Percy Sladen Trust Expedition (Boulenger 1909).

House Gecko *Hemidactylus frenatus*

A specimen collected on St. Joseph is now in the British Museum (Natural History); this species has not previously been recorded from the atoll.

Seychelles Skink *Mabuia sechellensis*

Very common on all islands of the atoll. It occurs on tree trunks like *Phelsuma*, but it is also observed on the ground, unlike the Gecko. This species is restricted to the Seychelles and the Amirantes, although it is quite closely related to the widely distributed African species *M. maculilatris*.

Insects

We have found only a single species of insect previously recorded from St. Joseph Atoll, the Rhinoceros Beetle (Scott 1912). The caterpillars of the small arctiid moth *Utetheisa p. pulchelloides* Hampson were found defoliating *Scaevola* on Ressource, 8 April 1976. Also collected were specimens of *Euconocephalus* sp. (Tettigonioidea); *Icerya seychellarum* (Westwood); *Cardiophorus* sp. (Elateridae); *Dactylosternum* sp.? (Hydrophilidae); *Aedes (Stegomyia) albopictus* Skuse (Culicidae); and the following Staphylinidae: *Philonthus bisignatus* Boh., *Philonthus reinekis* Schab., *Philonthus* species (four not determined and one possibly new), *Gabronthus* sp., *Oxytelus varipennis* ssp. *Pharaohnum* Koch., and *Aleochara trivalis*.

Other Arthropods

Hirst (1913) records two spiders, including *Nephila madagascariensis*, from St. Joseph. We collected a specimen of a young huntsman spider (Heteropodidae) from Fouquet. The orb weaver *Tetragnatha* sp. is very common on all islands where it spins its golden webs in great numbers. Local children collect the thicker strands of these webs for fishing. Three millipedes were collected from a rotten palm trunk, and have been identified as follows:

Mystalides bivirgatus (Karsh), recorded from Tanzania, Pemba, Comoros, Aldabra, Madagascar.
Spirostrophos naresii (Pocock), recorded from Madagascar and Seychelles and widely distributed in the East and West Indies.
Orthomorpha coarctata (Sauss), cosmotropical distribution.

Recent clearing operations in the coconut plantations have removed many fallen trunks from the surface. However it is possible to measure the rate of decomposition of fallen palm trunks remaining. The dead trunks examined were probably not more than six years old, yet during this time the whole interior had been reduced to a broken powder comprised mainly of arthropod frass. In addition to the very large numbers of millipedes present there were also huge numbers of a small Entomobryoid-like Collembolan. At the time of our visit to the atoll recent rain had probably accelerated decomposer microorganism and detritivore activity, which must for much of the year be water-limited.

Borradaile (1907) records the land hermit crab *Coenobita rugosus* H. Milne-Edwards from St. Joseph. We did not, however, find these crustaceans to be common. One male and one female were collected on Ressource, together with three individuals of *Coenobita perlatus* H. Milne-Edwards. Only a single colony was found of the large crab *Cardiosoma carnifex* (Herbst), and this too was on Ressource, under *Pemphis* scrub on the west shore. One female of this species and the specimens of *Coenobita* are in the British Museum (Natural History).

Ocypodid crabs were abundant on virtually all the beaches visited. Their excavations for the small bivalve mollusc *Donax faba* were especially prominent on the lagoonward shores of St. Joseph, where a female *Ocypode ceratophthalmus* (Pallas) was collected. These crabs play an important role in adding to and reworking the sediments of the beaches, in some of which *Donax* shells form a dominant component.

The Lagoon

The lagoon, which has general maximum depths of about 3 m, is divided into a series of basins by parallel flat-topped reef ridges trending northeast to southwest and concentrated in its western half. The upper surfaces and edges of these ridges are emergent during lowest tides and do not support living corals. They are covered with thick growths of marine angiosperms, mainly *Thalassodendron ciliatum* and *Thalassia hemprichii*, with a molluscan infauna characterised by *Pinna*. *Syringodium isoetifolium* has been collected on the reef flat at D'Arros but not at St. Joseph, though it is common in shallow water on the north side of the lagoon. Massive faviid and poritid corals grow on the flanks of the ridges, especially on their eastern (windward) sides; but they are clearly adversely affected by siltation, and the coralla are heavily bored and deformed. Presumably because of the absence of any open channel to the sea, the lagoon acts as a sediment sink. Wide fans of sediment are advancing into the lagoon from the peripheral reefs, especially on the south and southeast sides, and during our visit the lagoon water was extremely turbid, in marked contrast to that outside the seaward reef margins. Shallow surfaces in the lagoon are covered with thick silty sand sheets up to 30 cm deep.

Large rays are extremely common on shallow sandy reef flats. In several cases they were seen swimming in pairs, raising their pectoral fins above the water and diving one above the other, and it seems probable that they were courting. Seychellois on the atoll say that rays are always common in the lagoon. Black-tipped and White-tipped sharks (*Carcharinus melanopterus, Triaenodon abesus*) are seen in all parts of the lagoon. No Green Turtles *Chelonia mydas* were seen, but up to a dozen Hawksbill Turtle *Eretmochelys imbricata* were seen on the D'Arros aspect of the atoll and around the islets south of St. Joseph.

The shallow nature of the lagoon and the low rate of water turnover leads us to suspect that it is in a low state of productivity. Thus suggestion would seem to be supported by the fact that few fish shoals were observed in the lagoon during our visit. The presence of storm beaches and the width of the reef flats may well inhibit the transport of reef-generated nitrogenous particulate matter into the lagoon.

Settlement

The only settlement on the atoll at present is on St. Joseph island, though there are remains of huts some years old on both Fouquet and Ressource. The plantations were well established by 1905, when Tonnet reported that there were more trees on St. Joseph than on D'Arros. At that time there were 4000 coconut trees on Fouquet and 2500 on Ressource, as well as the main plantation on St. Joseph; together with small plantations on Benjamen and Cascassaye. The population in September 1905 was 26, including 3 each on Fouquet and Ressource.

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Plate 20. St Joseph Atoll: vertical air photograph mosaic. Reproduced by permission of the Chief Surveyor, Survey and Lands Department, Republic of Seychelles

Plate 21. St Joseph Atoll from the northeast; the island in the foreground is St Joseph Island

Plate 22. Southern reef of St Joseph Atoll, from the east. The islet in the foreground is Chien, and the large island in the background is D'Arros

Plate 23. Pelican Island from the south, with Fouquet in the background

Plate 24. The southern part of St Joseph Island (Cascassaye), from the east, with Pelican and other islets behind

Plate 25. Hammerhead shingle spit at Banc Coco, St Joseph Atoll

Plate 26. Banc Sable, St Joseph Atoll

Plate 27. *Scaevola* and *Suriana* shrubs on Banc Sable, St Joseph Atoll

Plate 28. Scrub of *Pemphis acidula* on Ile Poule, St Joseph Atoll

Plate 29. Scrub of *Tournefortia argentea* on Ile Poule, St Joseph Atoll

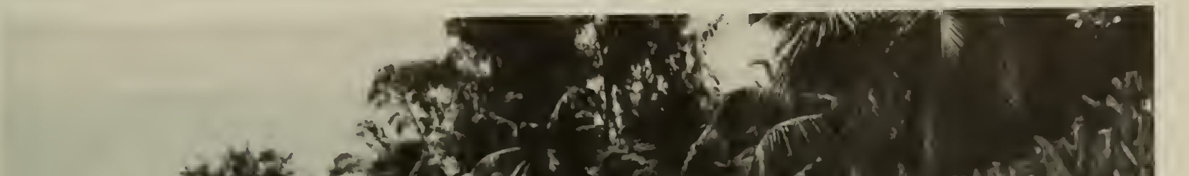

Plate 30. *Scaevola* scrub, seaward shore of Ile Fouquet, St Joseph Atoll

Plate 31. *Scaevola* scrub, coconuts and *Casuarina*, seaward shore of Ile Fouquet, St Joseph Atoll

Plate 32. *Scaevola* scrub, northern lagoon shore of Ile Fouquet, St Joseph Atoll

Plate 33. Pioneer *Scaevola*, southeast point of Ile Fouquet, St Joseph Atoll

Plate 34. Coastal *Guettarda* woodland, eastern seaward shore of Ile Fouquet, St Joseph Atoll

Plate 35. *Guettarda* woodland, west coast of Pelican Island, St Joseph Atoll

Plate 36. Coastal coconut and *Casuarina* woodland, lagoon shore of St Joseph Island, St Joseph Atoll

Plate 37. *Pemphis* scrub and cemented gravel on Ile Ressource, St Joseph Atoll

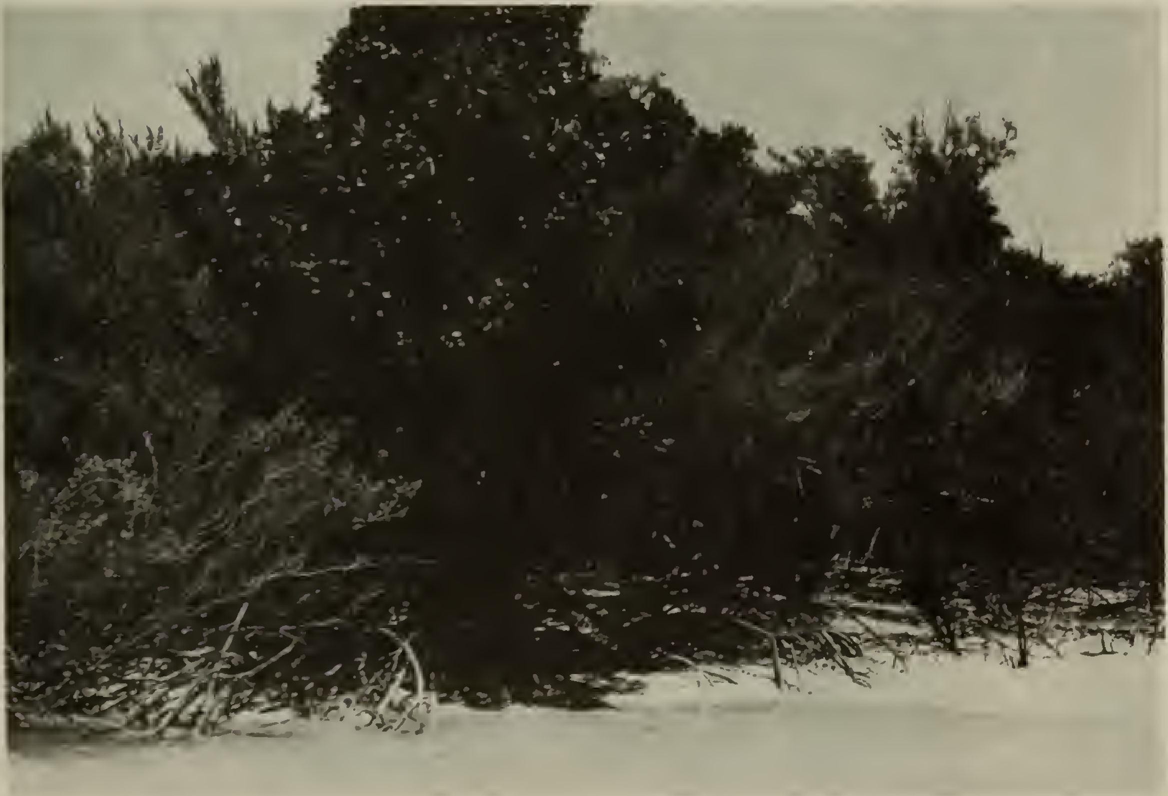

Plate 38. *Rhizophora* in *Pemphis* scrub, west shore of Pelican Island, St Joseph Atoll

Plate 39. Mudhole surrounded by *Suriana* scrub, with germinating coconuts, east end of Ile Fouquet, St Joseph Atoll

Plate 40. Mature coconut woodland, north end of St Joseph Island, St Joseph Atoll

Plate 41. Abandoned coconut plantation with juvenile coconuts, Ile Fouquet, St Joseph Atoll

Figure 5. St Joseph Atoll. Based on aerial photographs with detail added from Baker (1963) and Piggott (1968)

PLANTS OF ST. JOSEPH ATOLL

F.R. Fosberg

POTAMOGETONACEAE

Thalassodendron ciliatum (Forsk.) den Hartog
Cymodocea ciliata (Forsk.) Ehrenb. ex Aschers.
Gwynne and Wood 1057 (EA) (Fouquet); Stoddart 7167 (US), 7170 (US) (St. Joseph).

HYDROCHARITACEAE

Thalassia hemprichii (Ehrenb.) Aschers.
Gwynne and Wood 1056 (EA) (Fouquet); Stoddart 7168 (US), 7169 (US); (St. Joseph).

GRAMINEAE

Dactyloctenium aegyptium (L.) Willd.
Gwynne and Wood 966 (EA), 987 (EA) (St. Joseph); 1059 (Fouquet)

Dactyloctenium sp.
Stoddart 7147 (US) (Fouquet)

Eragrostis ciliaris (L.) R. & S.
Gwynne and Wood 967 (EA)

Eragrostis tenella var. *insularis* Hubb.
Gwynne and Wood 981 (EA) (St. Joseph)

Lepturus repens R. Br.
Gwynne and Wood 982 (EA) (St. Joseph)

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Lepturus repens R. Br. var. *subulatus* Fosb.
Stoddart 7140 (US)

Sporobolus virginicus (L.) Kunth
Stoddart 7155 (US) (St. Joseph)

Stenotaphrum micranthum (Desv.) Hubb.
Stenotaphrum subulatum Trin.
Gwynne and Wood 973 (EA), 985 (EA) (St. Joseph), 1061 (EA) (Fouquet); Stoddart 7145 (US) (Fouquet)

CYPERACEAE

Cyperus ligularis L.
Mariscus ligularis (L.) Urb.
Stoddart 7141 (US) (Fouquet)

Fimbristylis cymosa R. Br.
Fimbristylis obtusifolia sensu auct.
Gwynne and Wood 958 (EA), 959 (EA), 983 (EA) (St. Joseph); Stoddart 7139 (US) (Fouquet)

PALMAE

Cocos nucifera L.
Gwynne and Wood, sight; Stoddart, sight

AMARYLLIDACEAE

Crinum angustum Roxb.
Gwynne and Wood 957 (EA) (St. Joseph)

Hymenocallis littoralis (Jacq.) Salisb.
Stoddart 7176 (US) (St. Joseph)

CASUARINACEAE

Casuarina litorea L.
Casuarina equisetifolia L.
Gwynne and Wood 963 (EA) (St. Joseph); Stoddart 7150 (Fouquet)

AMARANTHACEAE

Achyranthes aspera L. var. *mollis* (Moq.) Townsend
Gwynne and Wood 1060 (EA) (Fouquet); Stoddart 7148 (US) (Fouquet)

NYCTAGINACEAE

Boerhavia repens L. var.
Stoddart 7146 (US) (Fouquet)

Pisonia grandis R. Br.
Gwynne and Wood 986 (EA) (St. Joseph)

PORTULACACEAE

Portulaca oleracea L.
Stoddart 7177 (US) (St. Joseph)

LAURACEAE

Cassytha filiformis L.
Gwynne and Wood 965 (EA) (St. Joseph); Stoddart 7136 (US) (Fouquet)

HERNANDIACEAE

Hernandia sonora L.
Gwynne and Wood 954 (EA) (St. Joseph); Stoddart 7154 (US) (St. Joseph), 7227 (US) (Ressource).

MORINAGACEAE

Moringa oleifera Lam.
Stoddart 7174 (US) (St. Joseph)

CRASSULACEAE

Kalanchoe pinnata (Lam.) Pers.
Bryophyllum pinnatum Lam.
Stoddart 7135 (US) (Fouquet)

LEGUMINOSAE

Leucaena leucocephala (Lam.) deWit
Leucaena glauca sensu auct.
Stoddart 7173 (US) (St. Joseph)

Pithecellobium unguis-cati (L.) Benth.
Gwynne and Wood 953 (St. Joseph)

SURIANACEAE

Suriana maritima L.
Gwynne and Wood 979 (EA) (St. Joseph); Stoddart 7138 (US) (Fouquet)

EUPHORBIACEAE

Euphorbia hirta L.
Stoddart 7172 (US) (St. Joseph)

Phyllanthus maderaspatensis L.
Gwynne and Wood 975 (EA), 989 (EA) (St. Joseph); Stoddart 7178 (US) (St. Joseph).

MALVACEAE

Hibiscus tiliaceus L.
Stoddart 7181 (US) (St. Joseph)

Sida parvifolia DC.
Gwynne and Wood 972 (EA) (St. Joseph); Stoddart 7185 (Ile Paul) (US)

TURNERACEAE

Turnera ulmifolia L.
Stoddart 7180 (US) (St. Joseph)

PASSIFLORAE

Passiflora suberosa L.
Gwynne and Wood 968 (EA), 984 (EA) (St. Joseph) 1062 (EA) (Fouquet); Stoddart 7144 (US) (Fouquet)

LYTHRACEAE

Pemphis acidula R. Br.
Gwynne and Wood 955 (EA), 980 (EA) (St. Joseph), 1058 (EA) (Fouquet); Stoddart 7143 (US) (Fouquet).

RHIZOPHORACEAE

Rhizophora mucronata Lam.
Stoddart 7182 (US) (Ile Benjamin)

COMBRETACEAE

Terminalia catappa L.
Stoddart 7152 (US) (St. Joseph)

LECYTHIDACEAE

Barringtonia asiatica (L.) Kurz
Stoddart 7153 (US), 7166 (US) (St. Joseph)

APOCYNACEAE

Catharanthus roseus (L.) G. Don
Vinca rosea L.
Gwynne and Wood 951 (EA) (St. Joseph); Stoddart 7171 (US) (St. Joseph)

CONVOLVULACEAE

Ipomoea macrantha R. & S.
Ipomoea tuba (Don) Schlecht.
Stoddart 7184 (US) (Ile Benjamin), 7228 (US) (Ressource)

BORAGINACEAE

Tournefortia argentea L. f.
Messerschmidia argentea (L. f.) Johnst.
Stoddart 7137 (US) (Fouquet)

VERBENACEAE

Stachytarpheta jamaicensis (L.) Vahl
Stoddart 7142 (US) (Fouquet)

SOLANACEAE

Capsicum frutescens L.
Stoddart 7175 (US) (St. Joseph)

SCROPHULARIACEAE

Striga asiatica (L.) O. Ktze.
Gwynne and Wood 969 (EA) (St. Joseph); Stoddart 7156 (US) (St. Joseph), 7183 (US) (Ile Benjamin)

RUBIACEAE

Guettarda speciosa L.
Gwynne and Wood 964 (EA), 978 (EA) (St. Joseph); Stoddart 7151 (US) (Fouquet)

GOODENIACEAE

Scaevola taccada (Gaertn.) Roxb.
Scaevola sericea Vahl
Scaevola frutescens sensu auct.
Gwynne and Wood 977 (EA) (St. Joseph); Stoddart 7149 (US) (Fouquet)

COMPOSITAE

Bidens pilosa L.
Gwynne and Wood 956 (EA) (St. Joseph)

Tridax procumbens L.
Gwynne and Wood 974 (EA) (St. Joseph)

Vernonia cinerea (L.) Less. var. *parviflora* DC.
Gwynne and Wood 970 (EA) (St. Joseph); Stoddart 7179 (St. Joseph)

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NO. 224

MICROATOLLS: REVIEW OF FORM, ORIGIN AND TERMINOLOGY

by D. R. Stoddart and T. P. Scoffin

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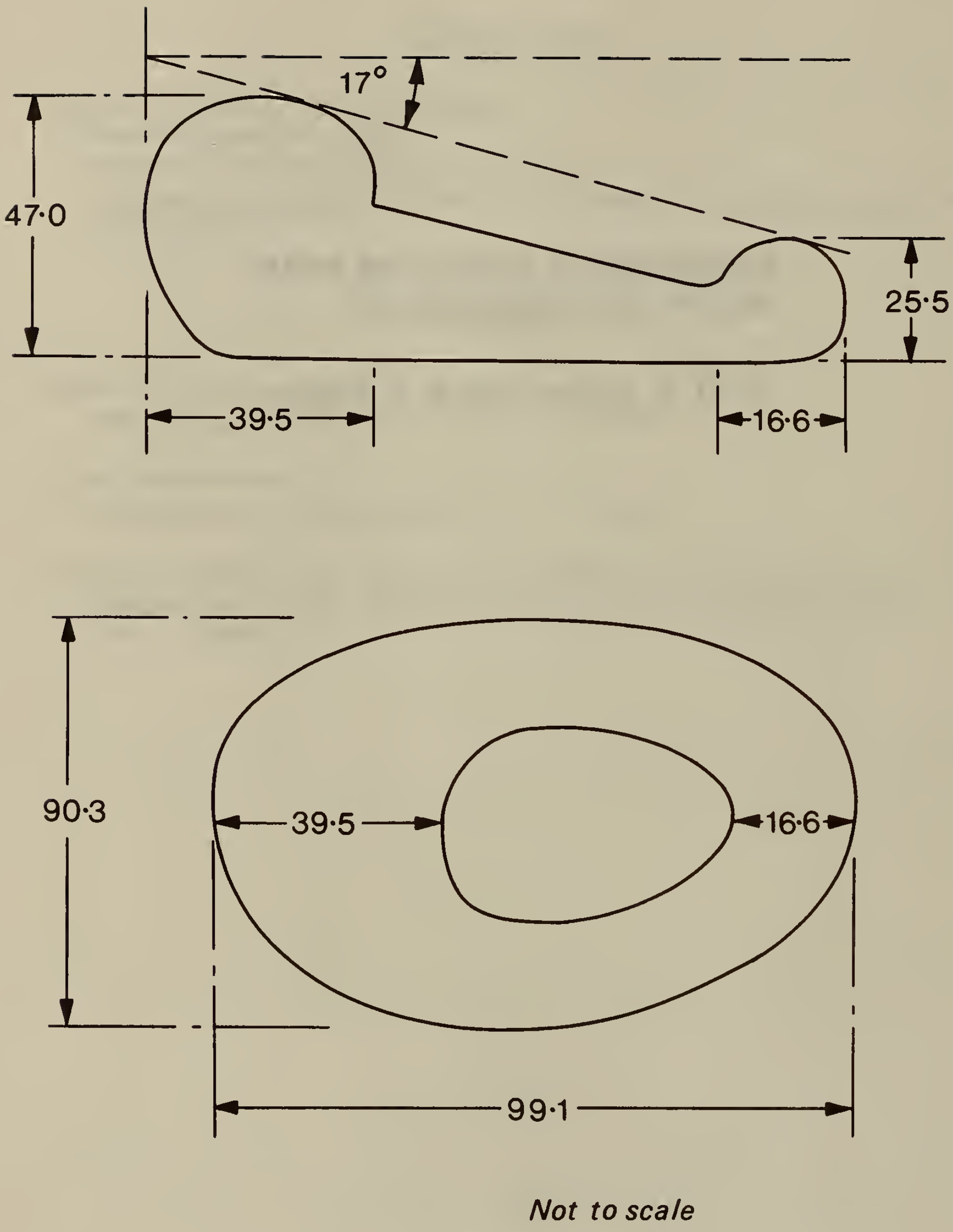

Figure 1. Dimensions of inclined microatolls of *Goniastrea aspera* (cm), after Abe (1937).

MICROATOLLS: REVIEW OF FORM, ORIGIN AND TERMINOLOGY

by D. R. Stoddart[1] and T. P. Scoffin[2]

Perusal of much recent literature reveals wide differences in usage of terms referring to microatolls (in the sense of individual coral colonies) and small atoll-shaped reefs. Though many writers mention differences in interpretation of such features, there is no comprehensive recent summary of work on the subject, other than R. W. Fairbridge's article on microatolls in his *Encyclopaedia of Geomorphology* (1968). Work by the authors on microatolls during the Royal Society and Universities of Queensland Expedition to the northern Great Barrier Reef in 1973 (Scoffin and Stoddart, *in litt.*) emphasised the need for such a summary, which is provided in the present paper.

GENERAL DEFINITION

Early descriptions of microatolls were given by Darwin (1842, 6), Dana (1872; 1875, 72, 94), Semper (1880; 1889, 224-226), and Guppy (1886), using general names such as coral head or coral block. Thus Dana (1849, 39) described situations where "corals, when growing beneath the water, form solid hemispheres, or rounded hillocks; but on reaching the surface, the top dies, and enlargement takes place only on the sides. In this manner the hemisphere is finally changed to a broad cylinder with a flat top". Possibly the earliest description of this phenomenon was that of Chamisso (1821, 143), who noted that "species, which otherwise assume a spherical form, spread out in places where sand is carried, into flat surfaces, with a raised edge, because the sand kills the upper part, and they can only live and grow on the circumference".

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Guppy (1886) spoke of "miniature atolls", Agassiz (1895) of "diminutive atolls", and Krempf (1927) of "dwarf atolls" ("atolls nains"). The term *micro-atoll* was first used by Krempf (1927, 13), but without concise definition. It was widely adopted and variously defined. Kuenen (1933, 64) used it for "a colony of corals" with "a raised rim, more or less completely surrounding a lower, dead surface". MacNeil (1954, 394) used it for "massive colonial corals growing peripherally in shallow areas and whose dead upper surface (sometimes made concave by solution) is exposed at low tide. Microatolls often form a pavement of closely spaced stepping stones". Such pavements have recently been termed "reef tables" by Fishelson (1973, 193). Most definitions of microatolls include elements of morphology, location, origin, and, rarely, internal structure.

CHARACTERISTICS

Most authors use microatoll "to designate a special type of growth of coral colonies" (Kuenen 1933, 90), not for ring-shaped assemblages of a variety of corals for which the word *faro* is more appropriate (Gardiner 1931, 19; MacNeil 1954, 399; Guilcher 1971, 77; Scheer 1972, 102). Typical microatolls comprise single colonies of massive corals ("monospecific microatolls" of Mergner and Scheer, 1974, 11), especially of *Porites,* usually round (though complexity of form is stressed by Kuenen 1933, 64), and with a flat or concave upper surface devoid of living polyps. Several authors have stressed the importance of a well-defined peripheral ridge of living coral several centimetres high and wide, surrounding the dead inner area (Krempf, 1927, 15); Semper (1899, 226) found this feature present only in larger colonies, and Pichon (1964, 135) found it generally absent in southwest Madagascar microatolls.

Most microatolls are found in pools on reef surfaces or on reef flats. Kuenen (1933, 65) stated that with respect to sea-level the surfaces of microatolls were higher on the windward than the leeward sides of reefs, and that exceptionally high microatolls could be found in ponded situations on reef-flats. Most microatolls described are up to 6 m in diameter. The general characteristics of microatolls may be derived from the following regional descriptions:

> *Cocos-Keeling Atoll.* "One large circular mass of *Madrepora* (with short branches), which measured 18 feet across and 2 feet in height, possessed a dead centre that was depressed 9 or 10 inches below the level of its living margin. ... An adjacent flat-topped mass of *Porites,* measuring 13 feet across, at the same condition of the tide presented an example of another miniature atoll. Its central portion was dead and hollowed out into a basin, which was occupied by a small pool of water" (Guppy 1886, 893).

Bikini Atoll. At Bikini, in the outer *Heliopora* zone of windward reefs, Emery et al. (1954, 28) describe microatolls in "1 to 4 feet of water at low tide ... large subcircular masses, 3 to 25 feet or even more in diameter, consisting largely of the blue alcyonarian, *Heliopora,* [and which] rise close to low-tide level. In the outer part of this zone the microatolls are formed mainly by the scleractinian coral, *Acropora palifera.* This zone is a part of the belt of microatolls. In these structures, as in true atolls, there is a concentration of living forms around the periphery, although live colonies, particularly *Heliopora* and algae, may be growing sporadically all over the structure. The *Acropora,* which apparently is not quite so hardy a form as the *Heliopora,* is concentrated around the edge of the microatoll, and most of the colonies are at a somewhat lower level than the Helioporas; at low tide the tips of many *Heliopora* colonies break water. The upward growth of the microatolls is definitely limited by low-tide level, but the growth around the rim of each structure is rich, and the masses appear to be expanding laterally in all directions. As they coalesce, they form a new reef surface — not so firm a surface as the pavement from which they grow but one that may become so eventually by continued organic growth and silting. Many of the dead Helioporas in the centers of the microatolls are covered by a film of sand very rich in Foraminifera".

Great Barrier Reef. "Typical of the reef flat is the microatoll which is formed by one of several species of coral that grow radially in the horizontal plane and produce a flat-topped mass that is circular in outline or consists of several merging circles. The top of the microatoll is encrusted by calcareous algae and the living coral survives mainly around the margins and outer face. The coral *Porites* forms the compact, purple and brown microatolls which are possibly the most common. The blue *Heliopora* and grey *Goniopora* are also responsible for compact microatolls, while more open structures, generally yellow and pale green in colour, are produced by certain branching species," e.g. at Heron Island (Maxwell 1968, 115). Earlier, fields of microatolls had been described forming "coral platforms" at Low Isles by Stephenson et al. (1931, 46-47): *"Montipora ramosa, Acropora hebes* and massive *Porites* ... exhibit a curious development connected with the shallowness of the water. They grow in a normal fashion until their tops project above the level of low water; they may then survive with projecting tips for a longer or shorter period; but sooner or later the projecting parts are killed, become infested by microphytic algae and sediment, and encrusted by nullipores (Melobesiae); so that ultimately the coral colonies are converted into flat-topped platforms, dead across the top and alive around the edges. This process may affect individual colonies or, if the growth has been dense so that fields of branching corals have been formed, it may convert a whole field into a platform. The general result of this is to create a bewildering maze of level platforms with pools between. ... The extent and composition of the platforms varies in different parts of the moat [at Low Isles]; massive

> *Porites* becomes converted into platforms as readily as the branched species, though the details are a little different. Astraeid corals, especially species of *Favia,* are common among the platform-building forms ... and these also often develop dead flattened tops".

It is clear from these descriptions that both massive (*Porites*) and branching (*Acropora*) scleractinian corals and also alcyonarians (*Heliopora*) commonly form microatolls. Wells (1957) lists six genera of massive scleractinians (*Favia, Favites, Platygyra, Cyphastrea, Goniastrea, Porites*) forming microatolls in the Marshall Islands, together with two species of branching corals (*Acropora palifera, A. brueggemanni*), and also *Heliopora*. Krempf (1927, 15) mentions *Porites, Acropora* and *Heliopora,* and also the hydrozoan *Millepora*. In Madagascar, Pichon (1964, 135) found *Porites somaliensis* Gravier to be the main former of microatolls up to 3 m in diameter, with smaller microatolls lacking a central depression built by species of *Acropora* and *Pavona,* and also *Turbinaria* sp. cf. *stephensoni* Crossland. At Alacran Reef, Gulf of Mexico, examination of 41 specimens of "atoll-shaped heads" and "atoll-shaped coral colonies" (the authors using the term microatoll for larger patch reefs) showed that nearly all species of massive corals found on the reef were represented, forming colonies 2-53 inches in diameter (Kornicker and Boyd 1962, 667). Microatolls are also described in the spicular skeletal material deposited in the tissues of the alcyonarian *Sclerophytum* in American Samoa (Cary 1931, 61).

In addition to "corals" *sensu lato* (Scleractinia, Hydrozoa, Alcyonaria), some authors consider that constructional features formed by other animals morphologically resemble microatolls to the extent of using the same term for them. Rock rims coated by the pelecypod *Brachyodontes erosus* at Point Peron, Western Australia, are termed microatolls by Fairbridge (1950, 52). Similar rock rims coated with tubes of serpulid worms at Bermuda have frequently been referred to as microatolls (Agassiz 1895; Krempf 1927; Fairbridge 1950). Constructions by vermetid gastropods are also so referred to by Krempf (1927) and by Safriel (1974). Coralline algal rims on reef flats and limestone terraces are termed microatolls at Cozumel, Yacatan, by Boyd, Kornicker and Rezak (1963), though where characteristically developed, e.g. in the western Pacific (Lister 1891; Stoddart 1969), they are not annular.

Microatolls have been described in the fossil scleractinian *Heliastraea reussana* Milne Edwards and Haime by Vasicek (1948), but reference to his figure shows that the typical microatoll form is not present in this lobate coral.

ORIGINS OF MICROATOLLS

A variety of modes of origin has been proposed for typical microatolls. Often these modes overlap in several particulars, but broadly three main explanations can be recognised.

(1) Low-water level control

Many authors have suggested that low-water level forms an upper growth limit for coral colonies; that when this is reached upward growth ceases and is replaced by lateral growth, leaving a dead, flat central area. Semper (1899, 224-226) described how up-growing small massive hemispherical colonies would be transformed to microatolls as their upper surfaces reached low-water level, and very similar explanations were given by Kuenen (1933, 64-65) and by Pichon (1964, 135-136). One of the earliest detailed accounts relating form of the corallum to measured water heights was that of Manton (1935, 300) at Low Isles, Great Barrier Reef. She states that: "The upper limit of coral growth is determined in the first place by the range of water level. In the Moat the height of the branched and massive coral platforms appears to be controlled by the permanent level of low water, and lies at 0.3 and 0.15 feet respectively above the latter. Outside the Boulder Tract and rampart coral growth starts at a lower level, just above datum [i.e. level of lowest low water springs] ..., so that corals are only exposed to the air intermittently at exceptionally low tides. No platforms are here formed with flat dead or living tops at a constant level since the water is continually changing, but over the level inshore part of Traverse II coral growth, except for *Acropora hebes,* is checked above 1.6 feet above datum. Massive corals with flat dead tops have been noted in other regions ... The distribution of such dead-topped corals on the traverses and on Low Isles generally, where they are found abundantly in Moats but rarely outside the Boulder Tract, even in regions where sediment is a limiting factor, and the direct correlation of the height of such colonies with low-water level, indicates that here water level and not sediment is the main factor responsible for such growth forms on Low Isles". This relationship is so close that the presence of microatolls in Pleistocene reefs has been used as an indicator of low-water spring tides (Braithwaite et al. 1973, 321).

More recently, Roy (1970, 12-13) has described microatolls, mainly of single colonies of *Porites compressa,* in Kaneohe Bay, Oahu, up to 20 ft in diameter, all rising to within a few inches of lower low water. He finds that the morphology of the microatolls is related to depth of surrounding water, though he does not discuss this relationship in his text (Table 1).

A tidal-level control could explain a flat, bevelled upper surface of the kind found by Pichon in Madagascar, but less easily the existence of a raised rim of living coral round the dead central area. Semper (1899) and Agassiz (1895, 258) both proposed that after growth ceased the central area was hollowed out by biological, chemical and mechanical erosion to form both the flat or concave centre and gullies and channels in it. Krempf (1927, 19) could find no evidence of such erosion: in Annam he found the central area sound, and often with small growing corals on it. Various conditions could form the specific cause of death at or near the sea-air interface. Fishelson (1973, 193) has suggested that exceptionally low tides, which may be aperiodic, could kill the upper surfaces of corals through emersion at Eilat in the Red Sea. In Bermuda Iams (1969, 70) has described several possibly pathological conditions leading to the disappearance of living polyps from otherwise healthy coral heads, and Garrett and Ducklow (1975) have described apparent evidence of disease from the same atoll. Once skeleton is exposed it is open to many processes of bioerosion, of which the activities of tridacnid clams are conspicuous on western Pacific microatolls (Figure 2 and 3).

Table 1. Relation of microatolls morphology to water depth, Kaneohe Bay, Oahu (source: Roy, 1970, table 3).

Depth of water on surrounding bottom (feet)	Microatoll morphology
1	No live coral on the rim: top dead, centre eroded nearly to the level of the surrounding bottom.
2	Part of the rim is live coral: top dead, centre partly eroded.
3	All of the rim is live coral: top dead, flat, not eroded.
4	All of the rim is live coral: some live coral on top, top tends to be domal rather than flat, not eroded.

(2) Sedimentation leading to differential growth

Wood Jones (1912, 107-109, 247-251) observed that coral colonies with dead upper surfaces were frequently found at Cocos-Keeling Atoll well below low-tide level. He proposed that the steady rain of sediment through the water led to accumulation on the flat upper surfaces of coral colonies, especially of massive hemispherical *Porites* colonies, the consequent death of living polyps, and the ultimate formation of an "atoll reef in miniature". Krempf (1927, 13) similarly observed deep microatolls in Annam. He argued that sedimentation on horizontal surfaces was aided by ectodermal mucus secretion trapping fine particles, though it is now usually held that mucus helps remove sediment from corals. This control was absent on vertical surfaces, which consequently grew faster, leaving a flat dead area within. An early stage in this process produced "umbilical" colonies, round with a central depression. Vasicek (1948) has pointed out that this process of control by sedimentation appears more applicable to massive than to branching and platy corals. He has also noted that the resulting differential growth of different parts of the skeleton should be clearly observed in skeletal structures.

Marshall and Orr (1931, 131) noted at Low Isles, Great Barrier Reef, that microatolls were formed near low tide level by both large-polyped *Favia* species and small-polyped *Porites* species, the former efficient sediment-removers and the latter not, and they concluded that microatolls were probably not therefore primarily caused by sedimentation. Other factors, such as growth form, could, however, affect the efficiency of sediment removal.

Interesting variations on normal microatoll form have also been described in shallow-water situations. In Iwayama Bay, Palau, Abe (1937, 253-256) described microatolls of *Goniastrea aspera* Verrill with inclined upper surfaces; such inclination was not found in *Porites somaliensis*. Figure 1 gives mean dimensions for 17 measured *Goniastrea* microatolls with inclined surfaces; Abe also gave data on 23 more colonies where the rim was incomplete because of the interruption of its narrower lower part. The mean orientation of the long axes of the complete microatolls was 117°, and the mean angle of inclination of the upper surface about 17°. These orientations are "to the direction of the upper stream at rising tide" (1937, 253); Abe believed that sediment in the current was probably an important control. Elsewhere, especially on shallow reef flats, sediment may accumulate to form conspicuous tails in the lee of microatolls, as near Gan, Addu Atoll, Maldive Islands (Stoddart et al., 1966, 19); both here, on *Porites,* and in the Gulf of Eilat on *Platygyra,* the dead upper surfaces of the microatolls are conspicuously colonised by the alga *Turbinaria* (Fishelson, 1973, fig. 3b).

(3) Food supply, currents, and differential growth

Some authors have suggested that as a coral grows, it will influence hydrologic conditions near it, and that in general currents and food supplies will be greater round the periphery than in the centre. Hence the margins will grow more rapidly than the centre and a microatoll form will result. This has been proposed for alcyonarian microatolls in Samoa (Cary 1931, 61) and for fossil corals by Vasicek (1948).

(4) Overgrowth on older coral colonies

Kornicker and Boyd (1962, 667-668, fig. 33) produced a novel explanation of microatoll development at Alacran Reef. Gulf of Mexico. Here microatolls "have developed principally (about 90 per cent) by peripheral growth around the rims of overturned coral heads; a few have formed after the central part of the dome was encrusted with calcareous algae that effectively stopped coral growth in that area but permitted continued growth around the edge. Atoll-shaped coral colonies formed on overturned heads have convex-downward bases. Specimens were collected that had evidently been turned over several times so that both top and bottom were atoll-shaped". Overgrowth on dead coral blocks, not necessarily overturned, to form microatolls was noted with *Porites* in Madagascar by Pichon (1964, 136), who also found it to be the sole mode of microatoll development in *Turbinaria*.

SUSCEPTIBILITY TO MICROATOLL FORMATION

Abe (1937) contributed important data on microatolls (termed by him "coral tables") at Iwayama Bay, Palau. He measured the depth from mean water level of the upper surfaces of microatolls and of round-topped colonies of three common species (*Porites somaliensis, Favia speciosa, Goniastrea planulata*) at three sites in the Bay (Stations 1 and 2 are reef margin sites, Station 3 a reef flat and pool site). His data are summarised in Table 2. The lowest tide recorded in 1935 was 100 cm below mean water level, though in such a topographic situation local variability must be considerable.

Table 2. Depth below mean water level of microatolls and hemispherical coral colonies at Iwayama Bay, Palau (from data in Abe 1937, 306-307)

	Microatolls				Hemispherical colonies			
	Mean depth	Minimum depth	Maximum depth	n	Mean depth	Minimum depth	Maximum depth	n
Porites somaliensis								
Station 1	101.9	86	124	25	122.8	106	144	12
Station 2	123.8	116	130	12	139.2	134	148	5
Station 3	115.3	108	124	21	-	-	-	-
Favia speciosa								
Station 1	96.5	78	114	4	126	-	-	1
Station 2	104	-	-	1	-	-	-	-
Goniastrea planulata								
Station 1	108	106	112	6	124	-	-	1

Depths in cm; depth of lowest low tide in 1935 100 cm.

At Station 1, for which data are fullest, Abe found (1937, 305-309) considerable differences between species in the levels at which microatolls form. *Favia speciosa* formed microatolls at the highest level (mean depth 96.5 cm), then *Porites somaliensis* (mean 101.9) and deepest *Goniastrea planulata* (mean 108). These differences must reflect variations in tolerance between different species of the controlling factors. Abe also found that the same species formed microatolls at different depths at the three different stations. Thus *Porites somaliensis* microatolls are found at a mean depth of 102 cm at Station 1 (round colonies at 123 cm); at 124 cm at Station 2 (round colonies at 140 cm); and 115 cm at Station 3 (no round colonies). Abe felt that these differences could not be explained by tidal control alone. He noted the prevalence of muddy sediments at Station 2, and argued (1937, 313-314) that microatolls formed at lower levels at this station because of the amount of suspended mud in the water.

MICROATOLLS AT ABNORMALLY HIGH LEVELS

Mention has already been made of Kuenen's (1933, 65) observation of microatolls in ponded situation on reef flats in the East Indies, and such a situation is implicit in the records of microatoll growth and elevation on the surfaces of low wooded island-reefs of the Great Barrier Reef by Manton (1935, 300). In describing reef-top pools at Low Isles, Fairbridge and Teichert (1947, 4) state that "there is often active coral growth reaching several feet above the normal upper limit of such growth, a significant point for those who would use coral which has grown *in situ* as a datum for former sea-levels". The height data used by Fairbridge and Teichert are the same as those used by Manton, derived from the careful surveys by Spender (1930). Clearly, if such reef-top pools are drained then such abnormally high microatolls might be killed; such changes could result from hurricane modification of reef topography (Moorehouse 1936).

High-standing dead microatolls which might be referred either to growth in formerly existing pools or to growth when sea-level itself was higher than at present were first described in detail at Funafuti Atoll, Ellice Islands. Here Sollas (1904, 20-22) noted an area of *Porites* microatolls and *Heliopora* colonies within a mangrove swamp, at a level submerged by several feet at high water but emerged during much of the day. The corals themselves were partly covered by a cemented shingle rampart. The flat tops of the corals were ascribed to "an arrest of upward growth ... by the level of low water". Sollas proceeded to discuss the interpretation of these microatolls:

> "If it be admitted that the surface of the *Porites* clumps marks an ancient level of low water, then it obviously becomes a problem of extreme interest to compare this level with that of the existing sea. ... the summits of the *Porites* clumps now stand 1 foot 4 inches above mean tidal level, i.e., 4 feet 6 inches above low water at spring tides or 3 feet 9 inches above low water at neap tides. I therefore concluded that a

> change in sea-level in a negative direction to the extent of about 4 feet had occurred over the site of the Mangrove Swamp since the growth of its ancient reef" (1904, 22).

David and Sweet (1904, 67) placed the downward movement of the shoreline so indicated at "from 4½ to 6¼ feet". Elsewhere on Funafuti, however, Finckh (1904, 138-139) found living *Heliopora* colonies at unusually high levels in moated situations similar to those later found at Low Isles. Both *Heliopora* and *Porites* were found at the north end of Amatuku Island, Funafuti, growing in a pool at a height of 2 feet above low-water spring tide: "great care was exercised to determine the exact height of this coral growth, since it would seem to offer an explanation for the occurrence *in situ* of dead *Heliopora* considerably above low-water mark in the Mangrove Swamp and in other localities on the main island of Funafuti". David and Sweet (1904, 67), however, while accepting this observation, did not feel that modern growth in pools could account for the main areas of dead microatolls. It "may explain small heads above low water level, but not the *Heliopora* slightly above high water level ... nor *in situ* heads of *Porites* "in many cases over a foot, some ... 4 feet above high water. These immense heads could not have grown in land-locked reef pools, but must have flourished under the most favourable conditions, such as free access to food-bringing currents, etc., would provide".

The Funafuti situation is directly analogous to that found on the northern Great Barrier Reef in 1973, and there is some suggestion in the literature that abnormally high dead microatolls (though perhaps not characterised as such) are fairly widespread in the western Pacific e.g. in the Marshall Islands (Emery *et al.* 1954, Buddemeier *et al.* 1975, Tracey and Ladd 1974) and the Gilbert Islands (Cloud 1952).

PROBLEMS OF TERMINOLOGY

Microatoll mis-used for patch reefs

As described above the usage of the term "microatoll" as introduced by Krempf is relatively unambiguous. Unfortunately several recent authors have used the term for quite different kinds of features and hence produced confusion.

In the Bahamas, Newell and Rigby (1957, 36) used the term for "certain ring-shaped patch reefs ... in many areas nearly circular ... measuring 10 to 200 metres across. As viewed from a boat or from the air, the faros [*sic*] stand out as dark rings or fringes of gorgonians upon a rim of stony corals. The central area is more or less dead, slightly depressed, and covered with coral fragments". Newell (1954, 12) considers the use of the term microatoll for single coral colonies "not very appropriate" and suggests it be reserved for such ring-shaped patch reefs (cf. Newell *et al.* 1951, 23; Illing, 1954); he does not explain why microatoll in this redefined sense and faro are used synonymously.

Similarly, at Raroia Atoll, Tuamotu Archipelago, Doty and Morrison (1954, 52) speak of larger reef patches "progressively like microatolls in that the centre is more apt to be a pool a few feet deep and the edge a rim a few feet wide more or less complete and higher, just below low tide level". Kinsey and Domm (1974, 51) described "a very large number of patch reefs "at One Tree Island, Great Barrier Reef, "many taking the form of microatolls. These vary from about 3 m to 200 m in diameter and are characterised by being fully or nearly fully enclosed by living reef. The walls are usually vertical on the sides and 2-5 m thick. Within these enclosures the water depth, during the 5-6 hr low-tide slack water period, is typically 0.5-2 m and the bottom has sparse coral cover being predominantly sandy with some rubble". Similar features of comparable size had earlier been termed "miniature atolls" at Pearl and Hermes Reef, Leeward Hawaiian Islands, by Galtsoff (1933, 14).

At Alacran Reef, Hoskin (1963, 27) used microatoll in an inclusive sense for "growths of massive corals which resemble a doughnut in shape. They range in size from single heads ... to very large and complex structures. ... The largest microatolls are called patch reefs ... [and] may be up to 20 feet in diameter". These Alacran reefs are also described by Kornicker and Boyd (1962, 658-659): "The upper surfaces of two microatolls about 2 miles north of Isla Perez were examined in detail. They rise within a few feet of the surface from a depth of about 40 feet, and their upper surfaces form circular areas 325 and 200 feet in diameter respectively. The water depths at the margins of these surfaces are typically about 5 feet to the base of the corals and 2½ feet to the tops of the corals. Between the outer edge and the central lagoon, depths are as shallow as 1½ feet to the coral tops and 3 feet to the base of the corals. The deeper parts of the lagoons are about 4½ feet beneath the surface. Beyond the outer edge of the larger microatoll, the slope is steep and was estimated at 30°. ... each of these microatolls could be mapped as a circular belt of massive corals enclosing a sand-bottom area and surrounded by sand bottom." These features are clearly quite different from classically-defined microatolls, and there seems no good reason for misusing this term to describe them.

Similar difficulties arise in new terminology proposed for lagoon patch reefs at Bermuda by Garrett *et al.* (1971, 650). These authors use "microatoll reef" for patch reefs which "resemble small atolls in possessing a growing perimeter and a sediment-filled interior". One example described measured 150 x 700 m, with an upper sandy surface 4 m deep; this they also term a "rough-topped mesa". A mesa reef is defined as a broad reef in the Bermuda lagoon bounded by steep slopes; further, "if the top is bowl-shaped and sandy, depth 4 m, the reef becomes a microatoll reef" (Garrett *et al.* 1971, 651). They also state that "continued lateral growth as well as coalescence of adjacent reefs results in poorer circulation for the central areas [of lagoon reefs], which die off; the reef is then a microatoll" (Garrett *et al.* 1971, 644). This misuses terms already well-defined and established in the literature, and it adds no precision to the features being described.

The need for a series of terms to differentiate members of a hierarchy of forms from microatoll *sensu stricto* to atoll was recognised by Scheer (1969, 1972). He proposed four terms: microatoll (classically defined as referring to individual colonies); mini-atoll; faro; and atoll. Mini-atoll is used for patch reefs in atoll lagoons with central depressions 2.5-3.5 m deep, comparable to the patch reefs described by Newell and by Doty and Morrison but termed by them microatolls. Scheer was quite clear that the term microatoll "should be reserved to the loaf-shaped, round coralla of the outer reef flat, whose upper parts are dead" (1972, 99-100). Faro refers to larger reefs of ring-shaped form, usually found round the margins of certain atolls in the Maldives instead of linear reefs (Gardiner 1903, 155; 1931, 19). The term is often restricted to peripheral reefs of atolls or outer reefs of barriers (Kuenen 1950, 426; MacNeil 1954, 393), in which sense it is close to the term "atollon" used by Guppy (1889, 472) and defined by Stamp (1961, 36), but it is also properly applied to ring-shaped patch reefs within atoll lagoons (MacNeil 1954, 399; Guilcher 1971, 77; Scheer 1972). "Bason-formed reef" of Darwin (1842, 106) and "lagoon atoll" of Davis (1928, 15) are obsolete versions of faro.

Cognate terms

Certain cognate terms have been introduced for features associated either with true microatolls *sensu* Krempf or for features improperly termed microatolls by some recent authors.

The dead central area or enclosed pool of true microatolls is termed a *microlagoon* by Vasicek (1948, 56) and by Boyd *et al.* (1963). *Micro-lagoon* is used for the larger patch reefs at Raroia, for "pool areas in the reef patch tops ... as a rule sand or sediment floored and a foot to a metre deep" (Doty and Morrison 1954, 52). Morrison (1954, 5) curiously uses micro-lagoon in a totally different sense, also at Raroia, for "brackish water lagoons ... [in] incomplete channels between islands [i.e. *hoa*] or small embayments close to the lagoon of the atoll, and more or less completely cut off from the salt water of the lagoon by sand barriers"; other terms, notably *barachois,* are available for this phenomenon (Bourne 1888, 442), and Morrison's usage is thus redundant as well as confusing. *Microatoll lagoon* is used by Garrett *et al.* (1971, 651) for the water up to 4 m deep over the wide sandy plain of their misnamed microatoll reefs.

In spite of the popularity of the term microatoll, there are few references to *microbarriers*. Fairbridge (1950, 345, fig. 4) applied this term to a submerged linear reef 1500-2000 ft seaward from the main reef rim on the south side of Pickersgill Reef, Great Barrier Reef; "patches of growing coral connect it with the main reef, but deep, rounded pools are left between".

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A LIST OF INSECTS CAUGHT IN LIGHT TRAPS ON WEST ISLAND, ALDABRA ATOLL, INDIAN OCEAN

by D. W. Frith

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A LIST OF INSECTS CAUGHT IN LIGHT TRAPS ON WEST ISLAND, ALDABRA ATOLL, INDIAN OCEAN

by D. W. Frith[1]

Collections made by J. C. F. Fryer during the Percy Sladen Trust Expeditions to the Indian Ocean (1908-1909) form the basis of several publications on the insect fauna of Aldabra Atoll, Indian Ocean. A bibliography of these and other pertinent literature is given by Stoddart (1971). Legrand (1965) published a comprehensive list of Lepidoptera based on collections made on the Seychelles and Aldabra during 1956 and 1958-60, and housed at the Muséum National d'Histoire Naturelle, Paris. Preliminary observations on the affinities and composition of the insect fauna of Aldabra were made by Cogan, Hutson and Shaffer (1971), their results being based primarily on collections made during the Royal Society Expedition to Aldabra 1967-68. Webb (1975) described species of Fulgoroidea (Hemiptera-Homoptera) collected during the above expedition.

Aldabra, the largest elevated coral atoll in the world, is situated 420 km northwest of Madagascar and 640 km from the African mainland in the southwest Indian Ocean, latitude 9° 24'S, longitude 46° 20'E (Stoddart and others 1971). The atoll is elongated east-west with a maximum length of 34 km and a maximum width of 14.5 km. At its highest point it is about 18 m above sea level, but most of the land mass lies approximately 5 m above sea level. The atoll consists of four main islands separated by tidal channels. The surface coral is mainly of two types, 'champignon', a deeply pitted and irregular solution-fretted reef rock, and 'platin', a smooth surfaced pavement-like cemented limestone (Fryer, in Stoddart *et al.* 1971). A third type, 'pavé' may be used to describe a surface that has similar features to platin but lies at a greater elevation (Stoddart 1970).

The study area was located on West Island or Ile Picard which measures 9.3 sq. km and forms the northwest corner of the atoll. It consists mainly of champignon apart from a small area of platin around Bassin Cabri and an area of pavé around Anse Var. The champignon is covered by mixed scrub except for coastal strips of palm grove and/or

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Casuarina equisetifolia L. woodland (for details of vegetation and place names see papers in Westoll and Stoddart 1971). The Royal Society Research Station, constructed in 1971, is located on the southern tip of West Island.

Insects were constantly trapped by the present author using two Heath light traps and a Rothamsted light trap during the period August 1971 - September 1972 whilst testing trapping techniques at the invitation of the Royal Society of London. Details of trap sites and trapping periods are given below. Insects were identified at the British Museum (Natural History) and Muséum National d'Histoire Naturelle, Paris (Lepidoptera only). Collections from the present study are housed at the British Museum (Natural History). Data on seasonal variation and abundance of insect families and predominant species only, caught by these three light traps, are given elsewhere (Frith, 1975), in a publication unsuitable for a comprehensive list of Aldabran insects. With future intensive zoological research on Aldabra and surrounding atolls, assured by the presence of the Royal Society Aldabra Research Station, there is a need for a continuously updated lists of flora and fauna. A list of Aldabran insects caught by the light traps is therefore presented here as a basis for future research. Whilst the present list is a preliminary one, the intensity of trapping and period involved is indicative of a fairly comprehensive study. Annual total numbers for orders and species are included as an indication of insect abundance. Many of the smaller insects remain unidentified to species and some species, obtained in very small numbers, were too damaged by trapping for identifications to be made, but numbers of these are given to indicate relative abundance within the family and genus.

Families are listed in the systematic order used in the Insects of Australia (CSIRO, 1970). Species are listed alphabetically within the family and genus.

Trapping techniques

The light traps were placed about the research station in areas which varied in floral composition. A list of plant species near to each trap is given in Appendix 1. It was initially intended to trap for about 7 nights per month per trap, but due to the large size of nightly catches during some months for the Heath light traps this period was reduced. Trap localities and trapping periods were as follows:

Heath trap 1 was situated 70 m inland behind the research station and placed in a box 50 cm. above the champignon. The trap was surrounded on three sides by poor mixed scrub predominantly consisting of *Pemphis acidula* Forst. and the fourth side faced a large tidal pool. Monthly samples (2-8 nights per sample) were taken from September 1971 to August 1972.

Heath trap 2 was situated 60 m. inland on champignon surrounded by species rich mixed scrub which bordered a coconut plantation just north of the research station. The trap was placed on a table 1 m. above the ground. Monthly samples (2-10 nights per sample) were taken from September 1971 until August 1972.

Rothamsted light trap was situated 50 m. in a clearing just east of the research station. The trap was placed on roughly dissected champignon and was surrounded by a relatively species rich mixed scrub, *Pemphis acidula* being the dominant species. Monthly samples (7-9 nights per month) were taken from October 1971 to September 1972.

A list of insects and their annual total numbers caught by Heath and Rothamsted light traps on West Island, Aldabra Atoll over a twelve month period.

[Species marked * are predominant species for which monthly population fluctuations are given in Frith (1975)]

		Annual total number		
Family	Species	Heath Trap 1	Heath Trap 2	Rothamsted light trap
LEPIDOPTERA				
Psychidae	*Pseudometisa* sp.	2	2	1
Ethmiidae	*Ethmia nigroapicella* Saalmüller	13	185	4
Cosmopterigidae	1 unidentified species	-	-	13
Alucitidae	1 unidentified species	-	-	1
Hyblaeidae	*Hyblaea puera* (Cramer)	1	12	-
Thyrididae	*Banisia aldabrana aldabrana* (Fryer)	34	7	35
Pyralidae (excluding Phycitinae)	*Bocchoris inspersalis* Zeller	2	9	-
	**Bradina* sp.	134	1198	1139
	Cirrhochrista oxylalis Viette	30	17	3
	Diaphana indica (Saunders)	-	1	-
	**Diastictis savyalis* Legrand	83	119	61
	**Duponchelia fovealis floeschalis* Legrand	23	70	185
	**Endotricha erythralis* Mabille	123	143	78
	**Epipagis prolalis* Viette and Legrand	21	76	65
	**Hymenia recurvalis* (Fabricius)	151	146	63
	**Hymenoptychis sordida* Zeller	331	116	57

	**Ischnurges lancinalis aldabrensis* Viette	28	199	235
	**Lamprosema aldabralis* Viette	86	289	78
	**Nausinoe capensis* (Walker)	27	267	138
	**Pardomima zanclophora* Martin	215	1770	153
	Pagyda sp.) *Pyrausta* sp.)	124	226	238
	Pyrausta incolaris Guenée	-	-	3
	Pyrausta nr. *prostygialis* Viette	4	60	3
	Synclera univocalis Walker)	50	17	12
	3 unidentified species	5	3	6
Geometridae	**Chlorissa* sp.	40	115	99
	**Chloroclystis* sp.	39	59	901
	**Comostolopsis* sp.	8	197	195
	**Erastria madecassaria* Boisduval	21	149	39
	Problepsis deducta Herbulot	8	74	11
	Scardamia sp.	4	37	5
	**Scopula minorata* (Boisduval)	106	116	183
	Scopula nr. *minorata* (Boisduval)	-	3	17
	**Scopula sparsipunctata menaiensis* Legrand	88	288	634
	Scopula sp.	14	11	5
	**Sterrha* sp.	82	355	450
	**Tephrina pulinda deerraria* (Walker)	17	288	30
	Xenimpia sp.	4	33	14
	5 unidentified species	37	63	5
Sphingidae	*Agrius convolvuli* Linne	8	-	-
	Hippotion geryon Boisduval	18	30	-
Notodontidae	*Iridoplitis malagassica aldabralis* Legrand	1	2	12
Arctiidae	**Celama* sp.	1434	878	490
	**Eilema aldabrensis* (Hampson)	697	1873	890
	**Eilema* sp.	1	93	121
Noctuidae	*Achaea catella* Guenée	-	2	-
	**A.violaceofascia* Saalmüller	267	405	11
	Acontia malagassica Mabille	2	13	2
	**Amyna octo* (Guenée)	88	72	2
	Attatha gaetana (Ch.Oberthür)	3	9	-
	Aulotarache decoripennis (Mabille)	3	2	2
	**Avatha extranea* Berio	20	165	3
	**Bryophilopsis griseoplaga* Legrand	1234	1648	153

	**B.nesta* (B. Fletcher)	72	102	20
	**Catephia squamosa* Wallengren	187	169	45
	Catephia sp.	2	13	-
	Chalciope delta (Boisduval)	3	11	-
	Dysgonia torrida (Guenée)	7	43	1
	Earias spp. (4 species)	1	10	2
	**Ericeia inangulata* (Guenée)	465	337	9
	Eublemma costimacula (Saalmüller)	2	6	-
	Eulocastra neoxcisa Berio	-	86	7
	Eutelia blandiatrix Guenée	2	1	-
	Heliothis assulta Guenée	5	10	-
	Mythimna madensis Berio	34	41	1
	Oedebasis ovipennis Hampson	2	2	-
	Oediplexia nr. *citrophila* Berio	4	36	7
	Oglasa aldabrana aldabrana Fryer	1	2	-
	Ophiusa legendrei Viette	8	7	-
	**Ozarba aldabrae* Berio	87	475	13
	**Perigea aldabrae* (Berio)	114	220	190
	Plusia chalcytes (Esper)	9	31	-
	Tarache rachiastris Hampson	2	19	1
	Trigonodes hyppasia anfractuosa (Boisduval)	8	3	-
	Zeuxinia aeschrina Legrand	40	69	24
	14 unidentified species	10	202	21
Tortricidae	Approximately 10 unidentified species			
Tineidae	Approximately 2 unidentified species	15447	38845	14487
Pyralidae - Phycitinae	Approximately 10 unidentified species			
ANNUAL TOTAL NUMBER OF LEPIDOPTERA		23586	54576	21793
HEMIPTERA -HOMOPTERA				
Cixiidae	**Achaemenes major* Jacobi	133	644	98
	Brixia stellata Distant	16	4	59
Achilidae	*Akotropis* sp	1	10	15
Ricaniidae	*Deferundata aldabrana* Distant	1	4	1
	Neoprivesa fuscovaria Distant	6	17	6
	Osaka hyalina Distant	2	10	2
	Privesa nr. *fryeri* Distant	15	37	11

Flatidae	**Chaetormenis madagascariensis* (Signoret)	53	718	517
Cicadellidae	*Balclutha* sp.	-	8	6
	Batracomorphus sp.	-	-	6
	Empoasca spp. (2 species)	-	-	48
	*nr.*Helionidia* sp.	4	5978	102
	**Limentius aldabranus* Distant	2	26	239
	Naevus subparallelus Knight	-	28	14
	Paganalia virescens Distant	1	-	-
	Penthima sp.	-	15	10
	*nr.*Vulturnus* sp.	236	297	2183
	Xestocephalus sp.	-	-	21
HEMIPTERA -HETEROPTERA				
Miridae	2 unidentified species	159	364	444
Tingidae	1 unidentified species	-	-	38
Coreidae	*Plinachtus* sp.	4	27	1
Stenocephalidae	*Dicranocephalus punctipes* (Stål)	2	8	8
Lygaeidae	**Dieuches* sp.A	1288	8591	551
	Dieuches sp.B	1	5	-
	**Lethaeus stellatus* Distant	1769	2704	1412
	2 unidentified species	9	-	36
Cydnidae	2 unidentified species	84	145	19
Pentatomidae	**Acrosternum* nr. *heegeri* Fieber	190	248	207
	Eysarcoris sp.	1	-	-
	Nezara viridula (Linnaeus)	-	1	1
	1 unidentified species	1	-	-
Notonectidae	1 unidentified species	-	3	-
Corixidae	1 unidentified species	20	-	-
ANNUAL TOTAL NUMBER OF HEMIPTERA		3998	19892	6055
Carabidae	**Aulocoryssus aciculatus pavoninus* Gerstaecker	194	149	12
	Callida rufoplagiota Jeannel	1	19	3
	Chlaenius nr.*allacteus* Alluaud	-	2	3
	C.bisignatus Dejean	1	7	-
	Egadroma laticolle Jeannel	7	8	1
	E.trivitte Fairmaire	-	3	-

	**Myriocile melancholica perplexa* Dejean	291	128	16
	Platymetopus interpunctatus Dejean	6	9	-
	Tachys sp.	-	21	-
	Tetragonoderus bilunatus Klug	6	5	2
Dytiscidae	*Copelatus* sp.	1	1	-
	Laccophilus posticus Aube	-	2	-
Hydrophilidae	**Berosus* sp.A	36	82	16
	**Berosus* sp.B	150	444	3
	Enochrus sp.	8	63	16
	Hydrobius sp.	-	1	-
Staphylinidae	**Bledius* sp.	61	17	5
	**Carpelimus* sp.	767	7	25
Scarabaeidae	*Comaserica granulipennis* Fairmaire	-	7	1
	**Phaecrous insularis* Linell	161	177	12
Elateridae	*Cardiophorus lutosus* Candèze	4	28	-
	**Cardiotarsus labidus* Erichson	43	100	20
	Elastrus aldabrensis Fleutiaux	13	31	7
	Megapenthes difformis Fleutiaux	10	14	15
	1 unidentified species	9	39	2
Bostrychidae	*Apate congener* Gerstaecker	7	3	-
	Ennaedesmus sp.	2	-	-
Cleridae	*Necrobia rufipes* DeGeer	2	3	2
Nitidulidae	*Cryptarcha* sp	1	-	-
Coccinellidae	*Exochomus laeviusculus* Weise	-	1	1
Tenebrionidae	*Alphitobius diaperinus* Panzer	1	-	-
	Leichenum canaliculatum Fabricius	-	1	-
	Platydema sp.	-	1	-
Alleculidae	*Cacoplesia* nr. *viriditincta* Champion	6	27	7
Monommidae	*Monomma pruinosum* Champion	-	9	-
Oedemeridae	**Ananca aldabrana* Champion	496	1112	790
	Oxacis sp.	7	4	3
	3 unidentified species	1	1	2

Cerambycidae	*Idobrium voeltzkowi* Kolbe	-	13	33
	nr.*Lygrus* sp.	1	19	14
	Paralocus semitibialis Fairmaire	4	7	14
Chrysomelidae	*Aspidomorpha apicalis* Klug	4	-	-
	Keeta fryeri Maulik	65	11	2
	**Rhyparidula insularis* Maulik	9	760	10
	Rhyparidula sp	2	49	5
Anthribidae	*Phloebius pustulosus* Gerstaecker	-	4	6
Curculionidae	*Camptorhinus* sp.	1	-	-
	**Cratopus viridisparsus* Fairmaire	3	33	60
ANNUAL TOTAL NUMBER OF COLEOPTERA		2381	3422	1108
DIPTERA				
Tipulidae	*Limonia corallicola mayotteana* Alexander *L.edwardsella* Alexander *Limonia* sp. 1 unidentified species	39	26	232
Culicidae	Unsorted to species	240	53	856
Chironomidae	Unsorted to species	977	102	15110
Tabanidae	*Aegophagomyia remota* Austen	13	15	12
Stratiomyidae	*Odontomyia* sp	-	4	1
Asilidae	*Ommatius pulchripes* Bigot	3	14	3
Bombyliidae	*Micomitra famula* Bezzi	2	1	-
Dolichopodidae	*Hydrophorus praecox* Lehmann	1	4	5
Tephritidae	*Ceratitis capitata* Wiedemann	-	4	-
	Coelotrypes vittatus Bezzi	7	11	8
	Dioxyna sororcula Wiedemann	-	1	-
	Psednometopum aldabrensis Lamb	5	56	1
Neriidae	1 unidentified species	-	-	5
Lauxaniidae	*Homoneura* sp.	106	498	82
	Sapromyza sp	2	20	18

Lonchaeidae	*Lamprolonchaea aurea* Macquart	1	14	1
Drosophilidae	1 unidentified species	-	7	10
Tethinidae	Approximately 3 unidentified species	1565	588	3825
Chloropidae	*Cadrema pallida* Loew	-	-	13
Anthomyiidae	*Anthomyia fasciata* Walker	3	1	-
Muscidae	*Atherigona* sp.	33	1	92
	Atherigona orientalis Schiner) *Coenosia strigipes* Stein)	1	9	32
	Helina sp.	39	282	42
	Limnophora sp.	1	5	2
	Lispe tetrastigma Schiner	24	1	1
	Musca sorbens Wiedemann	1	3	1
	Ophyra nigrisquama Stein	-	11	-
Calliphoridae	*Chrysomya* nr.*albiceps* Wiedemann	4	14	19
	Cosmina fuscipennis Desvoidy	11	4	6
	Rhinia nr. *apicalis* Wiedemann	-	15	-
	2 unidentified species	2	2	-
Sarcophagidae	*Sarcophaga* spp. (2 species)	15	12	4
Tachinidae	*Pleisiocyptera* nr. *hemimelaena* Bezzi	3	5	3
	6 unidentified species	31	25	7
Ceratopogonidae	*Forcipomyia* sp.) 1 unidentified species)	155	180	781
Scenopinidae	1 unidentified species)			
Ephydridae	*Brachydeutera* sp.) *Paratissa semilutea* Loew)			
Milichiidae	1 unidentified species)			
ANNUAL TOTAL NUMBER OF DIPTERA		3284	1988	21172
HYMENOPTERA				
Formicidae	**Anochetus* sp. A	164	181	750
	Anochetus sp. B	6	8	42
	**Camponotus* sp. A	1015	1832	275
	**Camponotus* sp. B	71	118	29
	**Camponotus* sp. C	1164	975	492
	Camponotus sp. D	12	-	12

	**Leptogenys maxillosa* F. Smith	7	130	134
	**Pheidole* sp.A	347	13	297
	Pheidole sp.B	-	4	3
	**Tetramorium simillimum* Emery	407	62	590
	1 unidentified species	-	112	-
Ichneumonidae	**Enicospilus* sp.	70	51	1
Braconidae	**Phanerotoma* sp.	43	234	159
Unsorted to families — 9 unidentified species		9	21	76
ANNUAL TOTAL NUMBER OF HYMENOPTERA		3315	3741	2860
ODONATA	5 unidentified species	3	-	3
DICTYOPTERA	3 unidentified species	2	34	11
ORTHOPTERA	3 unidentified species	1	30	16
EMBIOPTERA	1 unidentified species	1	-	1
NEUROPTERA	1 unidentified species	36	141	133
TOTAL NUMBER OF TRAPPING NIGHTS		48	56	87

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Appendix 1. Composition of vegetation surrounding the light and suction traps on West Island, Aldabra Atoll

Heath trap 1:

2 - 3 m. in height	*Pemphis acidula* Forst.
	Ipomoea macrantha R.& S.
Herb layer	*Achyranthes aspera* L.
	Portulaca oleracea L.

Heath Trap 2 and Johnson-Taylor Suction traps:

2 - 3 m. in height	*Euphorbia abbottii* Baker
	Acalypha claoxyloides Hutch.
	Allophylus aldabricus Radlk.
	Dichrostachys sp.nov.
	Polysphaeria multiflora Hiern
	Dracaena reflexa Lam.
	Maytenus senegalensis Exell
	Ochna ciliata Lam.
	Ipomoea macrantha R.& S.
	Azima tetracantha Lam.
	Pemphis acidula Forst.
	Premna obtusifolia R.Br.
Herb layer	*Euphorbia hirta* L.
	Dactyloctenium pilosum Stapf
	Passiflora suberosa L.
	Lomatophyllum
	Cyperus obtusiflorus Vahl
	Achyranthes aspera L.

Rothamsted light trap:

2 - 3 m. in height	*Pemphis acidula* Forst.
0.5 - 1 m. in height	*Vernonia cinerea* Less.
	Acalypha claoxyloides Hutch.
	Ipomoea macrantha R.and S.
	Passiflora suberosa L.
	Asparagus umbellulatus Bresler
	Scaevola taccada Roxb.
Herb layer	*Achyranthes aspera* L.

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ECOLOGY OF BIRD ISLAND, SEYCHELLES

by Christopher J. Feare

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ECOLOGY OF BIRD ISLAND, SEYCHELLES

by Christopher J. Feare [1]

INTRODUCTION

Bird Island (55° 12'E, 3° 53'S) is the northernmost island of the Seychelles archipelago, 83 km NNW of Mahé, the largest island of the group. Bird and neighbouring Denis are the only two sand cays of the group (Stoddart 1970) (all other islands are granitic) and they lie on the northern edge of the Seychelles Bank.

The main published scientific accounts are those of Fryer (1910), Ridley and Percy (1957), Baker (1963), Piggott (1968) and Feare (in prep.), but ornithological observations were made by Vesey-Fitzgerald (1941), Bailey (1967), and Feare (1973, 1974, 1975a). This paper is based on observations made in June 1972, from August-November 1972, from May-October 1973 and in July 1974, and is concerned primarily with the vertebrate fauna.

RECENT HISTORY

Coconut planting began early in this century, and in 1907 this was confined to a narrow belt across the centre of the island, (Fryer 1910). Apart from beach vegetation surrounding the island, the remainder of the land was occupied by an enormous Sooty Tern *Sterna fuscata* colony. Eggs were collected and exported to Mahé: according to Fryer (1910), in 1907 909,000 eggs were collected, but claims of much larger egg crops (Ridley & Percy 1957) are probably not well-founded (Feare, in press). In addition to coconuts, pawpaws *Carica papaya* were planted for their papain on the phosphatic sandstone, and in the late nineteenth and early twentieth century guano was exported.

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Despite poor growth of the coconuts (Fryer 1910, Piggott 1969) planting was continued until most of the island was covered. Sooty Tern eggs continued to be a source of income, although coconut planting had restricted the colony to the northwest corner of the island (Fig. 1) and consequently reduced the number of breeding birds. The annual egg crop declined (Ridley and Percy 1958) and exploitation of eggs, except for local consumption, was stopped in 1957. In 1967 the island was bought by Messrs. G. Savy and R. Delorie, who began clearing some of the coconuts adjacent to the Sooty Tern colony in the hope of increasing the number of birds. The cleared area was rapidly occupied, and so more trees were felled; by 1973 the colony occupied 11.7 ha, and numbered c.395000 pairs. For one year tomatoes were grown on part of the cleared area. Since this time no further felling around the colony area has been undertaken.

During the cruises of the *Lindblad Explorer* it became apparent that the Sooty Tern colony and the beaches of Bird Island could be a tourist attraction, and with the impending opening of an international airport on Mahé the owners decided to build a small hotel on the island, and provide access to the island by building two air-strips. This work was begun in 1971 and completed in 1973. The hotel caters for 20 residents and a small number of day visitors. Apart from tourists, the island has a population of about 20 Seychellois.

Tourism, based on the tern colony, game fishing in the surrounding waters and the relative isolation and low human population of the island, is now the main source of income, but coconuts are still exported in small quantities, and Sooty Tern eggs are collected for the Seychellois labourers and for the tourists.

CLIMATE

The climate of the Seychelles is tropical and humid. From May to October (these months are approximate as there is some annual variation) the south east trades affect the islands. In 1972 and 1973 the wind reached a maximum velocity of around 17-20 knots. From December to March the islands are influenced by the north-west monsoon, a period of variable wind velocity and frequent calms. The Seychelles fall outside the cyclone belt, but during the north-west monsoon the effects of tropical disturbances to the south are felt as squalls and rough seas. The average annual temperature is 26.7°C (Piggott 1968), being slightly cooler in the south-east trades and slightly warmer in the north-west monsoon. The transition periods are calm and hot.

Rainfall has not been systematically measured on Bird Island, but for Denis Piggott (1968) gave a mean annual rainfall of 1714 mm (range 1176-2644), most of this falling during the north-west monsoon, as occurs elsewhere in the Seychelles. In 1972 on Bird Island 703 mm fell between 15 August and 5 November, most of this falling as heavy showers over the periods 29 August-2 September, 16-20 September, 8-11 October, 16-19 October and 30 October-5 November. Rain fell on 43 out of the 83 days on which rain was measured. In contrast, in 1973 heavy showers fell on only 6 days between 28 May and 21 October, with light drizzle on a further 8 days. This dry trade wind period of 1973 is perhaps more usual, since local inhabitants remarked that the 1972 season was exceptionally wet.

GEOMORPHOLOGY

Bird Island has maximum surface dimensions of 1.7 x 0.7 km, and a land area of c.70 ha. It is situated on the northern rim of the Seychelles Bank, which is probably based on granite, which underlies the coral on the Seychelles Bank (Baker and Miller 1963). A patch reef extends around the south and east coasts, with a little coral also at the north of the island.

The beach sand is highly unstable and undergoes an annual cycle of erosion and deposition (Fig. 1). During the south-east trades the beaches on the west coast and in Hirondelle Bay, and to a lesser extent on the south-east coast, are eroded, but deposition occurs at the northern tip of the island to form an extensive sand spit. The amount of erosion that occurs each year varies: in 1972 it was severe and by October beach rock was exposed in Hirondelle Bay, while in 1973 the beach here remained wide. During the north west monsoon the process is reversed, with erosion of the sand spit and deposition on the west and north east coasts. The variable nature of these annual events is shown by various beach lines, marked by ridges of sand, driftwood (mainly dead *Tournefortia* and *Suriana* killed when vegetated sand was eroded) and *Cymodocea*. In 1972, and especially 1973, several of these beach lines were visible on the sand spit, and some were being colonized by *Suriana* and *Cyperus pachyrhiza*. Ridges on the sand spit contained much coarse sand with a little coral debris, but depressions were filled with very fine wind blown sand, occasionally up to ½m deep. Piggott (1968) said there was no evidence of coastal erosion, and that the island was increasing in size with the accumulation of sand from the reefs nearby: this interpretation seems to be incorrect.

In the centre of the island is a belt of phosphatic sandstone which represents the remains of a Jemo Series soil (Fosberg 1954), much of the guano having been exploited. In parts the remaining phosphatic horizon is 1 m deep (Piggott 1968). Elsewhere above the high-water mark the soil is Shioya Series with an organic horizon 5-22 cm deep (Piggott 1969). Wells have been sunk in both the phosphatic sandstone and the Shioya soils and these provide brackish water.

There is a little sea-borne pumice behind the beach on the western side of the island.

VEGETATION

Fryer (1910) found Bird Island completely surrounded by a scrub, mainly of *Tournefortia argentea* and *Scaevola taccada*. Inside this belt was a zone of bushes of the same species and also of "weeds", the only plant that he mentioned being *Tribulus cistoides* (Creole name "fagote"). The centre of the island he described as plain occupied by Sooty Terns, and with practically no vegetation, the birds having destroyed this. In addition, he mentioned a *Convolvulus* climbing bushes (= *Ipomoea macrantha*?) *Cassytha filiformis* and *Ipomoea pes-caprae,* and coconuts and pawpaws forming a belt across the middle of the plain.

In 1972-73 sight records were made of 58 species of plants on the island (Table 1) and seven associations were distinguished.

1. Stable beach fringe on sand

This is the belt of *Scaevola* and *Tournefortia* to which Fryer (1910) referred. It dominates the top of the beach on the more stable parts of the coast, from Hirondelle south down the eastern coast and up the western coast to just north of the settlement. Throughout this area *Casuarina* has been planted as a windbreak, although some of these trees were felled and the timber used for hotel construction. The only breaks in the *Scaevola/Tournefortia* belt are where the airstrips have been cut through.

2. Stable beach fringe on phosphatic sandstone

For about 200 m on the north-east coast the phosphatic sandstone reaches the shore, and in some south-east trade seasons the beach sand is eroded away to such an extent that sandstone on the beach becomes exposed. At the top of the beach here is a belt of trees, 7-10 m tall, of *Thespesia populnea* and *Cordia subcordata*. In 1973 *Ipomoea pes-caprae* grew out from beneath this tree fringe to produce an extensive mat over the beach.

3. Unstable beach fringe on sand

Parts of the beach at the northern end of the island were subject to considerable erosion and deposition. (Fig. 1). This varied considerably annually, and in 1972 and 1973 several beach lines were apparent on the north-west corner. These areas were dominated by *Suriana maritima* and *Cyperus pachyrhiza,* and recent beach lines lying outside the *Scaevola* belt on the south-west coast showed that these two plants were the first to colonize recently deposited sand. Interspersed amongst the *Suriana* were a few small *Scaevola* and *Tournefortia* bushes, but these appeared to reach a large size only on stable sand.

Table 1. List of sight records of plants on Bird Island 1972-1974

Abutilon indicum
Acalypha indica
Achyranthes aspera
Agave sisalana
Amaranthus oleraceus
Asystasia gangetica
Boerhavia repens
Calophyllum inophyllum
Capsicum minimum
Carica papaya
Cassia occidentalis
Cassytha filiformis
Casuarina equisetifolia
Catharanthus roseus
Cleome viscosa
Cocos nucifera
Cordia subcordata
Cucurbita moschata
Cynodon dactylon
Cyperus pachyrhiza
Dactyloctenium aegyptium
Datura metel
Eleusine indica
Euphorbia hirta
Euphorbia prostrata
Ficus sp.
Gossypium hirsutum
Guettarda speciosa
Gynandropsis gynandra
Ipomœa pes-caprae
Ipomoea macrantha
Kalanchoe pinnata
Lippia nodiflora
Malvastrum coromandelianum
Maranta arundinacea
Mariscus dubius
Mirabilis jalapa
Moringa oleifera
Musa sapientum
Nephrolepis biserrata
Passiflora suberosa
Phyllanthus casticum
Pisonia grandis
Portulaca oleracea
Ricinus communis
Scaevola taccada
Sida acuta
Solanum melongena
Solanum nigrum
Stachytarpheta jamaicensis
Stenotaphrum micranthum
Suriana maritima
Tabebuia rosea
Thespesia populnea
Tournefortia argentea
Tribulus cistoides
Turnera ulmifolia
Vernonia cinerea

(Procter (1970 and pers. comm.) recorded *Digitaria horizontalis, Enteropogon monostachyos, Enteropogon sechellensis, Eragrostis tenella,* and *Sporobolos viginicus* in July 1970. Fryer (1910) recorded a large *Hernandia peltata* at the settlement, but this is no longer present).

4. Sooty Tern colony

The main vegetation components of the original colony, i.e, that which was present before the felling of coconuts was begun, are *Portulaca oleracea, Boerhavia repens* and small areas of *Tribulus cistoides.* These species are characterised by an ability to survive burning off by the joint action of faeces and salt water from the birds. In 1973 this burning off was complete, and by October the colony was devoid of herb vegetation. However, in the much wetter 1972 season these plants continued growing to a limited extent; this may have been due directly to the presence of water, or indirectly through the unusually rapid leaching of salt and faeces. In 1972 the area of the colony which had been recently cleared of trees was dominated by grasses, but there were small areas of *Stachytarpheta jamaicensis* and *Achyranthes aspera,* and in parts, especially beneath Casuarina trees, *Lippia nodiflora.* Sooty Terns nested only at low density in the tall grass, and so before the birds returned to the island in March-May the grass was cut. This, together with the effect of salt water and faeces from the birds, killed some areas of grass, and by the beginning of the 1973 season *Portulaca, Boerhavia* and *Tribulus* had become established. To encourage the spread of these species remaining grass was burned off at the end of the 1973 season, and although grasses were still present in the area in 1974, *Portulaca, Boerhavia* and *Tribulus* had occupied more ground.

In addition to this form of management, bushes of *Tournefortia, Scaevola* and *Suriana* within the colony were cut down each year to provide more space for the birds. The cut bushes were stacked in piles around the colony, and while they provided some shade for Sooty Tern chicks, they also provided nesting areas for rats.

5. Coconut plantation in sand

The vegetation beneath coconuts on the sandy part of the island consists mainly of a herb layer, dominated by grasses of various species, *Lippia nodiflora* and *Boerhavia repens.* Where this vegetation was kept short eg. around the settlement, many other species were found including exotics, but where vegetation was allowed to develop occasional bushes of *Scaevola* occurred.

6. Coconut plantation on phosphatic sandstone

Here the vegetation was much more dense than on sand, doubtless due to the more fertile soil. Apart from *Carica papaya* which had gone wild, *Nephrolepis biserrata, Phyllanthus casticum* and *Kalanchoe pinnata* were abundant. A few bananas *Musa sapientum* had been planted but did not produce fruit.

7. Airstrips

The airstrips were cut through the coconut plantation on both sand and phosphatic sandstone. After clearance the parts of the airstrip on sand rapidly became carpeted with a binding mat of *Lippia nodiflora*. In 1972, during a break in the levelling operations on the sandstone, areas of broken sandstone supported dense areas of small *Carica papaya* and *Abutilon indicum,* but when levelling had been completed in 1974 phosphatic sandstone areas of the airstrips either consisted of bare sand or were colonised by *Lippia nodiflora*.

INVERTEBRATE FAUNA

No detailed observations on terrestrial invertebrates except ticks were made, but the following groups were recorded:

Crustacea

Two species of land crab were common, and one was an important scavenger in the Sooty Tern colony.

Myriapoda

A small millipede and a small centipede were occasionally seen around the settlement.

Insecta

Odonata
Dictyoptera
Isoptera
Hemiptera
Orthoptera
Coleoptera
Planipennia
Lepidoptera
Diptera: Mosquitoes were abundant during the wet 1972 season, but scarce in 1973. House flies periodically infested the island in July and August, but no direct relation with the state of the Sooty Tern colony was found.
Hymenoptera
Phthiraptera: Lice *Saemunssonia sternae* were found on the heads of a dead Roseate Terns *Sterna dougallii* and a louse, probably the same species was common on the heads of Sooty Terns.

Arachnida

Scorpionidea: A small scorpion was common under the bark of *Casuarina*.

Araneida

Acarina: Two species of tick were found. *Ornithodoros capensis* was common in the Sooty Tern colony in 1973 and caused part of the colony to desert (Feare 1976) and was found to carry Soldado virus. (Converse *et. al.* 1975). *Amblyomma loculosum* was found occasionally on Sooty Terns (Hoogstraal *et. al.* 1975), and specimens collected from two dead Roseate Terns were found to carry a new virus, Aride virus (Converse *et. al.* 1975).

AMPHIBIA

During this study Mrs. F.C. Feare and Mrs. M.F. Savy saw one frog, and frogs had been seen occasionally prior to this. This is most likely to be *Rana madagascariensis,* which may have been introduced to the Seychelles (Gaymer 1968), and is almost certainly an accidental introduction to Bird Island from the granitic islands.

REPTILES

The reptile fauna of Bird Island comprises a skink, two geckos, a snake, two marine turtles, and two tortoises.

Mabuya sechellensis

This endemic skink was common over most of the island, but was not found in the interior of the sooty tern colony. It occurs on most of the islands of the Seychelles, but Vesey-Fitzgerald (1947) thought that it may be an accidental introduction on the sand cays.

Phelsuma sp.

A *Phelsuma* gecko was common in the buildings around the settlement, and was also seen in the plantation. Again, this may have been an accidental introduction from the granitic islands, but the taxonomy of the *Phelsuma* geckos of the Seychelles is not clear (Gaymer 1968). Bird Island specimens appeared distinct from those seen on Mahe. Praslin, La Digue and Cousin. They were bright green, attained the size of those commonly seen at around 500 m on Mahe (i.e. smaller than those on Praslin and La Digue, but larger than on Cousin) and the red spotting on the back was sparse.

Hemidactylus sp.

A brown gecko, presumably introduced, was common in the buildings around the settlement.

Rhamphotyphlops braminus

Specimens of this parthenogenetic burrowing snake were found in damp soil under stones and timber. This species is widely distributed in the Indo-Pacific, and has also been found in Mexico and possibly in West Africa. It has previously been recorded in the Seychelles from Mahé (Vesey-Fitzgerald 1947) and Frigate (Gaymer 1968) and there are also specimens in the British Museum from Praslin and Cerf (J.C. Dring, pers. comm.). Specimens from Bird Island constitute the first Seychelles records from a coralline island, and two have been deposited in the British Museum (BMNH 1975. 1148-1149).

Vesey-Fitzgerald (1947) and Gaymer (1968) thought that *R. braminus* may have been introduced to the Seychelles, but in view of its wide distribution (in the western Indian Ocean it also occurs in the Maldives, Comores and on Mauritius - J.C. Dring, pers. comm.) it may in fact be indigenous. On coralline islands this may be less likely, and the importation of coconuts and various palm leaves (for use as thatch) from the granitic islands would facilitate introduction to Bird Island.

Chelonia mydas Green Turtle

The main laying season for Green Turtles on Bird Island is May-October, the period of the SE trades. In 1972 no search for nests or tracks was made, but at least six nests were known to have been made. In 1973, Green Turtles were known to have come ashore on 24 occasions between 2 July and 28 October, and 15 nests were made. All nests, and most attempts to come ashore, were on the north-east coast (Fig. 2), with two in July, nine in August, 11 in September and two in October.

How these figures compare with earlier populations is not known, but it is to be hoped that the prohibition of killing Green Turtles in the Seychelles will be effective, but the difficulties of policing isolated islands and the high regard which island dwelling Seychellois have for turtle meat will mitigate against this. At present, it appears that Bird Island (and possibly Denis?) are the Seychelles headquarters for Green Turtle.

Eretmochelys imbricata Hawksbill Turtle

Hawksbill Turtles are mainly north-west monsoon (November-March) breeders on Bird Island, and consequently few were seen during this study. One laid in November 1972, and in 1973 eggs were laid on 13 September and 28 October, while turtles came ashore but did not lay on 12 and 24 September.

Testudo gigantea Giant Tortoise

Two giant tortoises are free on the island, both having been recently imported.

Leopard Tortoise

The history of a Leopard Tortoise, sometimes kept in a pen and sometimes free-ranging, is not known.

MAMMALS

All mammals on the island have been introduced, and the 40 miles of sea separating Bird from the closest granitic island, Silhouette, appears sufficient to prevent fruit bats *Pteropus sechellensis* reaching the island. In 1972 and 1973 the only mammals present were a donkey, c.40 pigs, occasional mice ?*Mus musculus* seen around the settlement, and rats *Rattus rattus*. In the past a dog and goats, and possibly cats, have lived on the island.

The history of the rat infestation is notable. Until 1967 there were no rats, and it is thought that they were imported with a consignment of leaves for thatching from Praslin. They increased rapidly and by 1972 the entire island was infested. Attempts at control using warfarin and thallium sulphate in 1973 resulted in much reduced numbers around the settlement late in that year and in 1974. The rats lived all over the island and there appeared to be no noticeable movement into the Sooty Tern colony when the birds were breeding. Away from the colony the only food rats were seen to eat were pawpaws, but doubtless coconuts and other plants were taken, and eggs and chicks of Brown Noddies *Anous stolidus* and White Terns *Gygis alba* were known to have been eaten.

The number of rats did not therefore appear to be controlled by the seasonal appearance of the Sooty Terns, and the rats appeared to have little influence on Sooty Tern breeding success, being responsible for only small losses of eggs and chicks (Feare, in prep.). In 1973, six chicks, representing only 6.5% of total chick losses, that were known to have been killed by rats, had been losing weight prior to death, and in 1972 rat predation appeared to be restricted to weak or injured chicks. There is no evidence of a decline in the Sooty Tern population since the rats arrived (it is more likely that the colony is increasing, but counts are lacking), and the burrow-nesting Wedge-tailed Shearwater, *Puffinus pacificus* still breeds in cavities in the phosphatic sandstone. (Piggott's (1969) claim that fouquets - *P. pacificus* - disappeared long ago is erroneous.)

BIRDS

None of the land birds endemic to the Seychelles occur on Bird Island, but three of the land birds introduced to the Seychelles have become established on the island. Five species of seabird breed, and a further seabird, the Masked Booby, *Sula dactylatra* stopped breeding around 1940, when the birds are said to have been killed by the islanders. The only other breeding species is the Cattle Egret, but many migrants, especially from the palaearctic, were recorded in 1972-3. Apart from these domestic chickens *Gallus domesticus* run free, and one Peahen *Pavo* sp. seen in 1974-1973 appeared to be the sole survivor of a flock that used to breed on the island. Quail *Coturnix coturnix* were present up to 1968, but have not been seen since.

(i) Breeding seabirds

Wedge-tailed Shearwater *Puffinus pacificus*

Between May and October birds were seen off the island most evenings, but numbers increased in July and August, with birds calling over the island at night. In October newly excavated burrows were found - of three whose cavities could be reached two had no egg or chick and one had an egg, while in another burrow whose cavity could not be reached a call thought to be that of a chick was heard. On the granitic islands Wedge-tails breed from October to December (Lousteau-Lalanne 1963).

On Bird Island Wedge-tails excavated burrows in pockets of sand in the phosphatic sandstone, especially around the holes dug for planting coconuts. No estimate of numbers was obtained, but plenty of suitable habitat was available in the interior of the island. However, some of the potential habitat was destroyed by the construction of the airstrips.

White-tailed Tropic Bird *Phaethon lepturus*

Few pairs, perhaps less than 20, bred in coconut and *Casuarina* trees. A pair was found on a nest with no egg on 28 August, 1973 and they had an egg in mid-September but this was eventually lost. On Cousin White-tailed Tropic birds breed throughout the year (Diamond, in press) as they probably do on other islands of the Seychelles (pers. obs.).

Sooty Tern *Sterna fuscata*

On Bird Island as elsewhere in the Seychelles Sooty Terns breed only during the south-east trades, usually late May to October.

The biology and history of the Sooty Tern colony has been reviewed by Feare (in press). No estimates of population size at the beginning of the twentieth century exist, but the collection of 909,000 eggs in 1907 (Fryer 1910) suggests that probably over a million pairs bred in that year. In the mid 1930's Vesey-Fitzgerald (1941) estimated that 65,000 pairs bred but in 1955 the colony was reduced to 18,000 pairs (Ridley and Percy 1966, correcting their 1958 estimate of 8,300 pairs). Bailey (1968) estimated 20,000 well feathered chicks on 4 November 1963. Ridley & Percy (1966) estimated 120,000 pairs. In 1973 Feare (in prep.) estimated that 395,000 pairs had bred, while due to food shortage which affected many seabirds in 1974 (Diamond, in press) Sooty Terns arrived to breed late and in reduced numbers (as they did also on Aride in the Seychelles, and on Desneufs, but to a much smaller extent on African Banks, in the Amirantes). This colony expansion as more nesting area is provided suggests that in the Seychelles breeding space is at present limiting the population, rather than food, which Ashmole (1963) considered to be limiting Ascension Island Sooty Terns. However, the 1974 observations show that food shortage can restrict the number of breeding birds in some years.

Brown Noddy *Anous stolidus*

Before coconuts were planted noddies nested in the *Scaevola* and *Tournefortia* bushes, but now they nest almost exclusively in coconuts, with (in 1972) about 20 pairs nesting in young *Casuarina* on the south-eastern coast. In these habitats they build a substantial nest of seaweed, in contrast to the situation on some rocky islands e.g. Aride and Ile aux Vaches (Grande Anse) where when laying on rock no nest is built (pers. obs.). On Bird Island Noddies are present throughout the year and may breed for most of the year. Chicks were seen and heard in all months from May to October and breeding is certainly not restricted to the south-east trades. In fact here breeding appears to be much less synchronous than on Aride, Cousin and Ile aux Vaches where ground nesting birds predominate. It would be interesting to know whether the substantial nest building and extended breeding season birds of Bird Island represented a population distinct from the reduced or no-nest, and more restricted breeding season birds of other islands.

In September 1972 the population was (number of nests/coconut tree x number of trees) estimated at about 10,000 pairs. Ridley and Percy (1958) considered there to be only 1000 pairs in 1955, and they thought the population had not increased in 1966. However, Mr. G. Savy, resident owner since 1967, thought that noddies had not increased since he bought the island. To what extent the population has increased, or whether Ridley and Percy's estimate was too conservative - is not known. The biology of this species on Bird Island has not been studied. Some losses of chicks occur through them falling from the nest; when these were small their parents did not continue to feed them on the ground, and they were eventually killed by rats. There may be competition with rats for nest sites in the tops of the coconut trees.

White Tern *Gygis alba*

This species was not mentioned by Fryer (1910), and although it may have nested in small numbers in the *Scaevola* and *Tournefortia*, it may in fact be a recent colonist. It is now dependent for its nest sites on *Casuarina* and buildings at the settlement, though a few pairs lay their eggs on coconut fronds, on footholds on coconut trunks or even on pawpaw trees. In September 1972 the population was estimated at about 720 pairs.

This species is noted for its high egg and chick losses (Dorward 1963), and this situation prevails on Bird Island. Rats take both eggs and chicks from the buildings, but birds laying in *Casuarina* may not be subject to this loss. Breeding occurred throughout the south-east trades, but Mr. & Mrs. Savy thought that breeding stopped in January and February, when most birds left the island. If this is so, breeding on Bird Island differs from that on Cousin where it is continuous throughout the year (Diamond, in press).

(ii) Breeding land birds

Cattle Egret *Bubulcus ibis*

In 1972 there were seven nests (eggs and chick present mid-August) in two *Casuarina* trees at Passe Coco, but in 1973 these trees, with their nests, were cut down. Cattle Egrets on the island were very mobile, and no reliable estimate of the number of birds present was obtained, but there were probably over 40 birds. Sooty Tern eggs and young chicks, and regurgitated food, formed part of their diet during the tern breeding season (Feare 1975b) and egrets certainly bred at this time, but it is not known whether the egrets breeding season extended into the north-west monsoon; then their diet must consist almost entirely of insects, skinks, and refuse from around the settlement and pig enclosure. Cattle Egrets in the Seychelles appear to be an endemic subspecies *B.i. seychellarum* (Benson 1971), and they may be indigenous on the seabird islands. They were present on Bird Island in 1907 (Fryer 1910).

Ridley and Percy (1958) regarded Cattle Egrets as serious predators of Sooty Terns, but during the 1973 season on Bird Island very few losses of eggs and chicks could be attributed to egrets (Feare in press), and eggs and chicks that egrets did take had usually been left unattended by the terns. Losses would probably be increased as a result of human interference in tern colonies.

Barred Ground Dove *Geopelia striata*

Common all over the island, except the Sooty Tern colony, but no estimate of numbers was obtained. No nests were found between June and October, but increasing courtship in October of both years suggested that breeding occurred during the northwest monsoon. Fryer (1910) recorded ground doves on Bird Island.

Mynah *Acridotheres tristis*

Mynahs were not mentioned by Fryer (1910) and so it is presumably a recent arrival from the granitic islands. It was present all over the island in 1972 and 1973, and although no estimate of numbers was obtained there were probably well over 100 birds. Pawpaws appeared to form an important component of the diet, but birds were also frequently seen feeding in grassland on the airstrip and around the edge of the Sooty Tern colony. Nestbuilding in coconuts was seen in November 1972, so breeding presumably occurred during the north-west monsoon.

The most notable aspect of Mynah behaviour on Bird Island was the absence of noisy communal roosts typical of the species on the granitic islands. On Bird Island the Mynahs' food did not appear to be localised, while on Mahé, where ripe fruit, especially mangoes *Mangifera* sp. and guavas *Psidium* sp., was an important source of food, trees with ripening fruit were localised in space and time. The absence of communal roosting on Bird Island lends support to the hypothesis that such roosts assist bird populations to discover and utilize localised food sources (Ward 1965, Zahavi 1971, Feare *et. al* 1974).

Madagascar Fody *Foudia madagascariensis*

Common throughout the island, where unoccupied nests were found in coconut and *Casuarina* trees. Many birds roosted in a large *Ficus* tree at the settlement. Red males were uncommon from May to August, but a juvenile seen begging on 13 August 1972 suggested that limited breeding occurred during this period. Red and moulting birds were more abundant in September and October, when males became territorial. Breeding therefore occurred mainly in the north-west monsoon.

(iii) Migrants

Records of birds of which specimens or photographs have been deposited in Cambridge Zoology Museum have been published by Feare (1973, 1975) and a comprehensive account of shorebirds in Seychelles is given by Feare and High (in press). Full details are given in these papers.

Audubon's Shearwater *Puffinus lherminieri*

Commonly seen a few miles offshore from boats, but rarely seen from the island. One found dead on the beach 18 June 1973.

Wilson's Petrel *Oceanites oceanicus*

One seen close inshore around small fishing boat 2 November 1972.

Red-billed Tropic Bird *Phaethon aethereus*

One regularly seen over the island, frequently displaying to *Ph. lepturus,* in July-August and September-October 1973, and May-June 1974 (Feare 1975a). Recorded in the Amirantes by Stoddart and Poore (1970).

Red-tailed Tropic Bird *Phaethon rubricauda*

One adult over island throughout morning 25 September 1973.

Masked Booby *Sula dactylatra*

No longer breeds. Immatures occasionally seen, especially August-September and an adult 19 August 1972.

Red-footed Booby *Sula sula*

Single birds occasionally roosted with frigate birds in *Casuarina* trees.

Brown Booby *Sula leucogaster*

An immature flew over the Sooty Tern colony 20 June 1972.

Great and Lesser Frigate Birds *Fregata minor* and *F. ariel*

Frigate birds roosted in tall *Casuarina* at Hirondelle on most nights, and were frequently seen feeding during the day. Numbers varied considerably from day to day, with a maximum of 41 on 2 June 1973. Said to be more numerous November-April. Most were immatures, but adult males of both species were occasionally seen.

Purple Heron *Ardea purpurea*

Immatures seen 8 September (this bird found starving 20 September) and 4 October 1973 (Feare 1975a).

Little Green Heron *Butorides striatus*

One on the beach at Passe Coco on 28 September 1972 is the only record of this species, which is common on the granitic islands.

Madagascar Squacco Heron *Ardeola idae*

An immature Squacco, thought to be this species, was present 22-29 September 1973 (Feare 1975a).

Garganey *Anas querquedula*

Immatures seen 18, 20 and 21 September 1972, and one found dead November 1973 (Feare 1975a).

Black Kite *Milvus migrans*

A large raptor, thought to be this species, was seen flying north 21 September 1973. Vesey-Fitzgerald (1936) recorded several "buzzards" on Bird Island 1936]

Hobby *Falco subbuteo*

Recorded by Moreau (1938) in November 1936 and Feare (1973) in December 1972. Unidentified falcons were seen 18 and 23 October 1972, and Mr. G. Savy had seen several falcons on the island since 1967.

Corncrake *Crex-crex*

One 5-6 October 1973 (Feare 1975).

Moorhen *Gallinula chloropus*

Recorded by Fryer (1910), and seen occasionally since 1968, but not in 1972 and 1973. Presumably these birds come from the granitic islands.

Ringed Plover *Charadrius hiaticula*

Singles on 5 September and 1 October 1973.

Little Ringed Plover *Charadrius dubius*

One 13 November 1972.

Lesser Sand Plover *Charadrius mongolus*

Recorded in June and August-November 1972, and September 1973.

Great Sand Plover *Charadrius leschenaultii*

Small numbers May - late September increased October.

Caspian Plover *Charadrius asiaticus*

Singles June and September-October 1973, and three on 2 October.

Asiatic Golden Plover *Pluvialis dominica*

Singles 20 August and 19 October-mid November 1972 in the Sooty Tern colony.

Grey Plover *Pluvialis squatarola*

Present throughout year, migrants arrived September-October.

Turnstone *Arenaria interpres*

Present throughout year. Birds present during the Sooty Tern breeding season were egg predators and scavengers, but they fed throughout the coconut plantation, presumably on insects. At low spring tides they fed on the reef flat.

Rufous-necked Stint *Calidris ruficollis*

One in the Sooty Tern colony with Curlew Sandpipers 13-14 November 1972.

Temminck's Stint *Calidris temminckii*

Recorded by Bailey (1967) and one on airstrip 22 September 1972.

Pectoral Sandpiper *Calidris melanotos*

One feeding with Turnstones in the Sooty Tern colony 13 October 1972.

Curlew Sandpiper *Calidris ferruginea*

Seen singly and in small parties from September-May.

Sanderling *Calidris alba*

Present all year increasing in October. Usually restricted to the beach, but fed in Sooty Tern colony when the terns began leaving.

Ruff *Philomachus pugnax*

Singles 26 September-28 October 1972 and 24-30 September, 1973.

Greenshank *Tringa nebularia*

Singles 31 July 1972 and occasionally September-October 1972 and 1973.

Wood Sandpiper *Tringa glareola*

Singles 2-3 October, 16-18 October and 12-15 November 1972, on the airstrip and around the settlement.

Common Sandpiper *Actitis hypoleucos*

Recorded from late August in small numbers, mainly on island paths and around the settlement.

Terek Sandpiper *Xenus cinereus*

Singles 11-25 October 1972 and 9-19 October 1973.

Bar-tailed Godwit *Limosa lapponica*

Small numbers seen September-October 1972 and 1973.

Curlew *Numenius arquata*

Recorded June and September-October 1972, and May, but not autumn 1973.

Whimbrel *Numenius phaeopus*

Present all year, feeding mainly in the coconut plantation, but at low spring tides also on the reef flat.

Little Whimbrel *Numenius minutus*

Single 14 October 1972-April 1973 (Feare 1973).

Snipe *Gallinago* sp.

A snipe, probably *G. gallinago*, was flushed from *Scaevola* bushes 23 October 1972.

Jack Snipe *Limnocryptes minimus*

One 3 September 1973.

Crab Plover *Dromas ardeola*

Present all year. Family parties, each of two adults and one begging juvenile arrived October 1972 and September 1973. Only seen on the beach.

Collared Pratincole *Glareola pratincola*

Recorded by Bailey (1967) in November 1963. One seen daily 25 September-14 October 1972, with 4 27-29 September.

Lesser Black-backed Gull *Larus fuscus*

One adult 11 October 1972. Also recorded on Aldabra (Dawson 1966), and on Mahé in January-February 1972.

Roseate Tern *Sterna dougallii*

Occurs irregularly in small numbers, often associating with other terns on the beach. Usually in non-breeding plumage, but on 8 July 1973 two birds in breeding plumage were found dead with *Amblyomma loculosum* ticks on their feet. Breeds in the Seychelles and Amirantes.

Black-naped Tern *Sterna sumatrana*

Small numbers seen on the beach in June 1972 and 1973. Breeds in the Amirantes.

Bridled Tern *Sterna anaethetus*

Roosted at night in large numbers (5000+) in *Casuarina* trees throughout the periods of study, despite breeding every 7-8 months on some of the granitic islands (Diamond, in press). During two periods in mid July and mid August when Sooty Terns were short of food (Feare, in press) the number of roosting birds fell and several Bridled Terns were found starving or dead. Bridled Terns were rarely seen during the day, but roosting birds began returning in mid-afternoon.

Saunders Tern *Sterna ? saundersi*

From August-October in both 1972 and 1973 small terns congregated on the sand spit at the northern end of the island, the largest flock being 258 on 21 September 1973. Flocks of small terns have also been recorded on several other islands in the western Indian Ocean (Vesey-Fitzgerald 1941, Benson 1967, Bayne *et. al* 1970, Parker 1971). The identity of these birds is uncertain. Diamond (1971) thought that birds on Aldabra were *S.a. albifrons*, since they had yellow legs, but Vesey-Fitzgerald (1941) and Loustean-Lalanne (1963) considered them to be *S.a. saundersi* (regarded by Vaurie (1965) as a distinct species *S. saundersi*), while Mountford (1971) identified Bird Island individuals as *S. balaenarum*, Damara Tern of the cold waters of SW Africa, on account of their black bills. However, moulting birds in May had yellow bills with black tips, typical of *albifrons* and *saundersi*, and they never had complete black caps, which breeding plumage *balaenarum* has.

Crested Tern *Thalasseus bergii*

A party of 5-20 birds was present throughout the two study periods, with juveniles being fed by adults (Feare 1975c). The adults appeared to feed mainly inside the reef. The nearest known breeding colony is African Banks, about 240 km to the south west. Most adults were typical of the pale backed *T.b. thalassina* which breeds in the western Indian Ocean, but from 11 September-3 October 1973 an adult with a very dark back (as in British lesser black-backed gull *Larus fuscus graellsii*) and a more orange bill than *T.b. thalassina* was present in the flock. Comparison of photographs of this bird with specimens in the British Museum suggested that this bird was *T.b. velox,* which breeds around the coasts of the northern Indian Ocean. This individual was in breeding plumage, but during its stay on Bird Island it began primary moult.

Lesser Crested Tern *Thalasseus benghalensis*

Two on 28 May, 1975. Small flocks were occasionally seen round Mahé.

Black Noddy *Anous tenuirostris*

Occasionally a few birds roosted in *Casuarina* trees with Bridled Terns, but on each night from 10-14 September 1973 very large numbers roosted in coconut trees in the centre of the island. The birds assembled offshore in a flock estimated at well over 10,000 birds, and began flying into the island at 1830h (almost dark) usually in flocks of 30-50 birds, but some times in a long winding stream of birds. The movement continued until about 2130. They flew low over the water, but when they reached the shoreline they began erratic movements, each bird in the flock flying independently of the others. Throughout the flight they were silent, but once settled in the trees they called loudly. This behaviour, also seen in Brown Noddies returning to their nests, was reminiscent of defensive behaviour against aerial predators. However, in the Seychelles, there are no indigenous aerial predators, but migrant falcons could conceivably constitute a threat.

Turtle Dove *Streptopelia* sp.

An unidentified turtle dove was seen feeding in *Phyllanthus casticum* on 30 October 1972. It was uniform red/brown with no grey on head or rump, and no markings on the neck; the bill was the same colour, but the lower belly and undertail were buff; the tail had a narrow white terminal band.

Great Spotted Cuckoo *Glamator glandarius*

An immature seen 5-7 October 1973. Very long dark grey tail with white edges. Back grey, heavily spotted white. Chin, breast and belly warm cream with buffish tinge, especially on throat. Crown black, extending below eye and on to ear coverts, slightly crested. Rufous patch on primaries. Bill short and decurved. This is the only record for the Malagasy region.

Grey Cuckoo *Cuculus canorus*

Frequently seen 8 October-7 November 1972 with two on 1 November. The bird on 8 October was rufous, all others grey.

Barn Owl *Tyto alba*

A bird first seen 9 August 1973 remained for several months and was eventually found dead, but too decomposed for subspecific identification. Probably *T.a. capensis*, which was introduced on Mahé and spread to most of the granitic islands.

European Nightjar *Caprimulugus europaeus*

A ♀, nominate race, was found dead early December 1972 (Feare 1973).

Black Swift *Apus apus*

Black swifts (presumably this species, which has also occurred on Aldabra (Benson & Penny 1971), but on sight records *A. barbatus* cannot be ruled out) were seen in 1972 as follows: 2 on 30 September, singles 30 October, 6 November, 7 November and 14 November. All were all black except for white chin, and had slightly forked tails.

Pacific Swift *Apus pacificus*

Singles seen 20 October, 1 November and 13 November 1972, with three on 14 November and two on 15 November. These birds were black with pure white "square" rump patch; tail slightly forked. The bird on 20 October had pale whitish chin and a small white mark on under tail coverts. Birds on 14 November flying with *A. apus* were slightly smaller, had no white on under tail coverts, and an indistinct greyish throat patch. From these descriptions R.K. Brook thought they may be *A. pacificus* which had over-flown from S. India (but see Frith 1974 for white-rumped swifts on Aldabra).

Blue-cheeked Bee Eater *Merops superciliosus*

Four-five birds in November, 1972 were *M.s. persicus* (Feare 1975a).

European Roller *Coracias garrulus*

c.5 were present in November-December 1972, when others, both adult and juvenile, were present on Mahé.

Broad-billed Roller *Eurystomus glaucurus*

One on 14 November 1972 in fresh plumage was probably the nominate race, lost on its return from Africa to Madagascar (Feare 1975a). This is the first Seychelles record, but nominate *E. glaucurus* has occurred on islands further west (Benson & Penny 1971).

Swallow *Hirundo rustica*

From descriptions by Mr. & Mrs. Savy birds seen in several winters were this species, which has been recorded previously from the Seychelles (Crook 1960) and from Aldabra (Benson & Penny 1971).

Wheatear *Oenanthe oenanthe*

One from 26-29 October 1972 (Feare 1975a).

Tree Pipit *Anthus trivialis*

According to Mr. Savy pipits have been seen most years since 1968. In 1972, two were seen 21 October and three from 23 October to at least 15 November. In 1973 one present from 7 October until at least 21 October. They apparently remain throughout the northern winter. Crook (1960) also recorded this species from Frigate Island.

Red-throated Pipit *Anthus cervinus*

Singles 28 October and 10 November 1972. Identified by streaked rump, long hind claws, pink legs and call a loud "shup".

Grey Wagtail *Motacilla cinerea*

Present 8-13 November 1972, with maximum of three on 12 November (Feare 1975a).

Yellow Wagtail *Motacilla flava*

Winters on the island each year (G. Savy pers comm.). Singles seen October and November 1972, and October 1973. An ad. ♂ on 4 November 1972 had characters of *M.f. flava* with slate crown and nape with slightly darker ear coverts, and white eye-stripe, but one on Mahé in November 1972 resembled *M.f. beema*. Birds on Aldabra appear to be *M.f. lutea* (Benson and Penny 1971).

Ortolan Bunting *Emberiza hortulana*

An immature on 13 and 14 November 1972 (Feare 1975a).

Golden Oriole *Oriolus oriolus*

Frequently seen in October-November 1972, with three on 1 November. All were juveniles or ♀. Crown, head, nape and back yellow/green. Upper tail brownish green with yellow tip; rump, under tail and lower belly bright yellow. Breast grey/buff finely streaked brown; sides of breast yellowish buff. Belly buff with sparse fine streaking. These are the first records for the Seychelles, but Golden Orioles have occurred on Aldabra.

DISCUSSION

Bird Island, together with Denis and the islands of the Amirante group, probably have a Pre-Cambrian granite foundation (Baker and Miller 1963) and these sand cays and atolls may therefore be older than similar islands elsewhere which are based on more recent volcanic rocks. The phosphatic sandstone of Bird Island suggests that for much of its recent geological history the island has been dominated by birds, and man's influence has probably been felt for less than 100 years. During this 100 years, however, the island has been transformed to such an extent that it is now difficult to separate the indigenous elements of the fauna and flora from what has been recently introduced. For example, while *Rana madagascarienses*, the three breeding land birds, and the rat have certainly been brought by man, the distinctiveness of Bird Island *Phelsuma* geckos suggests that it may be indigenous, as may be the burrowing snake *Rhamphotyphlops*. Both of these animals could, however, have been transported from the granitic islands amongst coconuts that were brought for planting. Vesey-Fitzgerald (1947) considered this to have happened with the skink *Mabuya sechellensis*. Similarly, while both the stable and unstable beach fringe plant associations on sand are certainly indigenous, and much of the flora of the coconut plantations is undoubtedly introduced, the beach fringe association on phosphatic sandstone, dominated by the trees *Thespesia populnea* and *Cordia subcordata,* was not mentioned by Fryer (1910). These plants may therefore have been introduced by man, and have become established in the habitat with which they seem to be naturally associated on other islands (e.g. on elevated limestone on Astore, Assumption and Aldabra - Bayne *et. al* 1970, Stoddart *et. al* 1970, Stoddart and Wright 1967).

The introduction that has had the most far-reaching effects has been that of the coconut. While it has been claimed that over-exploitation of eggs may have reduced the Seychelles populations of Sooty Terns, on Bird Island the main factor in the reduction of the colony has been the removal of space in which the birds could breed. This has been demonstrated by the recent removal of part of the coconut plantation, the newly-available space having been rapidly occupied by Sooty Terns.

The planting of coconuts, therefore, brought to an end a long period of domination of the island by seabirds, during which guano deposits were formed with a layer of phosphatic sandstone beneath. Fryer (1910) found Sooty Terns, Brown Noddies and Masked Boobies to be the main species living on Bird Island in 1907, but whether these three species were always dominants, and were therefore responsible for the formation of guano and phosphatic sandstone, is moot. Fosberg (1954) considered that an essential element in the formation of Jemo Series soils was the litter of *Pisonia grandis*. At present this is an uncommon plant on Bird Island, and since Fryer (1910) did not mention it, it was probably uncommon before coconuts were planted. On islands in the Seychelles where *Pisonia* woodland is well developed (especially Aride, pers. obs.) tree-breeding species are the main guano producers. Currently the species involved are mainly the two noddies (especially Black) and White Terns, but in the past larger tree breeding species, e.g. Red-footed Boobies and Greater and Lesser Frigate Birds, may have bred in these habitats in the

Seychelles and may have made a much greater contribution to guano formation than the smaller species. The presence of Jemo Series soil on Bird Island (and on other sand cays with Sooty Tern colonies e.g., African Banks: Feare, in prep.) suggest that either *Pisonia* is not an obligatory precursor in phosphatic sandstone formation, or that Bird Island has at one time been more densely vegetated than when described early this century, and for some reason much of this vegetation disappeared.

A characteristic of Jemo soils is that some of the phosphatic sandstone exists in the form of loose boulders or slabs, which Fosberg (1954) thought were pushed up by *Pisonia* root systems. Piggott (1969) said that the phosphatic sandstone of Bird Island existed as numerous cracked blocks, rather than as a continuous sheet, but the removal of most of the A_o horizon during guano exploitation, and the breaking of the sandstone during the preparation of pits for coconut planting, renders interpretation of the present broken form of the sandstone difficult. Although *Pisonia* occurs on many of the Seychelles islands, and being bird-distributed must have many opportunities of being constantly introduced to seabird islands (Ridley and Percy (1958) demonstrated inter-island movements by Sooty Terns), the absence of *Pisonia* forest on any of the sand cays of the Seychelles and Amirantes, while it occurs on Aride, suggests that Bird Island may never have had such forest. *Pisonia* may therefore not be necessary for the formation of Jemo soil and its phosphatic sandstone.

Fosberg (1954) considered the requisites for Jemo soil formation to be humus, acid, calcium phosphate, calcareous sand and rain. Although the humus layer on Bird Island is nowhere as well-developed as under the *Pisonia* on Aride, plants found in the Bird Island Sooty Tern colony, notably *Scaevola, Tournefortia, Suriana* and *Cyperus pachyrhiza* do accumulate litter and humus beneath them. Whether this is as acid as the humus formed under *Pisonia* is not known. In addition the plants which dominate the tern colony, *Portulaca, Boerhavia* and *Tribulus*, have a pronounced seasonal cycle of growth and die-back. During the wetter north-west monsoon, the rain (in conjunction with the absence of seabirds) leads to a luxuriant growth of these three species especially *Portulaca,* in the tern colony. In the usually dry south-east trades this vegetation dies off under the influence of lack of rain, salt water and faeces deposited by the birds, and through trampling. There is therefore a seasonal production of humus even in areas of mat vegetation, while the growth of *Scaevola* and *Tournefortia* within the tern colony provides more organic material. This humus, which is probably acid, together with calcium phosphate from the birds' faeces may be sufficient to react with the calcareous sand after leeching in the manner suggested by Fosberg to produce phosphatic sandstone. Sandstone production may be slower in the absence of *Pisonia* or other plants which deposit large quantities of litter, or where large colonies of larger seabirds, e.g., boobies, breed.[1]

The future of the Bird Island Sooty Tern colony, probably the largest colony that is readily accessible to visitors, seems to be secure at present. In view of its being a tourist attraction, the colony will probably benefit from the presence of a small, exclusive hotel on the island, together with small number of day visitors, since the income from these may obviate the need for exploitation of eggs for all but local consumption. If the colony then continues its expansion it could become the main area from which recruitment to exploited colonies occurs: as such it will be vitally important to the Seychelles Sooty Tern population as a whole, and to the egg industry. It is doubtful whether aircraft using the airstrips will have a long term effect on the Sooties (they may cause tree-nesting noddies and White Terns to move away from the airstrips), and the airstrips in fact provide, together with the tern colony, a valuable habitat for migrants, especially shorebirds. Although Bird Island is the northernmost island of the Seychelles, and thus presents the first landfall for birds arriving from the north, the presence of expanses of open ground may be particularly attractive to arriving migrants, and this may account for the number of species that have been recorded from Bird Island but not from other islands of the group. Further potential habitat for migrants and breeding land birds is provided by the growth of a dense shrub layer under the coconuts, this resulting from the running down of the plantation under the influence of the falling value of coconut products and the increasing emphasis on tourism.

An important consequence of tourism is that steps have been taken to reduce the rat population, and through the use of warfarin rats had been almost eliminated from the settlement by July 1974. Although rats do not appear to be a significant mortality factor for the Sooty Terns, it is to be hoped that this recent introduction may be completely eliminated from the island in the near future.

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[1] It would be highly desirable that the possibility of Jemo soils being formed by interaction of guano with other types of humus than *Pisonia* be investigated more thoroughly — the amount and acidity of this humus should be determined and evidence of current formation of phosphatic sandstone searched for. This is essential in order to support or refute our present belief that the presence of Jemo phosphate is in itself sufficient evidence for the former presence of *Pisonia* forest on a coral island. In the Pacific native information of the former presence of *Pisonia* forest has led to location of phosphate beds where no *Pisonia* forest is now found. — F.R. Fosberg, Ed.

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Mr. S.M. Savy, Director of Agriculture, kindly provided desk space in the Department of Agriculture, and he and Mr. J. Procter allowed me access to the Department's herbarium for the identification of plants. The snake was identified for me by Mr. J. Dring, the louse by Mr. P. Kettle, and the ticks by Drs. H. Hoogstraal and M.N. Kaiser. Dr. Hoogstraal also arranged for a travel grant from the United States Naval Medical Research Unit No.3 (NAMRU-3) which enabled my wife to visit Bird Island in 1974.

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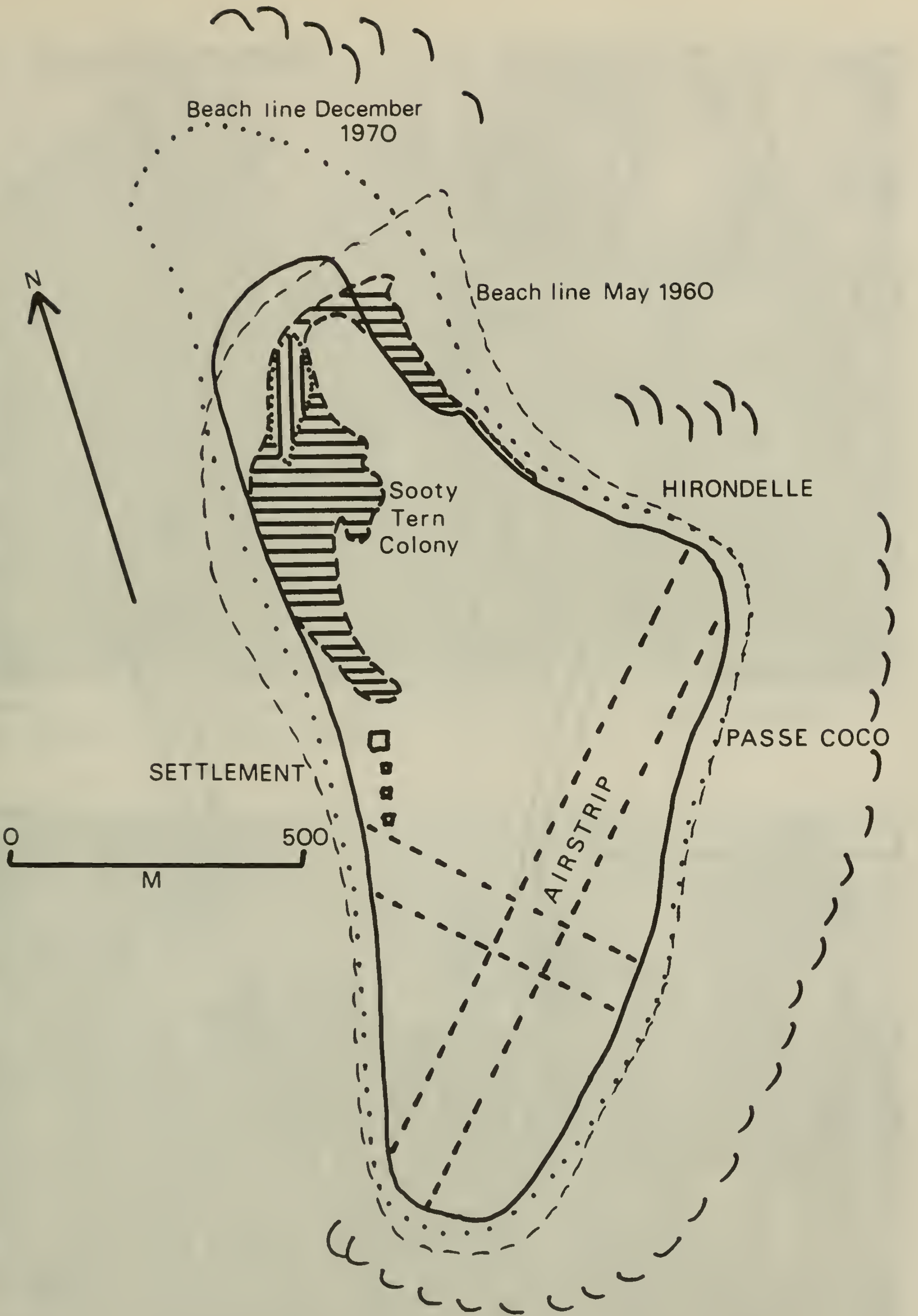

Fig. 1. Bird Island, Seychelles, drawn from aerial photographs. The May 1960 beach line shows the position at the end of the north-west monsoon, while the December 1970 beach line, at the end of the south-east trades, shows the northerly movement of sand forming an extensive spit at the north of the island. The area of the sooty tern colony in 1960 (vertical hatching) was taken from the aerial photograph, while the colony area in 1973 (horizontal hatching) was obtained by measurement with reference to land features.

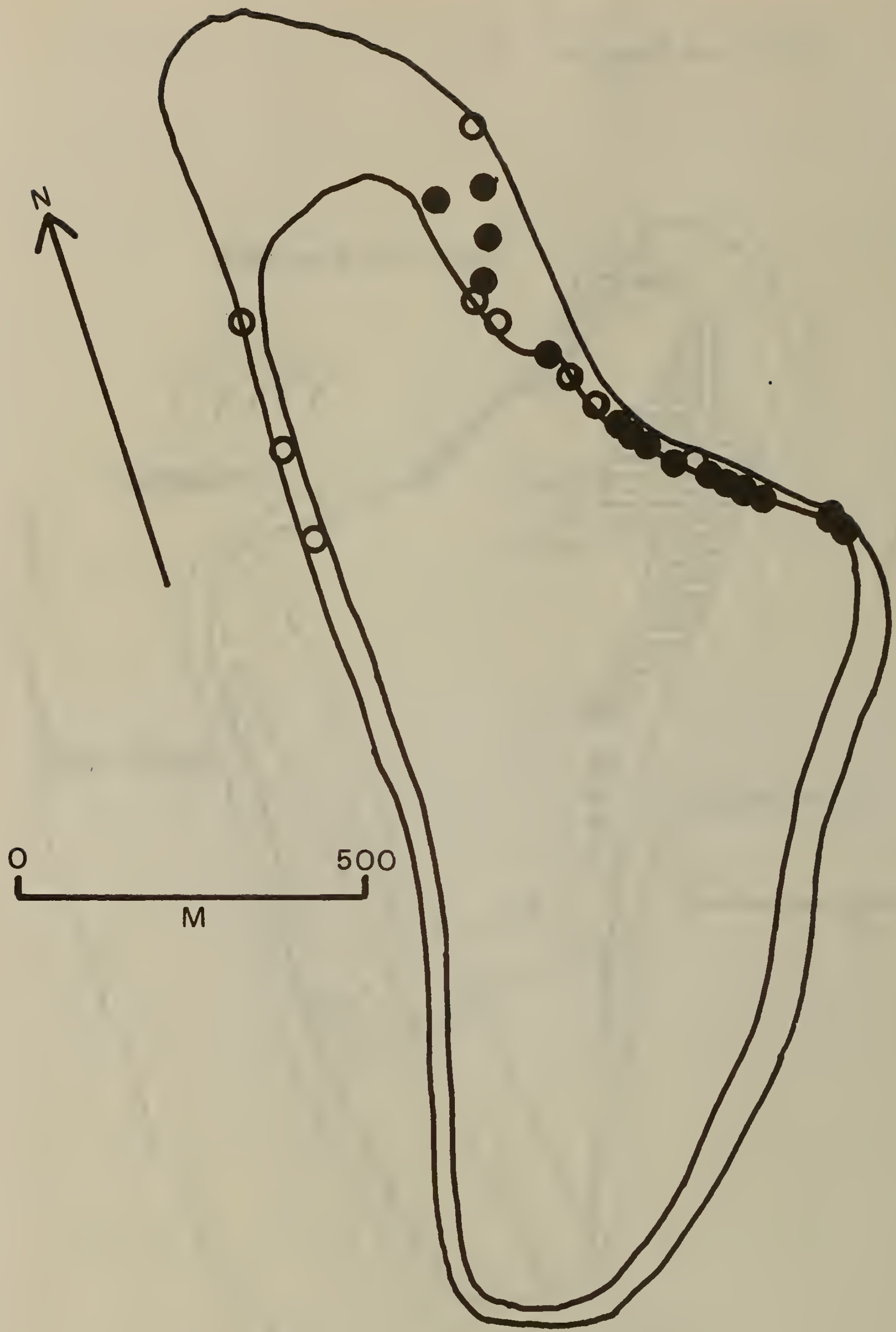

Fig. 2. The positions where Green Turtles came ashore in May-October 1973. Solid circles denote that a nest was excavated.

Plate 1. The settlement, with labourers houses in the foreground and chalets of the hotel behind.

Plate 2. The hotel on Bird Island.

Plate 3. The Sooty Tern colony in mid-May 1972.

Plate 4. A large *Tournefortia argentea* draped with *Cassytha filiformis* in the Sooty Tern colony, May 1973. Note the ground cover of *Portulaca oleracea* and *Tribulus cistoides*.

Plate 5. The Sooty Tern colony in October 1973. Note the absence of *Portulaca cleracea* and the mat of dead *Tribulus cistoides*.

Plate 6. Colonization of recently deposited sand by *Suriana maritima* and a few *Casuarina equisetifolia* seedlings. In the foreground are two *Tournefortia argentea* bushes killed by a new inundation of the sea.

Plate 7. Colonization of unstable sand on the west coast by *Suriana maritima* and *Cyperus pachyrhiza*. Behind this association is a belt of *Scaevola taccada* on stable sand, and the remnants of the *Casuarina equisetifolia* windbreak.

Plate 8. *Suriana maritima, Cyperus pachyrhiza* and a few young *Tournefortia argentea* and *Cocos nucifera* colonizing unstable sand on the sand spit at the northern end of the island. Behind this association is a belt of large *Scaevola taccada* on stable sand, and the coconut plantation.

Plate 9. The narrow belt of *Cordia subcordata* and *Thespesia populnea* growing on phosphatic sandstone in Hirondelle Bay on the north-east coast. At Hirondelle Point (left of picture) tall *Casuarina* are used for roosting by Frigate birds. On the beach is a mat of *Ipomoea pes-caprae* extending out from the *Cordia/Thespesia* belt. Note the beach driftwood, the remains of *Suriana maritima* and *Tournefortia argentea* killed by the sea during the annual erosion cycle. In the foreground is a Green Turtle *Chelonia mydas* nest.

Plate 10. *Cocos nucifera* interspersed with wild *Carica papaya* and *Phyllanthus casticum* growing on phosphatic sandstone near the east coast, September 1973. Note that the *Carica* and *Phyllanthus* are leafless, the trees having been defoliated during the south-east trades.

Plate 11. Rough and broken phosphatic sandstone exposed when vegetation was removed during airstrip construction.

Plate 12. Dense understory vegetation growing beneath *Cocos nucifera* on phosphatic sandstone. The dominant plant is *Phyllanthus casticum*, with some *Scaevola taccada*, *Cassia occidentalis*, *Ricinus communis*, *Kalanchoe pinnata* and *Passiflora suberosa*.

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ECOLOGICAL OBSERVATIONS ON AFRICAN BANKS, AMIRANTES

by Christopher J. Feare[1]

INTRODUCTION

Stoddart & Poore (1970b) reviewed scientific knowledge of the two African Banks islands, the northernmost islands of the Amirantes, following their visit to South Island on 26 September 1968. Apart from a visit to North Island by Ridley & Percy (1966) in June/July 1966, there has been no recent account of North Island. I visited North Island on 6-7 July 1974, and this paper is based mainly on observations of birds.

The island is small, approximately 230 x 130m (cf dimensions given by Stoddart & Poore 1970b). At the time of my visit honeycombed sandstone cliff, 1-2m high, was present all round the south, east and northern coasts, the only sandy beach being the west coast. However considerable expanses of sandbank within the reef that encloses the two islands suggested that sand may be very mobile, and the island may undergo seasonal changes in form as does Bird Island (Feare, *in press*).

The centre of the island was a phosphatic sandstone plain. Around the north east and southern fringes of this plain the sandstone was overlain with sand which extended almost to the top of the beach sandstone cliff. To the west of the central plain vegetated sand graded into an extensive sandy beach.

The most recent development has been the construction, in 1972, of an automatic lighthouse in the centre of North Island. This does not appear to have affected the ecology of the island.

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[1] Pest Infestation Control Laboratory, Ministry of Agriculture, Fisheries and Food, Worplesdon, Guildford, Surrey, England.
(Manuscript received November 1975 -- Eds.)

VEGETATION

Fosberg & Renvoise (1970) listed 15 species of plants from African Banks, mainly from South Island, and there appears to be no description of the flora of North Island. The most densely vegetated part of the island is the sand ridge at the top of the beach on the western coast. This is dominated by *Scaevola taccada* and scattered *Tournefortia argentea,* some of which had a little *Cassytha filiformis* growing on them. On the seaward side of the ridge are *Suriana maritima* and *Cyperus pachyrhiza,* which Feare (*in press*) considered to be flora typical of areas of sand subject to periodic erosion on Bird Island. The central part of the phosphatic sandstone plain was bare, but the remainder was dominated by *Portulaca oleracea, Tribulus cistoides* and *Boerhavia repens.* At the southern and eastern edges of the phosphatic sandstone and to a lesser extent at the south-eastern edge within the *Scaevola* belt was a dense growth of *Stachytarpheta jamaicensis,* while on higher sandy ground at the southern end was *Achyranthes aspera.* The sand above the cliffs was dominated by grasses, which were not identified. In 1955 there were only two coconuts, *Cocos nucifera,* but in 1974 there were four at the southern end of the island and one at the north.

FAUNA OTHER THAN BIRDS

A small Green Turtle *Chelonia mydas* was seen in the lagoon, and fresh tracks and a nest were found at the top of the beach on the morning of 7 July. There were many turtle excavations at the top of the beach, but the absence of tracks indicated that these were not recent (ie. not since the last spring tide).

Ornithodoros capensis ticks, mainly adults, were found in the scrapes of Sooty Terns and Roseate Terns, but were not as numerous as on Bird Island. They were not found in Crested Tern or Brown Noddy nests. No viruses were isolated from these ticks by U.S. NAMRU-3, Cairo (Converse *et al* 1975). While handling sooty terns a few *Amblyomma loculosum* fell off the birds, but the ground beneath the coconut trees at the southern end of the island was infested with this species, an infestation first reported by C. R. Grainger in March 1974 (*in litt.*). When the vegetation was disturbed the ticks ran out and rapidly climbed the legs of observers. Most of these ticks were adult (Hoogstraal *et al.* 1975). Stoddart & Poore (1970a) remarked on the absence of this tick from African Banks, having found it abundant on Farquhar. Infestations may therefore be temporary.

The only other invertebrate of which special note was taken was a large land crab (possibly a *Cardisoma* or *Sesarma* — J.D. Taylor *in litt.*), whose burrows were found in the phospatic sandstone and round the edge of the cliff at the southern end of the island close to a mixed group of Roseate and Crested Tern nests. Over the night of 6-7 July losses of eggs of Roseate and Crested Terns were noted. The eggs were left broken in the nest with remains of albumen and yolk in the cup. No skinks or other potential egg predators were seen, and these crabs may therefore be implicated. After disturbance Roseate Terns in particular take several minutes to return to their nests, and my disturbance may therefore have contributed to these egg losses.

BIRDS

Wedge-tailed Shearwater *Puffinus pacificus*

One in the lagoon 6 Jul. 1974.

Puffinus sp.

On 6 Jul. 1974 a shearwater, intermediate in size between *P. pacificus* and *P. lherminieri*, and less stockily built than the latter, black above and white below, was seen in the lagoon.

Red-billed Tropic Bird *Phaethon aethereus*

Recorded by Stoddart & Poore (1970b).

Masked Booby *Sula dactylatra*

Two immatures 6 Jul. 1974.

Red-footed Booby *Sula sula*

Recorded by Vesey-Fitzgerald (1941).

Brown Booby *Sula leucogaster*

A sub-adult in the lagoon 7 Jul. 1974.

Frigate Bird *Fregata* sp.

Five frigates seen feeding off North Island 6 Jul. 1974.

Grey Heron *Ardea cinerea*

Ridley & Percy (1958) recorded 2 nests in coconut trees on North Island, but no herons were seen in 1974.

Turnstone *Arenaria interpres*

Recorded on South Island (Stoddart & Poore 1970b). c.20 in the Sooty Tern colony on North Island 6-7 Jul. 1974.

Whimbrel *Numenius phaeopus*

One on beach North Island 6 Jul. 1974.

Greenshank *Tringa nebularia*

One on beach North Island 6 Jul. 1974.

Crab Plover *Dromas ardeola*

Recorded on South Island (Stoddart & Poore 1970b). One on beach North Island 7 Jul. 1974.

Roseate Tern *Sterna dougallii*

Breeding on North Island was recorded by Ridley & Percy (1958), and they (1966) estimated that 250-300 pairs were breeding in June/July 1966. In 1974 there were 3 sub-colonies on the southern point and the east coasts with 13, 4 and 4 nests, each with a single egg. Many seabirds bred late and in reduced numbers in 1974 (see Sooty Tern below) and this count is probably a low estimate of the island's population.

On 7 July 1974, two parties of c.30 Roseate Terns were seen c.15 km from the island and heading towards it, suggesting that they fed well away from the island. They were never seen feeding within the reef. (On returning from African Banks on the evening of 8 July several parties of Roseate Terns (10-20 birds per flock) were seen near Silhouette flying in the direction of Aride, probably the largest breeding colony in the Seychelles, again suggesting that they feed away from the colony).

Black-naped Tern *Sterna sumatrana*

Recorded breeding on South Island, with eggs in Sept.-Nov. (Vesey-Fitzgerald 1941) and breeding Jul.-Aug. (Ridley & Percy 1958). Not breeding North Island July 1974, but probably 100+ present feeding over shallows (dipping to surface) in the lagoon and roosting on sandbanks. Several birds on the beach of North Island were paired and courting (fish carrying).

Bridled Tern *Sterna anaethetus*

One in the lagoon 6 Jul., and another found dead on the island.

Sooty Tern *Sterna fuscata*

Recorded breeding by Vesey-Fitzgerald (1941), breeding on North Island but not South by Ridley & Percy (1958, 1966 — 43,300 pairs in 1955, 34,000 pairs in 1966), and breeding on South Island in large numbers in Sept. 1968 by Stoddart & Poore (1970). On 6-7 July 1974 20,300 pairs were estimated to have been breeding. Egg counts on the two days showed that laying had stopped, and on 6 July 1 newly hatched chick was found, with c.50 chicks on 7 July. In 1974 eggs were at a low density (av. $1.55/m^2$, cf. Bird Island $3.38/m^2$ in 1973) and did not occupy all of the ground that was potentially available to Sooty Terns —

the area of the colony was estimated at 1.31 ha., and that of the island at 2.27 ha, most of which could normally have been used by Sooties. In 1974 Sooty Terns, and other seabirds, bred late and in much reduced numbers on Bird Island, Desneoufs and Aride, this presumably being due to food shortage. However, it was interesting to note that while laying had stopped and hatching began on African Banks on 6 July, on Bird Island on 9-12 July laying was continuing and no birds had hatched. This supports the statement by Ridley & Percy (1958) that breeding begins earlier on African Banks than on other islands in the Seychelles and Amirantes, but the reason for this is unknown.

African Banks Sooty Tern eggs are not cropped commercially but the colony is poached. On our 1974 visit two shelters made of coconut leaves were found, and wings scattered around the colony showed that birds as well as eggs had been taken.

Saunders Tern *Sterna saundersi*

A large flock was recorded on 8 Nov. 1937 by Vesey-Fitzgerald (1941).

Crested Tern *Thalasseus bergii*

Eggs were found in Nov. 1937 (Vesey-Fitzgerald 1941). Ridley & Percy (1958) recorded this as a breeding species but did not say whether eggs or young were present in July-Aug. 1955. In Jul. 1974 there were 6 nests, all with 1 egg (weights of 5 eggs were 51g., 50g.,56g., 57g.,and 56g.) in two sub-colonies, and one very recently fledged juvenile on the beach. On Aldabra Diamond (1971) recorded breeding in Jan. and July, and they may breed at 6-months or irregular intervals on African Banks.

Brown Noddy *Anous stolidus*

Estimates of 5900 pairs on North Island in Jul.-Aug. 1955 but only 100 pairs in 1966 (Ridley & Percy 1958, 1966). In Jul. 1974 noddies, like Sooty Terns, bred late: c.200 bulky nests made of seaweed had been built about 0.25m above ground in the grass around the north-east and east coasts, but few contained eggs. Many more may breed in less abnormal years.

Black Noddy *Anous tenuirostris*

Not recorded breeding on North Island, but Stoddart & Poore (1970b) recorded them with eggs on South Island in Sept. 1968 in a *Scaevola* bush. This is an unusual breeding habitat in the Seychelles, where on Cousin, Cousine and Aride it generally nests in taller trees. In July 1974 there appeared to be no bush vegetation on South Island (viewing it with binoculars from North Island and from a boat) and it may not have bred that year: only one Black Noddy was seen, outside the reef.

White Tern *Gygis alba*

Not recorded breeding, although it breeds elsewhere in the Amirantes. Seen at sea in the vicinity of African Banks by Stoddart & Poore (1970b) and on the July 1974 visit.

Willow Warbler *Phylloscopus trochilus*

Recorded once in Nov. 1970 (Benson 1972).

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SPECIES-NUMBERS RELATIONSHIPS IN AN ASSEMBLAGE OF REEF-BUILDING CORALS: McKEAN ISLAND, PHOENIX ISLANDS

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SPECIES-NUMBERS RELATIONSHIPS IN AN ASSEMBLAGE OF REEF-BUILDING CORALS: McKEAN ISLAND, PHOENIX ISLANDS

by Thomas F. Dana[1]

ABSTRACT

Species-numbers relationships in the McKean Island assemblage of reef-building corals were investigated to discover how they changed along environmental gradients of the reef. For the purposes of the study, two gradients were identified — a complex depth gradient and a wave exposure gradient.

Sampling was carried out by means of point samples along three randomly located transects, each extending from the buttress and surge channel region across the two reef terraces and down the deep reef slope to a depth of 26 m. A total of 49 species in 21 genera of hermatypic scleractinians and 2 species of hermatypic hydrozoans were encountered.

The greatest number of species was found inhabiting the shallow terraces. Evident was a reduction in the numbers of species present below the sharp increase in reef slope at approximately 18 m.

Percent cover of living coral decreased with increasing exposure to surge and waves.

Significant heterogeneity in the coral assemblage was observed along the depth gradient, and a surprisingly large, but not statistically significant, heterogeneity also existed along the exposure gradient. Three times as many species were present over all segments of the exposure gradient as over similar segments of the depth gradient.

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Most species were represented by small numbers of individuals; only a few had high abundances. Species diversity was lowest on the least exposed portion of the exposure gradient sampled and at mid-depths along the depth gradient.

Zonation and spatial aggregation for single species populations of corals are suggested by variance-to-mean ratios in excess of one for 3 of the 9 species tested and by the position of most samples below the Hurlbert (1971) expected line.

A hypothesis is outlined for the organization of atoll seaward reef coral assemblages. Wave and surge action is suggested as the principal organizing factor.

INTRODUCTION

It is the purpose of this paper to explore certain static aspects of the organizational complexity of an assemblage of hermatypic corals. Examined in particular are how numbers of species, compositional similarity, species diversity, and spatial pattern (collectively referred to as species-numbers relationships) change along environmental gradients of the reef studied. The assemblage studied occupies a portion of the subtidal seaward reef of a Central Pacific atoll.[1]

The two gradients identified for the study are herewith defined. The depth gradient, a complex gradient (*sensu* Whittaker, 1967), is perpendicular to depth contours and extends from the base of the surge channel and buttress area at its shallow end to the steep reef slope below the 10 fathom (18 m) terrace at its deep end (Figure 1). Environmental variables judged to be important along this gradient are wave surge (or water movements in general), abrasion, light, plankton supply, and sedimentation. The exposure gradient is an atoll-encircling gradient in intensity of wave action (Figure 1).

This study is neither the first nor the most extensive to attempt either description or analysis of the differences in species-numbers relationships accompanying differences in the coral reef environment. Such observations date at least from Darwin (1889). The ecological surveys of Mayor (1918, 1924), Baker (1925), Manton (1935), and Abe (1937), depicting the zonation of coral species as the result of the varying degree to which corals are adapted for withstanding extremes of temperature and salinity, and of exposure to sedimentation and air,

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laid the groundwork from which much modern reef ecology springs. A plethora of zonation studies has followed, mostly qualitative and many confined to reef flats and shallow protected areas. In his review of coral reefs, Stoddart (1969) lists an entire page of such studies, and there have been more since.

Going beyond descriptions of species zonation and its possible cause, the works of Loya (1972), Porter (1972), Grigg and Maragos (1974), Maragos (1974b), and Connell (in prep.) have attempted to relate assemblage characteristics determined from species-numbers relationships to environmental factors and ecological theory. Such studies are important in that they may provide insight into community structure, identify non-obvious interspecific associations, suggest important variables for manipulative experiments designed to explore ecosystem controls, offer empirical evidence for the test of theory, and provide the information necessary to predict the consequences of perturbation of the reef ecosystem.

The particular significance of the present study is that it was carried out in the "mare incognitum" of Wells (1954, 1957). This is the region of active upward and seaward progradation that gives any coral reef its cohesiveness and persistence.

DESCRIPTION OF THE STUDY AREA

A quantitative study of the reef-building coral assemblage at McKean Island (3°36'S; 174°08'W) in the Phoenix Islands was undertaken during a brief visit in the summer of 1968. The atoll is slightly egg-shaped with a long axis of only some 1250 m (Figure 2). Such a small size means that there is no truly well protected lee, because the refraction of even moderate tradewind swell causes waves to break around the entire perimeter of the atoll. Mean tidal range is approximately 76 cm, winds are predominantly east and northeast trade winds, rainfall is on the order of 50 cm or less annually, and typhoons are extremely rare (Wiens, 1962).

The lagoon is filled, consisting presently of a salty guano and fine calcium carbonate mud flat. The mud flat is covered at high tides by a few centimeters of water that percolate through the atoll structure and flow in and out of the "lagoon" through several "springs" in the southeastern corner. The flat is surrounded by rubble ridges more or less filled with sand and small amounts of guano. Vegetation is sparse and low. Large numbers of sea birds use the island for nesting and roosting. The seaward shore along the western side of the island is backed by a high sandy beach used for nesting by the green sea turtle, *Chelonia mydas*. Around the remainder of the island the shore is backed by steep rubble ramparts (Figure 3). These ridges are highest along the northern shore, reaching heights of some 5 m.[1] There is a clear series of three of these ridges around the northern portion of the island, indicating that since the attainment of present sea level some 4,000 years ago (Shepard, 1963) there have been at least three episodes (or single events) of extremely high waves to strike McKean Island.

On the east and south sides of the atoll the reef flat is quite smooth, carpeted with a thick algal turf, and normally kept wet even during low tides by wave run up. Around the northern side there is a shallow moat (maximum depth approximately 1 m at low tide) between the seaward reef margin and the rubble ridge. This moat contains large quantities of coral fragments and scattered small colonies of living coral. The reef flat is narrower along the west side, has a very few widely scattered blocks of reef material deposited on it, lacks a dense algal turf as wave action is reduced, but has occasional colonies of living coral in the pools in its uneven surface. The entire reef margin consists of buttresses and surge channels with no prominent algal ridge at any point.

The small size of McKean Island made a series of spot dives and surveys from the surface around the entire atoll feasible. A remarkable abundance of the grey reef shark, *Carcharhinus amblyrhynchos,* inhibited carrying out a continuous underwater survey. A sharp increase in slope at approximately 18 m or 10 fathoms is clearly defined throughout with the exception of an area in the south-west where a more irregular, stepwise slope prevails. The region of the sharp increase in slope received the most attention during these extra-limital dives. A shallower change in slope between 8 and 10 m found on many Pacific atolls (W.A. Newman and J.R. Curray, unpublished) was much more difficult to distinguish and was not discernable at all on the southwestern portion of the reef. The deeper portions of the reef terraces in the northeast were covered with coral rubble encrusted with calcareous algae, with only scattered colonies of living coral (Figure 4a). The amount of living coral increased to the south and west, and the amount of rubble decreased rapidly. The reef slope below 18 m and the deeper portion of the terrace were covered with luxuriant coral growth in the south and west (Figure 4b). The shallower terrace area had scattered coral growth in the northeast, east, and south. The coverage by living corals was greatest in the west. In the northwest a considerable extent of dense alcyonacean growths was present. Fish were abundant everywhere.

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[1] These ridges are not unlike the ramparts reported by Maragos *et al.* (1974) from Funafuti formed during a rare typhoon strike. Similar ridges are also present at Fanning and at Christmas in the Line Islands (W.A. Newman, pers. comm., and Gallagher, 1970).

STUDY METHODS

Three transect lines of weighted 0.25 in. (0.635 cm) hard lay cotton were laid from the base of the buttresses and surge channels, across the seaward terraces, and down the outer reef slope to a depth of 26 m. The location of the initial transect was chosen arbitrarily as the most exposed point where, in the first day of field work, wave surge would not prohibit work in shallow water. Subsequent transects were located by running in a northerly direction (increasing exposure) along the reef in a small outboard-powered rubber boat for a number of seconds between 30 and 90 drawn from a table of random numbers. The distances between transects were never measured, but the overall distance between the first and last was an estimated 400 m. The approximate locations of these transects are shown in Figure 2.

The transect lines were marked at 1 m intervals. An ordinary wooden pencil was used to define a point sample below each mark. This procedure may be considered a systematic sample with a random start (Cochran *et al.*, 1954). When a point over lay living coral, a sample was collected for purposes of positive species identification. Only by examination under light and scanning electron microscopes could the various species of massive *Porites* and tuberculate *Montipora* be distinguished. Literature used for species identifications is given in an appendix. The primary data acquired by the sampling, which was performed with the aid of SCUBA, were the number of species and the number of individuals per species present.[1] These assemblage characteristics, and others computed or deduced from them, were then compared along the two nearly perpendicular environmental gradients (depth and exposure).

For analysing how species-numbers relationships change along the environmental gradients of exposure and depth, the sample points are grouped into two classes — transects and depth intervals, of three

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[1] In the strictest sense what was recorded was the number of "hits" rather than the number of individuals. This arises since colonies of several massive species may attain dimensions greater than 1 m and a few branching species may form thickets greater than 1 m in extent. For the McKean Island study, the only problem area was at depths greater than about 15 m where it was not always possible to be certain in defining the limits of massive, shelving colonies of *Porites*. Since such cases arose only two or three times in the sampling, the number of "hits" in this study may safely be referred to as the number of individuals.

sampling units each. Limits of the depth intervals were chosen to correspond to the terrace topography widely observed on seaward reefs of Pacific atolls, as these might represent habitat boundaries. Depth Interval 1 extends from the base of the buttress and surge channel system, found at depths between 1 and 2 m along the section of reef studied, to the slight change in slope between 8 and 10 m. Depth Interval 2 extends from the lower limit of Depth Interval 1 to the rather sharp break in slope at approximately 18 m. Depth Interval 3 extends from the lower limit of Depth Interval 2 down the steep deep reef slope to a depth of 26 m (Figure 1). Data for the depth intervals were obtained by pooling the points within each depth interval from each transect.

ANALYSIS TECHNIQUES AND RESULTS

A total of 49 species of hermatypic scleractinians representing 21 genera was found at McKean Island. Of this total, 36 species in 16 genera were encountered along the transects. The remainder were collected during the circum-atoll series of dives. Two species of the hermatypic hydrozoan *Millepora* were also present, one of which occurred under the transects. A list of species and their distribution in the samples is given in Table 1a and b.

Since Depth Interval 3 (the deepest) contains so many fewer sample points than any of the other sample units, it is necessary to demonstrate a sampling adequacy at least comparable to the other sample units before any meaningful interpretation can be made. This may be accomplished by comparing the relative shapes of the curves of cumulative number of species versus total numbers of individuals curves for the three depth intervals (Figure 5). These curves were constructed by successively adding the numbers of new species and total individuals from the segments of each of the transects lying within each particular depth interval. They appear to be a family of curves in which individuals of previously recorded species enter increasingly larger samples more frequently than do individuals of new species. This suggests that all three curves may be approaching plateaus, indicating relatively complete sampling. Depth Interval 1 (the shallowest) appears to have the poorest fit. Corroborating the suggestion of the plateauing of the Depth Interval 3 cumulative species-individuals curve is the paucity of additional species found in deep water during the series of dives all around the atoll (Table 1b).

The distribution of sample points, numbers of coral species, dominance, and a biased measure of percent living coral coverage are summarized in Table 2. The sampling indicates a decrease in the number of species with depth but little if any change over the range of the exposure gradient sampled.

The values for percent living coral coverage can be ignored except for the trends they suggest: decreasing coverage with increasing exposure but no discernable change along the depth gradient. It was, however, my subjective impression that coverage was lower along the shallowest portions of the transects. An upward bias has been introduced into the coverage values by the use of a sample point with finite dimensions (Grieg-Smith, 1964).

The similarity of species composition along the depth and exposure gradients was studied by comparing the numbers of species shared by pairs of sample units within sampling classes. This was done statistically by determining the probability that any two samples drawn from a randomly distributed population should be as or more similar than those actually obtained by sampling natural field populations. The formula for a single event (sample pair) is given by Glime and Clemons (1972).

Since the frequencies of the various species making up the total assemblage affect their chances of entering samples, it was necessary to include this distribution in the determination of probabilities of number of shared species. To do this, samples containing the numbers of species observed in the field samples were iteratively drawn at random (with replacement) by computer from the overall frequency distribution and sample pairs compared as to the number of shared species. The probabilities of observing given numbers of shared species were determined from these sample comparisons. These individual probabilities were summed to give the probability of observing as many or more shared species. Such probabilities for the McKean Island samples are given in Table 3. The numbers of species shared between each of the three possible transect pairs do not differ significantly from random expectation at the 5% level. However, in all three cases the number shared is on the "too few" side. Both Depth Intervals 2 and 3 have significantly too few species in common with Depth Interval 1, but do not themselves differ from random expectation. Too few shared species means differences in the species composition for portions of the assemblage being compared. In the actual field sampling, 15 species were found in common between all transects, but only 5 were common to all depth intervals. There is greater compositional similarity between transects than between depth intervals.

Changes in relative abundance along the depth and exposure gradients were explored by computing the degree of concordance in the rankings of species abundances for the sample units within each sampling class. Agreement in the rankings of the transect abundances of the 7 most common species and the depth interval abundances of the 5 species found in all three depth intervals, as well as for all species, was compared using Kendall's coefficient of concordance (Tate and Clelland, 1957). The coefficients of concordance are presented in Table 4. There is greater than 95% certainty that the transect rankings for all species are correlated, but not when only the most abundant species are considered separately. There is no significant agreement at the 5% level in the ranks of species from the depth intervals, even when only those species found at all depths are considered. The relative abundances of the various coral species are, at best, only slightly more alike between the transects than between depth intervals.

Species diversity (number of species, heterogeneity, and evenness or dominance) was explored using several different approaches. First, several indices that incorporate both the number of species present and the numbers of individuals per species as a summary statistic were calculated and ranked for each sample unit within each sampling class. These indices were 1 - Simpson's index (SI*), the Shannon-Wiener function (H'), the standard deviation about the mean (SD), and the number of moves index (NM) (Fager, 1972). Subsequently, each of these indices was scaled (see Fager, 1972, for methods) and ranked. The results of these calculations and rankings are presented in Table 5a and b. Next the antilogarithm of H' [Exp (H')] , the reciprocal of Simpson's index ($1/\Sigma p_i^2$) and the ratio of these two expressions (R 1:2, a measure of evenness or dominance) were calculated and are presented (after Peet, 1974) in Figure 6. Also, the actual sampling distributions are presented in Figure 7 as histograms of numbers of individuals per species versus species rank order for each sample unit in each sampling class. Dominance was further measured by calculating the minimum number of species needed to furnish 50% of the individuals contained in a sample unit (Fager, unpublished). This is most conveniently expressed as a percentage (given in Table 2). It is the trends in diversity along environmental gradients, as expressed in the rankings of Table 5b, the graphs of Figures 6 and 7b, and the species counts and dominance of Table 2, that are taken as of interest here rather than any actual calculated values. The outcome of the diversity analysis is contained in the discussion section.

Segments of the environmental gradients considered in this study were sampled with differing intensities, resulting in samples of different sizes. Hurlbert (1971) has presented a method of computing the expected number of species to be found in a sample of n individuals selected at random (without replacement) from a collection containing N total individuals and S total species. If such a computation is made for a series of sample sizes (n's) and these values are plotted and connected by a line, the numbers of species observed in small samples may be compared to the numbers of species found in large samples by noting their respective locations relative to the expected line. This was done for the sample units of this study using the pooled composite of all samples as the collection. Figure 8 illustrates the result. It may be noted from this figure that Depth Interval 3 (the smallest sized sample) departs less in absolute magnitude and proportionally the same from the expected line as Depth Interval 2 (the largest sized sample). This offers additional objective support to the earlier contention that the Depth Interval 3 sample may reasonably be considered adequate.

It may also be noted from the figure that only one point lies above the expected line, all the rest fall below, but most are quite close to it. Unfortunately with only three sample units per sampling class all three could be expected on the basis of chance alone to be located on one side or the other of the expected line 12.5% of the time (using a binomial distribution with p and q both equal to 0.5). Thus it is not possible to assess the significance of the observed frequencies of sample unit positions above or below the line with any confidence greater than about 90%. However the observed distribution of samples about the line, most having fewer species than expected, suggests that the coral assemblage is characterized by at least moderate spatial aggregation (Hessler and Jumars, 1973, explain the reasoning involved) along both environmental gradients.

DISCUSSION

Biogeography

The closest localities to McKean Island for which the hermatypic scleractinian faunas are relatively well known are Canton (also in the Phoenix Islands) and Fanning Island — roughly 650 km northeast of McKean in the Line Islands. Seventy-four species in 28 genera have been reported from Canton (P. Jokiel and J. Maragos, pers. comm.), and 69 species in 26 genera have been reported from Fanning (Maragos, 1974a). Three additional genera are reported (Maragos, pers. comm.) from Christmas Island, also in the Line Islands. Wells (1954) and Stehli and Wells (1971) place both the Phoenix and Line Islands within the boundaries of their 20 and 30 isopangeneric lines. The 21 genera reported here for McKean Island further suggests that at the generic level observations in this region are approaching completeness. All of the McKean genera are present elsewhere in the Phoenix or Line Islands.

The extremely small size of McKean Island, its relatively isolated location, the generally short duration of pelagic coral larval stages, and the occurence of catastrophic environmental disturbances — such as wave storms — make it seem quite likely that temporal disequilibria occur in extinction and immigration rates (see MacArthur and Wilson, 1967, for a discussion of island size and isolation in island biogeography.) Using the Canton and Fanning faunas as references, genera of hermatypic scleractinians likely to have species represented by at least a few individuals from time to time at McKean, but not observed there in 1968, are *Stylophora,* *Astreopora, Coscinaraea, Pachyseris, Herpolitha, Leptoria, Echinophyllia,* and *Merulina.*

Number of species

Wells (1957) has presented a general curve depicting a sharp decrease in the number of hermatypic coral species with depth. This curve was constructed from data collected at Bikini, Marshall Islands, and the steepness of the decline in numbers of species with depth certainly reflects the heavy sampling bias towards reef flats and shallow lagoon areas. Probably the most extensive and complete data on the depth distribution of hermatypic corals have been provided by Goreau and Wells (1967) for the north coast of Jamaica. Of the 48 hermatypic species they list, 36 have a distribution whose "optima" includes the depth interval 0 to 10 m, 26 include the interval between 10 and 20 m, and 22 have "optima" extending to depths greater than 20 m. The pattern of decreasing numbers of species along the complex depth gradient is similar even if the "maximum" and "minimum," rather than the "optimal," distributional limits are used: 42, 38, and 34 species for the respective depth intervals.

Sampling done on the seaward reef of McKean Island suggests that the number of species present there decreases only slightly with depth until the sharp increase in reef slope characteristic of Pacific atolls is encountered at approximately 18 m. At about that portion of the environmental gradient there is a reduction in the number of species present.

No one had ever challenged Wells's (1957) generality of a decrease in the number of hermatypic coral species with depth until Loya (1972) claimed that his study at Eilat showed "a successive increase in the number of species with depth." However, what Loya actually showed was that on the scale of 10 m line transects species *density* (number per unit of transect length) increased with depth. Maragos (1974b) arrived at a similar conclusion of high species richness at the deep end of his Fanning Island transect for the same reason. Hiatt (1957) first pointed out that all quantitative studies of coral assemblages up to and including his own employed fixed sample areas (same size quadrats) throughout and therefore measured densities on a particular scale. Stoddart (1966), Davies *et al.* (1971), Loya (1972), Porter (1972), Grigg and Maragos (1974), and Maragos (1974b) have all done likewise since.

Loya (1972) does give total species numbers for the reef flat (34) and the portion of the reef deeper than 20 m (59). No numbers are given in that paper for the intervening subtidal segments of the depth gradient. However, in an earlier paper (Loya and Slobodkin, 1971) dealing with the same reef at Eilat, a table similar to that presented by Goreau and Wells (1967) is given. Treating the distributional data in Loya and Slobodkin's table in the same manner as that of Goreau and

Wells, the distribution of numbers of hermatypic species is 77, 46, and 36. "Optimum" range is all that they give. The 77 species found in shallow water (0-10 m) is still greater than the 59 from deep water (>20 m) reported in Loya's 1972 paper. Sampling of an intensity comparable to that performed in Jamaica by T.F. Goreau and his associates would seem in order for both Fanning and McKean Islands before the final word on how the number of hermatypic coral species changes with depth can be spoken. Meanwhile, although Wells's (1957) curve may be too steep, the generality that the number of hermatypic coral species and the suitability of the environment for their growth decreases with depth on a reef appears to remain valid.

The exposure gradient

Changes in coral assemblage composition and characteristics along an axis paralleling the trends or faces of reefs have received very little attention in the past. Depending on size, shape, and location of any particular reef, environmental conditions may be similar for many kilometers or they may change rather rapidly. The principal factor of environmental change along or around the trend of an atoll reef is considered here to be exposure to wave action. Grigg and Maragos (1974) advance a similar hypothesis for their reef studies around the island of Hawaii. For the myriad zonation schemes determined for coral reefs to be meaningful, some measure of variation in species composition and relative abundances along the environmental gradient paralleling the reef trend must be made.

In a study of the reef front of Aldabra, Barnes *et al.* (1971) presented a figure depicting variation in the zonation pattern they determined. Their qualitative zonation scheme was based on coral growth forms, restricted species of hermatypic corals, and the presence of other distinctive taxonomic groups of benthos. Even though there is considerable variation in their scheme, that they were able to recognize similar zones over such a wide range of environmental conditions (their survey circled the entire atoll) seems remarkable. The lack of determination of species-numbers relationships however makes comparison with the McKean study impossible.

Having a series of systematic transects running parallel to each other and parallel to the shore at three stations, Loya (1972) tested for homogeneity of the data recorded at the different stations. Using an analysis of variance procedure, he found that means for the number of species, number of colonies, living coverage, and diversity (all per transect) for each of the various zones enumerated were not significantly variable between the three stations. Unfortunately neither of the papers dealing with this study (Loya and Slobodkin, 1971, and Loya, 1972) reveal how the stations were selected or how they were spaced. It is surmised from locality descriptions and figures in those two papers, however, that no strong environmental gradients are to be expected along the extent of any one of the Eilat fringing reefs. The results of Loya's (1972) analysis is then gratifying in that those assemblage characteristics analysed did not change significantly along an axis where environmental change was probably negligible.[1]

It should be added that all fringing reefs near Eilat are not necessarily alike in terms of species zonation. Mergner (1971) describes a rather considerably different zonation pattern for reefs there.

The seaward reef of McKean Island with its changing exposure to tradewind generated waves presents a situation rather different from that at Eilat.[2] Because of the small size of the atoll this gradient is noticeable over distances as small as a hundred meters or so, as judged by changes in heights of breaking waves.

The lack of a trend in the number of species found along the exposure gradient may result from there being no real changes in the number of species inhabiting the relatively narrow segment of the gradient sampled. Two other possible explanations are available. First, some species found shallow where exposure is low may be found deeper, but perhaps in reduced abundance, where exposure is greater. Or, second, there may be a regular faunal replacement series along the exposure gradient. On the first alternative the McKean data are certainly insufficient; the second will be treated in following discussion sections.

Percent cover

The decrease in percent coverage of living coral with an increase in exposure to waves may result from physical breakage and removal of corals by strong surge and wave action and also possibly from greater competition with coralline algae. Grigg and Maragos (1974) also

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[1] It does not necessarily follow from Loya's (1972) analysis that the coral assemblage is homogeneous in terms of its species and their relative abundances, but only that the summary statistics computed from his data are not significantly variable between stations.

[2] Munk and Sargent (1954) used a local wind rose to compute the wave power distribution around Bikini Atoll. Such a gradient in wave exposure may then be deduced from the local wind rose for McKean Island given in Wiens (1962, p. 143).

arrive at a similar conclusion for reefs around the island of Hawaii. Both of these factors should operate more strongly in shallow water. On the other hand, the decrease in coverage observed may be the result of either a gradation in the degree of coral destruction during the last catastrophic disturbance to strike McKean Island, or differential rates of recovery since such events, or both. The major obstacle to a firm answer is a lack of sampling (or observation) over a sufficient time span rather than any spatial deficiencies in the sampling program.

For the same reasons as above I would have expected lower coral coverage on the shallow portion of the depth gradient than on deeper segments. My subjective impression was that this was probably the case. However the numbers for percent living coral generated during the study are so similar for all three depth intervals that it is not sound to offer them as verification of that expectation. The changes in living coral coverage with depth reported by Loya (1972) are of little help here due to differences in reef topography and physical environments between the areas studied. Maragos (1974b) reports, like the McKean study, a qualitative impression of relatively low coral coverage in water shallower than 8 m at Fanning Island in an environment not too unlike that sampled at McKean Island.

Compositional similarity

The modification of Glime and Clemons' (1972) statistical approach to measuring compositional similarity, incorporating species abundances, is a measure of assemblage homogeneity. It was surprising that the numbers of species shared between pairs of transects is less than expected. All probabilities are well below 0.50, the level expected of species occur at random in the samples (Table 3). In fact, Transects 1 and 2 border on being significantly different from each other at the 5% level. Thus, while the number of species found along each transect is quite uniform (25, 27, and 21), the kinds present appear to change somewhat even along the rather narrow segment of the exposure gradient sampled.

The depth intervals also have too few shared species. The shallowest depth interval is significantly different from both the deeper depth intervals (Table 3). The shallowest depth interval appears to be distinctly different from deeper depths in the composition of its coral fauna. While the two deeper intervals are not significantly different at the 5% level, they too are on the side of fewer than expected shared species. Thus heterogeneity in the coral assemblage is more strongly indicated when preceeding along the depth gradient.

Concordance coefficients calculated for the sample units allow a more detailed look into the nature of the differences in compositional similarity. The high degree of concordance observed in the transect rankings should not be taken as being in disagreement with the heterogeneity along the exposure gradient suggested by the shared species method, but may be used to clarify the nature of that heterogeneity. The significant concordance in the transect rankings of all species stems mainly from the large number of tied ranks amongst the rare species, most of which are represented by only one or two colonies (Table 1). Differences in concordance are therefore largely precluded.

The lack of significant concordance in the rankings of the seven most common species indicates that the more common species show moderate variations in abundance along the portion of the exposure gradient sampled. This suggests that it is not only the presence or absence of uncommon species within the sample units that constitutes the coral assemblage heterogeneity along the exposure gradient but also the changes in relative abundance of the most common species.[1]

Compositional changes in the coral fauna along the depth gradient are much more striking. Not only were fewer species found in common between the three depth intervals than between the three transects, but the absolute and relative abundances of those species held in common by the depth intervals varied considerably. Even the presence of considerable numbers of species with abundances of only one or two individuals was not sufficient to obscure both the restricted distributions of some of the moderately abundant species and the rather large changes in relative abundance of the widely distributed ones.

I consider the concordance analysis and the shared species method to give consistent results. Both are needed to make the pattern of assemblage heterogeneity clear. Along the exposure gradient there were a moderate number of widespread species whose relative abundances changed moderately over the portion of the gradient sampled. There were a large number of species found in low abundance, but the magnitude of the sampling was insufficient to conclude whether or not these were widespread along the gradient. Changes in species composition and relative abundance were much more marked along the complex depth gradient. Only a few species appeared to be ubiquitous along it, and their relative proportions usually changed between depth intervals. Fewer still were found in large enough numbers, but only over a limited extent of the depth gradient, to suggest restricted depth distributions. Again, most species were not present in the samples in sufficient abundance to determine the extent of their distributions.

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[1] The degree of heterogeneity or concordance observed is relative to the scale of sampling and thus is best used for comparative purposes only.

Diversity

Preston (1969) observed that "every naturalist from Darwin downwards has felt aggrieved that a few species are very common and most are rare." Abe (1937), for the corals inhabiting a small lagoon reef at Palau, and Loya and Slobodkin (1971) for a collection from the fringing reef at Eilat, both present curves of species rank order versus numbers of individuals per species that have shapes virtually identical with that of the McKean coral fauna shown in Figure 7a. Data presented by Mayor for Murray Island (1918) and Samoan (1924) reef flats also indicate that species with high abundance are a minority. If the species pooling in his studies is taken into account the agreement with other studies improves. Hermatypic corals as a group appear to fit the general pattern noted by Preston.

Species diversity, its evolution, maintenance, and consequences has surely become an involved topic. Several older theories on the evolution of high species diversity required long-term stable (constant) environments (reviewed by Pianka, 1966). Additionally, diversity has been said to relate to community productivity, integration, evolution, niche structure, competition (McIntosh, 1967), and habitat complexity (Kohn, 1971). Further, Slobodkin and Sanders (1969) have theorized on the relationship between species diversity and environmental variability, unpredictableness and harshness. In this discussion coral species diversity is taken as a measure of environmental favorability for coral growth and as a measure of how well each species is doing relative to all others in its habitat. High numbers of species are considered positively related to environmental favorableness; low distributional skew means all species present are doing very nearly equally well.[1] The observed diversity pattern may then be correlated with changing physical conditions along environmental gradients.

Peet (1974), in the most recent review of the concept and measurement of species diversity, has discussed the various components comprising the concept and the methods employed in their measurement. He has also discussed the mathematical properties and interpretive limitations of the various measuring techniques. I wish to retain a dual concept approach; that is, species diversity is comprised of both a species "richness" and an "evenness" component.

Look first at the rankings for the unscaled diversity indices SI*, H', SD, and NM (numbers in parentheses in Table 5b). These are all indices classed as heterogeneity indices by Peet (1974) as they use various mathematical procedures in an attempt to summarize into a single statistic both the number of species in a sample and the distribution of individuals among species. As discussed by Fager

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[1] A potential problem not dealt with here would be the analagous situation of lumping trees, shrubs, and herbs in the calculation of diversity of terrestrial plant communities.

(1972), Hill (1973), and Peet (1974), these indices are sensitive to different aspects of these two components of diversity. Although these indices may pertain to slightly different questions about diversity (Fager, 1972), the choice of which one to use is largely arbitrary, and their lack of agreement in ranking samples suggests a tenuousness for hypothesis construction that would be better avoided.

Scaling these indices before ranking them improves their agreement somewhat. This probably results because, as pointed out by Grigg (pers. comm.) and Peet (1974), scaling in the manner proposed by Fager (1972) converts all the indices to measures emphasizing the evenness of the distribution of individuals among species. That is, the scaling procedure places each calculated index value on a scale relative to the values possible for maximum and minimum distribution skew for each sample. In the case under study here all four scaled indices do agree on which sample unit in each sampling class has the most uneven distribution (Transect 1 and Depth Interval 2), but they do not agree in discriminating between the others. As the choice of which index to use is still arbitrary (and they do not agree in the ranking of samples) and the units of expression have questionable biological meaning (bits, moves, or probabilities), I prefer to avoid their use just as the unscaled indices.

Graphical presentation of the sampling distribution (Figure 7b) shows the relationship between the number of species present and the distribution of individuals among them without losing or obscuring any of the information content of the original sampling. When coupled with the dominance calculations (given in Table 2), the graphic plots can be used to describe the diversity patterns along the environmental gradients of exposure and depth.

It can be readily noted from Figure 7b that Transect 1 has the most highly skewed distribution among the transects. Transect 1 also shows high calculated dominance (it takes only roughly 8% of the species present to furnish 50% of the individuals in the sample) and a high species count. Transects 2 and 3 have essentially the same number of species as does Transect 1, but they both show considerably greater evenness in their distributions. This pattern of maintained high numbers of species but decreasing dominance (or increasing evenness) with increasing exposure to wave action suggests that where the coral assemblage is exposed to a higher average level of wave action from either tradewind swell or large, long-period storm waves relatively fewer species are able to monopolize available space. Thus coral diversity may be enhanced by greater exposure to waves. Both Mayor (1918) and Grigg and Maragos (1974) invoke essentially this same hypothesis to explain the nature of the coral distributions they observed.

The graphical plots of the depth intervals show Depth Interval 2 to have the greatest distributional skew among the depth intervals, but at the same time this depth interval has a high species count. Depth Intervals 1 and 3 show nearly equivalent evenness with the dominance calculations suggesting that Depth Interval 3 is less dominated. Depth Interval 1, however, has a greater number of species than Depth Interval 3 and a number comparable to that of Depth Interval 2 and thus is the most diverse of the depth intervals. This pattern of species diversity suggests again that that portion of the environmental gradient in shallow water subject to a relatively constant and high wave energy level is prevented from having space highly monopolized by a few species. It further suggests that an assumed long-term constancy of the deep reef environment may be quite amenable to a rather equitable division of resources and that the sharp increase in reef slope at about 18 m represents a possible environmental threshold beyond which a greatly reduced number of hermatypic coral species find conditions favorable for growth and survival.

The methodology developed by Peet (1974) for studying species diversity was also employed in this study to check its agreement with the results of the graphical plots of the sample distributions. The overall shape of the Exp (H') curves are similar to those of the species counts. This was to be expected as H' is primarily sensitive to the number of species present (Fager, 1972) or, if you will, changes in the number of rare species (Peet, 1974). The index $1/\Sigma p_i^2$ is more sensitive to changes in abundance of the more common species (Peet, 1974), and the plots of it in Figure 6 show changes similar to those seen in the distributional plots of Figure 7b. The ratio of Exp (H') to $1/\Sigma p_i^2$, a measure of dominance or evenness (Hill, 1973; Peet, 1974) agrees with the distributional plots and the dominance calculations except for the relative dominance of Depth Intervals 1 and 3. The particular attractiveness of this procedure according to Peet (1974) lies in the nature of the response of the two diversity indices and the suggestion that their units (species) are both the same and ecologically meaningful. At this point their calculation appears to be unnecessary as the graphical plots of the sample distributions and the dominance calculations give at least as satisfactory results, without concealing the information contained in the actual sample distributions, without problems of "units," and without problems of interpretation.

The ordering of samples (or assemblages or communities) from the graphical plots is largely a subjective decision and hence may not always be clear cut. Where samples cannot be distinguished as to the more diverse on the basis of distributional plots, it probably is not safe to say they differ in diversity regardless of the method of measurement used. All of the methods currently used to measure species diversity are sample size dependent (Hill, 1973; Peet, 1974). Only in the graphical approach does this problem appear surmountable. This may be done through replicate sampling to verify the number, kinds, and relative frequencies of the species involved (Scanland, in prep.). This study begs to be repeated employing such a sampling design.

There have been three other studies recently of the diversity of hermatypic coral assemblages. All three studies employed the Shannon-Wiener function (H') as the diversity index for comparison. Loya (1972) reported an increasing trend in diversity (per 10 m of transect length) with depth for a fringing reef at Eilat. He also reported that at the 5% significance level there were no differences in diversity between stations (within zones only). Porter (1972) reported that diversity per 10 m transect reached a high level at a depth of 5 m and remained relatively high to the base of a lagoon reef in the San Blas Islands off the Caribbean coast of Panama. He also reported a trend of increased diversity values on "cliff edges." Maragos (1974b) reports highest diversity (per 10 m^2 of area) on the deepest segment (30-35 m) of his transect on the leeward seaward reef of Fanning Island, lowest diversity on the intermediate portion (20-25 m), and intermediate diversity at the shallow end (8-15 m).

The lack of agreement between the results, and to some degree also the hypotheses advanced to explain the patterns observed, of the McKean study and those of Loya, Porter, and Maragos may stem from several factors. The physical environment, particularly wave action and geological structure, of the reefs studied by Loya in the Gulf of Eilat and by Porter in the San Blas Islands are quite different from that at McKean, although the Fanning reef studied by Maragos may be somewhat comparable. Both Porter and Maragos used a measure of coral cover rather than individuals as the importance value for their diversity calculations.[1] The diversity (H') and evenness (H'/H'_{max}) indices used in each of these other studies are primarily sensitive to changes in the rare species only (Fager, 1972; Peet, 1974) and pay little attention to the concentration of dominance. Diversity values in each of the other three studies, unlike the McKean study, are reported in terms of fixed sized sample areas. Hopefully in the not too distant future some sort of common ground for sampling procedure and data analysis can be found so that generalizations regarding the structure of hermatypic coral assemblages can be realistically compared.

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[1] Loya (1972) used both individuals and coverage as importance values for calculating H' and found them strongly correlated. In addition to Loya's suggestion that this linear relationship showed that there were no significant differences in the sizes of the corals within a transect, that correlation may also have resulted from the distribution of cover closely matching that of individuals by chance and most likely from the fact that the same number of species was involved in each set of calculations. (H' shows extreme sensitivity to just the number of species involved (Fager, 1972.) Thus diversity based on individuals or coverage may or may not be equivalent.

Spatial Pattern

Spatial aggregation for single species populations of hermatypic corals along an environmental gradient parallel to depth is implied in the many determinations of reef "zones." Similarly, circumscribed species distributions have been referred to along an exposure gradient; for example, the differences in species present on windward and leeward seaward reefs (Wells, 1954). These propositions imply that any given species occupies only a limited range of the environment, the very basis of gradient analysis.

Likewise, the position of all three depth interval samples below the Hurlbert (1971) expected line suggest aggregation, or zonation, along the depth gradient. At best this offers limited statistical support for the zonation of corals with depth. The indirect gradient analysis technique of ordination employed by Loya (1972) provides a much stronger quantitative verification of zonation along the depth gradient. Maragos (1974b) also utilized an ordination procedure to show zonation.

Since the exposure gradient is generally much less steep (environmental conditions are assumed to change less rapidly per unit of distance) than the depth gradient, relatively similar environmental conditions may prevail for relatively large distances on many reefs. This makes the determination of patchy distributions for populations of coral species within arbitrary habitats lacking steep physical environmental gradients feasible and an inherently interesting feature of assemblage organization.

The relationship of the McKean transect samples to the Hurlbert (1971) expected line suggests a small degree of aggregation present in the coral assemblage when viewed along the exposure gradient. That a few of the more common species have variance-to-mean ratios in excess of one (Table 6) supports the aggregation hypothesis in the McKean Island assemblage.

There are now several reports in the literature concerning patterns of spatial distribution of hermatypic corals within limited habitats. Lewis (1970) reported highly aggregated distributions for three of the four species he studied on the reef crest of a Caribbean fringing reef. He states that the causes of such contagious distributions are under investigation, but suggests they are biological. He appears to reject heterogeneity of microhabitats, as the zone studied seemed to be physically homogeneous. Maragos (1974b) measured spatial pattern for several species (12) within a range of quadrats where each species was commonly found. He reports aggregated distributions for most of those species.

Stimson (1974) has determined an underdispersed pattern for *Pocillopora meandrina* in shallow water areas in Hawaii where it was virtually the only coral species present. He hypothesizes that this pattern probably results from larval settling behaviour.

On the reef flat at Heron Island near the southern end of the Great Barrier Reef, Grassle (1973) has found four species of hermatypic corals and several other invertebrates and algae to have patchy distributions on several scales. He suggests that this patchiness is a small scale response to the environment.

The aggregation present along the exposure gradient at McKean Island could result from such microhabitat differences as variations in exposure to waves, scour, sedimentation, and light that would lead to differential mortality rates or larval settling behaviour. It is also conceivable that interspecific aggressive behaviour might play a role. Clarification of the degree of aggregation exhibited by even a modest portion of the coral fauna inhabiting a relatively homogeneous reef environment other than the reef flat and the factors that lead to it must await a larger study properly designed to reveal spatial patterns.

CONCLUSIONS

The relative depauperateness of the McKean Island coral fauna probably results from a combination of very small island size, relative isolation, limited powers of coral larval dispersal, and catastrophic disturbances. The figures of 51 species in 22 genera of hermatypes are consonant with known biogeography.

Two gradients were studied at McKean — depth and horizontal exposure to wave action. The distribution of numbers of species appears to fit Wells's (1957) generality of a decline with increasing depth. The reduction seems most noticeable across the rather sharp increase in reef slope found at approximately 18 m. This reduction may result from changes in environmental variables, such as light, circulation, sedimentation, and plankton supply; reef topography; and/or biological interactions. The sampling at McKean revealed no changes in the numbers of species along the exposure gradient.

The McKean data are rather weakly suggestive of a decrease in living coral coverage with increasing exposure to wave action along both environmental gradients. Corals being broken free or damaged by strong surge and waves and space competition with coralline algae are possible explanations for such a pattern.

Comparisons of compositional similarity reveal the following characteristics of species and population distributions in the McKean coral assemblage: 1) Most species occur in relatively low abundances; these may or may not be widespread. 2) There are a moderate number of relatively abundant and widespread species along the exposure gradient;

there are considerably fewer such species along the depth gradient. 3) There are a small number of relatively abundant species that show restricted distributions along the depth gradient. This last group constitutes a break in faunal composition that separates that portion of the reef shallower than 10 m from the remainder. The average depth of surf base is the environmental factor implicated.[1] There must be a small suite of highly surge resistant species living in this shallow, more intensely wave and surge-swept habitat.

Graphical analysis, a simple dominance calculation, and various diversity indices were used to explore species diversity in the coral assemblage. The least exposed portion of the exposure gradient sampled appeared to be the least diverse. The middle segment of the depth gradient appeared to be the least diverse portion of that gradient. Along the exposure gradient it is the degree of dominance that appears to change rather than species richness. Along the depth gradient mid-depths are rich in species, but dominance is relatively high; shallow depths are also rich in species, but are dominated less; deep depths are less rich in species, but show greater evenness in species abundances.

Results of both the shared species comparisons and the positions of the depth interval samples relative to the Hurlbert (1971) line imply a degree of zonation in the coral assemblage with depth. Variance-to-mean ratios of common species and the positions of the transect samples relative to the Hurlbert (1971) line suggest at least a small degree of spatial aggregation in the McKean coral assemblage along the exposure gradient. Zonation with depth simply reflects the changing adaptive capabilities of the various species to relatively rapidly changing environmental conditions. Since the exposure gradient at McKean is subjectively less steep than the depth gradient, aggregation along it may reflect microhabitat differences although biological interactions cannot be ruled out.

Drawing upon knowledge of coral biology, the nature of the coral reef physical environment, observed coral assemblage species-numbers relationships, and aspects of ecological theory, I offer the following hypothesis for the organization of assemblages of reef building corals on atoll seaward reefs.

Shallow, subtidal, frequently wave-swept reef environments — the physiologically optimal region for coral growth — should have high temporal predictability, high temporal variability, and a high, steady rate of space production. But survival of individual colonies may be unpredictable. The result might be an arrested successional stage in

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[1] Surf base is the depth at which hard rock erosion ceases to occur (Bascom, 1964). For normal tradewind generated swell this depth lies between 7 and 9 m.

which there are many species found in rather equitable numbers, with at least a few restricted to such environments.[1]

Mid-depth environments should have relatively low temporal predictability, high temporal variability, and a fluctuating rate of space production due to irregular, unpredictable occurrences of heavy surge. Thus, while many species may persist, the assemblage is likely to be highly dominated a good deal of the time. This portion of the environmental gradient may be considered transitional, with very few species restricted to it, and in varying stages of succession depending on how much time had elapsed since the last space-creating episode.

Deep reef environments, perhaps slightly less favorable but no more variable physiologically than shallow water, may remain quite constant for lengthy periods of time and be disturbed only at great, but unpredictable, intervals by such events as particularly devastating typhoons or massive *Acanthaster* swarms. The number of species would be reduced and space utilized in an equitable manner. Only here may coral-coral competitive interactions be of any importance to coral assemblage organization. Deep reef assemblages, and perhaps some lagoon reef ones located in regions of low or zero typhoon frequency, are probably the only hermatypic coral assemblages reaching a true climax. Figure 8 summarizes this hypothesis.

Segments of the depth gradient where these various conditions prevail are likely to be displaced toward shallower depths only where the exposure gradient includes a long-term, well protected lee.

It is here suggested, as it has been by others (particularly Storr, 1964), that the organization of most coral assemblages is principally under the control of the physical factor of wave and surge action.

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[1] A rather similar conclusion of arrested succession in high wave energy environments has been reached by Grigg and Maragos (1974) for corals on exposed lava flows in Hawaii.

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APPENDIX

Literature utilized in the identification of the McKean corals.

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Table 1a. Hermatypic coral species observed at McKean Island and their distribution in the samples.

1b. Additional hermatypic coral species collected during the McKean Island study and the depth intervals where found.

Growth form abbreviations are as follows: B, branching; E, encrusting; M, massive; SM, submassive; U, unattached; and F, foliaceous.

Literature utilized in the identification of the McKean corals is given in the appendix.

a.

Growth form	Species	Transects			Depth Intervals			Total
		1	2	3	1	2	3	
B	*Pocillopora setchelli* Hoffmeister	2	0	0	2	0	0	2
B	*P. verrucosa* (Ellis & Solander)	1	2	0	0	2	1	3
B	*P. elegans* Dana	0	2	0	0	2	0	2
B	*P. damicornis* (Linnaeus)	0	1	0	1	0	0	1
B	*Acropora variablis* (Klunzinger)	2	0	0	2	0	0	2
B	*A. humilis* (Dana)	2	0	0	0	2	0	2
E-F	*Montipora verrilli* Vaughan	4	9	7	16	4	0	20
F	*M.* sp. cf. *M. aequi-tuberculata* Bernard	4	2	0	1	5	0	6
E	*M. granulata* Bernard	2	1	1	1	3	0	3
E	*M. informis* Bernard	4	2	2	8	0	0	8
E-SM	*M. socialis* Barnard	0	1	0	0	1	0	1
SM	*M. venosa* (Ehrenberg)	0	0	1	1	0	0	1
E	*Pavona varians* Verrill	0	3	1	3	1	0	4
M	*P. clivosa* Verrill	0	1	0	0	0	1	1
E	*Psammocora nierstraszi* van der Horst	0	0	1	1	0	0	1
U	*Halomitra phillippinensis* Studer	1	0	0	0	0	1	1
U	*Parahalomitra robusta* (Quelch)	0	1	0	0	1	0	1
M	*Porites lobata* Dana	1	3	4	3	2	3	8
M	*P. solida* (Forskal)	0	1	2	0	1	2	3
M	*P. lutea* Milne-Edwards & Haime	7	3	2	3	5	4	12
M	*P. australiensis* Vaughan	0	0	4	0	3	1	4
M	*P. fragosa* Dana	1	1	5	0	0	7	7
E-SM	*P. superfusa* Gardiner	0	1	0	1	0	0	1
M	*P. lichen* Dana	18	11	9	12	24	2	38
E	*P. (Synaraea) hawaiiensis* Vaughan	2	0	0	1	1	0	2
M	*Favia stelligera* (Dana)	13	19	4	12	18	6	36
M	*F. pallida* (Dana)	0	1	0	0	1	0	1
M	*Favites pentagona* (Esper)	1	0	0	1	0	0	1
M	*Plesiastrea versipora* (Lamarck)	2	3	1	5	1	0	6
M	*Platygyra daedalea* (Ellis & Solander)	1	0	1	0	0	2	2
B	*Hydnophora rigida* (Dana)	3	11	5	2	17	0	19
M	*H. microconos* (Lamarck)	1	1	1	1	2	0	3
M	*Leptastrea purpurea* (Dana)	1	1	1	3	0	0	3
M	*L. transversa* Klunzinger	2	2	1	1	4	0	5
M	*Cyphastrea microphthalma* (Lamarck)	2	3	5	10	0	0	10
F	*Echinopora lamellosa* (Esper)	45	3	17	5	50	10	65
M	*Millepora platyphylla* Hemprich & Ehrenberg	2	9	0	11	0	0	11
	Totals	124	98	75	107	150	40	297

b.

Extra-limital Species

Growth Form	Species	Depth Interval
B	*Pocillopora eydouxi* Milne-Edwards & Haime	2
B	*Acropora cymbicyathus* (Brook)	reef flat
B	*A. hyacinthus* (Dana)	2 and 3
B	*A.* sp. cf. *A.abrotanoides* (Lamarck)	2
F	*Pavona minuta* Wells	1
M	*P. clavus* (Dana)	1
SM	*P. (Polyastra)* sp.	1 and 2
F	*Leptoseris mycetoseroides* Wells	1
U	*Fungia (Pleuractis) scutaria* Lamarck	2
U	*F. (Verrillofungia) concinna* Verrill	2
M	*Favites abdita* (Ellis & Solander)	2
M	*Lobophyllia costata* (Dana)	2
F	*Turbinaria irregularis* Bernard	1
B	*Millepora murrayi* Quelch	reef flat

Table 2. Distribution of sample points, numbers of species, dominance, and percent living coral. Numbers in parentheses following the number of species are the number of species found only in that particular sampling unit when each sampling class is considered separately. Dominance is expressed as 100 minus the minimum percentage of species required to yield 50% of the individuals present. High dominance exists when only a small percentage of the species present are needed to constitute 50% of the individuals present.

Sample Unit	No. of Points	Coral	Non-coral	No. of Species	Dominance	% Living Coral
Transect 1	127	124	3	25 (6)	92	97.6
Transect 2	111	98	13	27 (7)	85	89.1
Transect 3	101	75	26	21 (3)	81	74.3
Depth Interval 1	127	107	20	25 (11)	83	84.3
Depth Interval 2	167	150	17	22 (5)	91	89.8
Depth Interval 3	44	40	4	12 (4)	79	90.9

Table 3. Probabilities and cumulative probabilities of as many or more shared species within sample unit pairs. For each sample unit pair comparison, the number of species in each and the number shared between them is also given.

Transects 1 and 2

Species in 1 = 25 Species in 2 = 27 Observed No. Shares Species = 18

No. Shared Species	Probability	Cumulative Probability
18	.06	1.00
19	.26	.94
20	.16	.68
21	.24	.52
22	.16	.28
23	.10	.12
24	.02	.02
25	.00	.00

Transects 2 and 3

Species in 2 = 27 Species in 3 = 21 Observed No. Shared Species = 17

No. Shared Species	Probability	Cumulative Probability
15	.02	1.00
16	.04	.98
17	.26	.94
18	.30	.68
19	.28	.38
20	.10	.10
21	.00	.00

Transects 1 and 3

Species in 1 = 25 Species in 3 = 21 Observed No. Shared Species = 16

No. Shared Species	Probability	Cumulative Probability
14	.02	1.00
15	.08	.98
16	.24	.90
17	.36	.66
18	.18	.30
19	.06	.12
20	.06	.06
21	.00	.00

Depth Intervals 1 and 2

Species in 1 = 25 Species in 2 = 25 Observed No. Shared species = 14

No. Shared Species	Probability	Cumulative Probability
15	.06	1.00
16	.10	.94
17	.34	.84
18	.18	.50
19	.26	.32
20	.06	.06
21	.00	.00
22	.00	.00

Depth Intervals 1 and 2

Species in 2 = 22 Species in 3 = 12 Observed No. Shared Species = 8

No. Shared Species	Probability	Cumulative Probability
8	.18	1.00
9	.24	.82
10	.26	.58
11	.22	.32
12	.10	.10

Depth Intervals 1 and 3

Species in 1 = 25 Species in 3 = 12 Observed No. Shared Species = 5

No. Shares Species	Probability	Cumulative Probability
8	.04	1.00
9	.16	.96
10	.48	.80
11	.26	.32
12	.06	.06

Table 4. Rank orders of abundance for the 7 most common species, all of which are present along all 3 transects, and the 5 species common to the 3 depth intervals with coefficients of concordance (w) for these rankings as well as for all the species. All W's have been corrected for ties.

Seven Most Common Species (present along all transects)	Rank Order of Relative Abundance Transect 1	 Transect 2	 Transect 3
Porites lichen	2	2.5	2
Echinopora lamellosa	1	6	1
Favia stelligera	3	1	6
Montipora verrilli	5	4	3
Hydnophora rigida	6	2.5	4.5
Porites lutea	4	6	7
Cyphastrea microphthalma	7	6	4.5

W for the 7 most common species = 0.43 $0.10 < p < 0.20$
W for all species by transects = 0.65 $p < 0.01$

Species Common to All 3 Depth Intervals	Rank Order of Relative Abundance Dpth.Intv.1	 Dpth.Intv.2	 Dpth.Intv.3
Echinopora lamellosa	3	1	1
Favia stelligera	1.5	3	2
Porites lichen	1.5	2	5
Porites lutea	4.5	4	3
Porites lobata	4.5	5	4

W for the 5 species in common = 0.56 $0.10 < p < 0.20$
W for all species by depth intervals = 0.42 $p = 0.27$

Table 5a. Scaled and unscaled values of the following diversity indices:
SI* = 1 minus Simpson's Index, H' = Shannon-Wiener function, SD = standard deviation,
NM = Number of Moves Index.

b. Rankings for the various diversity indices. Ranks in parentheses are for unscaled values.

a.

	SI*		H'		SD		NM	
	unscaled	scaled	unscaled	scaled	unscaled	scaled	unscaled	scaled
Trans 1: S = 25, N = 124	0.167	0.782	2.379	0.602	9.249	0.533	962	0.190
Trans 2: S = 27, N = 98	0.079	0.898	2.800	0.732	4.360	0.681	682	0.261
Trans 3: S = 21, N = 75	0.088	0.894	2.631	0.752	3,842	0.674	379	0.298
Dpth 1: S = 25, N = 107	0.073	0.926	2.771	0.773	4.468	0.728	683	0.306
Dpth 2: S = 22, N = 150	0.164	0.821	2.259	0.632	11.533	0.577	1070	0.204
Dpth 3: S = 12, N = 40	0.119	0.871	2.179	0.753	2.902	0.641	103	0.331

b.

	Transects		
Index	1	2	3
SI*	3 (1)	1 (2)	2 (3)
H'	3 (3)	2 (1)	1 (2)
NM	3 (1)	2 (2)	1 (3)
SD	3 (3)	1 (1)	2 (2)

	Depth Intervals		
Index	1	2	3
SI*	1 (3)	3 (1)	2 (2)
H'	1 (1)	3 (2)	2 (3)
NM	2 (2)	3 (1)	1 (3)
SD	1 (2)	3 (1)	2 (3)

Table 6. Spatial pattern of the more common and widespread species along the exposure gradient. At the 5% level of significance the three species marked with an asterisk are clumped, while none of the others depart from random.

Species	Distribution			$\bar{x}$	s^2	$s^2/\bar{x}$	χ^2	p
Montipora verrilli	4	9	7	20/3	12/3	0.60	1.20	$.50<p<.75$
Porites lobata	1	3	4	8/3	7/3	0.88	1.76	$.25<p<.50$
Porites lutea	7	3	2	12/3	21/3	1.75	3.50	$.10<p<.25$
Porites lichen	18	11	9	38/3	67/3	1.76	3.52	$.10<p<.25$
*Favia stelligera**	13	19	4	36/3	171/3	4.75	9.50	$.005<p<.01$
Hydnophora rigida	3	11	5	19/3	52/3	2.74	5.48	$.05<p<.10$
Cyphastrea microphthalma	2	3	5	10/3	3/3	0.30	0.60	$.50<p<.75$
*Echinopora lamellosa**	45	3	17	65/3	1372/3	21.6	43.2	$p<.005$
*Millepora platyphylla**	2	9	0	11/3	67/3	6.09	12.18	$p<.005$

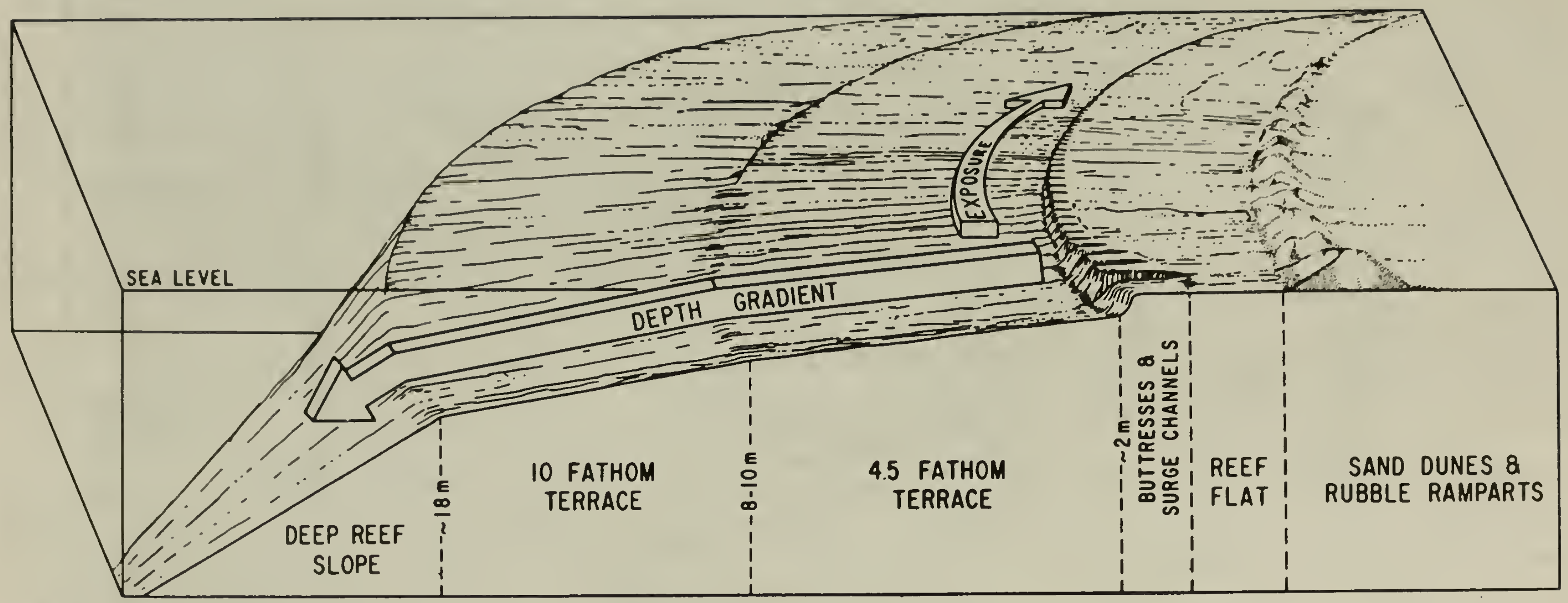


Figure 1. A generalized three-dimensional cut-away view of the seaward reef of an Indo-Pacific atoll located in trade wind regions. Terrace structure and environmental gradients are labeled. Prevailing wind would be from the upper right.

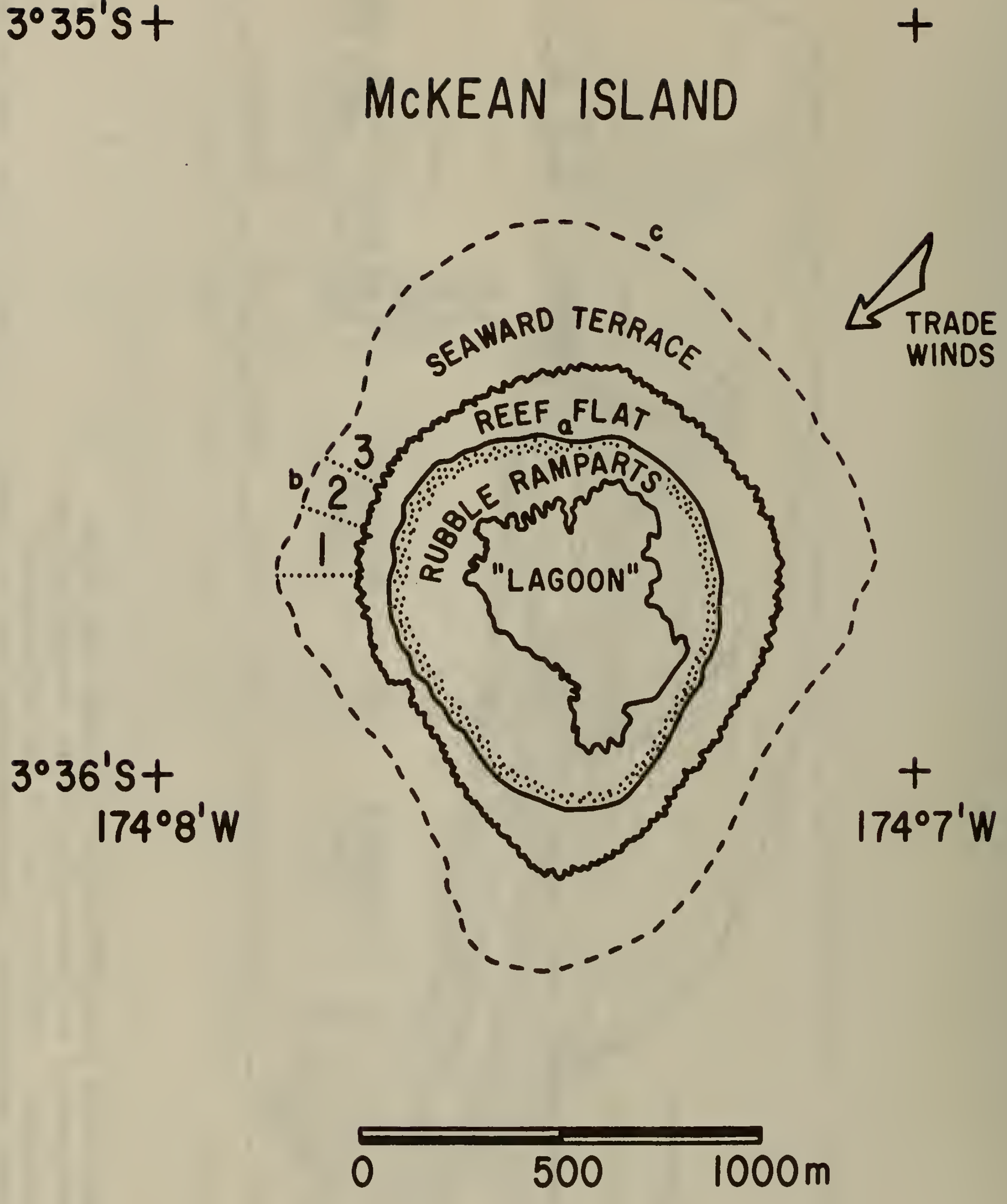


Figure 2. Plan view of McKean Island showing approximate location of the three transects. The contour indicated represents the 20 m contour. This figures was redrawn from HO Chart 83037. The lower case letters a, b, and c refer to the locations of the following two figures.

Figure 3. Rubble ridges along the northern shore of McKean Island. Here the ramparts reach a height of some 5 m. This photograph was taken at the point marked "a" on Figure 2.

Figure 4a. Region of the sharp break in reef slope in the northeastern sector of the reef. At this point virtually all living coral has been stripped from the reef and only rubble remains. This photograph was taken at the point marked "c" on Figure 2.

Figure 4b. Region of the sharp break in reef slope in the area of the transects. The abundance of large, shelving colonies of such species as *Porites solida, P. lutea, P. australiensis,* and *P. fragosa* can clearly be seen. This photograph was taken at the point marked "b" on Figure 2.

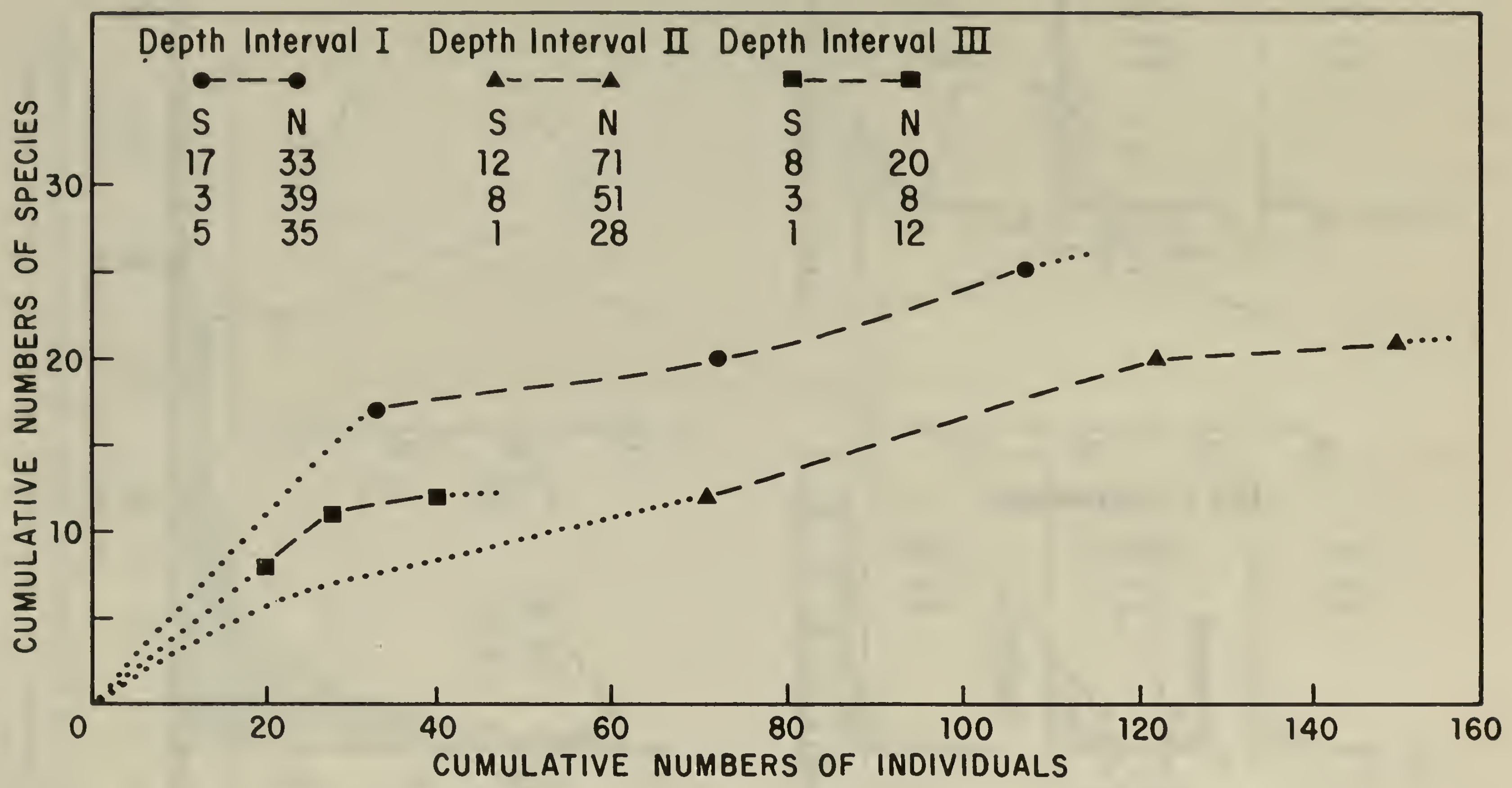


Figure 5. Plots of the cumulative numbers of species against the cumulative numbers of individuals for each of the depth intervals. These curves were constructed by successively adding new species and total individuals from the segments of each transect within each depth interval in the order of Transects 1, 2, and 3.

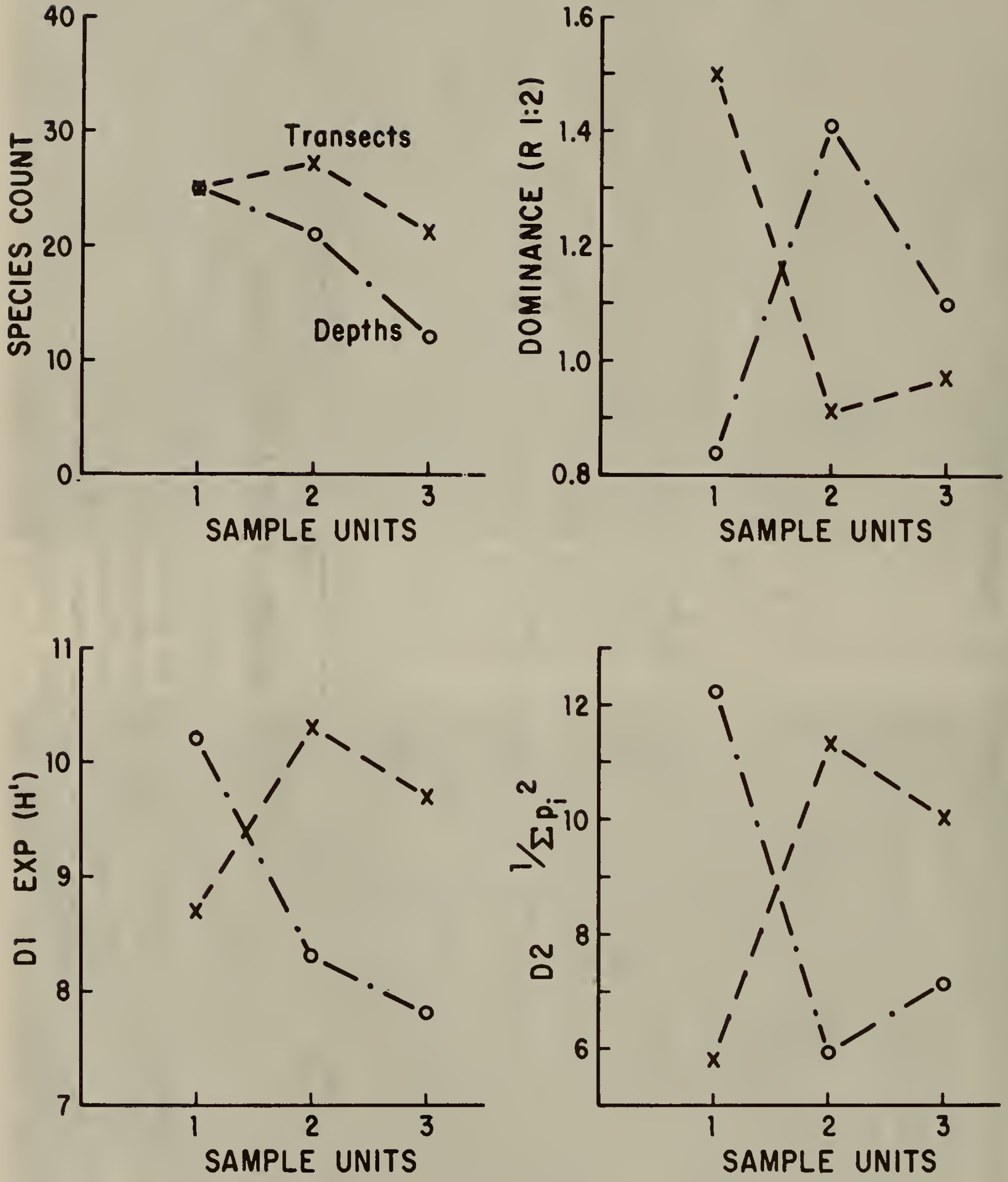
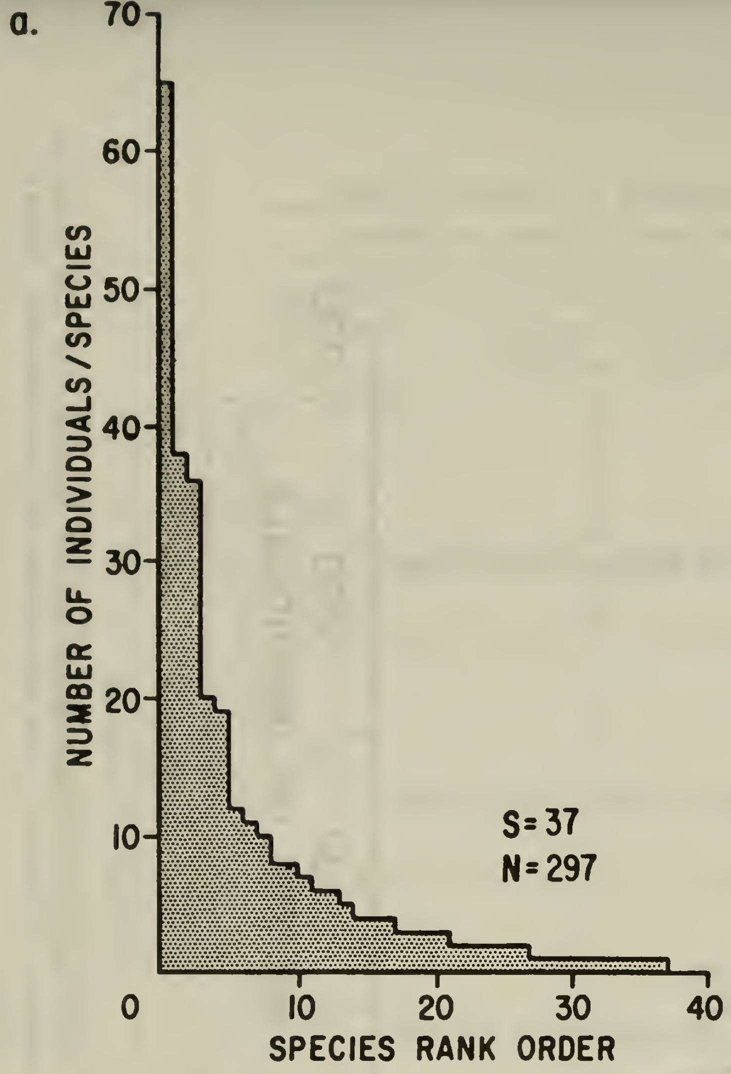


Figure 6. Plots of the species counts and Hill's diversity numbers as proposed by Peet (1974) for use in species diversity studies.



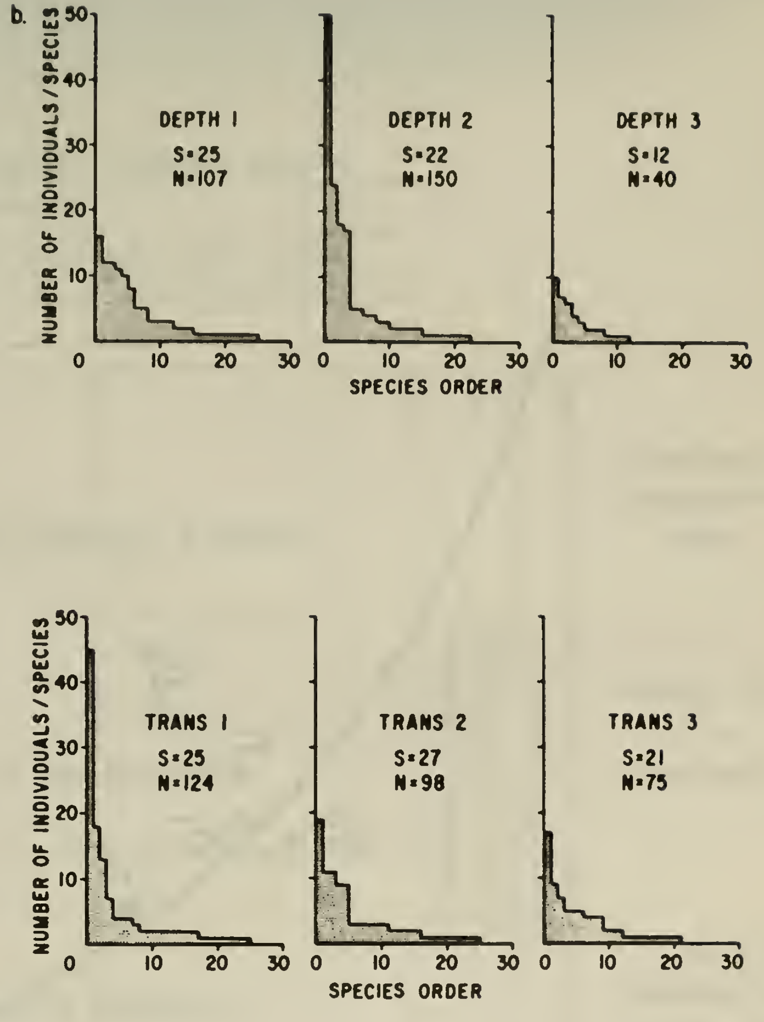


Figure 7a. Histogram of the number of individuals per species plotted against species rank order for the entire McKean Island coral collection.

Figure 7b. Histograms of the number of individuals per species plotted against species rank order for individual sample units.

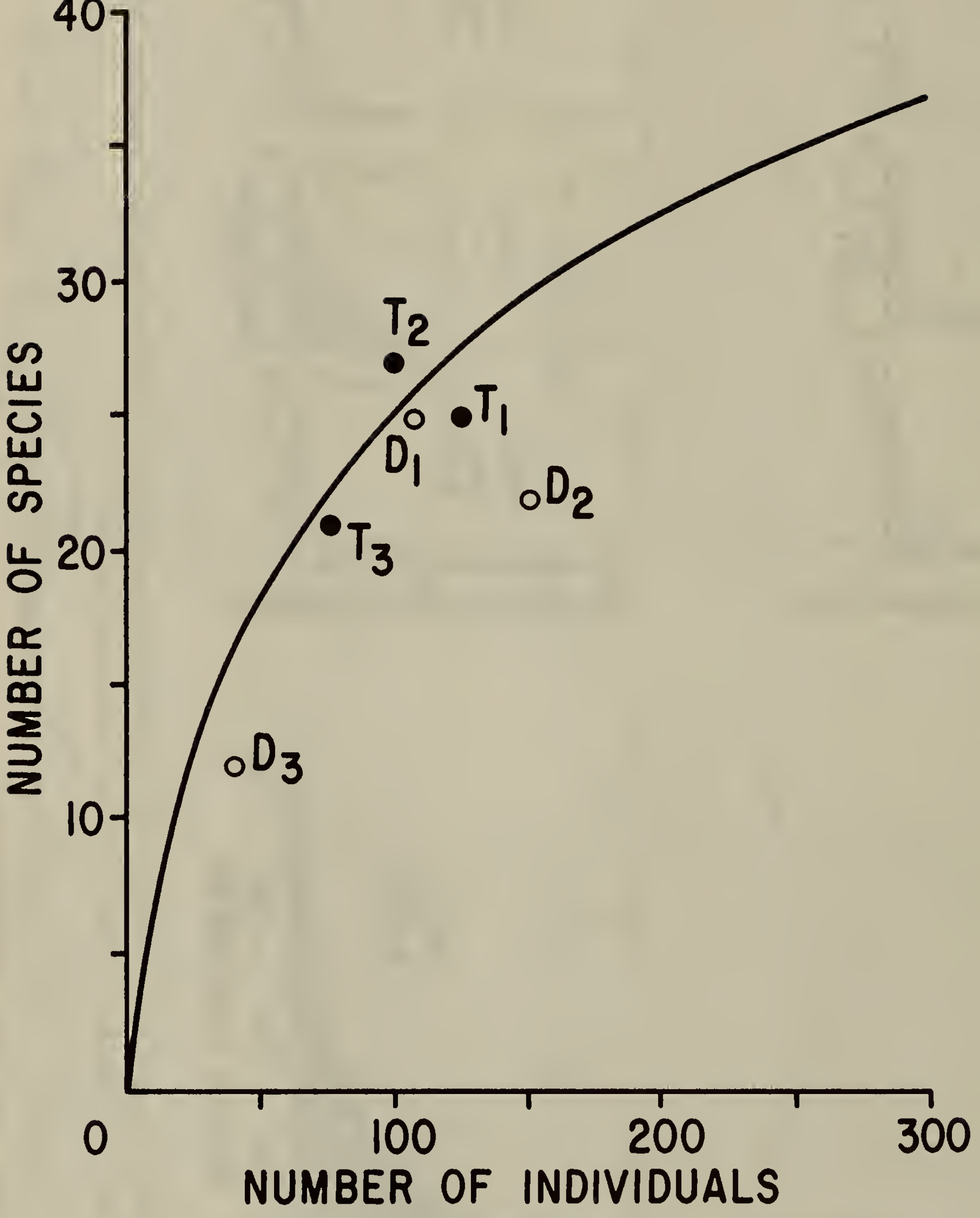


Figure 8. Distribution of the McKean samples relative to the expected number of species line calculated by the Hurlbert (1971) method.

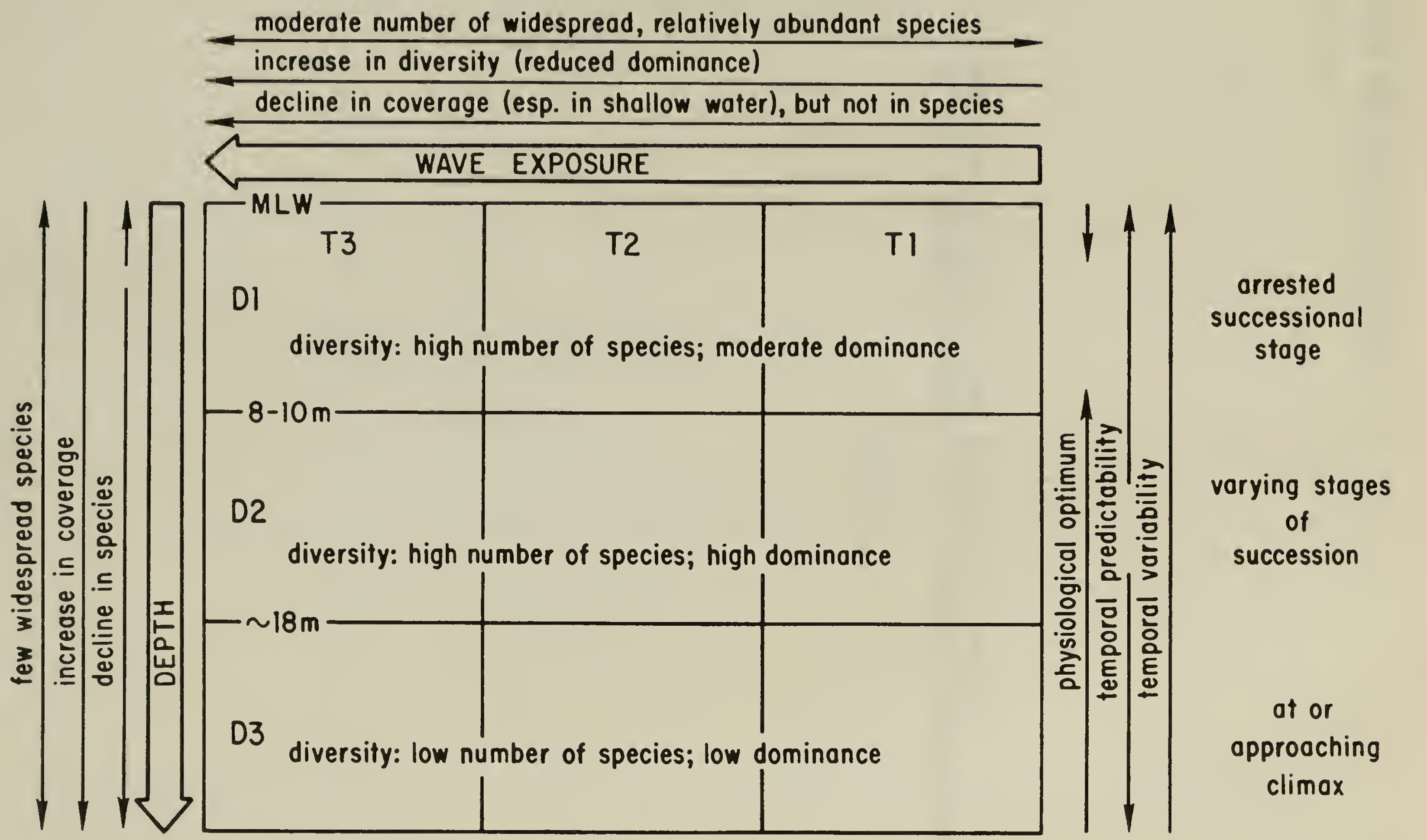


Figure 9. Graphical summary of the organization hypothesis for seaward reef coral assemblages.

ATOLL RESEARCH BULLETIN

NO. 229

THE PROPAGULES OF THE TERRESTRIAL FLORA OF THE ALDABRA ARCHIPELAGO, WESTERN INDIAN OCEAN

by G. E. Wickens

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THE PROPAGULES OF THE TERRESTRIAL FLORA OF THE ALDABRA ARCHIPELAGO, WESTERN INDIAN OCEAN

by G. E. Wickens[1]

The origins of the flora of the islands of the Aldabra archipelago, Aldabra, Assumption, Cosmoledo and Astove, and speculations on the modes of dispersal were discussed in an earlier paper (Wickens, 1979). In this paper the propagules are described, together with notes on their presumed status, distribution within the archipelago, and where known, information provided regarding long-distance dispersal and local dispersal. Dispersal information has been gleaned from the literature, or, in instances where no literature reference is provided, from unpublished data kindly supplied by C. B. Frith and Dr S. H. Hnatiuk.

The status of a species, whether native or introduced, is in some cases uncertain; the question is considered in some detail in Wickens (1979). Weeds are generally associated with areas of habitation, cultivation and waste places. Many are widely recognized as such in the literature, e.g. Haigh *et al.* (1951), Rochecouste & Vaughan (1959-66), Henderson & Anderson (1966), Ivens (1967), Henty & Pritchard (1975), and Holm *et al.* (1977). Cultivated plants are those believed to have been deliberately introduced for food, ornament, or some other utilitarian purpose. In both cases there are examples where the plant could have been naturally introduced.

Three categories are recognized for the native flora: 'strand' for the seashore littoral, 'lagoon' for the mangroves and tidal flats within the shelter of the lagoons, and 'inland' species, for which no designation is given in the text.

The method of dispersal has been gleaned from the literature, especially from Ridley (1930), whose encyclopaedic study is an uncritical catalogue of anecdotal evidence by numerous authors, which in the course of time has gained unquestioned universal acceptance. Effective dispersal involves transport and establishment. Thus evidence that a bird will consume a certain fruit or seed is not, *per se*, evidence for effective dispersal but of the possibility of dispersal by such a means. It must be admitted that the evidence of successful

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(Manuscript received July 1978 --Eds.)

establishment is often extremely difficult to obtain; many propagules may be successfully transported but never become established, as is evident from the many viable propagules washed up on the shores of Aldabra belonging to species not represented in the flora.

The nomenclature follows that of the local flora by Fosberg & Renvoize (1979). The term 'seed' is widely used for both true 'seeds' as well as 'stones' of drupes, etc. It is hoped that the information given will be of interest to all those interested in dispersal and that the descriptions of the seeds will be of some guidance to ornithologists examining the stomach contents of birds. The paper shows what is known about dispersal and, more important, how little is known and where observations are required.

POLYDODIACEAE

1. *Acrostichum aureum* L. Spores minute, tetrahedral, with a 3-radiate dehiscence scar, colourless. Native; Aldabra, Assumption. Wind dispersed (Ridley, 1930).

2. *Nephrolepis biserrata* (Sw.) Schott Spores minute, with an unbranched dehiscence scar, brown. Native; Aldabra, Assumption. Wind dispersed (Ridley, 1930).

ANNONACEAE

3. *Annona squamosa* L. Sweetsop. Fruit syncarpous, fleshy, globose or conical, 5-10 x 5-10 cm., formed of loosely cohering or almost free carpels. Cultivated; Aldabra. Seeds or seedlings planted by man; possibly sea dispersed, fruit buoyant for about 7 months, seeds not buoyant (Gunn & Dennis, 1976).

MENISPERMACEAE

4. *Cissampelos pareira* L. var. *hirsuta* (Buch. ex DC.) Forman Drupe obovoid, 3.5 mm. long, dorsally bearing 2 rows of 9-11, very prominent, transverse ridges, orange or red; seeds 1, depressed-globose, verrucose, c. 4 mm. in diameter. Weed of guano pits; Assumption. Drupes eaten by birds (Ridley, 1930).

CRUCIFERAE

5. *Brassica nigra* (L.) Koch Siliqua up to 20 x 2 mm., seed globose, 1.5 mm. in diameter. Weed or pot herb; Aldabra, Assumption, Cosmoledo Astove. Seed introduced by man.

CAPPARIDACEAE

6. *Capparis cartilaginea* Decne. Berry obliquely ovoid or ellipsoid, up to 5 x 3 cm., ribbed, red; seeds many, reniform, c. 3 x 2 mm., reddish-brown. Native; Aldabra, Assumption, Astove. Dispersal not known; possibly eaten by birds.

7. *Cleome strigosa* (Bojer) Oliver Capsule siliquiform, up to 3.5 x 0.3 cm., with 2 dehiscing valves and persistent replum. Seed cochleate, c. 1.2-1.5 x 0.7-0.9 mm., tuberculate, reddish brown. Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Dispersal not known, possibly eaten and transported by birds or on driftwood.

8. *Gynandropsis gynandra* (L.) Briq. Capsule siliquiform, up to 15 x 0.8 cm., with 2 dehiscing valves and persistent replum. Seed cochleate, c. 1.5-1.8 mm. in diameter, transversely rugose. Weed; Aldabra. Seed accidentally introduced by man.

9. *Maerua triphylla* A. Rich. var. *pubescens* (Klotzsch) De Wolf Berry golobse to cylindrical, 1-5 cm. long, torulose, woody; seeds ovoid to subglobose, up to 6 mm. in diameter. Native; Aldabra, Assumption, Cosmoledo, Astove. Dispersal not known.

FLACOURTIACEAE

10. *Flacourtia ramontchii* L'Herit. var. *renvoizei* Fosberg Berry globose, 7-10 mm. diameter, 5-lobed, black; seeds 6-8, obliquely ovoid, 4 x 2 mm., rugose, brick red with cream mottles. Endemic; Aldabra, Astove. Fruit eaten by turtledoves, blue pigeon, white-eyes and bulbuls (Benson & Penny, 1971).

11. *Ludia mauritiana* Gmel. Fruit baccate, globose, c. 10 mm. in diameter, thinly fleshy, red; seeds 2-3, oval to suborbicular, c. 1.5-2 mm. in diameter, arilate. Native; Aldabra. Fruit presumably eaten and dispersed by birds.

PORTULACACEAE

12. *Portulaca mauritiensis* Poelln. var. *aldabrensis* Fosberg Capsule globose, 3 mm. in diameter, circumscissile dehiscence. Seeds reniform, plump, 0.7-0.8 mm. across, irridescent blue. Endemic; Aldabra, Assumption, ? Cosmoledo. Dispersal unknown, seeds possibly eaten and dispersed by birds, locally dispersed by tortoise (Hnatiuk, in press,a).

13. *Portulaca mauritiensis* Poelln. var. *grubbii* Fosberg Fruit and seed as above. Endemic; Cosmoledo. Dispersal as above.

14. *Portulaca oleracea* L. var. *oleracea* Capsule ovoid, 4 x 2-3 mm., circumscissile dehiscence. Seeds many, reniform, somewhat compressed, c. 0.7 x 0.7 mm., black or dark brown, glossy, tessellate. Status uncertain, possibly naturalised weed of cultivation; Aldabra, Assumption. Seeds transported by drift pumice (Guppy, 1917) but sea dispersal considered a rare event by Ridley (1930) who records it as a pot-herb introduced by man, a weed of cultivated land and transported internally by birds. Also propagated by portions of broken stem (Henty & Pritchard, 1975, Holm *et al.*, 1977).

15. *Portulaca oleracea* L. var. *delicatula* Fosberg Capsule as above. Seeds reniform, somewhat compressed, c. 0.7 x 0.7 mm., dark brown, glossy, with star-shaped markings. ? Endemic; Aldabra. Seed dispersal as above.

16. *Portulaca oleracea* L. var. *granulato-stellalata* Poelln. Capsule as above. Seeds reniform, somewhat compressed, c. 0.7 x 0.7 mm., black, tuberculate. ? Native; Aldabra, Assumption, Cosmoledo, Astove. Dispersal as for var. *oleracea*.

GUTTIFERAE

17. *Calophyllum inophyllum* L. var. *takamaka* Fosberg Drupe globose, c. 2.5 cm. in diameter, mericarp thin, endocarp thin; seed 1, globose, c. 2 cm. in diameter, oily. Endemic, strand; Aldabra, Assumption, Cosmoledo, Astove. Drupes of var. *inophyllum* eaten by birds and bats, also dispersal by man (Ridley, 1930); drupes float for 126 days, sea dispersed (Ridley, 1930; Fosberg, 1974; Gunn & Dennis, 1976). Sea main vector, locally dispersed by bats (Pijl, 1957).

MALVACEAE

18. *Abutilon angulatum* (Guill. & Perr.) Masters Regma depressed-globose, 1.5 cm. in diameter, surrounded by persistent calyx; mericarps c. 20-30, oval in outline, 4 x 8 mm., with lateral wings, dehiscent; seeds reniform, 2.5 x 2 mm., verruculose or smooth. Weed; Aldabra, Astove. Accidentally introduced by man.

19. *Abutilon fruticosum* Guill. & Perr. Regma depressed-cylindrical, 7 x 10 mm.; mericarps 7-8, broadly keeled in the apical half, obliquely truncate — convex at the apex, dehiscent; seeds reniform, c. 1.5 x 1.5 mm., rugose, greyish brown. Weed; Assumption. Accidentally introduced by man.

20. *Abutilon pannosum* (Forst.f.) Schlecht. Regma depressed-cylindrical, c. 10 x 15 mm.; mericarps 16-20, obliquely oblong-elliptic, 8 x 6 mm., ends obtuse, dehiscent; seeds reniform-infundibuliform, 3 x 2 mm., hirsute. Weed; Aldabra, Cosmoledo,

Astove. Accidentally introduced by man.

21. *Gossypium hirsutum* L. Capsule globose, c. 3 cm. in diameter, enveloped by persistent calyx, loculicidally dehiscent; seeds ovoid 8 x 5 mm., with copious white wool. Cultivated and naturalised; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man.

22. *Hibiscus abelmoschus* L. Capsule ellipsoid, up to 8 x 3 cm., loculicidally dehiscent; seeds reniform, 3 x 2.5 mm., concentrically ribbed or rugose. Cultivated and naturalised; Astove. Introduced by man.

23. *Hibiscus tiliaceus* L. Capsule subglobose, 2-2.5 cm. in diameter, loculicidally dehiscent; seeds subreniform, 4.5 x 3 mm. Native, strand; Aldabra, Astove. Sea dispersed (Muir, 1937); seed buoyant 3-4 months (Guppy, 1917), carried by pumice (Guppy, 1890).

24. *Sida acuta* Burm. f. Regma depressed-globose 4 mm., dehiscent; mericarps 6-10, obliquely tetrahedral-reniform, 2 x 4 mm., birostrate, dehiscent; seeds 1, triangular, 1 x 1 mm., smooth. Weed; Aldabra, Assumption, Cosmoledo. Seed accidentally dispersed by man; mericarps adhere to coats of animals or carried by muddy feet (Holm *et al.*, 1977).

25. *Sida parvifolia* DC. Schizocarp hemispherical, 3 x 1.5-2 mm.; mericarps 5, dorsally shield-shaped, 2 mm. long, birostrate; dehiscent; seed obliquely pyriform, 2 x 1.5 mm. Native; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known.

26. *Sida rhombifolia* L. Regma depressed-globose, 4 mm. in diameter; mericarps 8-12, 3 x 2 mm., birostrate, dehiscent; seed triangular, 2.5 x 2 mm., red-brown, glossy. Weed; Aldabra. Accidentally introduced by man.

27. *Thespesia populnea* (L.) Sol. ex Correa Capsule depressed-globose, 2.5 x 1.8 cm., epicarp indehiscent, irregularly crumbling with age; seed broadly ovoid, 15 x 9 mm., slightly angled, with long silky pubescence. Native, strand; Aldabra, Astove. Capsule breaks up after a week at sea, seeds escape and float (Ridley, 1930); seeds buoyant, germinate after a year in sea (Guppy, 1906, 1917); viable seeds found along Aldabra strand line. Seeds eaten and locally dispersed by tortoise (Hnatiuk, in press, a).

28. *Thespesia populneoides* (Roxb.) Kostel. Capsule depressed-globose, 4 x 2 cm., leathery, brown exocarp separated from the tough, fluted endocarp by a loose, fibrous mesocarp, which partially disintegrates, exocarp then dehiscing into (4-)5(-6) valves (Fig. 1, 1a). Seeds broadly obovoid, (Fig. 1, 2b), 1.3 x 0.9 cm., covered with short, clavate pubescence (Fosberg & Sachet, 1972). Native, lagoon; Aldabra, Assumption, Cosmoledo, Astove. Dispersal presumably as for *T. populnea*.

TILIACEAE

29. *Corchorus aestuans* L. Capsule up to 2.5 x 0.3-0.6 cm., 3-5 valved; seeds shortly cylindrical, c. 0.8 x 0.8 mm., brown. Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man.

30. *Grewia aldabrensis* Baker Drupe (2-)4-lobed, 7 x 4 mm., each lobe obovoid, woody. Endemic; Aldabra. Method of dispersal not known, possibly by birds.

31. *Grewia salicifolia* Schinz Drupe 4-lobed, ± cuboid, 15 x 23 mm.; woody, densely reddish-brown, pubescent (Fig. 1, 12). Endemic; Aldabra, Cosmoledo. Method of dispersal not known, possibly by birds.

32. *Triumfetta procumbens* Forst.f. Drupe globose, 1.5 cm. in diameter, including the pilose prickles (Fig. 1, 3). Native, strand; Astove. Fruit not buoyant, sinks in 3-7 days, fide Guppy (1906), buoyant for at least a month (Gunn & Dennis, 1976); transported on drift pumice (Guppy, 1890, 1917; Muir, 1937). Fruit attached to feathers of boobies (Ridley, 1930).

ERYTHROXYLACEAE

33. *Erythroxylon acranthum* Hemsley Drupe ovoid, 3-4 x 2 mm. (immature), red. Endemic; Aldabra, Assumption, Cosmoledo. Drupe presumably eaten and dispersed by birds.

ZYGOPHYLLACEAE

34. *Tribulus cistoides* L. Schizocarp breaking up into 5 mericarps, c. 10 x 5 x 5 mm., armed with 2 ± divergent spines in the upper part and 2 small ones in the lower part. Weed; Aldabra, Assumption, Cosmoledo, Astove. Mericarps accidentally dispersed by man and animals, adhering by the spines (Holm *et al.*, 1977).

OXALIDACEAE

35. *Oxalis* sp. near *O. bakerella* Exell No specimens seen. Presumed introduced as an ornamental.

RUTACEAE

36. *Citrus aurantifolia* (Christm.) Swingle Lime. Berry, broadly ellipsoid to globose. Cultivated, now believed extinct; Aldabra. Introduced by man.

SURIANACEAE

37. *Suriana maritima* L. Nucules obovoid, 3.5-4 x 3 mm., blackish-purple, pubescent, indehiscent (Fig. 1, 19). Native, littoral; Aldabra, Assumption, Cosmoledo, Astove. Nucules buoyant, float 3-5 months (Guppy, 1917), also carried by floating pumice and logs (Guppy, 1917; Muir, 1937); carried by mud attached to feet of birds (Guppy, 1917; Ridley, 1930).

OCHNACEAE

38. *Ochna ciliata* Lam. Fruiting calyx red, reflexed; torus accrescent, red, fleshy, drupelets up to 10, oblong-ovoid, 8-10 x 5-7 mm., black; seed 1, ovoid, 8-9 x 5-6 mm. Native; Aldabra. Fruit obviously attractive to birds; eaten by Malagasy turtle dove (Benson & Penny, 1971), also by bulbul, locally dispersed by tortoise (Hnatiuk, in press, a).

MELIACEAE

39. *Malleastrum leroyi* Fosberg Drupe obliquely ovoid, 9 x 7 mm. (immature), 2-celled, seeds 1 per cell. Endemic; Aldabra. Drupe presumably eaten by birds.

40. *Xylocarpus granatum* Koenig Capsule globose, 10-20 cm. in diameter, glossy, orange-brown, ? dehiscent; seeds irregularly obpyramidal, 3.5-8 x 3-5 cm., light, corky, testa c. 10 mm. thick. Native, lagoon; Aldabra, ? Cosmoledo. Seeds buoyant, float for many months, tend to germinate while floating, lessening the effectiveness of dispersal (Ridley, 1930; Muir, 1937); stranded seeds often attached by crabs.

41. *Xylocarpus moluccensis* (Lam.) Roem. Capsule globose, 10-15 cm. in diameter, glossy orange-brown, tardily dehiscent; seeds 6-12, irregularly obpyramidal, 3.5-7 x 3-5 cm., light, corky, testa c. 10 mm. thick (Fig. 1, 10). Native, lagoon; Aldabra, Cosmoledo. Dispersal as for *X. granatum;* long range drifting of viable seeds apparently does not occur. (Gunn & Dennis, 1976).

ICACINACEAE

42. *Apodytes dimidiata* E. Mey. ex Arn. Crustaceous drupe subcompressed ovoid-reniform, 6-7 x 5-7 x 3 mm., black with a fleshy, lateral, red appendage (Fig. 1, 13); seed 1, compressed, oblong, 4 x 2.5 mm. Native; Aldabra, Cosmoledo, Astove. Fruit eaten and seed dispersed by pigeons (Ridley, 1930). Fruit eaten by turtle doves, bulbul and white-eye (Benson & Penny, 1971), also by crow; viable seeds obtained from bulbul regurgitate.

CELASTRACEAE

43. *Maytenus senegalensis* (Lam.) Exell Capsule globose to pyriform, 2-6 x 3-4 mm., dehiscing loculicidally, pink or crimson; seeds 4, ovoid, 3 x 2 mm., dark, glossy reddish-brown with a fleshy rose-pink aril obliquely covering the lower $^1/_3$-$^2/_3$. Native; Aldabra, Assumption, Cosmoledo, Astove. Seeds believed to be attractive to birds.

44. *Mystroxylon aethiopicum* (Thunb.) Loes. Drupe globose to ovoid, 8-10 x 7-8 mm., slightly fleshy, red; seeds 1, ovoid, 7 x 4 mm. Native; Aldabra, Assumption, Astove. Fruit eaten and viable seed obtained from bulbul regurgitate (Hnatiuk, in press, a); also eaten and locally dispersed by tortoise.

RHAMNACEAE

45 *Colubrina asiatica* (L.) Brongn. Schizocarp globose, 6-9 mm. in diameter, shallowly 3-lobed, dehiscing to form 3, crustaceous, 1-seeded mericarps, releasing the seed through a longitudinal, ventral slit, seed ventrally dihedral, dorsally convex, 4.5-6 x 4.5 mm., reddish brown (Fig. 1, 16). Native, littoral; Aldabra, Cosmoledo, Astove. Seeds of low specific gravity, float for many months (Guppy, 1906, 1917; Ridley, 1930; Muir, 1937); locally dispersed by tortoise (Hnatiuk, in press, a).

46. *Gouania scandens* (Gaertn.) R.B. Drummond Schizocarp compressed-orbicular, 3-winged, up to 17 x 18 mm. (Fig. 1, 6a), separating into 3, indehiscent, 1-seeded mericarps (Fig. 1, 6b); seed plano-convex, 5 x 4 x 2 mm. (Fig. 2, 6c). Native; Aldabra, Cosmoledo. Wind dispersed (Ridley, 1930), locally dispersed by tortoise (Hnatiuk, in press, a).

47. *Scutia myrtina* (Burm.f.) Kurz Drupe obovoid to spherical, up to 8 mm. in diameter, purplish-black; seeds 2, plano-convex, 6 x 6 x 1.5 mm., grey. Native; Aldabra, Assumption, Cosmoledo, Astove. Drupe eaten by blue pigeon, turtle dove and bulbul (Benson & Penny, 1971).

SAPINDACEAE

48. *Allophylus aldabricus* Radlk. Drupe obovoid, 4-6 x 4 mm., red or orange, 1-seeded; seed acutely-obovoid, 6 x 4 mm., reddish-brown. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Bird dispersed, other species eaten and dispersed by birds (Ridley, 1930); fruits eaten and seed locally dispersed by fody.

49. *Dodonaea viscosa* L. Double (or triple) samara, laterally compressed, subcircular in outline, c. 1 cm. in diameter, somewhat inflated, indehiscent, wings c. 5 mm. wide (Fig. 1, 15a), samaras eventually separate; seed (1-) 2, ovoid, 3 x 2 mm., black

(Fig. 1, 15b). Native, strand; Aldabra (lagoon islet). Order of effectiveness of dispersal according to Guppy (1917) is granivorous birds, sea (buoyant for 2 months) and man. Also wind dispersed (Muir, 1937).

50. *Macphersonia hildebrandtii* O. Hoffm. Fruit baccate, globose, 8-10 mm. in diameter, black; seed 1, depressed - ovoid, 6 x 5 mm. with thin arillode. Native; Aldabra, Assumption, Cosmoledo, Astove. Drupe presumably eaten by birds.

ANACARDIACEAE

51. *Operculicarya gummifera* (Sprague) Capuron Drupe ovoid, 7-8 x 5-7 mm., purplish; seed 1, reniform-obovoid, 8 x 6 mm., somewhat angular, reddish brown. Native; Aldabra. Drupe presumably eaten by birds.

MORINGACEAE

52. *Moringa oleifera* Lam. Horseradish Tree. Capsule torulose, up to 40 x 2 cm., slightly 3-angled, 2-ribbed between the angles, dehiscing by 3 valves; seeds orbicular, c. 1 cm. in diameter, with 3 papery wings c. 3 x 0.7 cm. Cultivated; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man.

LEGUMINOSAE — CAESALPINOIDEAE

53. *Caesalpinia bonduc* (L.) Roxb. Pod ± oblong-elliptic, 4.5-7.6 x 3.5-4.5 cm., densely prickly, dehiscent; seeds globose to subglobose, 1.5-2 cm. in diameter, lead grey (Fig. 1, 7). Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Seeds very hard shelled and will float and retain power of germination unimpaired after 2½ years at least (Guppy, 1906; Dupont, 1907; Ridley, 1970; Muir, 1937; Brenan, 1967; Gunn & Dennis, 1976); seeds also found in the stomachs of frigate birds and boobies (Guppy, 1890).

54. *Cassia aldabrensis* Hemsley Pod oblong, 3-4.5 x 0.2-0.3 cm., flat, dehiscent; seed compressed-rhomboid, 2 x 1 mm., brown. Endemic; Aldabra. Mode of dispersal not known.

55. *Cassia occidentalis* L. Pod oblong, up to 13 x 1 cm., flat, not or tardily dehiscent; seeds compressed ovate-suborbicular, 4.5 x 5 x 4-4.5 mm. Weed; Aldabra, Assumption, Cosmoledo, Astove. Accidentally introduced by man.

56. *Delonix regia* (Hook.f.) Raf. Flamboyant. Pod up to 50 x 5 cm., woody, dehiscent, opening before the pod falls; seeds narrowly oblong, 2-2.2 x 0.6-0.8 cm., light brown with purple markings. Cultivated; Aldabra. Introduced by man as an ornamental tree;

drifting valves of pod seedless, seeds not sea dispersed (Gunn & Dennis, 1976).

57. *Tamarindus indica* L. Pod sausage-like, 6-14 x 2-3 cm., woody, indehiscent; seed ± rhombic to trapeziform, 11-17 x 10-12 mm. Believed cultivated; Aldabra. Fruit edible and dispersed by man.

LEGUMINOSAE — MIMOSOIDEAE

58. *Calliandra alternans* Benth. Pods linear, 15 x 0.8 cm., woody, tardily dehiscent; seed not seen. Native; Aldabra. Method of dispersal not known.

59. *Dichrostachys microcephala* Renv. Pod oblong, 2.5-3 x 0.5 cm., flattened, dehiscent. Seed ovoid, 3 x 2.5 cm., flattened. Native; Aldabra, Cosmoledo, Astove. Method of dispersal not known.

LEGUMINOSAE — PAPILIONOIDEAE

60. *Abrus precatorius* L. subsp. *africanus* Verdc. Pod oblong, somewhat swollen, 2-3.5 x 1.4-1.5 cm., dehiscent (Fig. 1, 9); seed ovoid, 5-7 x 4-5 mm., scarlet with a black area around the hilum, shiny, remaining attached to the edges of the opened valves for some time. Native; Aldabra, Assumption. Seeds not buoyant (Guppy, 1906, Muir, 1937); false aril makes seeds attractive to birds (Ridley, 1930).

61. *Canavalia rosea* (Sw.) DC. Pod linear-oblong, 10-17 x 2.5-3 cm., flattened, usually somewhat curved and with a double ridge on the sutural edge, dehiscent; seed ellipsoid, slightly compressed, 1.5-2 x 0.9-1.4 x 0.5-1.1 cm., brown with darker mottles, hilum 7-8 mm., long, brown. Native, strand; Aldabra, Assumption. Seeds buoyant and float unharmed for long periods (Guppy, 1906, 1917; Ridley, 1930; Muir, 1937; Gunn & Dennis, 1976). Viable seed found along Aldabra strand line.

62. *Clitoria ternatea* L. Butterfly Pea. Pod linear-oblong, 6-12.5 x 0.7-1.2 cm., flattened, dehiscent; seeds ellipsoid, oblong or oblong-reniform, 4.5-7 x 3-4 x 2-2.5 mm., pale brown to deep reddish-brown. Cultivated; Aldabra. Introduced by man as an ornamental.

63. *Crotalaria laburnoides* Klotzsch var. *laburnoides* Pod broadly oblong-ellipsoid to oblong-ovoid, 1.4-2.3 x 0.8-1.4 cm., inflated, dehiscent; seeds obliquely cordiform, ± 2.5 mm. long, orange brown. Native; Aldabra, Cosmoledo. Mode of dispersal not known; the dilation of the pod is not an adaptation for wind dispersal since pods dehisce and do not break off entire when ripe (Ridley, 1930).

64. *Erythrina variegata* L. Pod cylindrical, up to 30 x 3 cm., tardily dehiscent; seeds oblong, up to 2 x 1 cm., pinkish or purplish-red. Status uncertain, probably native, strand, possibly planted at Settlement; Aldabra. Seeds readily float, common in sea drift (Ridley, 1930; Muir, 1936, Gunn & Dennis, 1976); fruit eaten by pigeons (Ridley, 1930), also planted by man as an ornamental tree (Muir, 1937).

65. *Indigofera* sp. Pod linear oblong, 10 x 2 mm., densely silvery-grey, appressed pubescent, ? dehiscent. Seeds immature. Native; Aldabra. Seeds presumably dispersed by birds.

66. *Sophora tomentosa* L. subsp. *tomentosa* Pod torulose, up to 9 cm. long, slowly dehiscent (seeds emerge 1 by 1, Ridley, 1930); seeds subglobose, 5 mm. in diameter, glossy dark brown. Native, strand; Aldabra, Assumption. Seeds float, some for at least 104 days (Muir, 1937).

67. *Tephrosia pumila* (Lam.) Pers. var. *aldabrensis* (J.R. Drummond & Hemsley) Brummitt. Pod linear, 2.5 x 0.3 cm., twisting when dry, dehiscent; seeds cuboid or rhomboid, c. 2 x 1.2 mm., brown. Native, strand; Aldabra, Astove. Method of dispersal not known, possibly by birds.

68. *Teramnus labialis* (L.f.) Spreng. subsp. *arabicus* Verdc. Pod linear, 2.5-6 x 0.35 cm., dehiscent; seeds oblong or almost cylindrical, 2.3 x 1.2-2 x 1.2-1.5 mm., dark brown. Native; Aldabra. Method of dispersal not known, possibly by birds.

69. *Vigna marina* (Burm.) Merr. Pod linear-oblong, 3.5-6 x 0.8-0.9 cm., slightly curved, inflated, dehiscent; seeds oblong, slightly narrowed at one end, 6-7 x 5-6 x 4.5-6 mm., yellow brown or red brown. Native, strand; Aldabra, Cosmoledo. Seeds buoyant (Ridley, 1930).

70. *Vigna unguiculata* (L.) Walp. Cowpea. Pod linear, cylindrical, up to 10 x 1 cm., dehiscent; seeds oblong or reniform, 3.5-5 x 2-3.5 x 2.2 mm., white to dark red or black. Cultivated; Aldabra, Astove. Introduced by man.

BREXIACEAE

71. *Brexia madagascariensis* (Lam.) Ker-Gawl. Drupe ovoid to cylindrical, 4-10 x 1.9-3 cm., (Fig. 1, 17a) sometimes tapering, prominently 5-ribbed, walls woody, cavity with large air spaces (Fig. 1, 17b); seeds many, irregularly compressed-ellipsoid, 4.5-7.5 x 3-3.5 mm., keeled, minutely rugulose in ridges, brown or blackish. Native, strand; Aldabra. Fruits capable of floating in the sea for several months without the seeds losing their viability (Verdcourt, 1968).

RHIZOPHORACEAE

72. *Bruguiera gymnorrhiza* (L.) Lam. Berry viviparous, enclosed by the campanulate 10-14-lobed calyx, hypocotyl cigar-shaped, 25 x 1.5 cm., slightly curved, greenish brown. Native, lagoon; Aldabra, Cosmoledo, Astove. Sea dispersed (Muir, 1973; Gunn & Dennis, 1976). Seedlings float for 117 days (Ridley, 1930).

73. *Cassipourea thomassetii* (Hemsley) Alston Capsule conical, red, fleshy, dehiscent; seed with conspicuous yellow aril, *fide* Alston (1925) *pro* genus, fruit from Aldabra not known. Endemic; Aldabra. Method of dispersal not known, possibly by birds.

74. *Ceriops tagal* (Perr.) C.B. Robinson Berry viviparous, hypocotyl slender, up to 40 x 80 cm., olive brown, arising from a yellow or orange brown, obconical embryophore, c. 2 cm. long, with 5 calyx lobes c. 3 mm. long at the base. Native, lagoon; Aldabra, Assumption, Cosmoledo. Fruits sea dispersed (Muir, 1937; Gunn & Dennis, 1976).

75. *Rhizophora mucronata* Lam. Berry viviparous; hypocotyl slender, lanceolate up to 40 x 2 cm., embryophore green, c. 20 mm. long, projecting from a brown, pear-shaped growth (ovary) c. 3.5 x 2.5 cm., terminating in 4-5 reflexed calyx lobes. Native, lagoon; Aldabra, Cosmoledo, Astove. The ovary (pear-shaped growth) falls with the seedling, and becomes immediately detached; the seedling floats away, usually horizontally or steeply inclined, on reaching shallow water the sharp point of the seedling becomes embedded in the sand and is pushed to a vertical position with the rising tide and grows (Ridley, 1930; Gunn & Dennis, 1976).

COMBRETACEAE

76. *Lumnitzera racemosa* Willd. var. *racemosa* Pseudocarp compressed-ellipsoid, 10-12 x 3-5 mm., obliquely angled, ± woody, crowned by the persistent, 5-lobed, calyx. Native, lagoon; Aldabra, Astove. Buoyancy due to the accrescent receptacle, floats for months (Ridley, 1930).

77. *Terminalia boivinii* Tul. Drupe ovoid, 8-12 x 4.5-6 mm., woody. Aldabra, Assumption, Astove. Fruit eaten by pigeon and bulbul (Benson & Penny, 1971), also by tortoise (Hnatiuk, in press, a).

78. *Terminalia catappa* L. Drupe ovoid or ellipsoid, 3.5-7 x 2-6.5 cm., ± laterally compressed, woody with rigid wing c. 2 mm. wide and scarcely conspicuous (Fig. 1, 18). Believed native, littoral, possibly planted; Aldabra, Assumption, Cosmoledo, Astove. Fruit buoyant, also locally dispersed by bats, rats, land crabs (Ridley, 1930; Gunn & Dennis, 1976); viable fruits washed up along Aldabra strand line. Sea main vector, locally dispersed by bats (Pijl, 1957).

MYRTACEAE

79. *Eugenia elliptica* Lam. var. *levinervis* Fosberg Berry globose, c. 1 cm. in diameter, fleshy; seed 1, not seen. Endemic; Aldabra. Other species of the genus dispersed by birds, fruit-bats and for short distance by water (Ridley, 1930).

LYTHRACEAE

80. *Pemphis acidula* Forst. Capsule globose, enclosed by the persistent calyx, 5-8 x 3.5 mm., reddish brown, capsule splitting transversely near the apex when ripe; seeds cuneate, 3 x 2 mm., with the spongy testa drawn out into a wing, reddish-brown. Native, littoral; Aldabra, Assumption, Cosmoledo, Astove. Seeds float for months or carried by drift pumice (Guppy, 1906; Ridley, 1930; Muir, 1937); occasionally the capsule becomes attached by the broken peduncle to the feathers of boobies and frigate birds (Guppy, 1890; Ridley, 1930).

SONNERATACEAE

81. *Sonneratia alba* Sm. Multilocular berry, obconic-turbinate, 2-3 x 3-4 cm., green with persistent style base, free from calyx lobes at maturity; seeds cuneate, 2 x 2 x 0.7 cm. Native, lagoon; Aldabra, Cosmoledo. Berry softens and breaks up at sea, releasing the seeds (Ridley, 1930); sea main vector but berries eaten and locally dispersed by fruit bats (Pijl, 1957).

TURNERACEAE

82. *Turnera ulmifolia* L. Capsule globose-ovoid, 8 x 7 mm., 3-valved; seeds many, clavate, 2-3 x 0.7-1 mm., arillate, longitudinally ribbed, yellow-brown. Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man.

PASSIFLORACEAE

83. *Passiflora foetida* L. var. *hispida* (DC. ex Triana & Planch.) Gleason Granadilla Berry globose to subglobose, 2-3 cm. in diameter, yellow to orange; seeds many, ovate-cuneiform, 2.5 x 2.5 mm. Weed, sometimes cultivated; Assumption. Introduced by man; may be dispersed by bulbuls (Ridley, 1930).

84. *Passiflora suberosa* L. Berry globose, 1-1.5 cm. in diameter, blue-black; seeds many, flattened, slightly curved, 3-4 x 2 mm., apex acute. Cultivated; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man. Fruit eaten by bulbul. (Benson & Penny, 1971) and fody (Frith, 1976), occasionally by coucal.

CARICACEAE

85. *Carica papaya* L. Pawpaw. Berry orbicular, ovate-oblong or oblong, up to 30 cm. long, yellow; seeds many, ovoid, 7 x 4 mm. Cultivated; Aldabra. Introduced by man.

CUCURBITACEAE

86. *Cucumis anguria* L. Gherkin. Berry subglobose or shortly ellipsoid, 3-4.5 x 3.2-3.4 cm., dark and light green stripes becoming yellow; seeds elliptic, 6 x 3 mm., flattened. Cultivated; Astove. Introduced by man.

87. *Cucumis melo* L. Canteloupe. Berry ovoid to oblong-elliptic, 3.5-10 x 2-7.5 cm., green to orange; seeds elliptic, 5-8 x 2.5-4 x 1-1.5 mm., compressed. Native; Assumption, Cosmoledo (wild form), uncertain whether the plants on Assumption are the wild form or cultivated; mode of dispersal for wild form not known.

88. *Cucurbita moschata* (Buch. ex Lam.) Poir. Pumpkin. Berry globose, c. 30 cm. in diameter, buff, flesh yellow to dark orange; seeds ovate-acute, 20 x 12 mm., compressed, dingy white to dark brown, margin wavy, hyaline. Cultivated; Aldabra, Cosmoledo. Introduced by man.

89. *Lagenaria siceraria* (Molina) Standley Bottle Gourd. Berry subglobose to clavate, up to 13 cm. in diameter, green, hairy; seeds oblong, c. 17 x 7 x 3.2 mm., compressed, slightly tapered, slightly 2-horned on the shoulders at the broader end. Cultivated; Aldabra. Gourds float up to 347 days without affecting the germination of the seeds; seeds may remain viable for 6 years (Whitaker & Carter, 1961).

90. *Momordica charantia* L. Bitter Gourd. Berry ovoid to attenuate-ellipsoid, 3.5-11 x 2-4 cm., reddish orange, tuberculate, splitting into 3 valves exposing the seeds sheathed in a sticky red pulp; seeds oblong, 8-11 x 4.5-6 x 2.5-3.5 mm., black with crimson aril. Cultivated; Aldabra, Assumption. Colour of fruit and seeds attracts birds (Ridley, 1930); introduced by man.

91. *Peponium sublitorale* C. Jeffrey & J. S. Page Berry ellipsoid 5-5.5 x 2.5-4 cm., pubescent; seeds oval, 5-6 x 3-4.5 x 1.5-2 mm., (immature), compressed, marginate. Endemic, strand; Aldabra. Method of dispersal not known, possibly by sea or birds.

92. *Trichosanthes cucumerina* L. Snake Gourd. Berry linear-cylindrical, up to 2 m. long, green and white striped; seeds embedded in greenish-black pulp; slightly compressed ovoid, 9-10 x 4-5 mm. Cultivated; Aldabra. Fruit eaten by crows (Ridley, 1930); introduced by man.

AIZOACEAE

93. *Sesuvium portulacastrum* (L.) L. Capsule ovoid, 5 mm. in diameter, circumscissile; seeds reniform 1.6 x 1.5 mm., reddish-black. Native, lagoon; Aldabra, Cosmoledo, Astove. Seeds found in drift pumice and logs (Guppy, 1917; Ridley, 1930); vegetative parts float (Muir, 1937, Carlquist, 1974); vegetative part found in nests of boobies (Ridley, 1930); transported by rafting and by mud on bird's feet (Muir, 1937).

94. *Trianthema portulacastrum* L. Capsule ovoid-cylindrical, 4 x 2.5 mm., circumscissile, the operculum retaining 1-2 seeds, the rest falling free; seeds reniform, cochleate, 1.5 x 1.5 mm., reddish-black, faveolate. Native; Aldabra. Two seeds retained in the closed, buoyant operculum and sea dispersed (Henty & Pritchard, 1975); possibly distributed by mud on bird's feet; usually a weed, but not on Aldabra where it occurs on a small rocky islet in the lagoon.

95. *Mollugo nudicaulis* Lam. Capsule ovate, 3 x 2.5 mm.; 3-valved; seeds obliquely reniform, 0.7 x 0.5 mm., plump, estrophiolate. Weed; Assumption. Introduced by man.

96. *Mollugo oppositifolia* L. Capsule ovate, c. 2 mm. long; 3-valved; seeds ± reniform, 0.5 x 0.3 mm., tuberculate, with a distinct, long, filiform-appendaged strophiole. Native; Aldabra. Method of dispersal not known.

RUBIACEAE

97. *Canthium bibracteatum* (Bak.) Hiern Drupe globose, c. 10 mm. in diameter, fleshy, orange or orange-brown to black; pyrenes 2, ovoid-cylindrical, 6 x 2.5 mm., light reddish-brown to black. Native; Aldabra. Drupe presumably eaten and transported by birds.

98. *Guettarda speciosa* L. Drupe woody, globose, 3 cm. in diameter, brown; seed 1. Native, littoral; Aldabra, Cosmoledo, Astove. Seed buoyant, floats for at least 50 days (Guppy, 1890; Ridley, 1930); fruit eaten and locally dispersed by bats (Pijl, 1957); locally dispersed by tortoise (Hnatiuk, in press, a).

99. *Hedyotis corallicola* Fosberg Capsule globose to somewhat obovoid, up to 1.5 x 1-2 mm, crowned by erect calyx lobes, thin walled, dehiscent; seeds somewhat oblong, c. 0.4-0.5 mm. in diameter, bluntly angular, shallowly alveolate-reticulate, somewhat glossy, almost black. Endemic; Cosmoledo, Astove. Presumably bird dispersed.

100. *Hedyotis lancifolia* Schum. var. *brevipes* (Bremek.) Fosberg Capsule turbinate-globose, c. 2 mm. in diameter, crowned by persistent, erect calyx lobes, thin walled, loculicidally dehiscent; seeds somewhat oblong, angular, c. 0.3-0.4 mm. long,

dull brown, cellular-reticulate. ? Weed; Astove. Presumably accidentally introduced by man.

101. *Hedyotis prolifera* Fosberg Capsule turbinate or obovoid, 1-1.5 (-2) x 1-1.5(-2) mm., crowned by persistent calyx lobes; seed irregularly bean-shaped to angular-peltate, c. 0.2-0.3 mm. in diameter, dark brown to black, cellular reticulate. Endemic; Aldabra, Assumption. Seeds locally dispersed by tortoise (Hnatiuk, in press, a); viable seed obtained from blue pigeon regurgitate.

102. *Pavetta verdcourtiana* Fosberg Drupe globose, 5-6 mm. in diameter, black; pyrenes 1-4, arranged radially, concave surface dull brown, gently rugose, a deep pit on inner angle. Endemic; Aldabra, Assumption. Fruit eaten by blue pigeon.

103. *Polysphaeria multiflora* Hiern Drupe globose, c. 1 cm. in diameter, purple-black; pyrenes 2, hemispherical, 6 x 5 mm., mottled light reddish-brown, gelatinous. Native; Aldabra, Cosmoledo, Astove. Drupe eaten and seeds locally dispersed by birds; viable seeds obtained from bird regurgitates.

104. *Psychotria pervillei* Baker Drupe depressed globose, 4 mm. in diameter, pale blue-grey; pyrenes 2, hemispherical, 3 x 2 mm., dorsally ribbed. Native; Aldabra. Drupe presumably eaten and seed dispersed by birds.

105. *Tarenna supra-axillaris* (Hemsl.) Bremek. Drupe globose, 3 mm. in diameter, black; pyrenes 1 or 2, subglobose, 2.5-3 mm. in diameter, with deep, somewhat irregular cavity in one side, reddish-brown mottles. Endemic; Aldabra. Drupe presumably eaten and transported by birds.

106. *Tarenna trichantha* (Baker) Bremek. Drupe globose, 3-5 mm. in diameter, black; pyrenes 2-4, hemispherical, 2-3.5 mm. in diameter, a deep linear scar along one side. Native; Aldabra, Assumption, Cosmoledo, Astove. Drupe eaten by doves and blue pigeons; viable seed obtained from blue pigeon regurgitate.

107. *Triainolepis fryeri* (Hemsl.) Bremek. Drupe globose, 8.5 mm. in diameter, white to pink; pyrenes 1, narrowly oblong-ellipsoid, 2-2.4 x 0.9-1 x 0.5-0.6 mm. Endemic; Aldabra. Drupe eaten by doves (Benson & Penny, 1971), also by blue pigeon.

108. *Tricalysia sonderana* Hiern Drupe globose, 7 mm. in diameter, reddish-black; pyrenes 6-9(-12), trigonous, dorsally convex, 3 x 2 mm., light brown, cellular-alveolate. Native; Aldabra, Assumption. Drupe eaten by blue pigeon and bulbul, viable seed obtained from bulbul regurgitate.

COMPOSITAE

109. *Bidens pilosa* L. Cypsela cylindrical-oblong, c. 11 mm. long, with 3 apical, retrorsely barbed bristles. Weed; Astove. Cypsela adheres to clothing or fur of animals; accidentally introduced by man.

110. *Launaea intybacea* Jacq. Cypsela oblong, 3-4 mm. long, 4-ribbed, pappus setose, 6-8 mm. long (Fig. 1, 5). Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man; locally wind dispersed.

111. *Launaea sarmentosa* (Willd.) Alston Cypsela cylindrical-oblong, 3.5-5 mm. long, pappus setose, 6-10 mm., detachable. Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Dispersed by sea currents (Ridley, 1930); cypsela descends rapidly in still air, 2 m. in 6 seconds.

112. *Melanthera biflora* (L.) Wild. Cypsela triquetrous, oblong, 2.5-3 mm. long, pappus absent (Fig. 1, 4). Native, strand; Aldabra, Assumption. Sea dispersed (Ridley, 1930; Muir, 1937); cypsela floats for at least a month (Gunn & Dennis (1976)).

113. *Synedrella nodiflora* (L.) Gaertn. Cypsela of tubular florets spindle-shaped, 0.5 mm. long, with 2-3 apical hair-like bristles 3 mm. long; cypsela of ligulate florets oblong, 4 mm. long, flattened, margins winged, lacinate, reduced to a slender spur 2-3 mm. long. Weed; Aldabra. Dispersed by its adhesive cypsela; accidentally introduced by man.

114. *Tridax procumbens* L. Cypsela oblong or obovoid, 3 mm. long, pappus feathery, up to 5 mm. long, spreading. Weed; Aldabra. Originally introduced to Old World as an ornamental, now locally dispersed by its plumed cypsela (Ridley, 1930); accidentally introduced by man.

115. *Vernonia cinerea* (L.) Less. Cypsela oblong or ellipsoid, 1.5 mm. long, pappus one row, sparse, 3 mm. long, antrorsely ciliate, spreading. Weed; Aldabra, Assumption, Astove. Accidentally dispersed by man.

116. *Vernonia grandis* (DC.) H. Humb. Cypsela narrowly obovoid, 2-3 mm. long, ribbed and glandular, pappus one row of antrorsely ciliate or spinous bristles, 5-6 mm. long. Native; Aldabra, Assumption, Cosmoledo, Astove. Method of long distance dispersal not known, short distance by wind.

GOODENIACEAE

117. *Scaevola taccada* (Gaertn.) Roxb. Drupe ovoid or subglobose, c. 1.3 cm. in diameter, pithy, white or purplish; stone ellipsoid, 6 mm. in diameter, reticulate, yellowish-white, outer layer

aerogenous or corky. Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Exocarp soon shrinks and decays, mesocarp corky, buoyant, floats for at least 12 months (Guppy,1890, 1917; Ridley, 1930); also carried by drift pumice (Guppy, 1890; Ridley, 1930); drupe eaten by blue pigeon, turtle dove and bulbul (Benson & Penny, 1971); also eaten and locally dispersed by tortoise (Hnatiuk, in press, a). Germination improved with length of immersion in sea water (Hnatiuk, in press, b).

PLUMBAGINACEAE

118. *Plumbago aphylla* Boj. ex Boiss. Anthocarp 8 x 2 mm., the enveloping persistent calyx with numerous viscid glands. ? Native; Aldabra, Assumption, Cosmoledo, Astove. Adheres to passing birds, animals and man by means of the viscid hairs (Ridley, 1930).

SAPOTACEAE

119. *Sideroxylon inerme* L. subsp. *cryptophlebia* (Baker) Hemsley Berry globose, 6 mm. in diameter, black; seeds 1, depressed-globose, up to 4.5 mm. in diameter, the ridges obscure, yellow-brown. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Fruit eaten by blue pigeon (Benson & Penny, 1971). Berry and seed of subsp. *inerme* non-buoyant; fruit eaten by birds, animals and man (Muir, 1937).

OLEACEAE

120. *Jasminum elegans* Knobl. Drupe globose, 8-12 mm. in diameter, purplish-black; stone globose, 6 mm. in diameter. Native; Aldabra. Drupe presumably eaten and dispersed by birds.

SALVADORACEAE

121. *Azima tetracantha* Lam. Berry globose, 7.5-8 mm. in diameter, cream; seeds 2, discoid, 6 mm. in diameter, black. Native; Aldabra, Assumption, Cosmoledo, Astove. Presumably berry eaten and dispersed by birds; locally dispersed by tortoise. Seeds not buoyant (Muir, 1937).

122. *Salvadora angustifolia* Turrill var. *angustifolia* Drupe ovoid-pyriform, not known, (c. 6 mm. in diameter, pink in var. *australe*). Native; Aldabra, Cosmoledo. Presumably drupe eaten and dispersed by birds.

APOCYNACEAE

123. *Carissa edulis* L. (Sens. lat.) Berry, globose, ovoid or oblong-

ovoid, 5.5-16 x 5-16 mm, apex rounded or apiculate, purple or black; seeds 2-4, ovate, flattened, up to 7 x 4 mm., light brown (fruiting material from Aldabra not seen). Native; Aldabra. Presumably eaten and dispersed by birds.

124. *Catharanthus roseus* (L.) G. Don Fruit of 2, linear, terete follicles, 3 x 0.2 cm., ribbed, pubescent, with a double false septum; seeds cylindrical, 2 x 1 mm., dark brown, prominently rugose. Cultivated and now naturalised; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man.

125. *Pandaca mauritiana* (Poir.) Markgraf & Boiteau Twin, ellipsoid capsules, 4.5 x 2.5 cm.; seeds ovoid-cuneate, 8 x 5 mm., light brown. Native; Aldabra. Seeds presumably dispersed by birds.

ASCLEPIADACEAE

126. *Pentopetia androsaemifolia* Decne. Follicles narrowly fusiform, 12 x 0.5 cm.; seeds oblong, 10 x 2 mm., flattened, with detachable apical tuft of silky hairs, 3.5 mm. long. Native or possibly introduced as an ornamental; Assumption. Method of dispersal not known as pappus regarded not suitable for long distance wind dispersal.

127. *Pleurostelma cernuum* (Decne.) Bullock Follicle fusiform, 4-6 x 0.8 cm.; seeds ovate, 4 x 2 mm., with detachable apical tuft of silky hairs, 40 mm. long. Native; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known as pappus regarded as not suitable for long distance wind dispersal.

128. *Sarcostemma viminale* (L.) R. Br. Follicle linear of fusiform, up to 12 x 1 cm.; seeds ovate, 8 x 3 mm., flattened, with detachable apical tuft of silky hairs, 20 cm. long. Native; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known as pappus regarded as not suitable for long distance wind dispersal.

129. *Secamone fryeri* Hemsley Follicle fusiform, 4-8 x 1 cm.; seeds ovate, 5 x 1 mm., flattened, with a detachable apical tuft of silky hairs, 35 mm. long. Endemic; Aldabra, Assumption, Astove. Method of dispersal not known as pappus regarded not suitable for long distance wind dispersal.

130. *Tylophora indica* (Burm.f.) Merr. Follicle clavate-acuminate, 4-9 x 1 cm.; seed ovate, 6 x 3 mm., flattened, with detachable apical tuft of silky hairs, 25 mm. long. Native; Aldabra. Method of dispersal not known as pappus regarded not suitable for long distance wind dispersal.

BORAGINACEAE

131. *Cordia subcordata* Lam. Drupe subglobose, 2 x 3 cm., woody,

enclosed by persistent calyx (Fig. 1, 2). Native, strand; Aldabra, Cosmoledo, Astove. Drupe buoyant, floats for over a year (Guppy, 1917; Ridley, 1930); sea main vector but also eaten and locally dispersed by fruit bats (Pijl. 1957); viable seed found along Aldabra strand line.

132. *Ehretia corymbosa* Boj. Drupe globose, 6 mm. in diameter, fleshy, orange turning black; stone trigonous, dorsally convex, 4 x 4 mm. reticulate. Native; Aldabra. Drupe presumably eaten and dispersed by birds.

133. *Tournefortia argentea* L.f. Drupe globose, 6 mm. in diameter, containing 4, pithy, 1-seeded pyrenes (Fig. 1, 11). Native, littoral; Aldabra, Assumption, Cosmoledo, Astove. Drupe floats for over 40 days, exocarp shed after 2 weeks and endocarp splits into two (Guppy, 1890); also found in drift logs and pumice (Guppy, 1890).

CONVOLVULACEAE

134. *Evolvulus alsinoides* (L.) Capsule ovoid, 3-4 mm. in diameter, 3-4 valved; seeds trigonous, dorsally convex, 1.7 x 1 mm., brown to black. ? Native; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known, possibly introduced as a weed of cultivation.

135. *Ipomoea batatas* (L.) Lam. Sweet Potato. Capsule ovoid, 5-6 mm. in diameter, 4-valved; seeds triquetrous, ovoid, 4 x 3 mm. glabrous. Cultivated and now naturalised; Aldabra, Assumption, Astove. Introduced by man, locally dispersed, possibly by birds.

136. *Ipomoea macrantha* Roem. & Schultes Capsule globose, 1.5-2 cm. in diameter, 4-valved, enveloped by calyx; seeds triquetrous, ovoid, 1 x 0.8 cm., hairy. Native, littoral; Aldabra, Assumption, Cosmoledo, Astove. Seeds sea-dispersed, float for at least 10 weeks (Guppy, 1917; Gunn & Dennis, 1976); viable seeds found amongst beach drift on Aldabra.

137. *Ipomoea obscura* (L.) Ker-Gawl. var. *obscura* Capsule subglobose-mamilliform, c. 0.7 x 1 cm., beaked; seed triquetrous, ovoid, 3.5 x 3.5 mm., plump, dark brown, sericeous-tomentose. Native, littoral; Aldabra (recent introduction). Seeds presumably sea-dispersed.

138. *Ipomoea pes-caprae* (L.) R. Br. subsp. *brasiliensis* (L.) van Ooststr. Capsule globose, up to 2 cm. in diameter, 4-valved; seeds triquetrous, ovoid, 6-10 x 6-10 mm., densely brown-tomentose, dull yellow-brown when tomentum is worn off. Native, littoral; Aldabra, Assumption, Cosmoledo, Astove. Seeds buoyant for over 6 months, sea, dispersed (Guppy, 1917; Ridley, 1930; Muir, 1931; Gunn & Dennis, 1976); viable seed found amongst beach drift on Aldabra.

SOLANACEAE

139. *Capsicum annuum* L. Red Pepper Berry globose to turbinate, 3-10(-30) x 1.2-8 cm., red, orange or yellow; seeds reniform, flattened, 3-5 x 2.5-4.5 mm., pale yellow. Cultivated; Aldabra. Introduced by man.

140. *Capsicum frutescens* L. Bird Chillies. Berry turbinate, 0.7-2.5 x 0.3-1 cm., red or yellow; seeds reniform, 3-5 x 2.5-4.5 mm., flattened, pale yellow. Cultivated; Aldabra. Introduced by man.

141. *Datura metel* L. Capsule globose, 3 cm. in diameter, reddish-brown, dehiscing irregularly; seeds triangular in outline, 0.5 x 0.5 mm., with a white raphe. Weed; Aldabra, Assumption, Astove. Introduced by man either accidentally or as a medicinal herb.

142. *Nicotiana tabacum* L. Tobacco. Capsule ovoid, 1.5-2 x 1.2-1.5 cm., 2-valved; seeds oval to spherical, 0.5 x 0.3 mm., brown. Cultivated; Aldabra, Assumption. Introduced by man.

143. *Solanum indicum* L. var. *aldabrense* (C.H. Wright) Fosberg Berry globose, 1.2 cm. in diameter, orange-red; seed subdiscoid, 2 mm. in diameter, pale yellow-brown. Endemic; Aldabra, Cosmoledo, Astove. Berry eaten by blue pigeon, dove and bulbul (Benson & Penny, 1971), also by tortoise (Hnatiuk, in press, a).

144. *Solanum lycopersicum* L. Tomato. Berry globose or depressed-globose, 1.5-10 cm., in diameter, fleshy, red; seeds obovate, 3-5 x 2-4 mm., flattened, light brown, hairy. Cultivated; Aldabra, Assumption. Introduced by man.

145. *Solanum melongena* L. Aubergine. Berry ovoid, oblong or obovoid, 5-15 x 5-8 cm.; seeds subdiscoid, 3 mm. in diameter, light brown. Cultivated; Aldabra, Cosmoledo. Introduced by man.

146. *Solanum nigrum* L. var. *americanum* (Mill.) O. E. Schulz Berry globose, 5 mm. in diameter, black; seed obovate, 1.5 x 1 mm., pale yellow-brown. Native; Aldabra, Assumption, Cosmoledo, Astove. Berry eaten by birds (Ridley, 1930).

SCROPHULARIACEAE

147. *Bacopa monnieri* (L.) Wettst. Capsule globose, 5 mm. in diameter; seed cuniform, 0.5 x 0.3 mm. Native; Aldabra. Method of dispersal not known, possibly on birds' feet.

148. *Bryodes micrantha* Benth. Capsule globose, 1 mm. in diameter; seeds oval, 0.5 x 0.2 mm. Native; Aldabra. Method of dispersal not known; presumably on birds' feet.

149. *Striga asiatica* (L.) Kuntze Capsule ovoid, 6 x 2.5 mm., enclosed by persistent calyx, splitting into 2 valves; seeds ellipsoid, 0.3 x 0.2 mm. Weed; Aldabra. Accidentally introduced by man.

BIGNONIACEAE

150. *Tabebuia pallida* (Lindl.) Miers Capsule cylindrical, 15 x 1 cm., longitudinally dehiscent; seed oval-oblong with membranous wings at either end, 7 x 15 mm. Cultivated; Astove. Introduced by man.

ACANTHACEAE

151. *Asystasia gangetica* (L.) T. Anders. Capsule clavate, 5 x 2 mm., longitudinally dehiscent; seeds ± rhombic-discoid, c. 3 mm. in diameter, brown; tuberculate. Native; Aldabra, Assumption, Astove. Method of dispersal not known.

152. *Barleria decaisneana* Nees Capsule oblong-ovoid, 1.6 x 0.6 mm., enclosed by the persistent calyx, longitudinally dehiscent; seeds 4, angular-discoid; 3-4 mm. in diameter, reddish-black, hygroscopic, hairy. Weed; Astove. Accidentally introduced by man.

153. *Hypoestes aldabrensis* Baker Capsule clavate, 6-8 x 3 mm., longitudinally dehiscent; seeds 4, broadly obovate or oblong, 2 x 1.2 mm., flattened, beaked, prominently longitudinally ribbed. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known.

154. *Justicia procumbens* L. Capsule oblong-ovoid, 3 x 2 mm., longitudinally dehiscent; seeds 4, depressed ovoid, 0.7 mm. in diameter. Native; Aldabra, Assumption. Method of dispersal not known, probably by birds.

155. *Ruellia monanthos* (Nees) Bojer ex Thwaites Capsule clavate, 7-10 x 3 mm., longitudinally dehiscent; seeds (4-)6(-8), reniform-ovate, 2 x 1 mm., flattened, glabrous except for marginal hygroscopic hairs. Native; Aldabra, Assumption. Method of dispersal not known.

VERBENACEAE

156. *Avicennia marina* (Forssk.) Vierh. Capsule broadly ovate, 2.5 x 2.5 cm., compressed, greyish-green, pubescent, calyx persistent, 1-seeded, viviparous. Native, lagoon; Aldabra, Cosmoledo, Astove. Sea dispersed (Ridley, 1930, Muir; 1937).

157. *Clerodendrum glabrum* E. Meyer var. *minutiflorum* (Bak.) Fosberg Drupe globose, 6-7 mm. in diameter, woody, orange-yellow; pyrenes

1(-2), 1-seeded, turbinate, 7 x 4 mm. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Drupe presumably eaten and dispersed by birds, also eaten by tortoise.

158. *Congea griffithiana* Munir Drupe obovoid, 4 x 3 mm., enveloped by the persistent calyx. Cultivated; Assumption. Introduced by man as an ornamental.

159. *Lantana camara* L. var. *aculeata* (L.) Mold. Drupe globose, 5 mm. in diameter, purple-black; seeds sub-globose, 3 mm. in diameter, somewhat angular. Cultivated; Aldabra. Introduced by man as an ornamental; seeds bird dispersed (Holm *et al.*, 1977), locally dispersed by bulbul.

160. *Premna obtusifolia* R. Br. Drupe globose, 3 mm. in diameter, black; seed reniform, 1.5 x 1 mm. Native; Aldabra, Assumption, Cosmoledo, Astove. Drupe eaten by blue pigeon (Benson & Penny, 1971).

161. *Stachytarpheta jamaicensis* (L.) Vahl Capsule elliptic-oblong, 3.5 x 1.2 mm., enclosed in the dry calyx, finally splitting; nutlets 2, elliptic-oblong, 3 x 0.6 mm. Weed; Aldabra, Assumption, Astove. Accidentally introduced by man; locally dispersed by tortoise (Hnatiuk, in press, a).

162. *Stachytarpheta urticifolia* Sims Capsule elliptic-oblong, 3.5 x 1.5 mm., enclosed in the dry calyx, finally splitting; nutlets 2, 3 x 0.6 mm. Weed. Astove. Accidentally introduced by man.

DICRASTYLIDACEAE

163. *Nesogenes dupontii* Hemsley Drupe globose, 2 mm. in diameter, enveloped in persistent mauve calyx; seed 1, globose 1.5 mm. in diameter, yellow-brown. Endemic; Aldabra, Assumption, Astove. Method of dispersal not known; locally dispersed by tortoise (Hnatiuk, in press, a).

LABIATAE

164. *Leonotis nepetifolia* (L.) Ait.f. Nutlets 4, oblong-triquetrous, 4 x 2 mm., light brown with purple mottles. Weed; Aldabra, Assumption. Accidentally introduced by man or possibly introduced as an ornamental.

165. *Ocimum basilicum* L. Nutlets 4, oblong-ovoid, 2 x 1.5 mm., reddish-black. Cultivated; Aldabra. Introduced by man as a pot-herb.

166. *Ocimum canum* Sims Nutlets 4, oblong-ovoid, 1.2 x 0.6 mm., reddish-black. Cultivated; Astove. Introduced by man as a pot-herb.

167. *Ocimum gratissimum* L. Nutlets 4, globose, 1.5 mm. in diameter, mucilagenous when moistened. Cultivated; Aldabra. Introduced by man as a pot-herb.

168. *Ocimum sanctum* L. Nutlets 4, ovoid, 0.7 x 0.5 mm., reddish brown. Cultivated; Aldabra. Introduced by man as a pot-herb.

NYCTAGINACEAE

169. *Boerhavia africana* Lour. Anthocarp subcylindrical, 3.5 x 0.7 mm., weakly 10-ribbed, with long sticky glands near the apical portion. ? Introduced; Assumption. Anthocarp adheres to fur, feathers and clothing.

170. *Boerhavia crispifolia* Fosberg Anthocarp narrowly ellipsoid to subclavate, c. 2 x 0.7 mm., 5-ribbed, intervals glandular or not. Endemic; Aldabra. Anthocarps adhere to fur, feathers and clothing.

171. *Boerhavia repens* L. var. *maris-indici* Fosberg Anthocarp ellipsoid to ± clavate, 2.5-3 x 0.7 mm., 5-ribbed, glandular. Endemic; Aldabra, Cosmoledo, Astove. Anthocarps adhere to fur, feathers and clothing.

172. *Mirabilis jalapa* L. Belle de Nuit. Anthocarp obovoid or subglobose, 10 x 5 mm., 10-ribbed, dark brown to black. Cultivated; Aldabra. Introduced by man as an ornamental or for medicinal purposes.

173. *Pisonia aculeata* L. Anthocarp narrowly oblong, 10-12 x 5 mm., ribs 5, prominently glandular. Native; Aldabra. Anthocarps carried externally by birds (Ridley, 1930).

174. *Pisonia grandis* R. Br. Anthocarp clavate, 10 x 3 mm., strongly 5-ribbed, ridges spinulose with stalked, very sticky glands, (Fig. 2, 14). Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Anthocarps not buoyant, adhere to boobies and frigate birds (Guppy, 1890; Ridley, 1930; St. John, 1951).

AMARANTHACEAE

175. *Achyranthes aspera* L. var. *fruticosa* (Lam.) Boerl. Utricle fusiform, 4-5 mm. long, indehiscent, closely invested by pungent, perianth segments and bracteoles. Weed, possibly native; Aldabra, Assumption, Cosmoledo, Astove. Fruit readily adheres to clothing, hair or feathers (Ridley, 1930; Ivens, 1967).

176. *Achyranthes aspera* L. var. *velutina* (Hook. & Arn.) C.C. Townsend Utricle etc. similar to var. *fruticosa*. Native?; Aldabra, Cosmoledo, Astove.

177. *Alternanthera pungens* Kunth Utricle ovate, c. 1.5 x 1.5 mm., flattened, corky, indehiscent, bracteoles and perianth segments pungent, adherent to the utricle. Weed; Assumption. Accidentally introduced by man. Propagated by seed or runners (Haigh *et al.*, 1951), fruit adheres to skin of man and animals, soles of shoes, etc. (Ivens, 1967).

178. *Amaranthus dubius* Mart. ex Thell. Utricle broadly elliptic, c. 1 x 0.5 mm., dehiscence circumscissile; seed 1, ovate, 0.7 x 0.5 mm., flattened, dark glossy brown. Weed; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man.

179. *Amaranthus viridis* L. Utricle globose, c. 1 mm. in diameter, indehiscent; seed 1, discoid-ovate, c. 0.8 mm. in diameter, dark glossy brown. Weed; Aldabra, Assumption, Cosmoledo. Introduced by man.

180. *Deeringia polysperma* (Roxb.) Moq. Fruit baccate, depressed-globose, 4-5 mm. in diameter, white, fleshy; seeds many, ovate-reniform, c. 1 x 0.7 mm., compressed, glossy, black, the short funicle persistent. Native; Aldabra. Method of dispersal not known.

181. *Lagrezia oligomeroides* (C.H. Wright) Fosberg Utricle ovoid, c. 1 mm. long, compressed, indehiscent, somewhat adherent to the seed; seed 1, discoid, c. 0.8 mm. in diameter, black, shiny. Native; Aldabra, Assumption, Cosmoledo. Method of dispersal not known.

CHENOPODIACEAE

182. *Arthrocnemum pachystachyum* (Bunge ex Ung.-Sternb.) A. Chev. Utricle ovoid, c. 1.5 x 1 mm. dehiscent; seed 1, oblong, 1.5 x 1 mm., brown, with few long hairs near the apex, perianth cork-like when mature, adheres to utricle. Native, lagoon; Aldabra. Corky perianth enables utricle to float (Tölken, 1967).

LAURACEAE

183. *Cassytha filiformis* L. Drupe globose, 5 mm. in diameter, basally enveloped by a white, fleshy cupule (enlarged hypanthium). Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Fruit eaten and dispersed by birds (Ridley, 1930) also dispersed by currents (Guppy, 1917; Muir, 1937); drupe floats for at least a month (Gunn & Dennis, 1976).

HERNANDIACEAE

184. *Hernandia peltata* Meissn. Nut globose, 2-2.5 x 1.5-2 cm., woody, longitudinally 9-ribbed to almost terete, black, enveloped by an

inflated, hemispherical involucel 4 x 3 cm. Native, strand, or possibly cultivated; Astove. Nut sea dispersed, floats for at least 42 days (Guppy, 1890; Ridley, 1930; Muir, 1937; Gunn & Dennis, 1976), possibly introduced by man.

LORANTHACEAE

185. *Bakerella clavata* Desr. Berry ellipsoid, 18 x 8 mm., green; seed 1, ovoid, c. 3.5 x 2.5 mm. apex truncate with 5 blunt points, gelatinous. Native; Aldabra. Berry eaten by birds, seeds usually not eaten, adhere to beak, etc. (Ridley, 1930).

VISCACEAE

186. *Viscum triflorum* DC. Berry globose, 3.5 mm. in diameter, yellow pulp, viscid; seed 1, ovoid or ellipsoid, c. 2-2.5 x 1.5-2 mm., brown with a black, apical, peltate appendage. Native; Aldabra. Berries eaten by birds.

EUPHORBIACEAE

187. *Acalypha claoxyloides* Hutch. Regma ± globose, c. 3 mm. in diameter; seeds ovoid, 2 x 1 mm., reddish. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Seeds eaten by fody (Frith, 1976).

188. *Acalypha indica* L. Regma globose, 3-lobed, 1.5-2 mm. in diameter; seeds ovoid, 1 x 0.6 mm., grey-brown. Weed; Aldabra, Assumption, Cosmoledo, Astove. Accidentally introduced by man.

189. *Euphorbia hirta* L. Regma 3-lobed, 1 x 1 mm., explosively dehiscent; seeds ovoid, 0.5 x 0.2 mm., reddish-brown. Weed; Aldabra, Assumption, Cosmoledo, Astove. Accidentally introduced by man.

190. *Euphorbia indica* Lam. var. *pubescens* Pax Regma 3-lobed, 1 x 1 mm.; seeds ovoid, 1 x 0.5 mm. ? Native; Assumption. Method of dispersal not known.

191. *Euphorbia mertonii* Fosberg Regma ± cuboid, c. 1-1.2 x 1.2 mm.; seeds ovoid-quadrangular, 0.8 x 0.4 mm., apex rounded or obtuse, base subtruncate, shallowly and irregularly cross-rugose, dull salmon-pink. Endemic; Aldabra. Method of dispersal not known.

192. *Euphorbia prostrata* Ait. Regma 3-lobed, 1 x 1.2 mm.; seeds ovoid, 0.8 x 0.4 mm. ? Native; Aldabra, Assumption. Method of dispersal not known. Seed locally dispersed by tortoise (Hnatiuk, in press, a).

193. *Euphorbia pyrifolia* Lam. Regma 3-lobed, 4 x 8 mm.; seeds globose, 3 mm. in diameter; Aldabra, Assumption, Cosmoledo. Method of dispersal not known, possibly eaten by birds.

194. *Euphorbia stoddartii* Fosberg Regma bluntly turbinate, c. 1.2 x 1.2 mm.; seeds oblong, weakly quadrangular, c. 1 x 0.5 mm., apex bluntly acute, base truncate, weakly rugose, white to grey or pinkish. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known.

195. *Margaritaria anomala* (Baill.) Fosberg var. *cheloniphorba* (Hutch.) Fosberg Capsule globose, 5 mm. in diameter, irregularly dehiscent into segments; seeds trigonous, dorsally convex, 3 x 2 mm., yellow brown, hilum conspicuous. Endemic; Aldabra, Cosmoledo, Astove. Method of dispersal not known, possibly eaten by birds, locally dispersed by blue pigeons.

196. *Pedilanthus tithymaloides* (L.) Poit. Regma subglobose, 7 x 7 mm., flattened, red; mericarp ovoid, 4 mm. in diameter, grey; seed turbinate, 2 x 1.2, with flared base, reddish-brown. Cultivated; Aldabra, Assumption, Cosmoledo, Astove. Introduced by man as an ornamental.

197. *Phyllanthus amarus* Schum. Regma globose, 1.5 mm. in diameter; seed trigonous, dorsally convex, 1 x 0.5 mm. Weed; Aldabra, Assumption, Cosmoledo, Astove. Accidentally introduced by man.

198. *Phyllanthus casticum* Soy.-Willem. Regma globose, 4 mm. in diameter, reddish; seeds trigonous, dorsally convex, 1 x 0.5 mm., orange-brown. Native; Aldabra. Regma eaten by blue pigeon and bulbul (Benson & Penny, 1971).

199. *Phyllanthus maderaspatensis* L. var. *frazieri* Fosberg Regma depressed-globose, 3 mm. in diameter; seed trigonous; dorsally convex, 1 x 0.5 mm., brown; transversely rugose. Native; Aldabra, Astove. Method of dispersal not known, possibly by birds; locally dispersed by tortoises. (Hnatiuk, in press, a).

200. *Phyllanthus mckenzei* Fosberg Regma strongly depressed-globose, up to 1.5 x 0.6-0.8 mm; seeds trigonous, dorsally convex, 0.4-0.6 mm. long, inner angle acute, dull orange to salmon or dull chocolate-brown. Endemic; Aldabra, Cosmoledo. Method of dispersal not known.

201. *Ricinus communis* L. Castor Oil Plant. Regma globose, c. 1.5 cm. in diameter, spinose; seed ovoid, 8 x 6 mm., streaky brown and grey. Weed, possibly an escape from cultivation; Aldabra, Cosmoledo, Astove. Seeds reported still viable after floating 93 days; also eaten by turtle doves but doubtful if viable afterwards (Ridley, 1930); Muir, 1937, found only 4 out of 60 seeds viable and floating after 10 days.

URTICACEAE

202. *Laportea aestuans* (L.) Chew Achene ovoid, 1.2 x 1.2 mm., flattened, umbellate, readily disarticulating from the lower portion of the pedicel and inverted by the persistent lateral perianth segments. Native; Aldabra. Method of dispersal not known, possibly by birds.

203. *Obetia ficifolia* Gaud. Achene ovoid, c. 1 x 0.8 mm., compressed, included in the accrescent perianth. Native; Aldabra. Method of dispersal not known, possibly by birds, seeds locally dispersed by birds, viable seed obtained from bulbul regurgitate.

MORACEAE

204. *Ficus avi-avi* Bl. Fig globose, 8 mm. in diameter, yellow brown, pubescent. Native; Aldabra, Assumption, Cosmoledo, Astove. Fig eaten by blue pigeon, locally dispersed by tortoise.

205. *Ficus nautarum* Baker Fig globose, 1-2 cm. in diameter, yellow-brown. Native; Aldabra, Assumption. Figs eaten by blue pigeons (Benson & Penny, 1971).

206. *Ficus reflexa* Thunb. Fig globose, 4-7 mm. in diameter, reddish, glabrous. Native; Aldabra, Assumption, Cosmoledo, Astove. Figs presumably eaten by birds.

207. *Maillardia pendula* Fosberg Drupe ovoid, 12-15 x 7-8 mm., reddish-brown; seed 1, oblong-oval, 9 x 5 mm., strongly inrolled-grooved on one side. Endemic; Aldabra, possibly now extinct. Drupe eaten by blue pigeons (Benson & Penny, 1971).

CASUARINACEAE

208. *Casuarina litorea* L. Cone globose, 1.5-2 cm. in diameter (Fig. 1, 8a); fruits with terminal wing, oblong-oval, 7 x 2.5 mm. (Fig. 1, 8b). Native, strand, or possibly introduced; Aldabra, Assumption, Cosmoledo, Astove. Cones float 1-2 days (Guppy, 1890); seeds soon sink Guppy, (1906); disseminule float for at least a month (Gunn & Dennis,1976); seeds possibly rafted or even wind-blown for short distances (Sauer, 1967); seeds eaten by turtle dove, white-eye and fody (Benson & Penny, 1971); may have been introduced by man for shade but Ridley (1930) considers this unlikely. Fruit found to be viable after floating for more than 8 weeks.

ORCHIDACEAE

209. *Acampe rigida* (Buch.-Ham. ex J.R.Sm.) P.F. Hunt. Capsule fusiform, 4-5 x 1.5 cm., ribbed, longitudinal dehiscence; seeds minute.

Native; Aldabra. Seed believed to be wind dispersed.

210. *Angraecum eburneum* Bory Capsule fusiform, 4.5-5 x 1.5 cm., longitudinal dehiscence; seeds minute. Native; Aldabra. Seed believed to be wind dispersed.

MUSACEAE

211. *Musa* sp. banana or plantain. No specimens seen, no longer extant. Cultivated; Assumption. Suckers or corms planted by man.

DIOSCOREACEAE

212. *Dioscorea bemarivensis* Jumelle Regma 3-winged, each wing suborbicular, 1-1.5 cm. broad, and containing 1-2 seeds; seeds oblong, 4 x 2 mm., with brown encircling wing, the whole disseminule being up to 1 cm. in diameter. Native; Aldabra, Assumption, Astove. Regma not blown by the wind but seeds wind dispersed (Ridley, 1930).

LILIACEAE

213. *Agave sisalana* Perr. Sisal. Capsules and seeds rarely formed due to formation of abscisson layer, bulbils formed after flowers absciss (Purseglove, 1972); seeds rounded- triangular, 10 x 8 mm., thin, flat, papery. Cultivated and naturalised; Aldabra, Cosmoledo, Astove.

214. *Asparagus umbellulatus* Bresler Berry globose, 5-7 mm. in diameter, pale orange to brown; seeds 2-4, trigonous, dorsally convex, 2.5 x 2.5 mm., black. Endemic; Aldabra, Cosmoledo, Astove. Berries of other species eaten by birds (Ridley, 1930). Fruit eaten, viable seed obtained from bulbul regurgitate.

215. *Dracaena reflexa* Lam. var. *angustifolia* Baker Berry globose, 10 mm. in diameter, brick red; seeds 2, subglobose, 4 mm. in diameter, orange-brown. Native; Aldabra, Assumption ? Cosmoledo, ? Astove. Berries of other species eaten by birds (Ridley, 1930).

216. *Lomatophyllum aldabrense* Marais Berry globose-oblong, 10 mm. in diameter, purplish-red; seeds strongly triquetrous, c. 3 x 3 mm., reddish-black. Endemic; Aldabra, Assumption, Cosmoledo, Astove. Berry eaten by blue pigeon, (Benson & Penny, 1971); viable seed obtained from bulbul regurgitate.

COMMELINACEAE

217. *Commelina benghalensis* L. Capsule oblong, 4-5 x 3 mm., the

2 dehiscing valves 2-seeded; seed oblong, 1.5-2.5 x 1.5-2 mm., greyish-brown, rugose. Weed; Assumption. Broken pieces of stem readily root; underground stem with reduced leaves and cleistogamous flowers, (Henderson & Anderson, 1966; Ivens, 1967; Holm *et al.*, 1977). Accidentally introduced by man.

PALMAE

218. *Cocos nucifera* L. Coconut Palm. Drupe elliptic or ovoid, 10-40 x 10-15 cm., 3-sided with tough endocarp, fibrous mesocarp and hard 'nut'. Native, strand, or possibly cultivated; Aldabra, Cosmoledo, Astove. Ocean-borne nuts capable of germination (Hill, 1929; Sauer, 1967; Dennis & Gunn, 1976), even after periods of up to 110 days at sea (conservative estimate of distance travelled 3,000 miles), visible growth very slow, over 1 year before shoot appears (Edmondson, 1941).

219. *Lodoicea maldivica* (Gmel.) Pers. Coco de Mer, Drupe ovoid, flattened, 40-50 cm. long, covered by thin, fibrous husk, nut 2(-4)-lobed. Cultivated; Aldabra. Introduced by man but no longer extant; no specimen seen. Nuts sea dispersed but apparently sterile (Bailey, 1942); nuts sink in water, specific gravity 1.2 (Corner, 1966; Dennis & Gunn, 1976).

220. *Phoenix dactylifera* L. Date Palm. Drupe cylindrical, 2.5-7.5 x 2.5 cm., seed cylindrical, up to 2.5 x 0.8 cm., grooved. Cultivated; Aldabra. The solitary specimen at Settlement is presumed to have been planted, and is too young to have provided a source of seed for the second specimen near Bras Takamaka to have been naturalized; it too must have been planted, probably accidentally by man.

PANDANACEAE

221. *Pandanus aldabraensis* St. John Aggregate fruit (syncarps) globose, 7-8 cm. in diameter; phalanges (syncarps) rhomboidal, 3.2-3.4 x 1.8-2.4 x 1.5-2.1 cm., apex pyramidal, 5-6 angled, stigmas 1-3; seed broadly ellipsoid 6 mm. long. Endemic; strand; fruit eaten and seeds locally dispersed by tortoise.

222. *Pandanus tectorius* Park. Aggregate fruit (syncarps) ellipsoid, 15-24 x 12-19 cm.; phalanges fusiform, 4-7 x 3.8-7.3 x 3.7-5.1 cm., apex ± truncate, stigmas 9-17; seeds broadly ellipsoid, 9-15 mm. long. Endemic, strand; Aldabra. Phalanges float, sea dispersed (Ridley, 1930; Muir, 1937). Fruit eaten and seeds locally dispersed by tortoise.

NAJADACEAE

223. *Najas graminea* Del. Nutlet cylindric-ellipsoid, 1.7-2 x 0.5 mm.,

indehiscent, beaked, decaying or rupturing to release the seed; seed 1, ovoid 1.6-2 x 0.6 mm., areolate. Native, aquatic; Aldabra. Seed dispersed by birds (Ridley, 1930).

CYPERACEAE

224. *Bulbostylis basalis* Fosberg Achene obovoid, 1-1.2 mm. long, trigonous, apex rounded, base substipiform, brown, rugose. Endemic; Aldabra. Presumably achenes eaten and dispersed by birds; locally dispersed by tortoise (Hnatiuk, in press, a).

225. *Bulbostylis hirta* (Thunb.) Svenson Achene broadly ovoid, c. 0.5 x 0.5 mm., trigonous, angles blunt, faces transversely rugose, dirty white or straw-coloured. Native; Assumption. Achenes probably carried in mud adhering to the feet of migrant birds.

226. *Cyperus aromaticus* (Ridley) Mattf. & Kük. var. *elatus* (Steud.) Kük. Achene obliquely ovoid or oblong, 1.2 mm. long, somewhat compressed, glossy dark brown with white isodiametric cellular reticulation. Native; Aldabra. Presumably achenes eaten and dispersed by birds.

227. *Cyperus bigibbosus* Fosberg Achene oblong-elliptic, 1.4-1.8 mm. long, strongly compressed, biconvex, dark brown. Endemic; Aldabra. Presumably achenes eaten and dispersed by birds.

228. *Cyperus bulbosus* Vahl Achene obovate, 1-1.2 mm. long, trigonous, grey. Adventive; Assumption, associated with rail tracks in the guano works.

229. *Cyperus conglomeratus* Rottb. Achene slightly obovoid to ovoid, 1 x 1.5 mm., rounded at base and apex. Native; Aldabra. Presumably achenes eaten and dispersed by birds.

230. *Cyperus dubius* Rottb. Achene obovoid or ovoid, 1 x 0.5 mm., strongly trigonous, base and apex subtruncate, brown. Native; Aldabra, Assumption. Presumably achenes eaten and dispersed by birds.

231. *Cyperus ligularis* L. Achene obovoid, 1.5 x 0.8 mm., strongly trigonous, dark blood-red to brownish. Native; Aldabra, Assumption, Cosmoledo, Astove. Presumably achenes eaten and dispersed by birds; locally dispersed by tortoise (Hnatiuk, in press,a).

232. *Cyperus niveus* Retz. var. *leucocephalus* (Kunth) Fosberg Achene oblong-obovoid, 1.2 x 1 mm., strongly trigonous, angles black, sides grey. Native; Aldabra. Achenes eaten by fody (Frith, 1976).

233. *Cyperus pumilus* L. Achene ovoid, 0.5 x 0.3-0.4 mm., apex subtruncate to slightly retuse, dull brown to grey. Native; Aldabra. Presumably achenes eaten and dispersed by birds; locally dispersed by tortoise (Hnatiuk, in press, a).

234. *Fimbristylis cymosa* R. Br. Achene obovoid, 0.5 x 0.4 mm., somewhat trigonous or flattened, blackish or dark brown, tuberculate or smooth. Native; Aldabra, Assumption, Cosmoledo, Astove. Presumably achenes eaten and dispersed by birds.

235. *Fimbristylis ferruginea* (L.) Vahl Achene broadly obovoid to subglobose, 1 x 0.8 mm., white to dull yellow or reddish-tan. Native; Aldabra. Presumably achenes eaten and dispersed by birds; locally dispersed by tortoise. (Hnatiuk, in press, a).

GRAMINEAE

236. *Bambusa vulgaris* Schrad. ex Wendl. Bamboo. Caryopsis not seen. Cultivated; Aldabra. Propagated by clonal material, seldom flowers.

237. *Cenchrus echinatus* L. Spikelets 2-6, 4.5-6 mm. long, enclosed by a retrorsely scabrid involucre of bristles. Weed; Astove. Burrs attach themselves to clothing and coats of animals (Henty & Pritchard, 1975; Holm *et al.*, 1977).

238. *Cymbopogon citratus* (DC.) Stapf Citronella Grass. Spikelets pairs oblong-lanceolate, 3.5-5.5 x 1 mm., awnless. Cultivated; Aldabra. Rarely found in flower because harvesting inhibits flowering (Bor, 1960). Propagated by clonal material.

239. *Dactyloctenium ctenoides* (Steud.) Bosser Floret narrowly ovate, 2.8-3.4 mm. long; lemma cuspidate with scabrid keel; caryopsis broadly ovate, 0.7-0.8 mm. long. Native, strand; Aldabra, Assumption, Cosmoledo. Locally dispersed by tortoise (Hnatiuk, in press, a).

240. *Dactyloctenium pilosum* Stapf Floret narrowly ovate, 2.3-3 mm. long, lemma acute, with scabrid keel; caryopsis elliptic, 0.8 x 0.6 mm., laterally compressed. Native, littoral; Aldabra, Assumption. Method of dispersal not known; locally dispersed by tortoise (Hnatiuk, in press, a).

241. *Daknopholis boivinii* (Camus) W.D. Clayton Floret ± ovate, 1.5-2.5 mm. long, lemma bidentate and tipped by a slender straight awn 3-12 mm. long. Native, strand. Aldabra, Cosmoledo, Astove. Method of dispersal not known.

242. *Digitaria horizontalis* Willd. Spikelet narrowly lanceolate, 2.5-3 mm. long. Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man, or possibly by birds since spikelets eaten by fody (Frith, 1976).

243. *Digitaria setigera* Roth Spikelet lanceolate to elliptic-lanceolate, 2-3 mm. long. Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man, or possibly by birds since spikelets eaten by fody (Frith, 1976).

244. *Eleusine indica* (L.) Gaertn. subsp. *indica* Floret broadly lanceolate, 2.4-3.6 mm. long, lemma keel scabrid, grain elliptic, 1-1.3 mm. long, enclosed by lemma and palea. Weed; Aldabra, Cosmoledo. Accidentally introduced by man; no evidence for bird or sea transport (Ridley, 1930), although transported internally or externally by animals, also wind dispersed (Holm *et al.*, 1977).

245. *Enteropogon seychellensis* (Baker) Dur. & Schinz Spikelets 3-flowered, 5-7 mm. long, lower lemma bidentate with awn 10-20 mm. long. Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Method of dispersal not known.

246. *Eragrostis decumbens* Renv. Caryopsis ovate or elliptic, 0.5 mm. long. Endemic; Aldabra. Locally dispersed by tortoise (Hnatiuk, in press, a).

247. *Eragrostis subaequiglumis* Renv. Caryopsis elliptic, 0.5 mm. long. Native; Aldabra, Assumption, Cosmoledo, Astove. Locally dispersed by tortoise (Hnatiuk, in press, a).

248. *Eriochloa meyeriana* (Nees) Pilger Spikelet elliptic, 2.3-3.5 mm. long, acute. Native; Aldabra, Assumption. Method of dispersal not known.

249. *Eriochloa subulifera* Stapf Spikelet ovate-lanceolate or oblong, 2-2.5 mm. long, awn subulate, 1 mm. long. Native; Assumption, Astove. Method of dispersal not known.

250. *Ischaemum rugosum* Salisb. Spikelet pairs oblong-ovate, 4-7 mm. long, falling entire at maturity, awn geniculate, c. 20 mm. long. Native; Aldabra. Method of dispersal not known.

251. *Lepturus repens* (G. Forster) R. Br. Spikelet 6-14 mm. long, sessile, solitary, embedded in the hollow on the opposite sides of the jointed axis of a solitary spike, the axis breaking up at the joints at maturity, (Hubbard & Vaughan, 1940). Native, strand; Aldabra, Cosmoledo, Astove. Sea dispersal (Ridley, 1930; Bor, 1960); spikelets eaten by fody (Frith, 1976); locally dispersed by tortoise (Hnatiuk, in press, a).

252. *Panicum aldabrense* Renv. Spikelets ovoid, 1-1.3 mm. long. Endemic; Aldabra. Method of dispersal not known, possibly eaten by birds.

253. *Panicum assumptionis* Stapf Spikelets ovoid or obovoid-elliptic, 1-1.3 mm. long. Endemic; Assumption. Method of dispersal not known, possibly eaten by birds.

254. *Panicum maximum* Jacq. Spikelets oblong, 3-4 mm. long, plump, slightly acute. ? Weed; Aldabra, Cosmoledo, Astove. Accidentally introduced by man or possibly cultivated for fodder; propagated by seed or by division of the rootstock (Hubbard & Vaughan, 1940).

255. *Panicum voeltzkowii* Mez Spikelet ovoid, 1.5-1.75 mm. long. Native; Cosmoledo, Astove. Method of dispersal not known, possibly by birds.

256. *Paspalum vaginatum* Swartz Spikelets oblong-ovate to ovate-elliptic, 3-4.5 mm. long, acute. Native, strand; Aldabra, Cosmoledo. Dispersed by currents, floating logs and pumice and adhering to birds' feet (Ridley, 1930; Muir, 1937; Bor, 1960).

257. *Pennisetum polystachion* (L.) Schultes Spikelet solitary, ovate-oblong, 2-3 mm. long, enclosed by an involucre of ciliate bristles, 5-15 mm. long; the fertile upper spikelet can be shed in transit. Weed; Aldabra, Assumption, Astove. Accidentally introduced by man.

258. *Sclerodactylon macrostachyum* (Benth.) A. Camus Florets ovate, 3 mm. long. Native, strand; Aldabra, Assumption. Florets sea dispersed (Ridley, 1930); locally dispersed by tortoise (Hnatiuk, in press, a).

259. *Sporobolus aldabrensis* Renv. Seed tetragonal, 0.7-0.9 mm. long. Endemic; Aldabra. Naked seed exuded from mucilaginous pericarp when spikelet moistened, possibly aids adhesion to feet and feathers of birds.

260. *Sporobolus testudinum* Renv. Seed elliptic, truncate, 0.5-0.7 mm. long. Endemic; Aldabra. Naked seed exuded from mucilaginous pericarp when spikelet moistened, possibly aids adhesion to feet and feathers of birds. Locally dispersed by tortoise (Hnatiuk, in press, a).

261. *Sporobolus virginicus* (L.) Kunth Floret narrowly ovate-elliptic, 1.7-2.5 mm. long. Native, strand; Aldabra, Assumption, Cosmoledo, Astove. Floret and rhizome sea dispersed, less likely to be carried by birds externally (Ridley, 1930; Bor, 1960). Fragments sea dispersed (Muir, 1937). Locally dispersed by tortoise (Hnatiuk, in press, a).

262. *Stenotaphrum clavigerum* Stapf False spikes of 5(-6); spikelets 2 mm. long, embedded in corky clavate rachis which disarticulates at maturity, the caryopsis retained within the spikelet. Endemic, strand; Aldabra, Assumption. Caryopsis does not imbibe water, but too heavy to float; rachis segments buoyant at first, being waterlogged after 5-7 days (Sauer, 1972).

263. *Stenotaphrum micranthum* (Desv.) Hubbard False spikes of 1-6; spikelets oblong to oblong-lanceolate, 2.5-3.5 mm. long, embedded in corky rachis which disarticulates at maturity. Native, strand,

Cosmoledo, Astove. Dispersal as for *S. clavigerum*.

264\. *Zea mays* L. Maize. Caryopsis subglobose, obovate or cuniform, c. 6 x 3 mm., yellow. Cultivated; Aldabra, Cosmoledo. Introduced by man.

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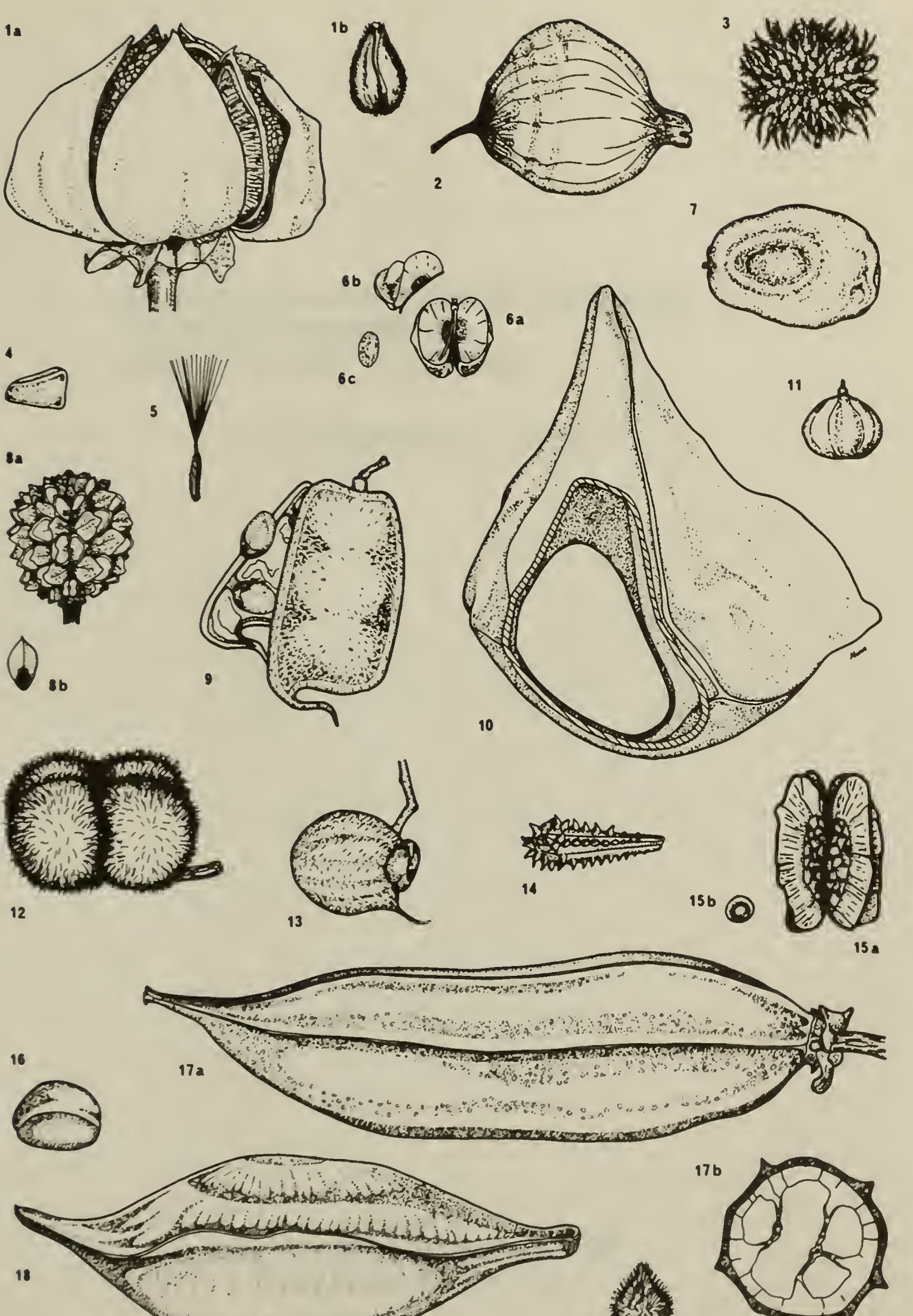
Figure 1. 1. *Thespesia populneoides*: a, capsule; b, seed. 2. *Cordia subcordata*; drupe. 3. *Triumfetta procumbens*: drupe. 4. *Melanthera biflora*: cypsela. 5. *Launaea intybacea*: cypsela. 6. *Gouania scandens*: a, schizocarp; b, mericarp; c, seed. 7. *Caesalpinia bonduc*: seed. 8. *Casuarina equisetifolia*: a, cone; b, fruit. 9. *Abrus precatorius*: pod. 10. *Xylocarpus moluccensis*: capsule with side cut away to expose seed. 11. *Tournefortia argentea*: drupe. 12. *Grewia salicifolia*: drupe. 13. *Apodytes dimidiata*: drupe. 14. *Pisonia grandis*: anthocarp. 15. *Dodonaea viscosa*: a, double samara; b, seed. 16. *Colubrina asiatica*: seed. 17. *Brexia madagascariensis*: a, drupe; b, cross-section of drupe to show air cavities. 18. *Terminalia catappa*: drupe. 19. *Suriana maritima*: nucule.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ATOLL RESEARCH BULLETIN

NO. 230

RECHERCHES SUR LA GÉOMORPHOLOGIE DE L'ATOLL FARQUHAR (ARCHIPEL DES SEYCHELLES)

par R. Battistini et C. Jouannic

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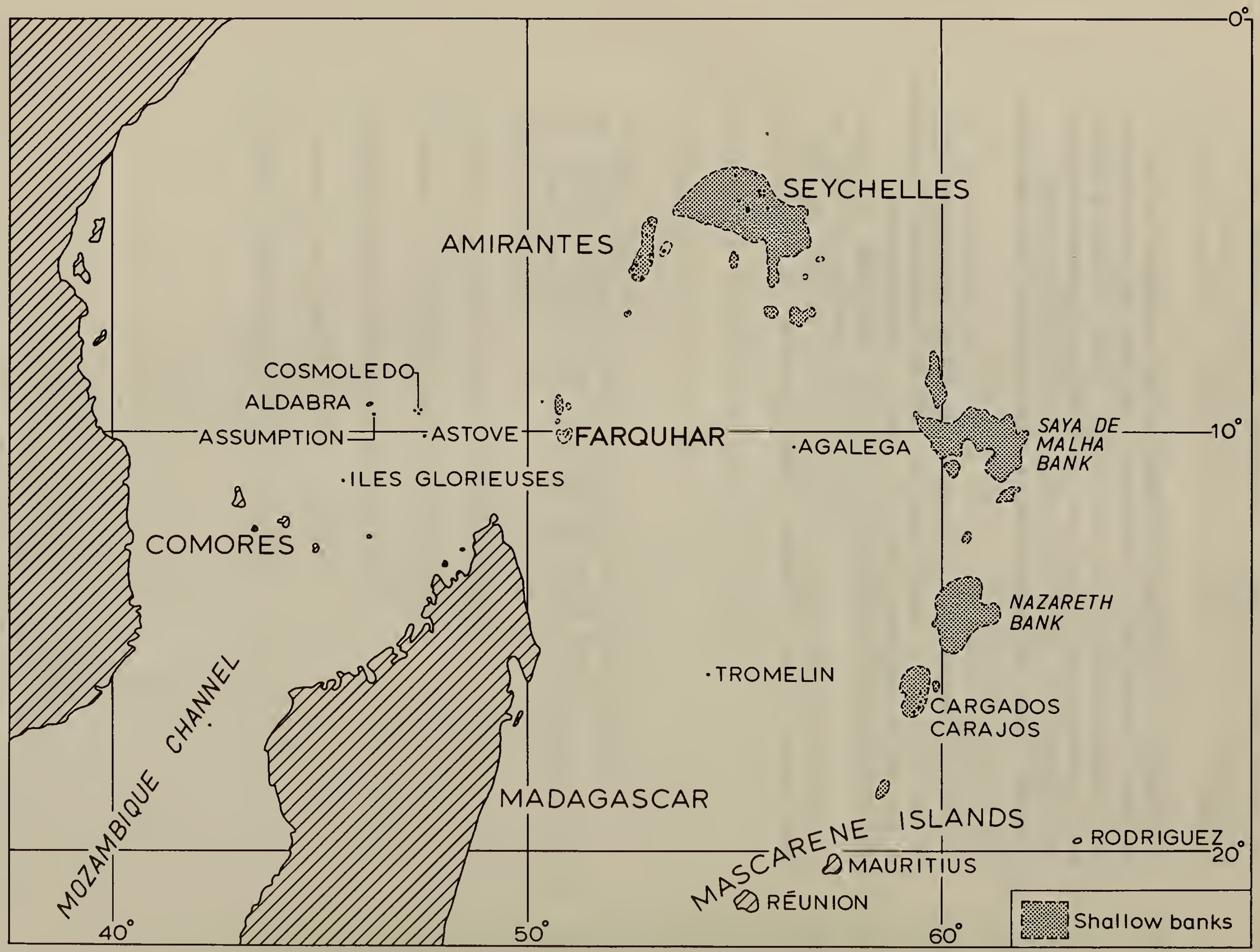

Fig. 1. Croquis général de localisation

RECHERCHES SUR LA GÉOMORPHOLOGIE DE L'ATOLL FARQUHAR (ARCHIPEL DES SEYCHELLES)

par R. Battistini[1] et C. Jouannic[2]

Découvert par João de Nova en 1504, portant d'abord ce nom, puis rebaptisé en 1824 du nom d'un Gouverneur de l'Ile Maurice, Sir R. Farquhar, l'atoll Farquhar est situé dans la partie méridionale de l'archipel des Seychelles, à 250 kilomètres au nord-est de Madagascar, et à 1150 kilomètres de la côte africaine, par 10°11' S et 51°07'E. Les îles les plus proches sont Saint-Pierre et Providence, au nord, qui font partie du même groupe, et à l'ouest les îles du groupe d'Aldabra, entre 200 et 300 kilomètres, comprenant Astove à environ 200 kilomètres, ainsi que Cosmoledo, Assumption, et Aldabra. L'atoll, de forme grossièrement triangulaire, mesure 20 kilomètres du nord-est au sud-ouest, et près de 25 kilomètres si l'on tient compte de ses prolongements au sud de la couronne enserrant le grand lagon. Il y a une seule passe, au nord-ouest. La couronne récifale (atoll rim) porte deux grandes îles à l'est au nord-est, l'île du Nord et l'île du Sud, ainsi que plus au sud la petite île Goëlette. Au nord-ouest il existe aussi plusieurs îlots, l'île Lapin, l'île du Milieu et l'île des Déposés.

La première carte de Farquhar fut celle dressée par M. Margaro en 1776. La carte 718 de l'Amirauté publiée en 1878 reprend, avec les additions faites par Owen en 1824, la carte de Margaro. La carte marine actuellement utilisée, très rudimentaire, résulte d'une révision, faite par Wharton en 1878, puis par White, en 1879, de la carte 718.

L'atoll a fort peu été visité par les scientifiques : une première fois en 1822 par Moresby, puis durant trois jours en 1905 par Gardiner et Fletcher, spécialement pour l'étude des insectes, et en 1937 par

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Vesey-Fitzgerald, pour l'étude des oiseaux. En 1960 eut lieu la visite de Baker, géologue, et Piggott, agronome, suivie en 1967 par celle de Parker, Wood et Gwynne chargés de collecter des oiseaux et des plantes pour le National Museum de Nairobi. En septembre 1968 Farquhar est visité, pour la dernière fois avant notre venue, par une expédition de la Royal Society comprenant Westoll, Poore, et Stoddart. C'est à ce dernier que nous devons la première étude géomorphologique de l'atoll, publiée dans le N°136 de l'*Atoll Research Bulletin* d'août 1970, et qui inclut un croquis morphologique général établi grâce à l'excellente couverture photographique aérienne datant de 1960, dont nous avons nous-même bénéficié.

Organisée en 1973 en accord avec les chercheurs de la Royal Society et avec leur chef le docteur Stoddart, la mission, dont il est fait ici le compte-rendu géomorphologique et sédimentologique, comprenait R. Battistini, géomorphologue, professeur à l'Université de Madagascar, et trois chercheurs de l'ORSTOM, C. Jouannic, géologue et sédimentologue marin, P. Morat, botaniste, et D. Van Waerebeke, entomologiste. Arrivés à Farquhar le 20 mai, la mission est demeurée jusqu'au 23 mai au soir. Le navire utilisé a été le *Vauban*, ancien chalutier transformé de 25 mètres, rattaché au centre ORSTOM de Nosy-Bé à Madagascar. Au cours de la même mission furent visitées Aldabra, le 18 mai, ainsi que Providence le 24 mai. Pour circuler dans le lagon les chercheurs ont disposé du hors-bord pneumatique de type Bombard du *Vauban* ; le *Vauban* lui-même est resté durant toute la mission au mouillage à l'extérieur de la passe.

DESCRIPTION GENERALE DE L'ATOLL

Les grands traits de la morphologie de l'atoll Farquhar ont déjà été décrits par D.R. Stoddart (D.R. Stoddart et M.E.D. Poore 1970).

A. Climatologie

On ne possède pas de données chiffrées relatives à la pluviosité. M.E.D. Poore (1970) tenant compte de ce que Farquhar est plus humide estime la pluviosité moyenne annuelle à environ 1200 millimètres.

L'atoll possède une façade au vent (côté sud et sud-est), exposée à l'alizé du sud-est et aux grandes houles océaniques formées dans le lit de l'alizé. Cela ne signifie pas qu'il ne soit pas battu sur ses autres faces, par la grande houle d'alizé qui le contourne, d'une part, mais aussi par des houles océaniques d'autres directions, en particulier en saison chaude lorsque la zone de convergence intertropicale est au sud, pendant la période de la mousson du nord-ouest. Par alizé fort, il se forme dans le lagon, du fait de sa grande taille (17 kilomètres de longueur et 7,5 kilomètres de plus grande largeur), d'assez fortes vagues capables de jouer comme nous le verrons un rôle morphologique notable.

L'atoll Farquhar est placé sur la route des cyclones, qui, en saison chande (novembre à avril) l'abordent en venant de l'est. Les plus grands cyclones notés dans les annales furent ceux de 1893, 1926, 1950 et 1954.

B. Les grandes unités morphologiques et la dissymétrie de l'atoll (fig. 2).

La couronne du grand lagon peut se diviser en trois parties en fonction de la forme générale triangulaire de l'atoll :

1. La partie orientale, au vent (voir les figures n°4,5 et 10)

C'est elle qui porte les grandes îles, l'Ile du Nord, qui s'allonge sur 8,5 kilométres depuis North Point jusqu'à la passe des Manaha, avec une largeur comprise entre 200 m et 1 km ; l'Ile du Sud, longue de 5,7 km, et large de 600 à 800 mètres ; l'Ile Goëlette, longue d'environ 600 m; enfin, entre les deux îles du Nord et du Sud, les trois petites îles Manaha. Toutes ces îles sont des accumulations très récentes de sable et de graviers, parfois de blocaille corallienne, reposant en certains endroits sur un socle induré constitué par les même matériaux et apparaissant ici et là sur l'estran sous la forme d'affleurements rocheux plus ou moins lapiazés. Ces îles sont précédées du côté externe par une plature corallienne large de 500 à 700 mètres, sur le bord de laquelle viennent briser les grands déferlements : cette plature, à structure rainurée caractéristique, ne porte pas de véritable levée détritique externe de blocs, mais seulement des ébauches, fait noté déjà par Gardiner (1936 pp. 432-433). Du côté du lagon il existe un vaste estran sableux, se terminant de manière brutale par un tombant lui aussi sableux sur des fonds de 5 à 10 mètres.

2. La partie nord-ouest, sous le vent, séparée de la précédente et de l'extrémité de l'île du Nord par la passe (figure n°9).

Dans ce secteur, long de 16 kilomètres, la couronne est constituée par une plature entièrement submersible large de 1 à 1.5 km, portant de vastes herbiers à Cymodocées. Contrairement au secteur oriental, il existe ici, particulièrement à l'ouest de la passe et sur environ 8 km, une levée détritique externe bien caractérisée, à rebord interne en dents de scie constituées par des traînées de matériaux non fixés venant recouvrir l'herbier. Cette vaste plature à herbiers porte dans sa partie orientale des témoins rocheux surbaissés et à sommet plat, au nombre d'une dizaine, qui dominent l'herbier de 2 à 2.5 mètres par de grands lapiés ou par un ressaut à encorbellement. La roche est un calcaire compact à gros massifs de corail certains en position de croissance et brèches coralliennes recimentées. Les trois témoins les plus importants portent une levée de tempête et de la végétation : îles du Lapin, du Milieu, et des Déposés (fig. 3).

3. La partie sud, de structure très compliquée (fig. 8).

A la couronne proprement dite de l'atoll, enserrant le grand lagon, s'adjoint de ce côté, et à l'extérieur, une prolongation triangulaire atteignant 5 km dans sa plus grande largeur. Ce qui, ailleurs, correspondait à la couronne sensu-stricto, se morcelle ici longitudinalement en un système de crêtes séparées par des sillons profonds remplis de pinacles ou de pâtés de corail (coral patches) constituant autant de petits lagons séparés du lagon principal. Situé en position interne, ce système n'est plus exposé à la grande houle. La plature corallienne actuelle, de type rainuré, est reportée plus à l'extérieur, et alimente de vastes accumulations sableuses en migration, en forme de dunes hydrauliques paraboliques qui déferlent par une pente raide sur un assez grand lagon profond et contenant de très nombreux pâtés de corail.

Enserré et délimité par la couronne de l'atoll, le grand lagon présente lui-même une structure complexe, avec des alignements énigmatiques en forme de levées étroites et allongées parfois subaffleurantes. D.R. Stoddart a reconnu, en fonction de ce système de rides ou de levées, l'existence de trois parties dans ce lagon, mais nous en distinguerons cinq :

1. une partie occidentale, limitée au sud-est par la levée I (fig. n°9). Cette partie a, d'après la carte marine, des profondeurs de 10 à 15 m. On n'y trouve pas de pâtés coralliens subaffleurants comme dans le reste du lagon;

2. une partie centre-sud, à l'ouest de la levée IV. Probablement profonde de 8 à 10 m, cette partie contient des centaines de pinacles ou pâtés de corail régulièrement répartis mais non alignés, qui apparaissent sur la photographie aérienne verticale comme autant de petites taches blanches sur fond noir;

3. une partie centrale, à l'est de la levée III, caractérisée par l'existence de centaines de pâtés de corail mais ici clairement disposés en 15 à 20 alignements qu'ils jalonnent. Couvrant une zone large d'environ 2 km, et longue de 6 à 7 km, ces alignements sont orientés NNE-SSW;

4. une partie nord-est, débouchant sur la passe, avec des profondeurs de 4 à 11 mètres. Cette partie est moins riche en pinacles ou pâtés de corail que les deux parties précédentes;

5. une partie sud-est, à l'est de la levée IV, caractérisée par l'existence d'au moins cinq grands alignements identiques à ceux de la zone 3, d'orientation NE-SW.

L'examen des cotes bathymétriques autour de l'atoll permet de mettre en évidence une dissymétrie bien nette dans la répartition des profondeurs. Il existe un plateau sous-marin peu profond du côté oriental, avec des fonds généralement inférieurs à 40 mètres jusqu'à 1 à 2,5 km en avant du bord externe du récif. Du côté occidental la carte marine indique aussi l'existence de faibles profondeurs jusqu'à 6 km de l'atoll. Par contre au nord on observe une chute brutale sur les grandes profondeurs : une cote moins 1000 est indiquée à 3 km au nord de l'île des Déposés, et une cote 183 à moins d'un kilomètre de la bordure du récif.

LE PROBLEME DES TEMOINS DE CALCAIRES RECIFAUX DU HAUT-FLANDRIEN

A. Dans l'est et le nord-est

Les grandes îles de l'est et du nord-est, île du Nord, île du Sud, et île Goëlette, sont des accumulations très récentes de matériaux meubles, et surtout de sable, mais qui reposent en plusieurs endroits sur un socle de matériaux calcaires variés indurés qui donnent ici et là le long du littoral des îles des affleurements rocheux lapiazés alternant avec de grandes plages de sable. Ces mêmes calcaires coralliens se retrouvent en témoins éxigus, servant de socle aux îles Lapin, des Déposés, et du Milieu, sur la partie nord-ouest de la couronne de l'atoll. Une datation par la méthode Thorium-Uranium a été effectuée sur un échantillon de corail en position de croissance prélevé dans la partie moyenne de cette formation à 2 mètres au-dessus du niveau des basses mers. L'âge obtenu a été de 3700 ans B.P. et de 4300 ans B.P. :

I. Corail mort: échantillon prélevé au sommet de la visière [corniche?], à peu près au niveau des plus hautes marées, de la base consolidée de l'Ile Déposés

1) Datation par la méthode Th/Ur (G. Elbez, Laboratoire des Faibles Radioactivités, Gif-sur-Yvette):

3.100 ± 700 B.P.

2) Datation du même échantillon par la méthode C 14 (Dr. G. Délibrias, Laboratoire des Faibles Radioactivités, Gif-sur-Yvette):

3.640 ± 100 B.P.

II. Corail mort provenant de la même brèche, Ile Déposés, prélevé à 2 mètres dans la même région que l'échantillon précédent, environ 50 cm au-dessus du niveau des marées les plus hautes.
Datation par la méthode Th/Ur (G. Elbez, Laboratoire des Faibles Radioactivités, Gif-sur-Yvette):

4.900 ± 600 B.P.

(Datations effectuées par Mlle. Elbez à Gif-sur-Yvette)

Les affleurements de ce platier ancien induré sont particulièrement nombreux dans l'île du Nord (voir la figure n°4); près du village à l'est de la passe, à North Point, le long du littoral côté lagon, de multiples affleurements alternent avec des plages de sable. Le platier ancien induré affleure aussi largement aux îles Manaha : il constitue, entre 0,5 et 1 m, au dessus du platier actuel qu'il domine par un petit escarpement bien net lapiazé, le socle des trois îles, formées elles-mêmes par des accumulations de sables et de graviers coralliens. Dans l'île du Sud il affleure largement dans la partie nord, mais plus rarement ailleurs : nous en avons relevé cependant trois affleurements, reportés sur la figure n°10. L'île Goëlette, plus au sud, est une accumulation peu élevée de sable, de graviers, et de blocs coralliens, supportée par un socle de ce platier ancien qui affleure largement au nord-est, donnant de grands affleurements rocheux lapiazés qui dominent de 1 m à 1,5 m la plature corallienne actuelle.

Ce platier ancien est constitué essentiellement de brèches coralliennes bien cimentées incluant de gros blocs de corail mais surtout beaucoup de gravier corallien et des lits de plage bien stratifiés : c'est alors un grès de caye (cay sandstone). Sa granulomètrie est donc très variée. Lors-qu'il y a litage, ces lits sont subhorizontaux, ou présentent un pendage, mais fait fondamental, ces pendages n'ont aucun rapport avec la pente de la plage actuelle dans le même lieu. Il ne s'agit donc pas de beach-rocks d'induration des plages sub-actuelles. Lorsqu'il existe de tels beach-rocks, comme par example à North Point (fig. n°4), à côté de ces formations anciennes, la distinction entre les deux formations est évidente et on ne peut les confondre.

Dans l'ensemble ce platier induré semble correspondre, dans cette partie est et nord-est de Farquhar, à un niveau marin supérieur de un mètre, ou un peu plus, au niveau marin actuel. Il sert de socle à toutes les îles, qui sont des accumulations meubles très récentes, et n'a été conservé que là : son extension a certainement été plus grande, mais partout ailleurs la corrosion l'a ramené au niveau de la plature actuelle.

L'interprétation que nous donnons de cette formation ancienne, dans l'est et le nord-est de Farquhar, est la suivante : il s'agirait de témoins d'une situation ancienne, où existait une plature corallienne à un niveau légèrement supérieur au niveau de la plature actuelle, portant des cayes de sable et de gravier corallien qui ont été elles-mêmes indurées. Une étude minutieuse des pendages des formations anciennes litées permettrait sans doute de se faire une idée du nombre et de la position de ces cayes, mais il est certain que leur disposition était différente de celle des îles actuelles. La discontinuité des affleurements rocheux dans l'île du Sud, et dans la partie septentrionale de l'île du Nord, font penser qu'il existait alors entre les cayes, en ces endroits, de larges passes : cela permettra de mieux comprendre l'origine et la disposition des grandes rides ou levées et des alignements du lagon.

B. Dans le nord-ouest

Le couronne récifale porte, dans sa partie nord-ouest, huit témoins isolés d'assez grande taille de l'ancienne plature corallienne indurée, ainsi que quelques rochers plus petits lapiazés. Ces témoins se présentent comme des îlots rocheux surbaissés à sommet plat vus de loin, hérissés de lapiés vus de près, dominant les herbiers de 2 à 2,5 mètres par un ressaut à encorbellement. Trois de ces témoins portent des accumulations de tempêtes récentes (gros blocs de corail, graviers et sable) sur lesquelles pousse de la végétation : l'île Lapin, l'île du Milieu et l'île des Déposés. A l'île des Déposés (voir fig. n°3), le socle rocheux est un calcaire corallien très dur contenant de gros massifs de coraux dont certains semblent en position de croissance ; l'essentiel est cependant une brèche corallienne à gros blocs très bien recimentés incluant des coquilles de *Tridacna*. L'ensemble de la formation monte nettement plus haut que dans l'est et le nord-est de l'atoll, la différence étant d'au moins un mètre.

Ces témoins permettent de reconstituer l'existence d'un ancien platier situé entre 2 et 2,5 mètres au-dessus du platier actuel, que la datation de l'île des Déposés place à 3700 ans B.P. Ce platier ancien a été complètement démantelé en fonction du niveau marin actuel, et ses témoins isolés sont en voie de réduction rapide par la corrosion. Les trois îles n'existent qu'en fonction du socle rocheux qui les supportent et sont donc destinées à disparaître.

L'aspect très induré du calcaire corallien aurait pu laisser supposer un âge plus ancien, par exemple pré-Würm. Deux datations par la méthode Thorium-Uranium, ont donné respectivement 3700 ans et 4300 ans B.P. De telles indurations de formations flandriennes ont été observées dans divers atolls du Pacifique, où elles donnent les "feos", résidus émergés d'un récif fossile, mais parfois très récent, déchiquetés par la corrosion, comparables aux formes décrites ici. On reste confondu toutefois devant la rapidité de la corrosion capable, en si peu de temps, de réduire un volume rocheux aussi considérable, et sur d'aussi grandes surfaces, pour le ramener au niveau du platier actuel.

LE PROBLEME DES LEVEES ET DES ALIGNEMENTS DU LAGON

Ces formes ont déjà été signalées par D.R. Stoddart (1970). Elles sont étroites, peuvent atteindre plusieurs kilomètres de longueur, et sont plus ou moins profondément immergées mais parfois subaffleurantes. Les plus longues traversent presqu'entièrement le lagon du nord au sud. Elles constituent une énigme, et ont fait écrire à

D.R. Stoddart "that Farquhar lagoon is one of the most complex in topography and presumably in geomorphologic history of the world" (opus cité p.11).

Nous distinguerons les grandes levées de ce que nous appellerons les "alignements", bien qu'il y ait passage de l'une à l'autre de ces catégories de formes, et que les unes et les autres aient très probablement la même origine.

A. Les grandes levées

Quatre grandes levées recoupent transversalement le lagon, les trois premières numérotées I, II et III ayant une direction NE-SW, la quatrième numérotée IV une direction presque nord-sud. Aucune n'a pu être examinée au sol.

La levée I est presque rectiligne, sur une longueur de 5 kilomètres. Sa largeur varie entre 100 et 200 mètres. Autant qu'on puisse en juger d'après la photographie aérienne, elle est entièrement sableuse, et porte à son extrémité un vaste ensemble d'herbiers subaffleurants ; une autre petite tache d'herbier existe dans sa partie septentrionale. Elle porte aussi sur toute sa longueur, et principalement sur ses bordures qui tombent en pente douce sur des fonds d'une dizaine de mètres, d'abondants peuplements de coraux en petits massifs sur fonds de sable.

Les levées II et III sont enracinées au nord à la couronne de l'atoll. Dans leur partie septentrionale elles sont couvertes par de l'herbier, qui prolonge dans le cas de III les vastes herbiers à Cymodocées de la partie interne de la couronne. Larges d'une centaine de mètres, l'une et l'autre sont couvertes dans leur partie centrale et à leur extrémité par de très nombreux massifs de coraux sur fond de sable, ces massifs devenant jointifs par endroits sur les bordures. La levée II se divise à son extrémité en deux levées légèrement arquées, à concavité orientale.

A la différence des trois premières, la levée IV s'enracine à la partie sud-est de la couronne. Elle est dans la continuité de l'une des levées qui, nous le verrons, semblent constituer la couronne elle-même dans sa partie méridionale. Large de 100 à 200 mètres, elle a un dessin moins régulier que les levées précédentes, mais s'intègre parfaitement par sa direction générale aux systèmes d'alignements que nous allons examiner maintenant. Elle est peuplée, comme les précédentes, de milliers de petits massifs de coraux sur fond de sable.

B. Les alignements (figures n°4, 6 et 7).

Ils ont de toute évidence la même origine que les grandes levées, puisqu'ils s'intègrent dans les mêmes faisceaux directionnels, mais sans avoir en général un aspect aussi massif qu'elles. Ces alignements s'ordonnent en deux faisceaux, l'un correspondant à ce que nous avons appelé la partie centrale du lagon (partie n°3), l'autre la partie sud-est (partie n°5).

Le premier de ces faisceaux, qui occupe la partie centrale du lagon, s'enracine à la partie septentrionale de la couronne comme les levées II et III et parallèlement à ces dernières. Ce faisceau est constitué par 15 à 20 alignements parallèles, orientés NNE-SSW, et très légèrement arqués avec concavité vers l'est. Près de leur enracinement, leur continuité est nette et ils se présentent comme les grandes levées précédemment décrites. Vers le sud et le milieu du lagon, leur continuité se devine seulement grâce à l'alignement des pâtés coralliens (coral patches). Ce faisceau de la partie centrale du lagon couvre une largeur d'environ 3 kilomètres. Certains des alignements se suivent jusqu'aux abords de la levée IV, ce qui veut dire que ce système d'alignements traverse et barre complètement le lagon dans sa partie centrale.

Le second faisceau occupe la partie sud-est du lagon. Il est constitué par quatre alignements très nets orientés NE-SW, et par un cinquième plus externe NNE-SSW subparallèle à la levée IV, qui vient s'intégrer au faisceau de la partie centrale du lagon. Ces cinq alignements présentent eux aussi une concavité vers l'est.

Les trois alignements les plus proches du rivage interne de l'île du Sud, qui sont aussi les plus beaux, ont pu être examinés en plongée. Ils sont longs de 3 km (alignement le plus proche du rivage) à 5 km (alignement n°3 à partir du rivage).

Leur continuité, bien visible sur les photographies aériennes, est confirmée par l'examen au sol. Les taches plus claires de la photographie aérienne, disposées en chapelet et qui les jalonnent, correspondent à de gros pâtés sableux peu immergés (2 à 3 mètres), d'un diamètre généralement de l'ordre de 50 à 150 mètres, qui tombent en pente parfois progressive, parfois relativement raide, sur les sillons intermédiares où l'on trouve des profondeurs d'une douzaine de mètres. Entre deux pâtés sableux successifs, il y a 4 à 8 mètres d'eau sur la levée elle-même, la continuité de celle-ci se devinant d'ailleurs par transparence sur les photographies aériennes. Sur les parties les plus élevées des pâtés sableux existe une couverture de petits massifs coralliens, souvent en patates, et peu serrés (10 à 30% de corail en moyenne), d'où la teinte très claire perçue sur les photographies aériennes. Généralement la densité des massifs de coraux augmente sur les pentes latérales, ainsi que dans les ensellements entre deux pâtés successifs, jusqu'à devenir localement jointifs, avec la possibilité de donner parfois un tombant. L'alignement n°2 est en certaines de ses parties presqu'uniquement sableux, et porte fort peu de massifs de coraux.

Les trois alignements les plus proches de la côte ont été systématiquement fouillés afin de rechercher s'il n'existait pas sous le sable une ossature résistante, de grès-calcaires par exemple : aucun indice allant dans ce sens n'a pu être découvert.

Un prélèvement du fond sableux a été effectué sur le deuxième alignement sous-marin à partir du rivage, par 5 m de profondeur, sur le bord de l'un des pâtés qui surmontent le bourrelet, et entre des petits massifs de corail (échantillon no11). Il s'agit d'un sable blanchâtre à légèrement verdâtre, grossier, dans lequel on observe de très gros débris coquilliers et d'algues encroûtantes. Le sable est composé essentiellement par des grains calcaires, anguleux mais informes, qui semblent provenir de la destruction par des organismes lithophages de tests calcaires d'organismes préexistants. On distingue encore des débris de Lamellibranches, de petits Gastéropodes, et de Foraminifères (dont des Textulariidés). Ce sédiment est moyennement classé, avec une médiane de 0,41 mm, et un mode peu prononcé vers 0,30 mm.

C. Essai d'interprétation

Les formes que nous avons décrites ne semblent pas assimilables aux "kaoa" (murs), décrits dans l'atoll Hao par exemple, dans le Pacifique, et qui sont plus étroites et à parois verticales, ce qui n'est pas le cas ici. Les "kaoa", dont l'origine demeure inexpliquée, s'enracinent perpendiculairement à la couronne et cloisonnent partiellement le lagon. Rappelons que l'on connaît d'autres structures énigmatiques dans des lagons, comme la structure en nid d'abeilles de l'atoll de Mataia, elle aussi inexpliquée.

L'interprétation que nous adoptons pour les formes décrites à Farquhar est celle de cordons littoraux sableux ayant, à un certain moment, colmaté au moins partiellement l'aquarium lagunaire. Les grandes levées I, II et III, peut-être aussi IV, peuvent être interprétées comme des flèches littorales enracinées à la couronne, puis ensuite partiellement tronquées par l'érosion, qui a coupé la levée I de son enracinement primitif. Il est logique de penser que chronologiquement c'est la levée I qui s'est formée la première, suivie par II puis part III. Le colmatage a ensuite gagné vers l'est avec la formation du faisceau central, constitué d'un grand nombre de crêtes de plages séparées par autant de sillons. A ce stade, l'aquarium se trouvait limité à la partie orientale actuelle du lagon, à moins qu'il soit demeuré, ce qui est possible, un plan d'eau étendu à l'ouest de la levée I, ainsi qu'au sud du lagon actuel.

L'une des difficultés de cette interprétation tient dans la profondeur des sillons intermédiaires (jusqu'à moins 12 mètres), et à la dénivellation importante entre le fond de ces sillons et le sommet des crêtes ou levées (4 à 8 mètres), dans le cas du faisceau oriental étudié au sol. Dans le cas de ce faisceau, l'espacement entre deux bourrelets ou alignements successifs est aussi trop important (150 à 300 mètres) pour qu'il s'agissent de crêtes de plages séparées par autant de sillons. On peut admettre par contre l'hypothèse de flèches d'avant côte, plus ou moins exhaussées par une reprise ultérieure du sable par le vent, puis par la construction corallienne.

L'hypothèse de crêtes de plages parallèles est plus vraisemblable pour le faisceau central, qui comprend un plus grand nombre d'alignements et surtout plus serrés (les sillons intermédiaires ont entre 50 et 100 mètres de largeur en moyenne).

Dans le cas des grandes levées I, II et III, il s'agit sans doute de flèches qui se sont allongées successivement à partir du littoral en s'avançant en eau relativement profonde.

Quoiqu'il en soit, il faut admettre que ce colmatage du lagon s'est effectué en fonction d'un niveau marin inférieur d'au moins une dizaine de mètres au niveau marin actuel. Un tel niveau a existé il y a 7000 à 6000 ans, durant la phase finale de la transgression flandrienne mais il ne s'est maintenu que fort peu de temps. Ultérieurement il est peu probable que le niveau marin soit redescendu, entre les maxima du Haut-Flandrien, au-dessous de moins 5 mètres.

En ce qui concerne la dénivellation entre le fond des sillons intermédiaires et le sommet des bourrelets, on peut penser que, par rapport aux formes littorales originelles, il a pu se produire une exagération de cette dénivellation par action dunaire d'une part, par la construction corallienne sur les pâtés et l'accumulation de débris coquilliers d'autre part (voir l'analyse de l'échantillon n°11).

La disposition des systèmes de crêtes de plage, et l'orientation des flèches que seraient les grandes levées, s'expliqueraient le mieux dans le cas d'ouvertures dans la couronne du côté nord-est et est, là où sont actuellement les deux îles du Sud et du Nord, ouvertures suffisamment larges pour laisser pénétrer la houle d'alizé. On peut supposer que la mer, durant la transgression flandrienne, a réoccupé le lagon d'un ancien atoll pré-würmien qui pouvait être largement ébréché au nord-est et à l'est ; elle a alors construit ces formes de régularisation dans le lagon, par remaniement des matériaux sableux disponibles. L'étude du vieux platier recimenté du Haut-Flandrien a montré qu'ultérieurement (vers 3700 ans B.P.), il pouvait encore fort bien demeurer des ouvertures de ce côté entre les accumulations en cayes de sable ou de graviers, aujourd'hui consolidées en "cay sandstone".

On peut se demander aussi pourquoi le matériel de ces cayes haut-flandriennes a été cimenté, et pas celui des "levées et crêtes de plages" du lagon, constituées pourtant par un matériel sensiblement identique. La raison est sans doute la suivante : la cimentation a pu se faire pour les premières dans la zone intertidale ou un peu au-dessus ; les secondes par contre sont restées au-dessus du niveau des plus basses mers depuis leur formation, et leur cimentation a été impossible.

LA STRUCTURE DU SUD DE L'ATOLL (figures n° 5 et 8)

La couronne de l'atoll, dans sa partie méridionale, présente une structure complexe (fig. N°8). A la couronne proprement dite qui enserre le grand lagon s'adjoint une prolongation triangulaire du côté externe, qui atteint 5 km dans sa plus grande largeur. Cette prolongation externe comprend les platures externes battues par les grands déferlements, qui délimitent un lagon large de 3 km. Ce "lagon externe" est complètement séparé de la haute mer d'une part, du grand lagon de l'atoll d'autre part. Dans la description des formes, faite essentiellement à partir des photographies aériennes puisque cette partie de l'atoll n'a été visitée qu'aux abords de l'île Goëlette, nous distinguerons donc la partie la plus interne ou "couronne sensu-stricto", le lagon et les platures externes.

A. La partie interne ou "couronne sensu-stricto"

Cette partie n'est pas atteinte par les grands déferlements, dont la protègent les platures externes. Nous y retrouvons, sur une largeur d'un kilomètre environ, une structure à éléments longitudinaux en saillie qui s'apparentent aux levées décrites dans le lagon, séparés par de profonds sillons remplis de pinacles et de pâtés coralliens. Immédiatement à l'ouest de l'île Goëlette il y a entre 4 et 6 "levées" sub-parallèles séparées par des microlagons allongés et très profonds (14 à 16 mètres d'après la carte marine). Le contact entre "levées" et sillons intermédiaires occupés par les micro-lagons se fait en général par un tombant corallien. La surface des levées présente des fonds sableux subaffleurants portant un semis serré de têtes de corail vivant, ou dans d'autres parties de grands herbiers donnant des taches noires sur les photographies aériennes.

Cette structure se poursuit à l'est de l'île Goëlette dans le vaste élément de plature, large de 2,5 km, qui sépare l'île Goëlette de l'île du Sud. Cette prolongation et la continuité des formes apparaissent de manière évidente sur les photographies aériennes (voir la figure n°5) : la plature présente en effet des parties foncées, à rainures transversales, en larges trainées prolongeant les "levées" du secteur plus à l'ouest, séparées par des parties plus claires qui sont sableuses, et qui correspondent aux "micro-lagons" des sillons mais ici remblayés. Sur le terrain, ces parties foncées correspondent à des peuplements de coraux en traînées transversales (d'où l'aspect rainuré), et localement, près de la pointe méridionale de l'île du Sud, et près de l'île Goëlette, à de l'herbier à Cymodocées. Il s'agit d'espèces coralliennes massives (pas d'*Acropora* par exemple). Ces peuplements n'émergent pas, mais sont recouverts par une mince pellicule d'eau, de 0,5 à 1,5 m.

Il apparaît aussi de manière fort nette que la grande levée IV du sud du lagon est dans le prolongement de la plus interne des levées qui constituent la couronne.

Il existe une différence entre la morphologie des grandes levées I, II et III du lagon, d'une part, et celle des levées constituant la couronne dans le sud de l'atoll, et de la grande levée IV, d'autre part. Les levées qui constituent la couronne dans le sud de l'atoll, ainsi que la levée IV du lagon qui appartient au même système, présentent des contours irréguliers, avec de multiples échancrures ; cela n'est pas le cas pour les grandes levées I, II et III du lagon. Les premières ont subi de toute évidence une érosion de détail plus importante. La profondeur et les parois raides des micro-lagons occupant les sillons intermédiaires suggèrent une érosion karstique durant une période de régression : il serait intéressant d'effectuer des plongées dans ces micro-lagons pour examiner si les levées intermédiaires ne sont pas grésifiées dans la masse sous le recouvrement sableux superficiel. Quoiqu'il en soit, on est amené à supposer que l'ensemble de ce système est plus ancien que les grandes levées I, II et III du lagon.

<u>B. Les platures et le lagon externe</u> (fig. n°8)

Ces vastes éléments de platures rainurées, de formation certainement très récente, témoignent, comme le pense D.R. Stoddart (1970 p.11), d'une vie corallienne intense sur la pents externe sud et sud-est de l'atoll. Ils semblent résulter de la coalescence de massifs coralliens primitifs distincts ayant poussé en avant de l'ancienne couronne sur un plateau sous-marin peu profond, d'où un contour externe en grands lobes séparés par des "passes" peu profondes.

En avant de ces éléments de platures, une structure orientée liée à l'action des grandes houles, et s'apparentant à la structure en "spurs and grooves", est parfaitement visible sur les photographies aériennes verticales (voir photographies n°52 et 63 par exemple). De multiples sillons sableux, ayant une largeur d'ordre métrique, s'allongent perpendiculairement à la houle, certains sur plusieurs centaines de mètres de largeur, séparés les uns des autres par 5 à 15 mètres. La zone des faibles profondeurs s'étend largement en avant des brisants, et le fin lacis des sillons, qui parfois s'anastomosent, est visible par transparence jusqu'à parfois un kilomètre de ces derniers. En face des "passes" et des plus grandes des criques externes cette disposition orientée du corail passe à de gros massifs d'abord ovales, puis subcirculaires.

Aucune levée détritique de blocs n'apparaît sur les photographies aériennes. Par contre la fourniture de matériaux sableux est considérable ; ces matériaux, qui transitent vers l'intérieur, sous l'action des grands houles, en suivant les "rainures", alimentent du côté interne de la plature d'énormes accumulations sableuses en nappes qui sont des dunes hydrauliques paraboliques ; elles déferlent par une pente raide, qui est la pente d'équilibre du sable sous l'eau, sur le lagon externe qui tend ainsi à être progressivement comblé de ce côté.

Ce lagon est un vaste plan d'eau de 2 km de largeur et 6 de longueur. Il contient des centaines de "coral patches", certains subaffleurants. Dans sa partie interne il est traversé par des éléments tronçonnés de "levées" appartenant au système longitudinal déjà précédemment décrit, et portant des taches d'herbier.

L'existence de ce lagon important et profond, bien distinct du grand lagon délimité par la couronne de l'atoll, est l'une des grandes originalités de l'atoll Farquhar.

Le surplus d'eau apporté dans ce lagon par les grands déferlements, par dessus les éléments de platures externes, se déverse dans le grand lagon par des chenaux de décharge parfois profonds qui coupent le système longitudinal de levées de la couronne. Quatre de ces chenaux de décharge sont particulièrement nets.

L'EVOLUTION MORPHOLOGIQUE DES ILES DE L'EST ET DU NORD-EST

Dans sa partie est et nord-est, c'est à dire entre la passe du grand lagon et l'île Goëlette, la couronne porte un rempart quasi-continu d'îles sableuses : île du Nord, îles Manaha, île du Sud, île Goëlette. En avant de ces îles, la plature corallienne s'étend du côté au vent sur une largeur de 500 à 700 mètres. Ainsi que nous l'avons déjà dit, cette plature, de structure rainurée, ne porte pas de véritable levée détritique de blocs (boulder zone) mais seulement quelques trainées localisées de blocaille corallienne. Cette absence, déjà notée par Gardiner (1936), est interprétée par lui comme étant liée à une faible activité corallienne actuelle de ce côté. On peut penser aussi que, comme dans beaucoup d'atolls très battus du Pacifique, par exemple aux Tuamotu, la totalité des matériaux détritiques est balayée jusque dans la partie plus interne de la plature, c'est à dire, jusqu'au rempart quasi continu que forment les îles. Constituées surtout de sable, mais aussi de graviers et de blocs coralliens, ces dernières seraient à la fois des cayes sableuses, et l'équivalent de la "boulder zone".

A. L'île du Sud (figures n°10 et 11C)

Longue de 5,7 km, et large de 600 à 900 mètres, cette île est dans l'ensemble plate et basse (moins de 3 mètres) sauf le long de sa façade orientale où existe une étroite frange continue de dunes hautes de 10 à 20 mètres. Une coupe d'est en ouest dans la partie méridionale de cette île montre la zonation suivante (voir la figure n°11C):

1) la plature corallienne au vent, large de 500 mètres ;

2) la plage de sable, avec en arrière 3 à 10 crêtes de plages récentes couverte par la végétation ;

3) la ligne des dunes, qui domine brutalement de 10 à 15 mètres la zone précédente, couverte par de grands buissons de *Scaevola* et de *Tournefortia*. Le sable qui la constitue (échantillon n°4 prélevé en sommet de dune) est bien classé, avec une médiane de 0,38mm ; il contient surtout des Amphistégines et des Spicules d'Alcyonaires (genre *Alcyonium*);

4) en arrière de l'étroite ligne de dunes, une zone plate à 1 ou 2 mètres au-dessus du niveau des plus hautes mers, portant une partie de la cocoteraie ;

5) une pseudo-mangrove à *Pemphis*. L'échantillon n°5, prélevé dans cette zone, ne contient que 78% de fraction grossière (>50µ) ; il s'agit d'un sable mal classé, sans mode net, constitué essentiellement par des Amphistégines et des débris de Spicules d'*Alcyonium* ;

6) une série de crêtes de plage internes qui séparent la pseudo-mangrove du lagon. Topographiquement bien marquées, ces crêtes portent des filaos et des cocotiers. L'échantillon n°6, prélevé dans cette zone, est entièrement sableux, et constitué lui aussi surtout d'Amphistégines ;

7) la plage de sable côté lagon. Le sable (échantillon n°3 prélevé à mi-hauteur de la plage), de couleur blanc à beige, est très bien classé, de médiane et de mode 0,55 mm ; il est constitué presqu'exclusivement d'Amphistégines et de débris de Spicules d'Alcyonaires, associés à quelques débris de Mollusques, de baguettes d'Oursins, et de Bryozoaires ;

8) un vaste estran sableux, se prolongeant en dessous du niveau des plus basses mers sur une largeur d'environ 400 mètres, jusqu'à un grand tombant sableux en pente de 15 à 30%, par lequel on passe aux profondeurs du lagon.

Contrairement à l'île du Nord, les affleurements rocheux correspondant au vieux matériel du Haut-Flandrien induré, sont rares dans l'île du Sud : il y en a deux, très localisés sur le rivage interne côté lagon, un autre plus important qui supporte l'extrémité nord de l'île (affleurement dans la passe sud des Manaha) ; enfin le quatrième est à l'extrémité méridionale de l'île côté externe (voir la figure n°10).

Du côté lagon, les crêtes de plage les plus externes (zone 6 de la coupe précédente) correspondent à une régularisation récente par les vagues qui se forment sur le lagon. Elles ont isolé trois étendues partiellement sans végétation, et occasionnellement recouvertes par la haute mer, où pousse la pseudo-mangrove à *Pemphis*. La comparaison peut-être faite avec les "barachois" des Chagos (D.R. Stoddart 1970, 12).

B. L'île du Nord

L'île du Nord est longue de 8,5 km, et large de 0,2 à 1 km. Elle a une forme générale en croissant, qui épouse l'extrémité septentrionale de la couronne. L'extrémité de la corne septentrionale porte l'unique village de l'atoll, sur le rivage de la passe ; lors de notre passage, ce village comptait 28 habitants, la plupart vivant d'un travail salarié sur la cocoteraie, qui couvre presqu'entièrement l'île du Nord, et une grande partie de l'île du Sud.

La plature corallienne du côté au vent montre les mêmes caractères qu'en face de l'île du Sud, et ici aussi on remarque l'absence d'une véritable crête détritique externe de blocs.

Une coupe dans la partie centrale de l'île, là où elle est la plus étroite, permet de distinguer trois zones :

1) dominant la plage au vent, une ligne étroite de grandes dunes couvertes par *Scaevola* et *Tournefortia* ;

2) une partie centrale plate et peu élevée portant la cocoteraie ;

3) dominant la plage du côté lagon, des crêtes de plage remaniées en dunes de 5 à 6 mètres de hauteur avec des filaos.

Le vieux platier induré donne des affleurements rocheux jusqu'au niveau des plus haute mers, tant du côté externe que du côté lagon.

Une autre coupe depuis la grande anse sableuse côté lagon, jusqu'aux environs de North Point, dans la partie où l'île est la plus large, montre :

1) la plage externe avec un grand affleurement de beach rock décollant en arrécife ;

2) une zone de petites dunes fixées, large d'une centaine de mètres. L'échantillon n°14 a été prélevé au sommet de l'une de ces dunes : il s'agit d'un sable bien classé, de médiane 0,32 mm, constitué comme l'échantillon n°4 essentiellement d'Amphistégines et de Spicules d'Alcyonaires ;

3) sur 800 à 900 mètres de largeur, une zone plate et peu élevée couverte de cocotiers. Il s'agit en fait d'un grand nombre de crêtes de plage très récentes, disposées parallèlement jusqu'aux toutes dernières immédiatement en arrière de la grande plage actuelle côté lagon.

Le prélèvement n°15 a été affectué en face de cette plage, dans l'axe de la grande anse, par moins 4 mètres. Nous sommes là dans la partie la plus abritée du lagon, sur des fonds unis et sans corail. Il s'agit d'un sable fin à moyen blanchâtre, relativement bien classé, dont la médiane est de 0,35 mm ; il est constitué par de nombreuses petites coquilles de bivalves (Nucules), de nombreux petit Foraminifères (*Marginopora* de petite taille et Amphistégines), de petits Gastéropodes, enfin d'abondants grains calcaires informes petits à moyens.

La côte de l'île du Nord présente du côté du lagon une succession d'affleurements rocheux du vieux platier induré. La principale interruption dans ces affleurements correspond à la grande anse déjà citée, longue de près de 3 km. A la corne de l'île sur la passe, on retrouve le vieux platier, en un vaste affleurement à l'est du village. Du côté externe, il existe aussi un témoin de ce vieux platier à North Point, à 200 mètres environ à l'ouest du beach-rock, mais ensuite on n'en trouve plus aucun jusqu'à la passe. On peut raisonnablement penser que l'île du Nord s'est constituée par soudure de deux îles primitivement distinctes, la coupure se situant au droit de la grande plage et correspondant à la zone colmatée par le système des crêtes de plage récentes décrites dans la dernière coupe.

Les beach-rocks du côté au vent, à North Point et plus au sud-est, permettent d'autre part de se faire une idée de l'évolution actuelle des rivages de l'île. Il existe là deux lignes distinctes de beach-rock. La plus interne, à North Point, décolle de la plage actuelle vers le nord (voir la figure n°4). La seconde, au sud-est, est plus ancienne ; elle est complètement détachée sur toute la longueur de la plage, à une centaine de mètres en avant de cette dernière, et se suit, de manière discontinue, sur environ 1200 mètres. La position de ces beach-rocks témoigne d'un recul rapide de la côté au vent, tout au moins dans ce secteur.

C. Les îles Manaha

Entre l'île du Nord et l'île du Sud, les trois petites îles Manaha sont des accumulations de sable et de graviers coralliens, reposant chacune sur un socle façonné dans le vieux platier recimenté (voir la figure n°10). Ces îles, qui sont des "motu", sont séparées les unes des autres par des passes qui sont en réalité des traverses de déferlement du type des "hoa" des Tuamotu ou des îles de La Société. Ces traverses de déferlement fonctionnent en effet dans le sens océan-lagon, canalisant vers ce dernier les eaux des grands déferlements de la façade au vent. Les quatre "hoa" entaillent de 0,5 à 1 m les brèches calcaires du vieux platier recimenté, en un petit ressaut sub-vertical. Du côté du lagon ils ont construit un vaste delta interne en éventail constitué de sable et de graviers, qui est encore pleinement actif et non fixé par l'herbier.

On remarque au sud du delta interne actuel, un autre delta du même type, mais plus ancien, qui s'avance encore davantage que le delta actuel dans le lagon. Contrairement au delta actuel, ce delta ancien n'est plus fonctionnel, mais est entièrement fixé et colonisé par l'herbier. Sa présence montre qu'il a existé d'autres "hoa", au sud des quatre "hoa" actuellement fonctionnels, à une époque récente. De l'un de ces "hoa" seule demeure la partie aval, sous la forme de l'une des dépressions à pseudo-mangrove dont il a été question dans la description de l'île du Sud.

Une autre grande convexité, dans le dessin du grand tombant sableux décrit dans le sud de la même île du côté lagon, et dont l'axe se trouve à peu près exactement en face de l'exutoire de la pseudo-mangrove traversée par la coupe n°11C, doit avoir la même origine.

On peut penser que l'île du Sud s'est ainsi constituée à partir d'îlots d'abords distincts, de "motu", séparés par autant de "hoa", qui se sont ensuite progressivement soudés. Il y a eu ensuite régularisation, en particulier sous l'action des vagues formées dans le lagon.

L'échantillon n°10 est un sable de plage prélevé du côté interne de l'îlot central Manaha ; il est constitué surtout de *Marginopora* et d'Amphistégines, de débris d'Algues encroûtantes et de débris coquilliers (Mollusques divers). Ce sable est mal classé, avec deux modes peu prononcés à 1,1 mm (les *Marginopora*) et 0,45 mm (Amphistégines et débris divers) ; la médiane est de 0,82 mm.

L'échantillon n°12 a été prélevé sur la pente sous-marine du delta interne actuel. Les *Marginopora* et les Amphistégines constituent à égalité l'essentiel de ce sable. Quelques débris coquilliers blanchâtres et des baguettes d'Oursins leur sont associés. La médiane est de 0,53 mm. On observe dans ce sable moyennement classé deux modes, l'un à 0,90 mm correspondant aux *Marginopora,* l'autre à 0,30 mm correspondant aux Amphistégines. Il semble donc y avoir une réduction de taille des espèces par rapport à l'enchantillon n°10.

D. L'île Goëlette

Cette petite île, d'environ 600 mètres de grande dimension, est une accumulation basse de sable et de graviers coralliens, s'accrochant à un élément du vieux platier induré qui affleure à l'est. Elle porte une végétation de Graminées, et sert de rockerie à d'importantes colonies d'oiseaux.

Entre l'île Goëlette et l'île du Sud, les matériaux sableux transitent librement à travers le platier jusqu'au lagon ; de ce côté ils s'étalent en de vastes accumulations sableuses en nappe, et donnent sur le lagon des dunes hydrauliques paraboliques à pente interne tombant sur des fonds de 8 à 12 mètres, localement en voie de colonisation par des coraux massifs en grosses patates. L'échantillon n°2 a été prélevé dans la partie supérieure de ce tombant sableux, par moins 3 mètres, au nord de l'île Goëlette entre ces colonies de coraux : il s'agit d'un sable blanchâtre, moyen, constitué de *Marginopora* et d'Amphistégines, de très nombreux petite grains calcaires informes et anguleux, de Spicules d'Alcyonaires d'allure irrégulière, de débris coquilliers et d'Oursins, enfin de quelques débris d'algues calcaires.

CONCLUSION

L'atoll Farquhar est, par sa morphologie, l'un des atolls les plus étranges du monde. Son originalité tient à la topographie particulière de son lagon, cloisonné par des levées immergées longues de plusieurs kilomètres, et par des faisceaux d'alignements, ainsi que par la structure de la partie sud de sa couronne, où l'on retrouve ces mêmes formes.

L'interprétation adoptée est celle de flèches et de cordons littoraux anciens, aujourd'hui tronçonnés, plus où moins immergés, et colonisés par les coraux et par l'herbier. Il semble que l'on puisse distinguer un système ancien, constituant la partie sud et sud-est de la couronne, ainsi que la grande levée IV du lagon, qui pourrait être pré-Würm, et un système plus récent, contemporain de la phase finale de la transgression flandrienne (7000 à 6000 ans B.P.), auquel se rattacheraient les grandes levées I, II et III du lagon, ainsi que les deux grands faisceaux d'alignements.

Sans doute primitivement ébréchée au nord et à l'est, la couronne s'est d'abord reconstituée à un niveau légérement supérieur à son niveau actuel. A ce stade (3700 ans B.P.), existait déjà un certain nombre de cayes sableuses, dont on retrouve les témoins grésifiés (cay sandstone), qui reposaient sur une plature elle aussi indurée dont seuls demeurent d'étroits lambeaux résiduels sous la forme de témoins rocheux dominant par un ressaut de 0,5 à 1 m de hauteur (secteur est et nord-est), ou de 2 m (secteur ouest), la plature actuelle.

A une époque très récente, et en fonction du niveau marin actuel ou d'un niveau proche de l'actuel, est apparue une seconde génération de cayes ou de "motu", séparés par des traverses de déferlement. Ces nouvelles constructions, surtout sableuses, se sont soudées entre elles au fur et à mesure des apports nouveaux de matériaux, les flèches d'obturation des "hoa", évoluant sous l'action des vagues formées dans le lagon, isolant de ce côté des pseudo-mangroves à *Pemphis* : ainsi semble s'être formée, au moins en partie, la grand île du Sud. Il demeure encore trois "motu" caractéristiques, les îles Manaha.

Au point de vue sédimentologique, il apparaît que le corail intervient fort peu dans la composition des matériaux sableux ; tous les sables analysés sont constitués essentiellement de Foraminifères, et accessoirement de débris coquilliers, de Spicules d'Alcyonaires, de baguettes brisées d'Oursins, ou de débris d'Algues calcaires. Les matériaux de la taille des blocs, et une grande partie des graviers, sont par contre d'origine corallienne.

REMERCIEMENTS

Nous remercions le Centre océanographique de Nossi-Bé, et spécialement son directeur M. Alain Crosnier, qui a mis à notre disposition pour cette mission le *Vauban,* navire océanographique du Centre. Nous remercions aussi le commandant Fiurie et l'équipage du *Vauban*.

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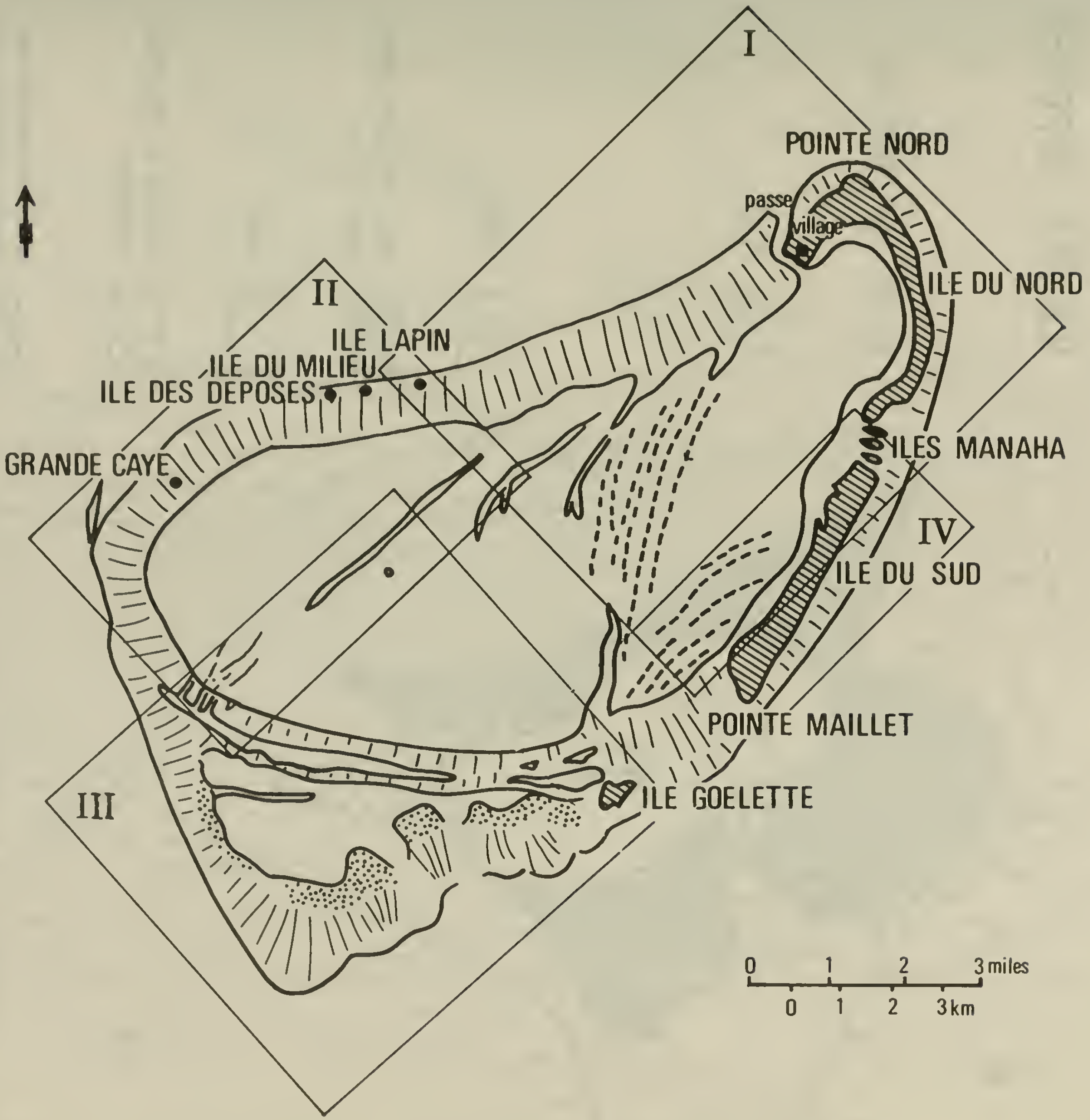


Fig. 2. L'atoll Farquhar: découpage des figures 4, 5, 9 et 10.

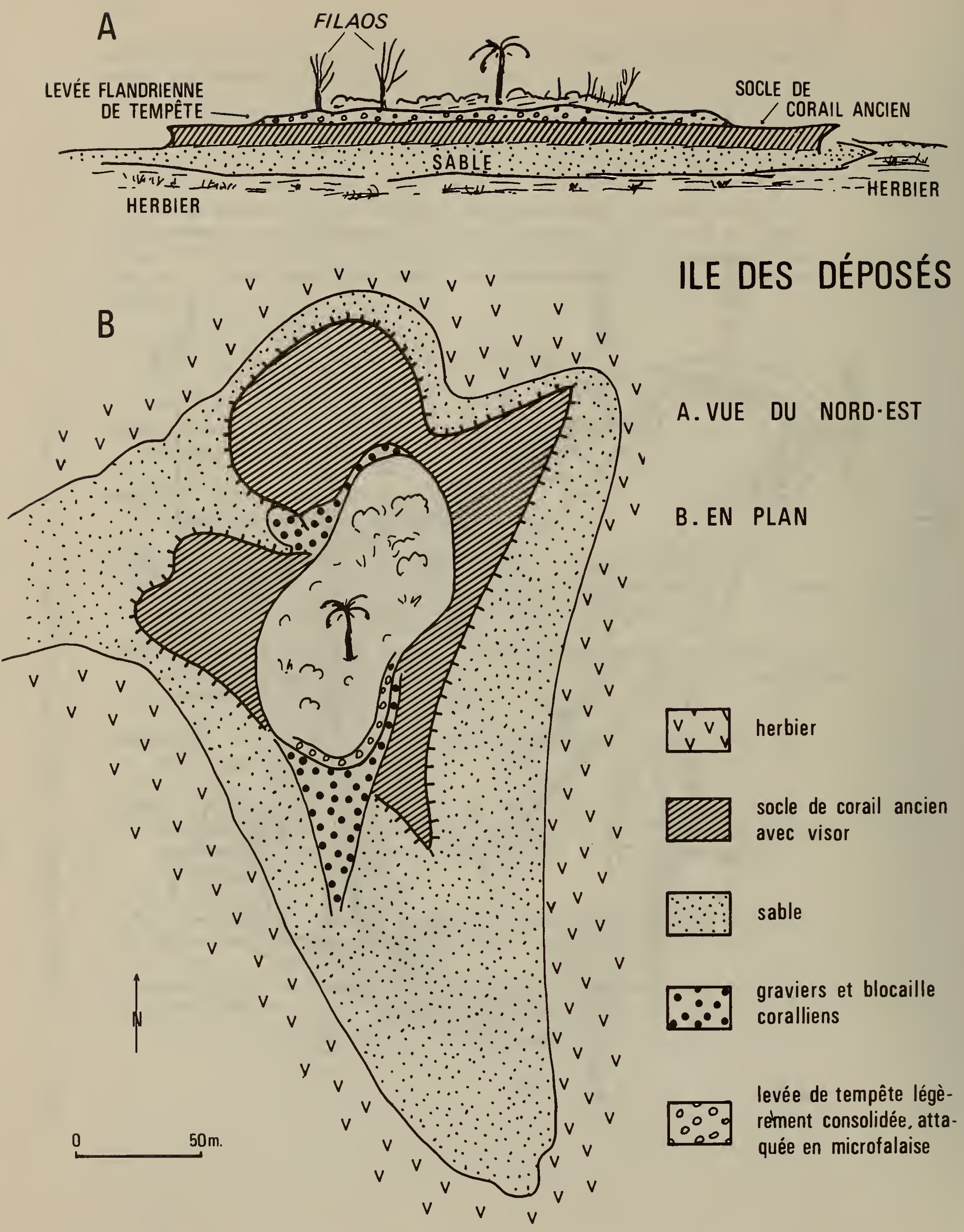


Fig. 3. L'île des Déposés. A: l'île vue du Nord; B: croquis géomorphologique.

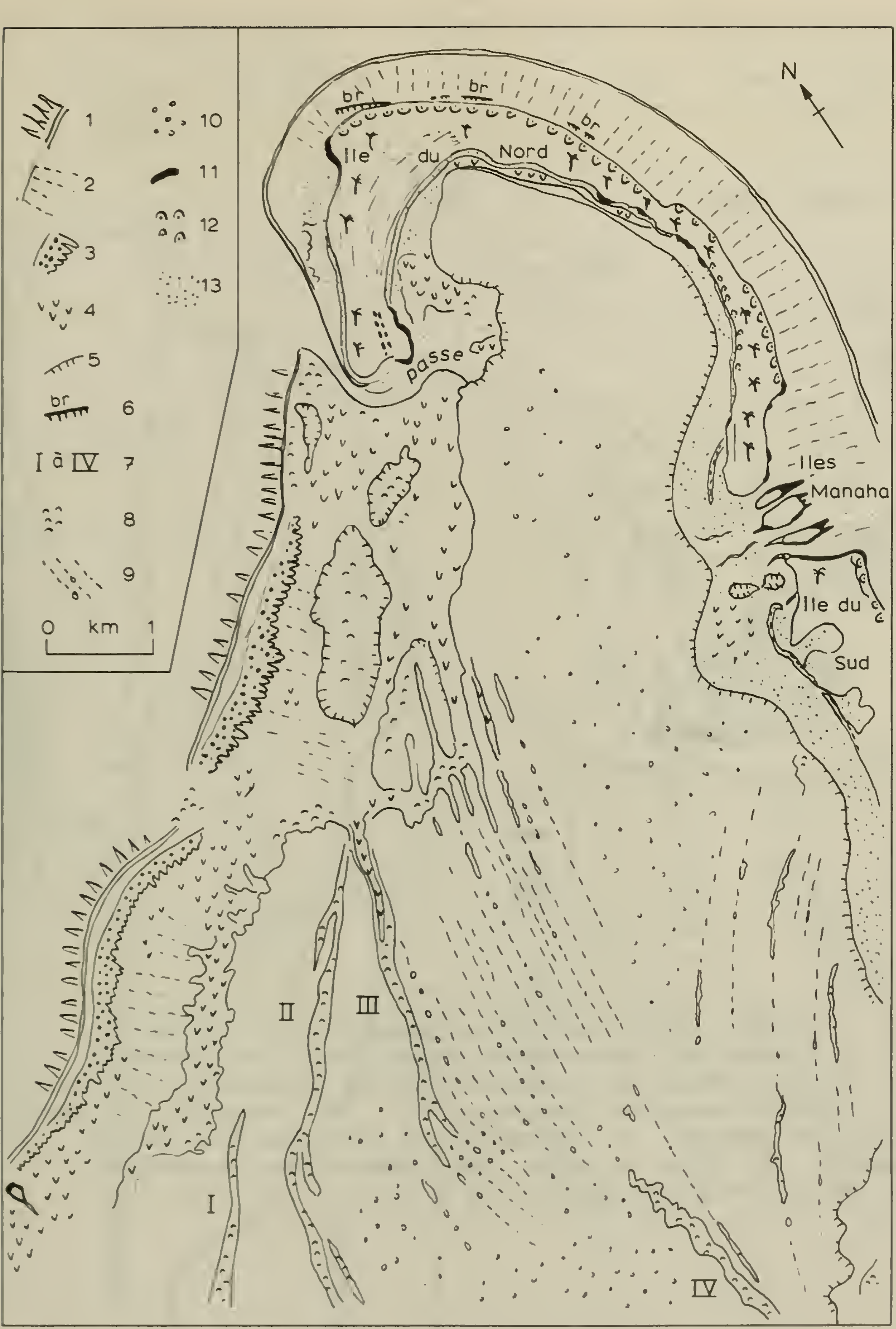


Fig. 4. Partie nord-est de l'atoll. (1) Pente externe à structure en peigne (spurs and grooves). (2) Plature striée. (3) Levée détritique externe de blocs. (4) Herbier à Cymodocées (5) Tombant sableux. (6) Beach-rock. (7) Grandes levées du lagon. (8) Peuplements subaffleurants de corail vivant dans le lagon. (9) Alignements du lagon. (10) Coral patches. (11) Affleurements rocheux du récif anciens. (12) Dunes. (13) Sable nu sur l'estran.

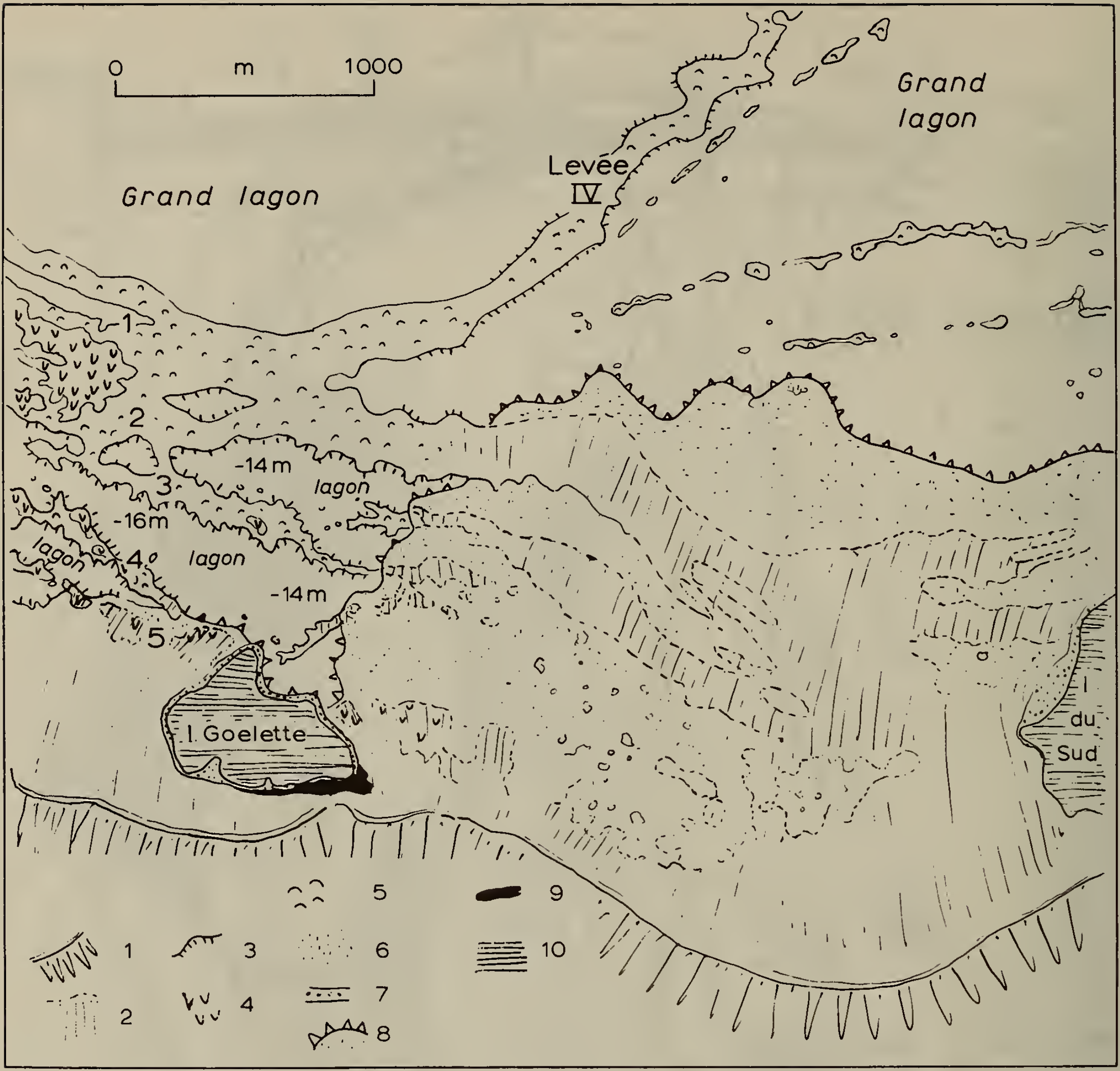


Fig. 5. Structure de la couronne aux abords de l'île Goëlette.
(1) Pente externe à structure en peigne (spurs and grooves).
(2) Parties striées de la plature révélant les anciens alignements.
(3) Tombant (rebord des lagons inclus). (4) Herbier. (5) Corail vivant peu immergé. (6) Accumulations sableuses nues sur la plature. (7) Plage de sable. (8) Tombant interne sableux.
(9) Socle (récif ancien) de l'île Goëlette. (10) Ile.

Fig. 6. A: Les alignements dans la partie sud-est du grand lagon.
B: Les alignements dans la partie nord du grand lagon au nord-est de la levée III.

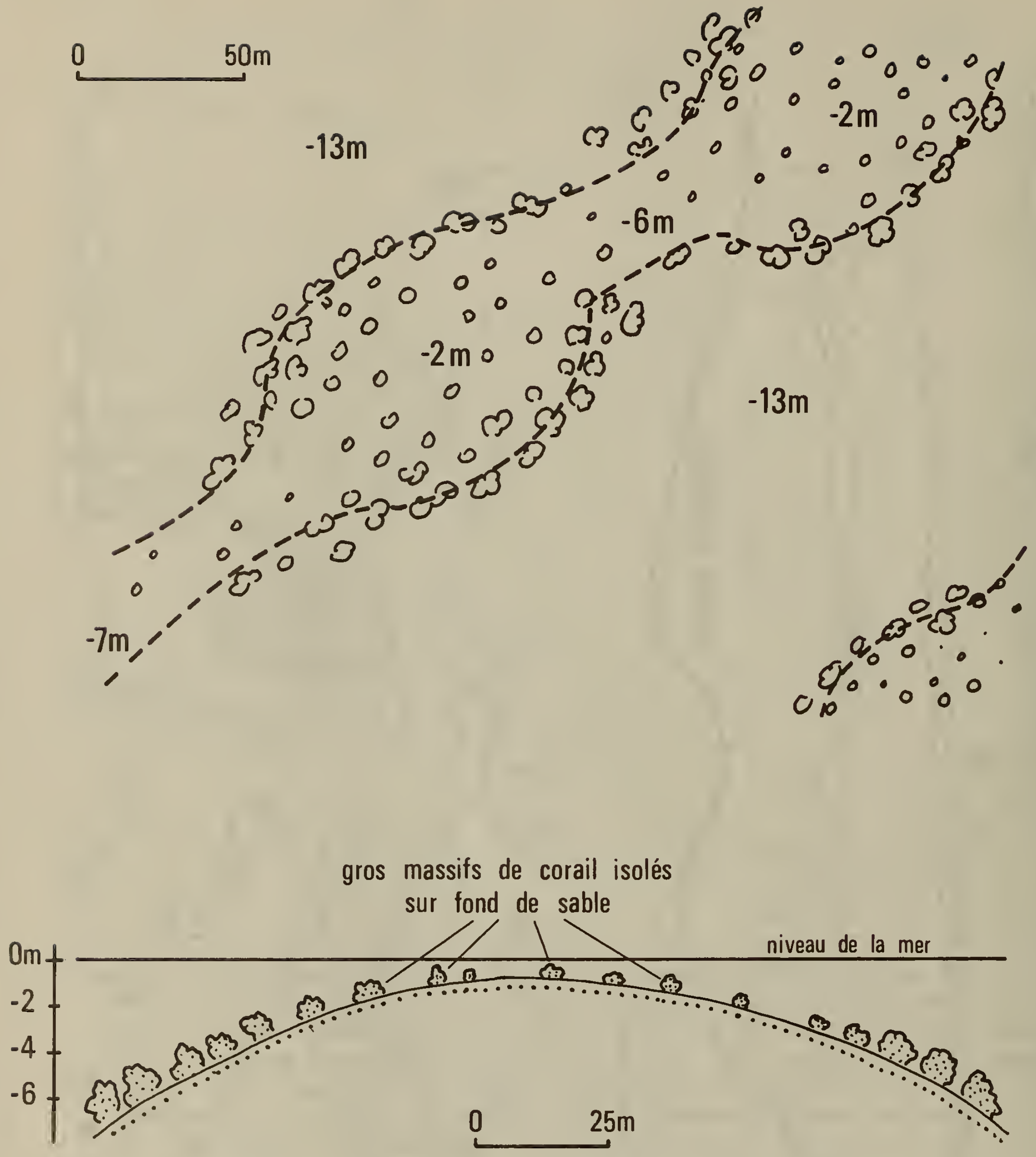


Fig. 7. Structure de détail de l'un des alignements du sud-est, en plan et en coupe transversale.

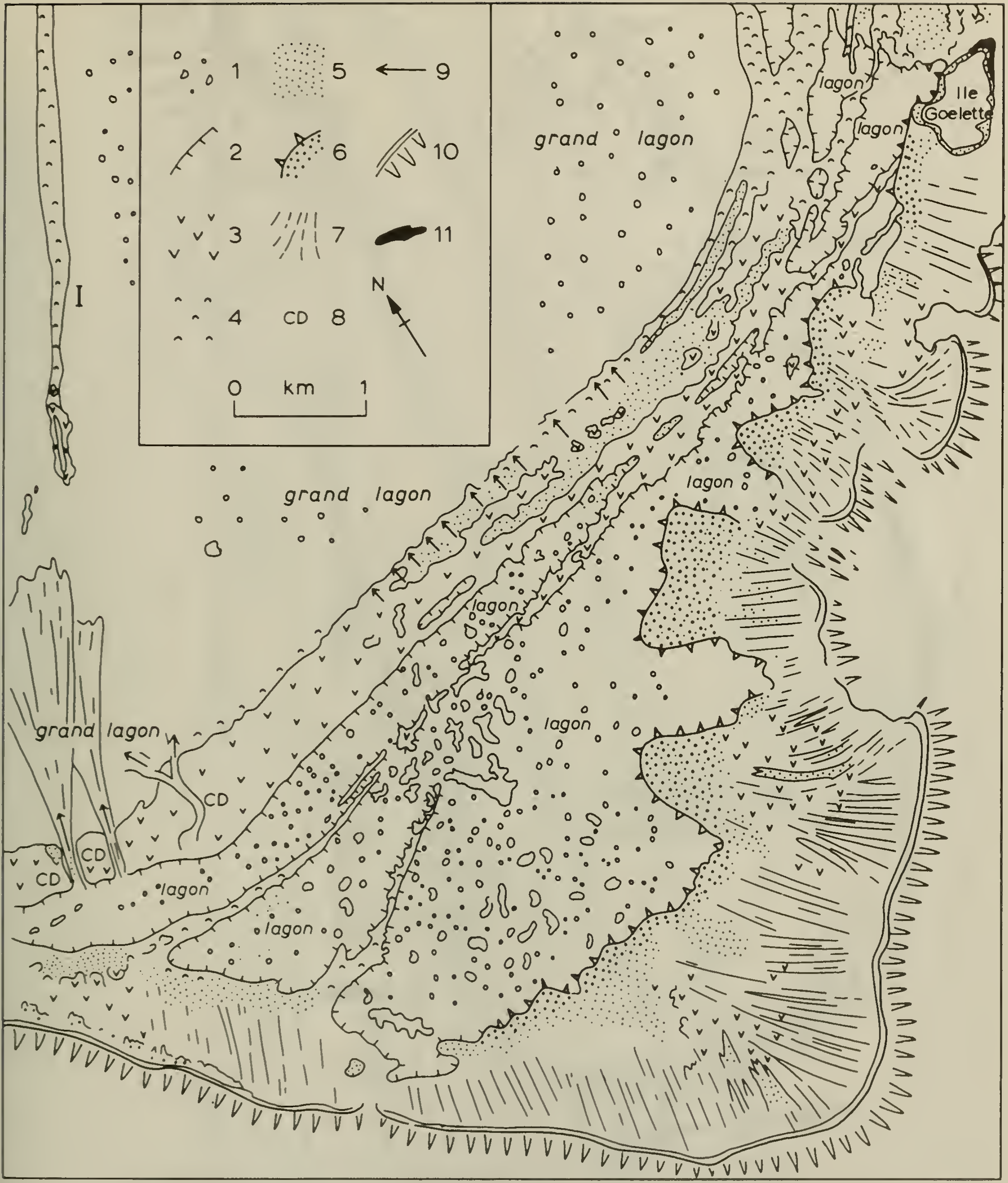


Fig. 8. Morphologie de la partie sud de l'atoll. (1) Eau profonde avec patés de corail. (2) Rebord des petits lagons inclus. (3) Herbier. (4) Corail vivant peu immergé. (5) Accumulations sableuses nues sur la plature. (6) Grandes accumulations sableuses paraboliques. (7) Parties striées des platures coralliennes. (8) Principaux chenaux de déversement dans le grand lagon. (9) Directions de déversement dans le grand lagon. (10) Pente externe à structure en peigne (spurs and grooves). (11) Socle (récif ancien) de l'île Goëlette.

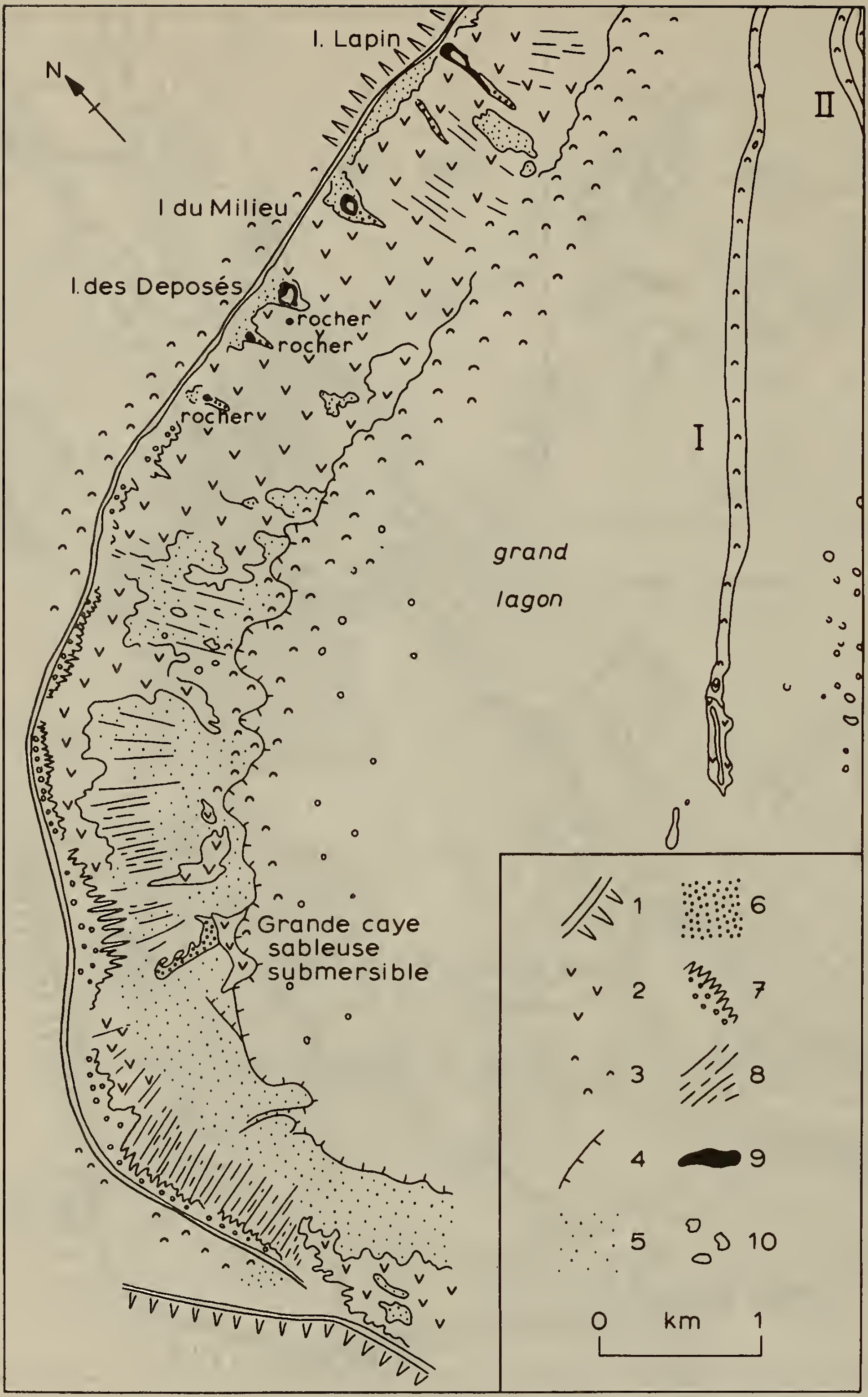


Fig. 9. Morphologie de la partie ouest de l'atoll. (1) Pente externe à structure en peigne (spurs and grooves). (2) Herbier. (3) Corail vivant peu immergé. (4) Retombée interne de la plature sur le grand lagon. (5) Accumulations sableuses nues sur la plature. (6) Caye de sable et accumulations sableuses en queue de comète derriére les ilots. (7) Levée détritique externe. (8) Parties striées de la plature corallienne. (9) Témoins du récif ancien. (10) Patés de corail dans le grand lagon.

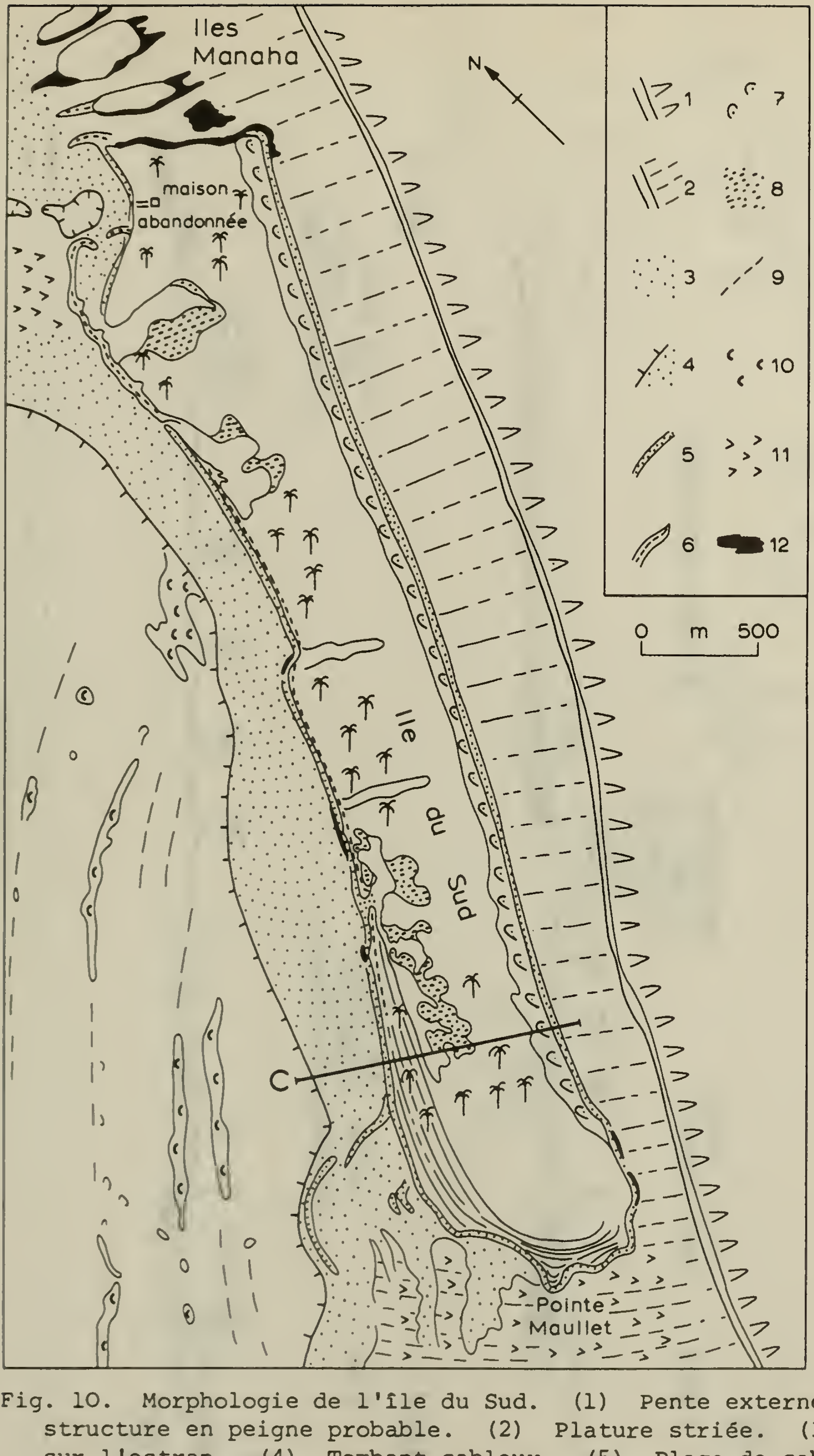


Fig. 10. Morphologie de l'île du Sud. (1) Pente externe, avec structure en peigne probable. (2) Plature striée. (3) Sable nu sur l'estran. (4) Tombant sableux. (5) Plage de sable. (6) Petite levée actuelle de régularisation du rivage interne. (7) Dunes. (8) Pseudo-mangrove à *Pemphis*. (9) Alignements du lagon. (10) Corail vivant peu profond sur les alignements. (11) Herbier à Cymodocées. (12) Affleurement rocheux du récif ancien.

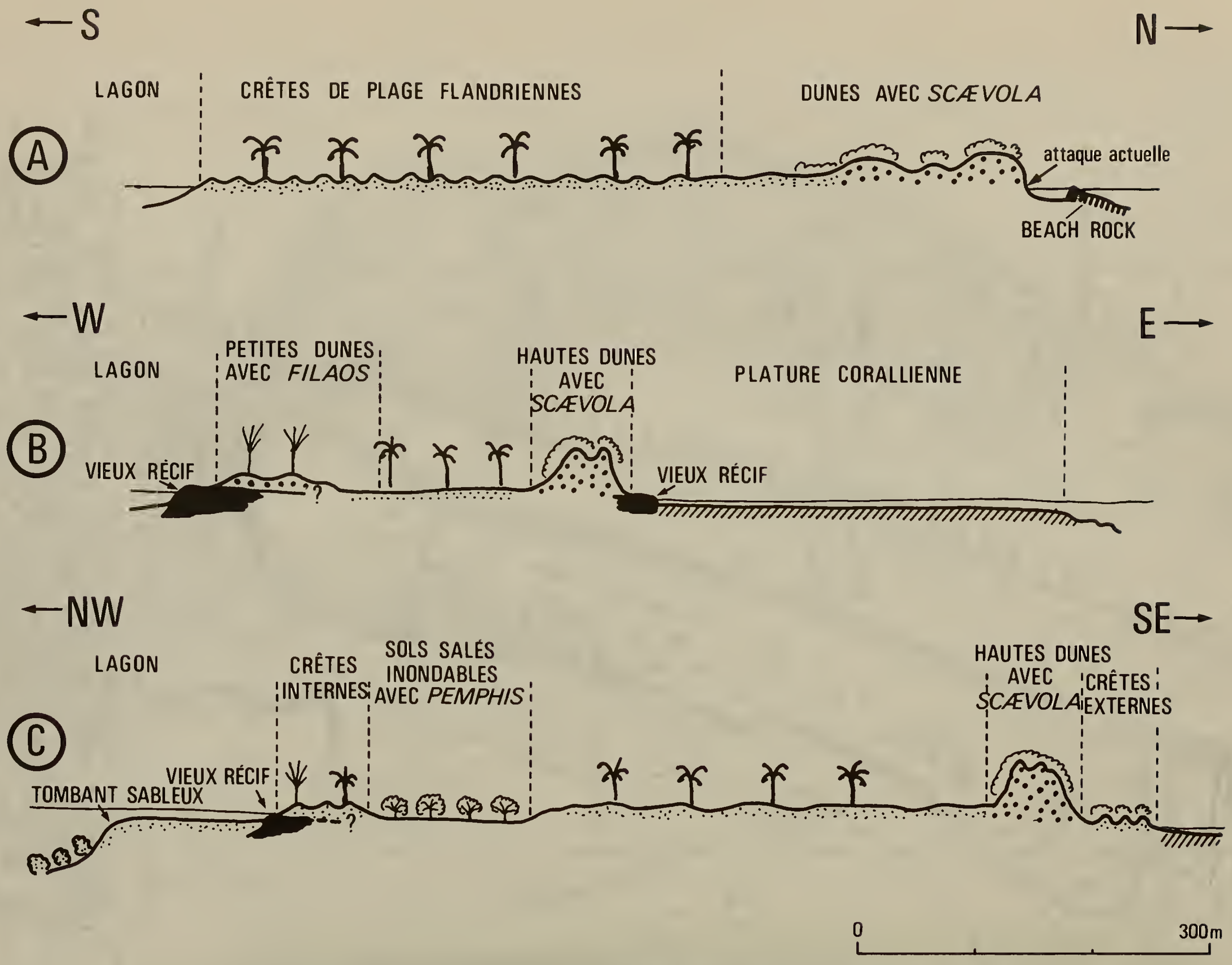


Fig. 11. Coupes transversales. A: Dans la partie septentrionale de l'île du Nord. B: Dans la partie centrale de l'île du Nord. C: Dans la partie méridionale de l'île du Sud selon C de la figure no. 10.

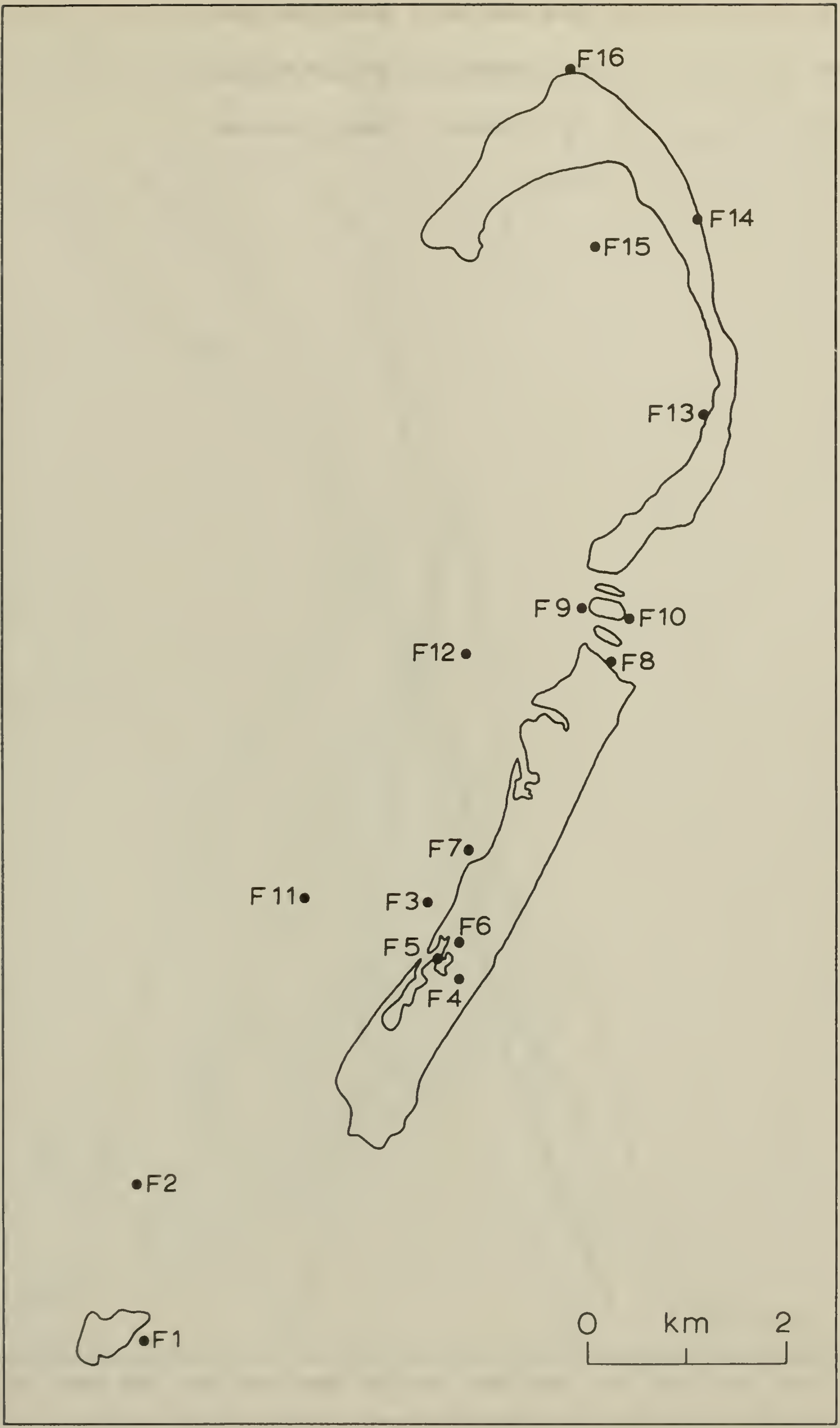


Fig. 12. Croquis de localisation des prélèvements.

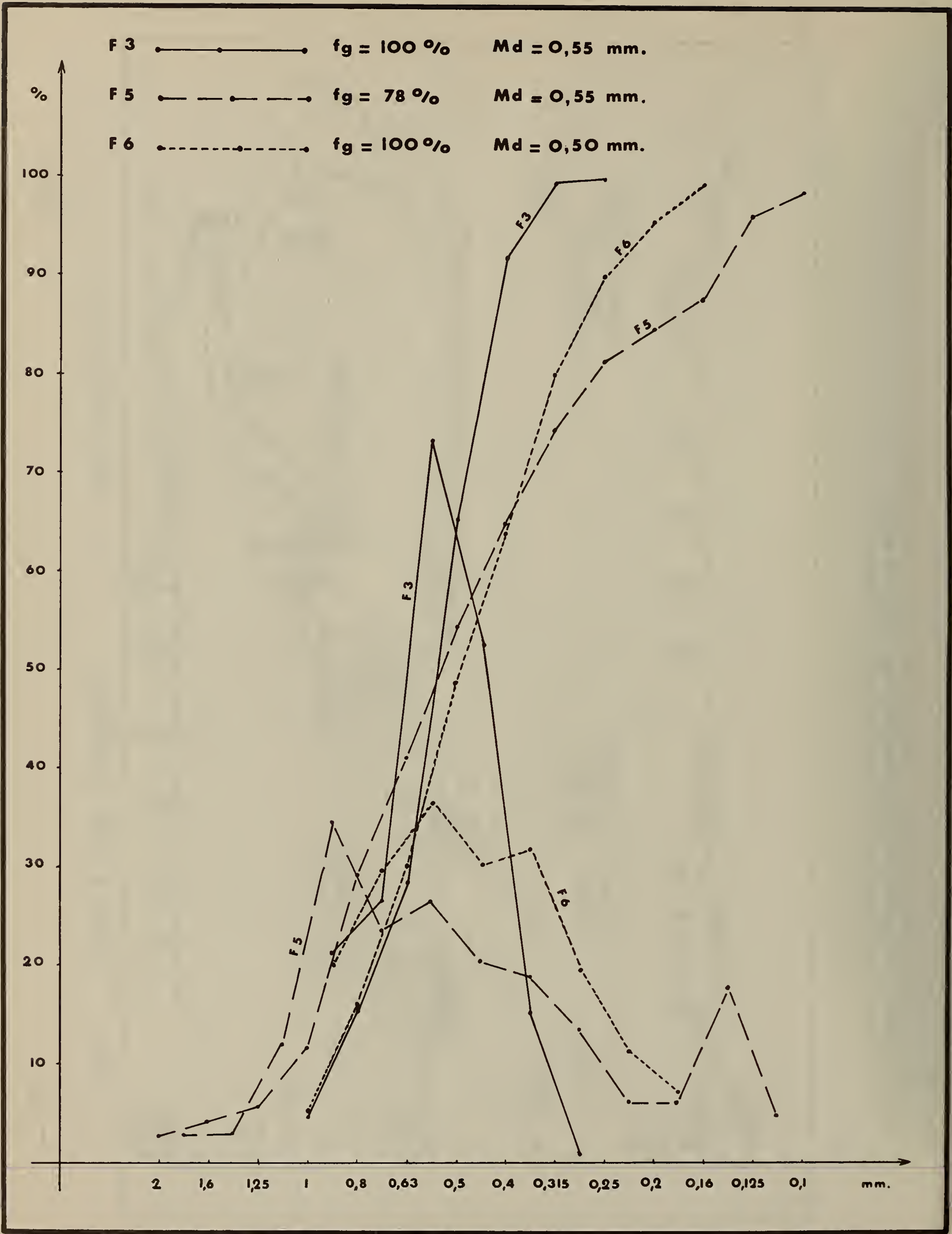
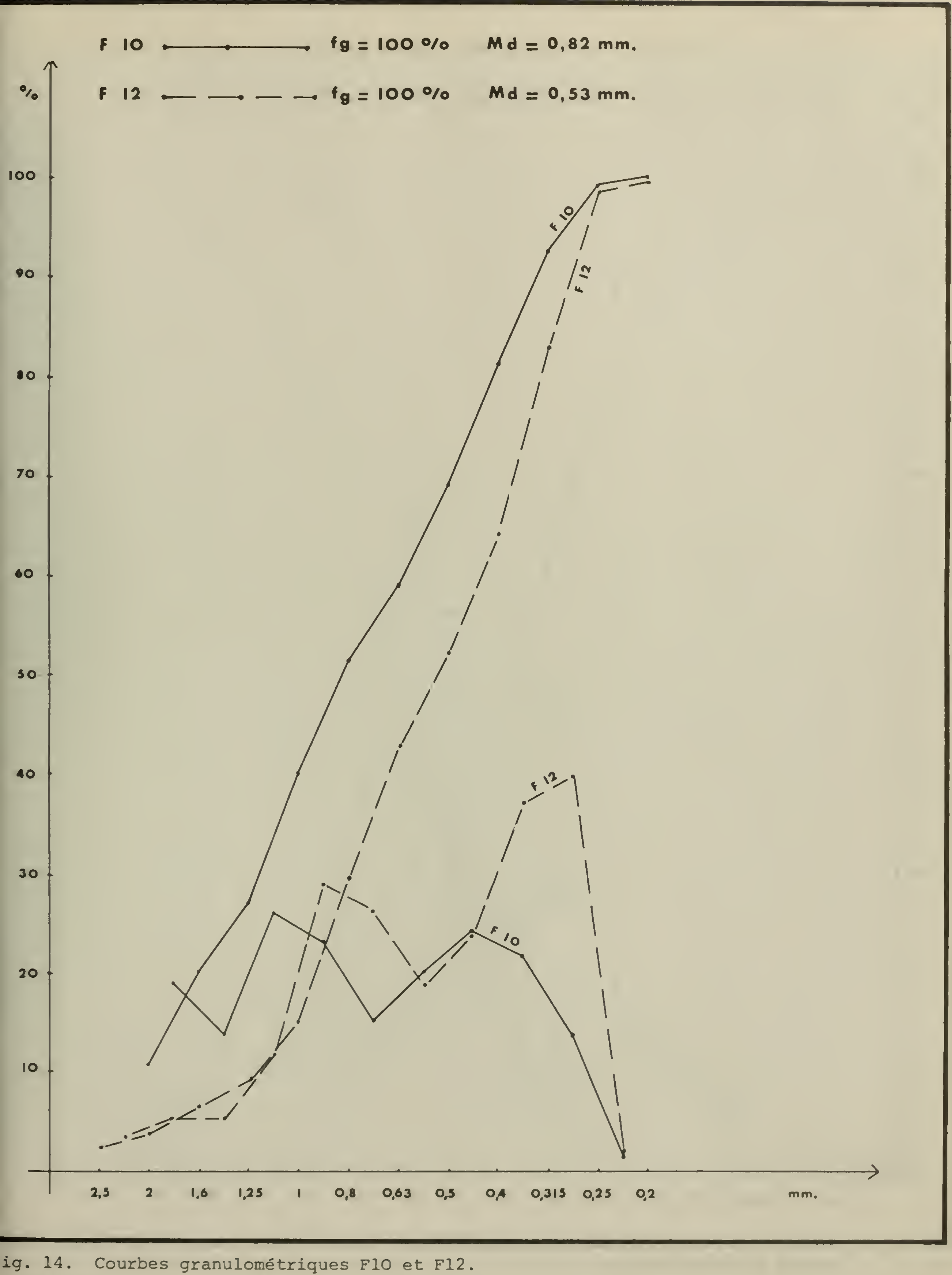


Fig. 13. Courbes granulométriques F3, F5 et F6.



ig. 14. Courbes granulométriques F10 et F12.

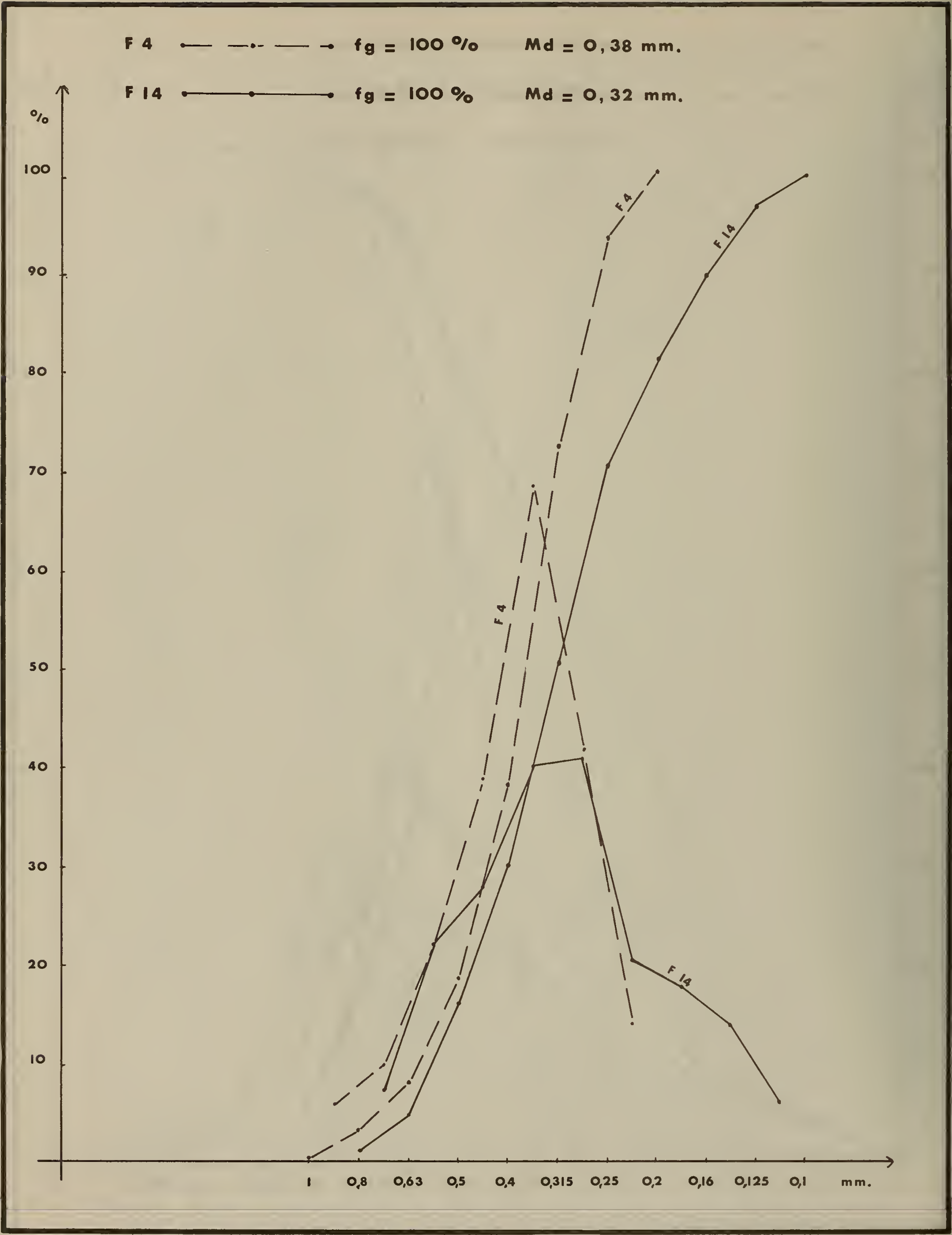


Fig. 15. Courbes granulométriques F4 et F14.

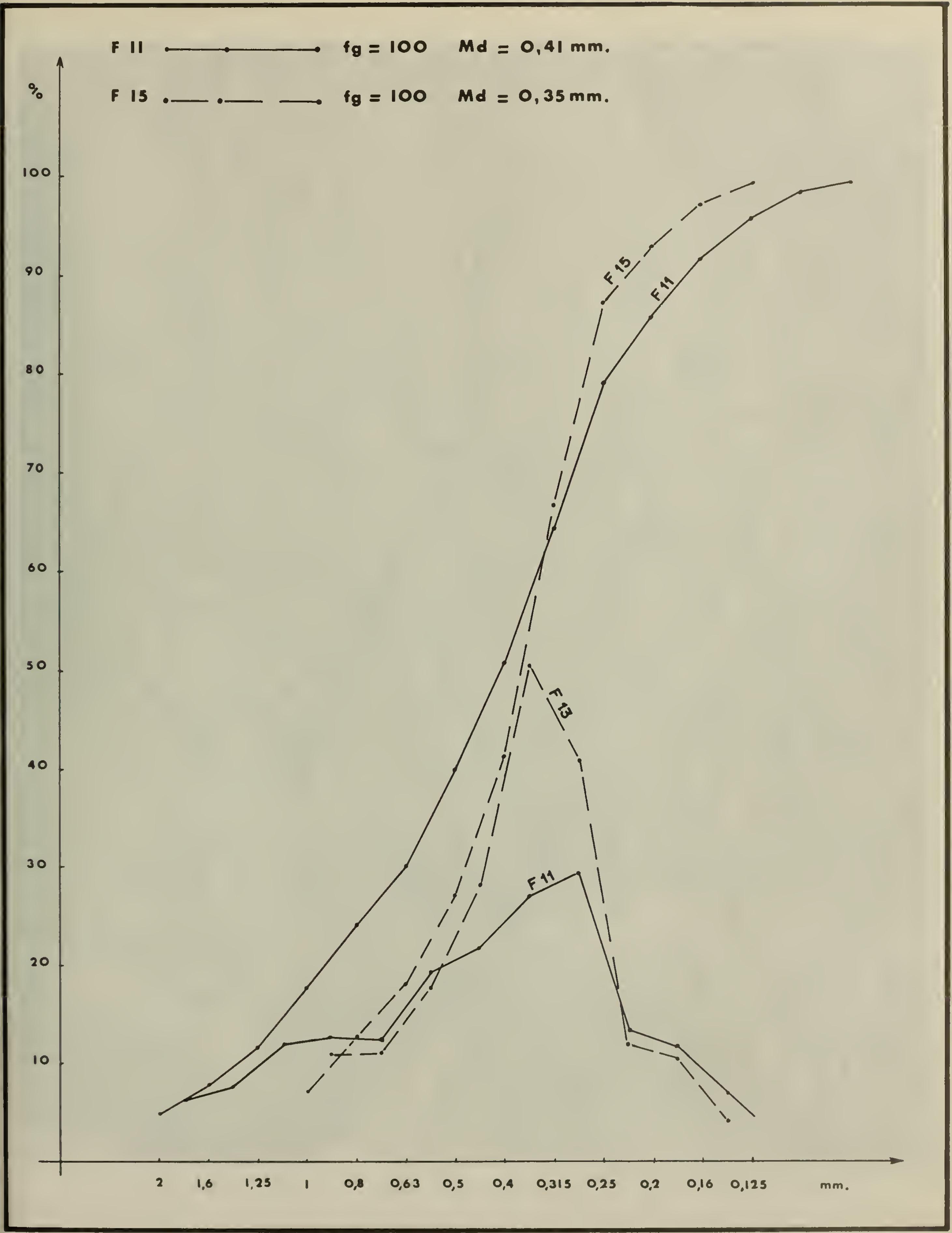


Fig. 16. Courbes granulométriques F11 et F15.

Photographie aérienne verticale no. 050. La grande levée IV, et la structure de la couronne de l'île Goëlette, avec les petits lagons inclus (voir la figure no. 5).

Photographie aérienne verticale no. 052. Structure de la couronne récifale au Sud-ouest de l'île Goëlette. Remarquer la structure complexe de la couronne (alignements avec taches d'herbier). Dans le coin Sud-est de la photographie, structure en Spurs and grooves dans les déferlements, et grands épandages sableux paraboliques actuels. Dans les lagons secondaires inclus, coral patches. Dans le coin Nord-ouest, le grand lagon.

Photographie aérienne verticale no. 048. L'extremité de la levée IV, et les quatres alignements de la partie Sud-est du grand lagon qui ont été examinés en plongée. Au bas de la photographie, les grandes accumulations sableuses paraboliques du Sud-est de la couronne (voir la figure no. 4).

Photographie aérienne verticale no. 044. Le Sud de l'île du Nord, le Nord de l'île du Sud, et les îles Manaha. Dans le lagon, coral patches.

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ATOLL RESEARCH BULLETIN

NO. 231

THE TERRESTRIAL VEGETATION OF AN INDIAN OCEAN CORAL ISLAND: WILINGILI, ADDU ATOLL, MALDIVE ISLANDS

I. TRANSECT ANALYSIS OF THE VEGETATION

by R. A. Spicer and D. McC. Newberry

II. A LIMITED QUANTITATIVE ANALYSIS OF THE VEGETATION DISTRIBUTION

by D. McC. Newberry and R. A. Spicer

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THE TERRESTRIAL VEGETATION OF AN INDIAN OCEAN CORAL ISLAND: WILINGILI, ADDU ATOLL, MALDIVE ISLANDS

I. TRANSECT ANALYSIS OF THE VEGETATION

by R.A. Spicer[1] and D.McC. Newbery[2]

ABSTRACT

The vegetation of a little-disturbed Indian Ocean coral island, Wilingili, Addu Atoll, is described both subjectively and in terms of three sea to lagoon transects. Exposure and edaphic factors were measured and the possible effects of these on vegetational pattern discussed. It is concluded that because soil maturity and exposure are both dependent on proximity to the strands, investigation of the relative importance of the influence of these variables on vegetational pattern is impossible from transect analysis in this case. However, the three transects spanning different widths of the island probably reveal vegetational differences determined by the salinity of the ground waters.

A list of plants collected in the course of the work is presented which represents practically the complete flora of Wilingili and includes eight confirmed new records for the Maldive Islands.

INTRODUCTION

The problems concerning the low floral diversity of oceanic islands and the factors influencing the distribution of vegetation

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have, to date, received little attention beyond a subjective appraisal. In the work reported here one island, Wilingili, was selected for detailed study in a more quantitative manner. Wilingili is a constituent island of Addu Atoll (0°38'S., 73°10'E.) which lies at the southern extremity of the Maldive Island chain.

The J. Stanley Gardiner expedition of 1899-1900 was the first to make extensive plant collections in the Maldive group. Soon afterwards Agassiz (1903) remarked "The vegetation..... of Wilingili .... [is] perhaps, as luxuriant as that of any island in the Maldives." Until 1972 the most recent work in this area was carried out by an expedition led by D.R. Stoddart in 1964. For political reasons work was confined to the heavily populated islands of Gan and Hittadu and it was suggested that the vegetation of a less disturbed island should be studied for comparison (Sigee 1966).

Wilingili with its lack of permanent human population provided a suitable site for such work which was undertaken by the authors during their six week (16 August to 28 September 1972) expeditionary visit to the Atoll.

GEOMORPHOLOGY

The total land area of Addu Atoll (Fig. 1) measures some 11.19 sq. km, with Wilingili, the sixth largest island in the group, occupying 0.79 sq. km. In 1836 Wilingili was charted as two separate islands but by 1900 (Gardiner 1903) it had become one and remains so to this day. Stoddart (1966) classifies the island as a seaward edge type since the seaward beach, lies only 90 m from the reef edge. This beach is mainly composed of rounded coral fragments 20 cm. or more in diameter.

The margins of coral islands usually show the highest relief due to the formulation of unconsolidated ridges of coral debris along seaward and, occasionally, lagoon shores. The material comprising the marginal ridges varies from fine sand through to cobbles and boulders (Fosberg & Carroll 1965). The Wilingili seaward ridge was noted by Agassiz (1903) as being "perhaps the highest we have seen in the Maldives". The vegetation, often consisting entirely of *Pemphis acidula* (Table 1), acts as a wind break with the result that a deposit of wind blown sand forms on the landward side of the seaward ridge. Unlike many Pacific islands the marginal ridge of Wilingili contained no large boulders, presumably because the high energy agents of transport and deposition, e.g. typhoons, are never experienced on Addu Atoll. No lagoon ridge was observed on Wilingili but there was some evidence of erosion along the southern lagoon shore which, like most of this beach is composed of fine coral sand.

Although drainage through unconsolidated coral debris is practically perfect, the porous nature of this material allows retention of often considerable amounts of rain water. The presence of a well (Fig. 2) indicates that a non-saline ground water lens is present, as on many other coral islands, and approaches the surface in numerous shallow hollows within the *Pisonia* forest (Fig. 2). Substantial amounts of fresh water are absent however in the narrower parts of the island and some hollows are at least periodically filled with brackish water.

CLIMATE

It was not possible to make extensive meteorological observations during the period of our stay on Wilingili, but the expedition of 1964 obtained data from the R.A.F. Staging Post on Gan and the following is summarized from Stoddart (1966).

The annual rainfall fluctuates between 300 cm and 188 cm with a mean of 229 cm and exhibits no clear seasonal pattern. The temperature, like the high humidity, is controlled by the surrounding ocean and has a mean of 28°C throughout the year. The diurnal temperature variation of 5.5°C far exceeds the annual range of 1.66°C.

Surface winds show the following pattern:

January	WNW - NNE
February	N - NE
March	W
April	W
May	W
June	SW - SE
July	S - SE
August	S - SE
September	SW
October	SW - W
November	W
December	WSW - NNE

Gales and strong winds are rare but winds up to 36 m/sec have been recorded during squalls.

TRANSECT METHODS

Three transect lines were set up in the positions shown in Fig. 2. Detailed measurement of microclimate was not possible, but an effective estimate of the relative exposure in different parts of the island was found from the loss of material tattered from 25 cm by 40 cm cloth flags (method of Lines & Howell 1963). Two flags were set up at the mid-point and extremities of the three transects and tattering proceeded over 35 days (21 August 1972 to 25 September 1972), after which the area lost was measured for each flag. The mean values for each site are shown in Fig. 3.

In the following studies of the vegetation representative specimens of each species encountered were collected and returned to the British Museum (Natural History) where they are now lodged, and were determined by Mr. E.W. Groves unless otherwise stated. It is considered that the species listed here (Appendix 1) represent the majority of those species to be found on Wilingili at the present time.

Records of the vegetation along each transect were made on a simple presence and absence basis for each metre interval of the transect length.

Soil pits, 30 - 40 cm deep, were dug every 20 m along the middle and southern transects and every 40 metres along the northern transect. pH measurements and soil samples (approx 150 g net weight) were taken at 5, 10 and 20 cm depths supplemented by observations on the appearance of the soils. It was not possible to dry the soils completely in the field, and therefore they were stored wet and dried on return to England. Analysis of the soils was then carried out as described in Newbery and Spicer (this issue).

SUBJECTIVE DESCRIPTION OF THE VEGETATION

The 'soil' of the southern tip of Wilingili was composed of coral blocks 10 - 20 cm in diameter in which *Scaevola taccada, Tournefortia argentea, Guettarda speciosa,* and *Pemphis acidula* survived.

To the north the vegetation increased in height to about two metres with *S. taccada* and *G. speciosa* predominating. Approximately 200 m from the southern tip *Pemphis acidula* was abundant under a canopy of coconut palms which continued northwards but with an increasingly dense understorey of *S. taccada*. Unlike the rest of the island the vegetation here was free of *Passiflora suberosa*. The seaward ridge supported *Pemphis acidula* which commonly grew down to, and often below, high water level.

Approximately 600 m from the southern tip of the island isolated individuals of mature *Pandanus* sp. were encountered along the lagoon shore though nowhere on Wilingili did this plant grow in abundance. Some 400 m south from the southern transect in the centre of the island a depression in the coral was found, covered with a pure stand of *Pemphis acidula*. It may be that this depression is periodically filled with brackish water.

Further north coconut palms formed dense vegetation, rich in such species as *Kalanchöe pinnata* and *Euphorbia* sp.

The area of the southern transect was rich in *Scaevola taccada*, many of the plants being covered in the parasitic leafless *Cassytha filiformis*. Many of the densely covered *S. taccada* had the appearance of being etiolated with long vertical stems crowned with a rosette of small chlorotic leaves. *Thuarea involuta* and *Lepturus repens* formed the ground cover in the clearings.

A number of individuals of *Cordia subcordata* were seen growing above cemented beach rock of a small bay on the Lagoon shore north of the southern transect. Northwards the coconut palms became sparse and stunted and the vegetation was composed mainly of *S. taccada, P. acidula* and *G. speciosa* with isolated plants of *Pandanus* sp., *Morinda citrifolia* and *Hibiscus tiliaceus*, many of which were covered in *Passiflora suberosa*. *Digitaria horizontalis* and *Boerhavia diffusa* occurred along the edges of trampled ground.

The open scrub vegetation reached as far north as the brackish water lake in the centre of the island (Fig. 2). Here the mangroves *Rhizophora mucronata* and *Bruguiera cylindrica* were found in abundance spreading north behind the seaward ridge.

The canopy of the northern part of the island was formed by *Pisonia grandis* and in the extremely high humidity of the forest community *Carica papaya, Morinda citrifolia, Neisosperma oppositifolia, Asplenium nidus* and *Tacca leontopetaloides* were to be found. Almost the entire understorey of the forest area was covered with the creeper *Passiflora suberosa*.

The most extensive coconut groves occurred on the lagoon side of the *Pisonia* forest. These areas are not planted as such but the growth of any germinating coconut appears to be encouraged by clearing the undergrowth around it.

An area of the forested region has been cleared and supports crops of *Zea mays* and castor oil *Ricinus communis*. Wherever the ground has been disturbed the weed *Wedelia biflora* was found in abundance.

The north-western tip of the island appeared to be similar to the southern tip in that the coral blocks comprising the extremely juvenile soil are subject to periodic marine disturbance and consequently only *P. acidula, S. taccada* and *G. speciosa* were found. In places however *Cassytha filiformis* was seen to be growing over bare coral debris and *Scaevola taccada*.

RESULTS

The occurrences of the various species encountered along the transects are given in Fig. 4.

Similarly the results of the soil analysis are presented in Figs. 5, 6 and 7, with pH measurements in Table 1.

Table 1. pH measurements of the soils sampled along the three transects.

Northern Transect Sample Sites

Depth	A	B	C	D	E	F	G	H
5cm	8.5	7.7	7.9	8.2	8.2	7.7	7.0	7.7
10cm	8.6	8.2	7.8	8.5	8.0	8.1	7.2	8.3
20cm	8.5	8.4	7.9	8.4	8.5	8.3	7.1	8.3

Middle Transect Sample Sites

Depth	A	B	C	D	E	F
5cm	8.3	7.9	7.8	7.7	7.6	8.4
10cm	8.7	8.5	8.3	7.8	8.2	8.8
20cm	8.7	8.5	8.3	8.5	8.3	9.2

Southern Transect Sample Sites

Depth	A	B	C	D	E	F
5cm	8.2	8.0	8.1	8.5	8.0	8.5
10cm	8.3	7.8	8.3	8.5	8.0	8.5
20cm	8.3	8.3	8.2	8.7	8.4	8.8

DISCUSSION

The flora of Wilingili, as with many other oceanic islands, is extremely restricted, being almost totally represented by the 72 species presented here. Consequently the expression, by the vegetation of environmental variables is often concealed (Stone 1953).

The primary sources of land material are reef organisms (except for pumice which is common on a number of atolls (Sachet 1955), and which is locally abundant on Wilingili), and it is only with time that the coral debris becomes altered to provide a variety of habitats that may be reflected by vegetational patterns. This differentiation into communities might be expected to reflect proximity to the sea and maturity of soil. Naturally these two factors are strongly linked.

As can be seen from the tatter flag data (Fig. 3) proximity to the sea is also associated with exposure, thus it may be difficult to isolate the effects of single environmental factors on the vegetation, from simple transect analysis.

If percentage organic matter is an indicator of maturity in atoll soils then the soils of the northern transect are the most developed (Fig. 6). Their most striking feature is the high phosphate levels associated with the more mature *Pisonia grandis* forest (Figs. 4 and 6). Such an association is commonly found in Pacific atolls (Fosberg 1953) and is probably the result of guano from roosting sea birds. It is not likely that *P. grandis* is dependent on the phosphate for its growth as has been suggested by Shaw (1952) since it is also found on relatively low phosphate soils e.g. sample site F. The association of *P. grandis*, phosphorus, and a layer of relatively acid raw humus has been discussed by Fosberg (1954, 1957a). He has pointed out that the acidity of raw guano (pH 6.0) is not sufficient to take the calcium phosphate present in guano into solution and it is only when guano falls onto the thin, acid, raw humus layer, characteristic of mature *P. grandis* forests, that the phosphate passes into solution later to be precipitated as a phosphate hardpan when the underlying coral debris is reached. Wiens (1962) concludes that while *P. grandis* does not necessarily require phosphate and acid soils for germination it undoubtedly thrives in such an environment since its relatively shallow root system is often directly exposed to such conditions. However the development of a raw humus layer and acid conditions characteristic of Jemo soils, as described by Fosberg (1954), are not fully developed on Wilingili (Table 1).

By comparison the middle and southern transects represent more open scrub vegetation. Here the island is only a third of the width of the northern transect, thus a substantial fresh water lens cannot be supported (Stone 1953), with obvious consequences in times of relative drought.

The absence of a non-saline groundwater lens is indicated in the southern transect by the widespread distribution of the salt tolerant bushes *Scaevola taccada* and *Guettarda speciosa*. These plants do however provide cover and locally humid conditions to allow *Passiflora suberosa* to survive.

The coconut palms on the southern half of the island appear to be less vigorous and set further apart than on the northern lagoon shore and it has been noted by Wiens (1962) that the density of coconut palms tends to be less on drier atolls. However Hatheway (1953) has stated that the coconut thrives over an extremely wide range of environmental conditions, consequently it is "utterly worthless as an indicator of environmental differences". Although this is true, particularly with reference to ground water salinity, the fronds appear to suffer from sea spray damage. It is thus a common practice to protect coconut groves from direct spray by leaving a band of essentially natural vegetation on the seaward side of an island, thus the greatest density of coconut palms is found along the lagoon shore of Wilingili.

It may be readily seen from Fig. 5 that the concentration of magnesium is consistently higher on both lagoon and sea strands. Stone (1953) has noted that some reef organisms, e.g. *Lithothamnion*, may contain up to 25% magnesium carbonate. However this is relatively soluble and becomes leached from the older soils, hence its lower concentration in the middle of the island. This hypothesis is also supported by a general increase in magnesium concentration with depth.

Sodium, however, shows a uniform distribution across the Island apart from the mangrove peat. Undoubtedly the contribution of sodium in spray must be considerably higher towards the strands but this is not reflected in the analyses. One is led to conclude, therefore, that any contribution by spray is rapidly leached from the surface soils.

CONCLUSIONS

Coral islands are generally considered to exhibit a strong environmental gradient from windward to leeward and from sea shore to lagoon shore. On Wilingili the former gradient is not evident due to the variable nature of the prevailing wind direction. Exposure however is considerably less in the centre of the island than along the strands and because of the proximity of the seaward ridge to the reef edge, the effect of spray is more marked on the seaward side. The maturity of soils as indicated by percentage organic matter and associated ionic availability, is mainly correlated with distance from the strands, hence it is difficult to isolate exposure effects from edaphic factors. This argument also applies to textural differences in the soils. However there are marked vegetational differences between the northern transect and the two more southerly ones which are probably determined by the salinity of ground waters. Where the island is wide enough to support a fresh ground-water lens the development of a *Pisonia* forest has in turn greatly modified the soil.

Superimposed upon this natural vegetation pattern are the activities of man especially with regard to the managing of coconut groves and ground disturbance. Where this is most marked weeds such as *Wedelia biflora* are able to grow in abundance.

ACKNOWLEDGEMENTS

As members of the 1972 Imperial College Maldive Islands Expedition we should like to record our thanks to the many who supported and financed us, especially the Imperial College Exploration Board, The Royal Geographical Society, The Royal Air Force, the Maldivian Government and the British Museum (Natural History). We would also like to take this opportunity of expressing our gratitude to Mr. E.W. Groves for determining plant specimens and preparing the species list. Sincere thanks go to Dr. A.J. Morton of this department for helpful discussion and Professor A.J. Rutter for use of facilities for soil analysis.

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Appendix 1. Botanical Specimens collected on the Imperial College of Science & Technology (London) Expedition to the Maldive Islands, Indian Ocean, 1972.

Material determined by Mr. E.W. Groves, Dept. of Botany, British Museum (Natural History) London unless otherwise stated. The collection has been deposited in the Herbarium of that Museum.

* indicates new species recorded to the Maldives.

ANGIOSPERMS

DICOTYLEDONS

Portulacaceae

Portulaca tuberosa (Roxb.) Trin.

Guttiferae

Calophyllum inophyllum L.

Malvaceae

Hibiscus tiliaceus L.
Sida humilis Willd.

Tiliaceae

**Triumfetta procumbens* Forst. f.
Corchorus aestuans L.

Surianaceae

Suriana maritima L.

Oleaceae

**Ximenia americana* L. var. *americana* (det. F.R. Fosberg July 1973)

Rhamnaceae

Colubrina asiatica (L.) Brongn.

Leguminosae

Caesalpinia bonduc (L.) Roxb.
Canavalia cathartica Thou.
Cassia occidentalis L.
Vigna marina (Burm.) Merrill

Crassulaceae

Kalanchoe pinnata (Lam.) Pers.

Rhizophoraceae

Bruguiera cylindrica (L.) BI.
Rhizophora mucronata Lam.
**Ceriops tagal* (Perr.) C.B. Robinson (det. F.R. Fosberg July 1973)

Lythraceae

Pemphis acidula Forst.

Turneraceae

Turnera ulmifolia L.

Passifloraceae

Passiflora suberosa L.

Caricaceae

Carica papaya L.

Cucurbitaceae

Cucumis melo L.

Aralisceae

Polyscias guilfoylei (Bull.) Bailey (det. F.R. Fosberg July 1973)

Rubiaceae

Morinda citrifolia var *bracteata* Hook. f.
Guettarda speciosa L.

Compositae

Launaea pinnatifida Cass.
Wedelia biflora (L.) DC.
Tridax procumbens L.
Conyza bonariensis (L.) Crong.
Vernonia cinerea var. *parviflora* (Bl.) DC.

Goodeniaceae

Scaevola taccada (Gaertn.) Roxb.

Apocynaceae

Neisosperma oppositifolia (Lam.) Fosberg & Sachet.
(*Ochrosia oppositifolia* (Lam.) K.Schum).

Boraginaceae

Tournefortia argentea L.f.
Cordia subcordata Lam.

Convolvulaceae

Ipomoea pes-caprae L.
Ipomoea macrantha R. & S.
Jacquemontia paniculata (Burm.f.) Hallier f.

Scrophulariaceae

Bacopa monnieri (L.) Wettst.

Nyctaginaceae

Pisonia grandis R. Br.
Boerhavia diffusa L.

Amaranthaceae

Alternanthera sessilis (L.) R.Br.
Achyranthes aspera L.

Lauraceae

Cassytha filiformis L.

Hernandiaceae

Hernandia peltata Meissn.

Euphorbiaceae

Ricinus communis L.
Euphorbia cyathophora Murray
**Euphorbia indica* Lam.
**Laportea interrupta* (L.) Chew (det. F.R. Fosberg, July 1973)
Agyneia bacciformis (L.) Juss.
Phyllanthus urinaria L.

Moraceae

Ficus benghalensis L.

MONOCOTYLEDONS

Amaryllidaceae

Crinum asiaticum L.

Taccaceae

Tacca leontopetaloides (L.) O.Ktze.

Pandanaceae

Pandanus sp. (juvenile material)

Aroideae

Colocasia esculenta L.

Cyperaceae

Cladium jamaicense Crantz. var *chinense* (Nees) Koyama
Cyperus ligularis L.
Cyperus conglomeratus Rottb. forma *pachyrrhizus* (Nees) Kukenth.
Cyperus dubius Rottb.
**Fimbristylis cymosa* ssp. *spathacea* (Roth) Koyama
Fimbristylis ferruginea (L.) Vahl

Gramineae

Eragrostis tenella (L.) Beauv.
Apluda mutica L.
**Digitaria horizontalis* Willd.
Dactyloctenium aegyptium (L.) Willd.
Thuarea involuta (Forst) R.Br.
Lepturus repens (Forst.f.) R.Br.
**Oplismenus* sp. (possibly *O. compositus*)

PTERIDOPHYTES

Psilotaceae

Psilotum nudum (L.) Beauv.

Aspleniaceae

Asplenium nidus L.

Davalliaceae

Nephrolepis hirsutula (Forst.f.) Presl

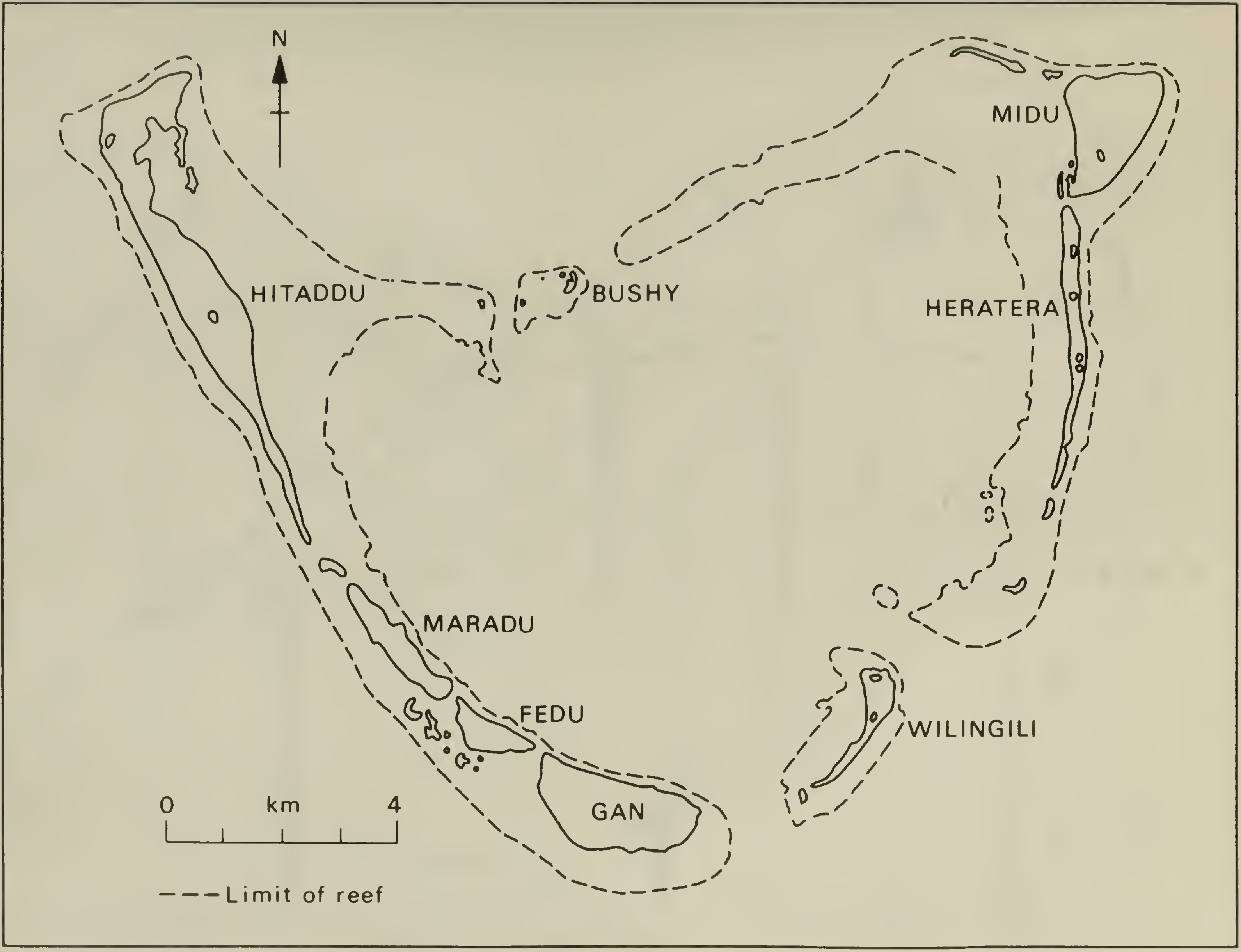


Fig. 1. Addu Atoll, Maldive Islands.

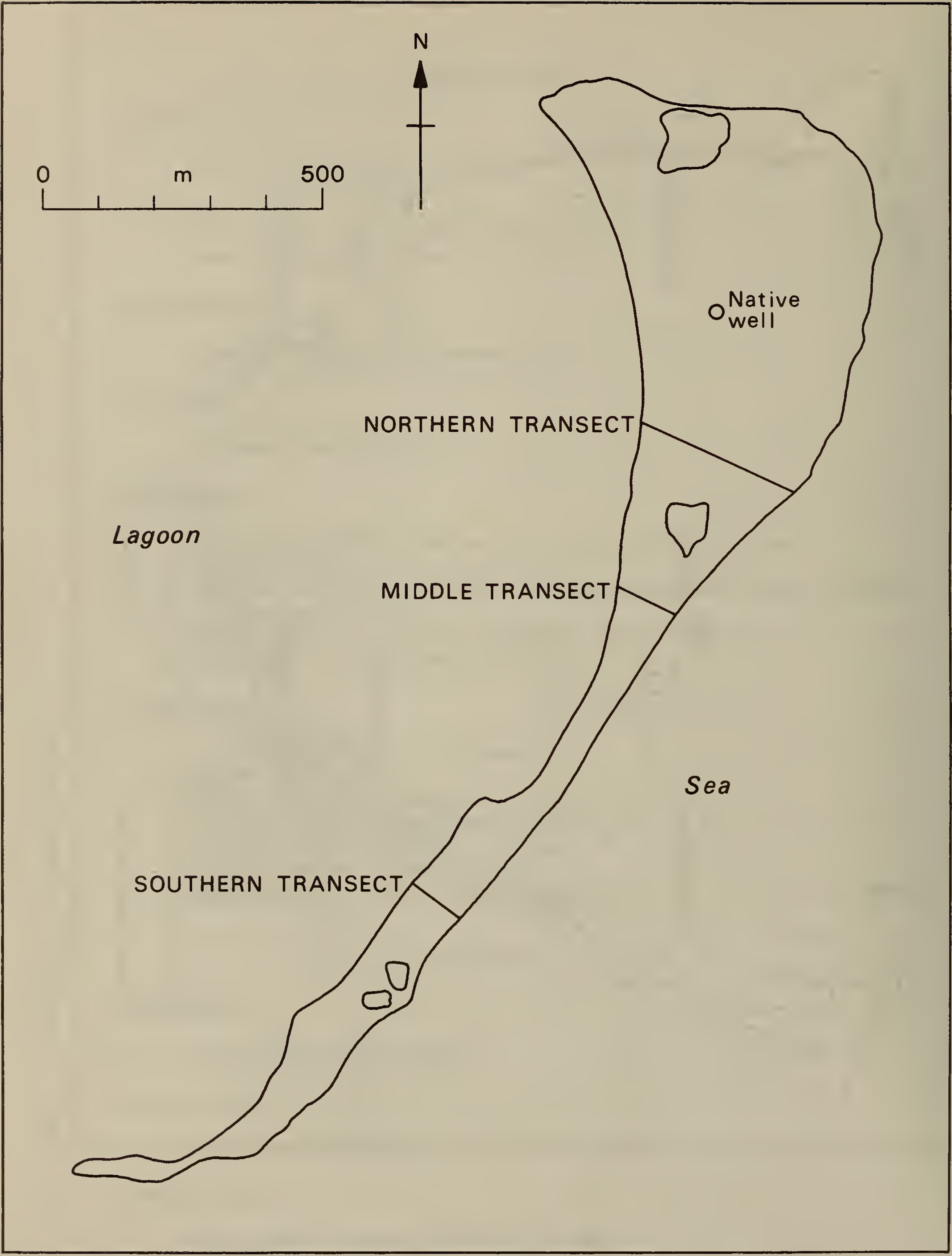


Fig. 2. Wilingili, Addu Atoll, showing the positions of the transects. Tatter flags were positioned in the centre and at the ends of the three transects.

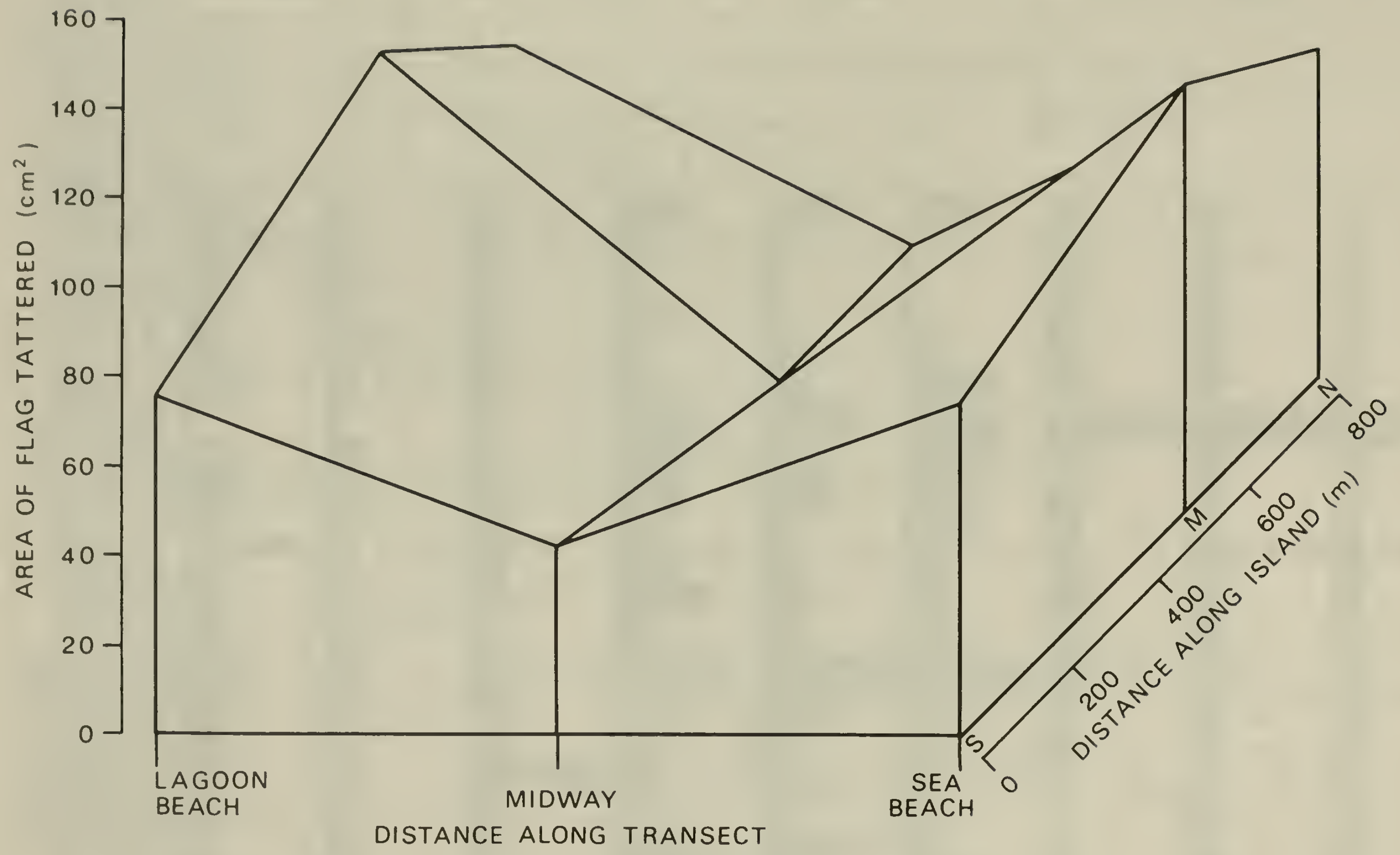


Fig. 3. Three dimensional representation of relative exposure at nine points on the Island as measured by tatter flags.

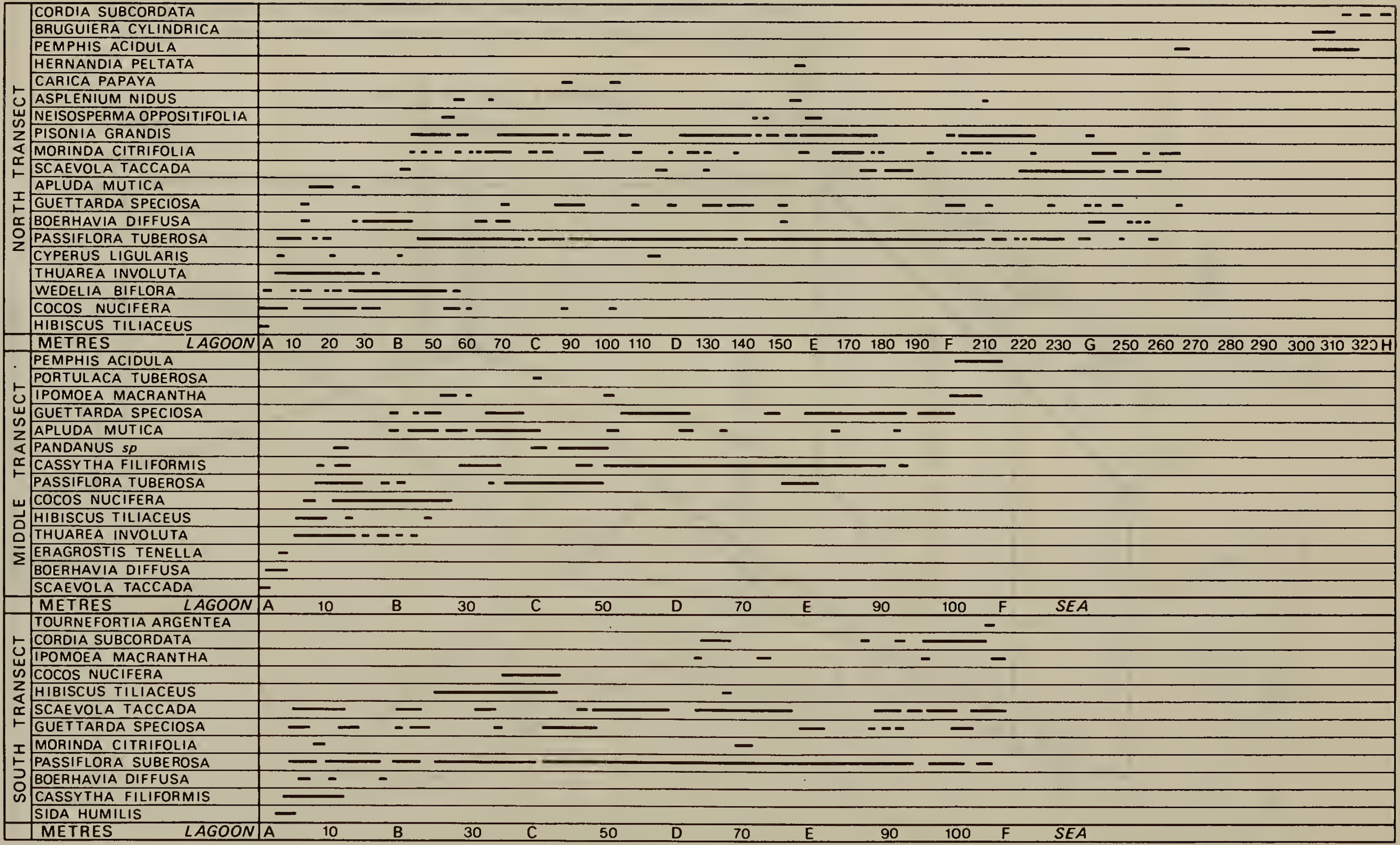


Fig. 4. The distribution of species along the transects. The presence of a species in every 1 metre section of the transect is marked by a horizontal bar.

Fig. 5. The distribution of the elements Sodium, Magnesium and Calcium in the soil samples from three transects spanning the width of Wilingili. The values represent the total amounts of the elements present.

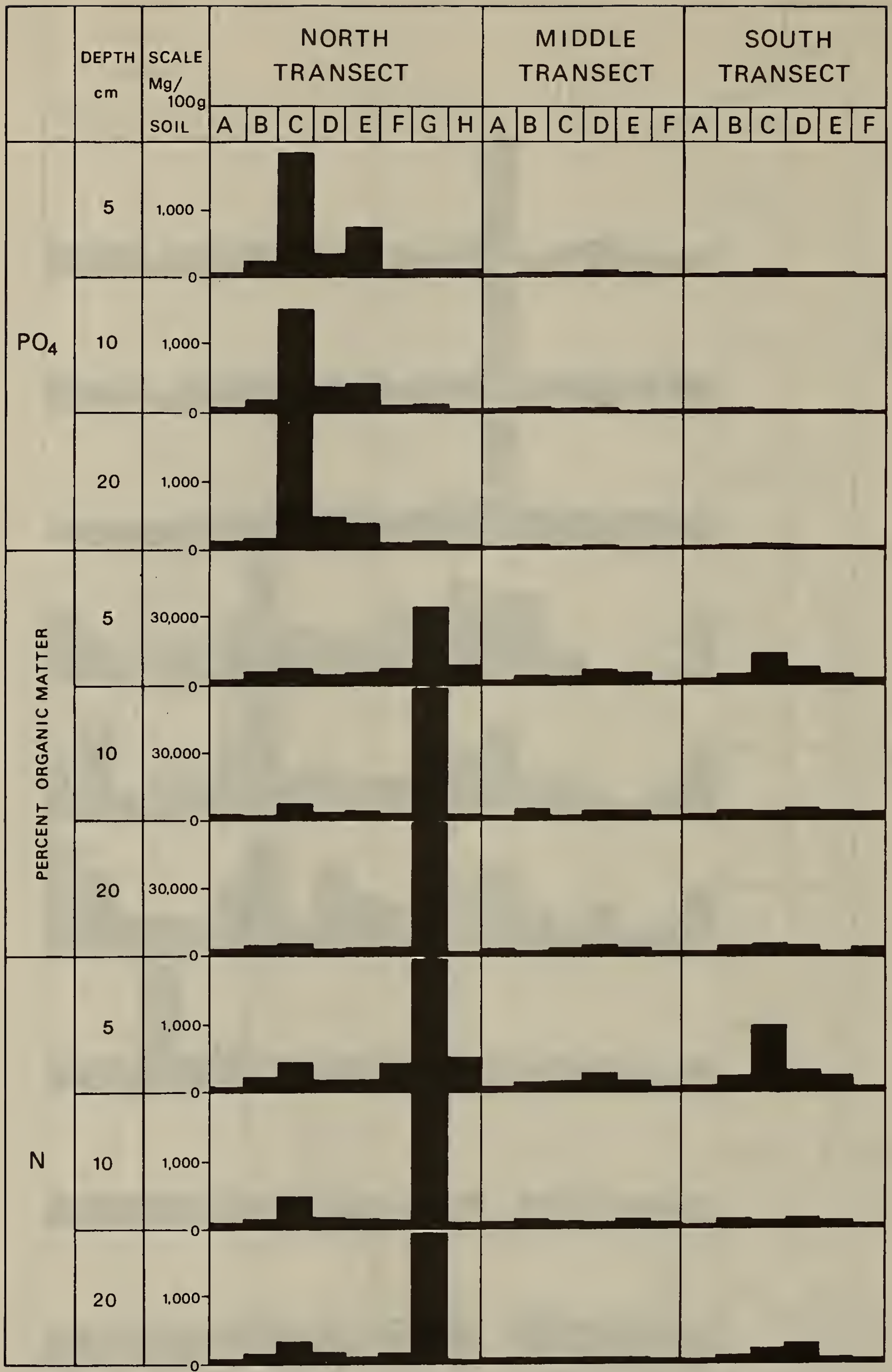
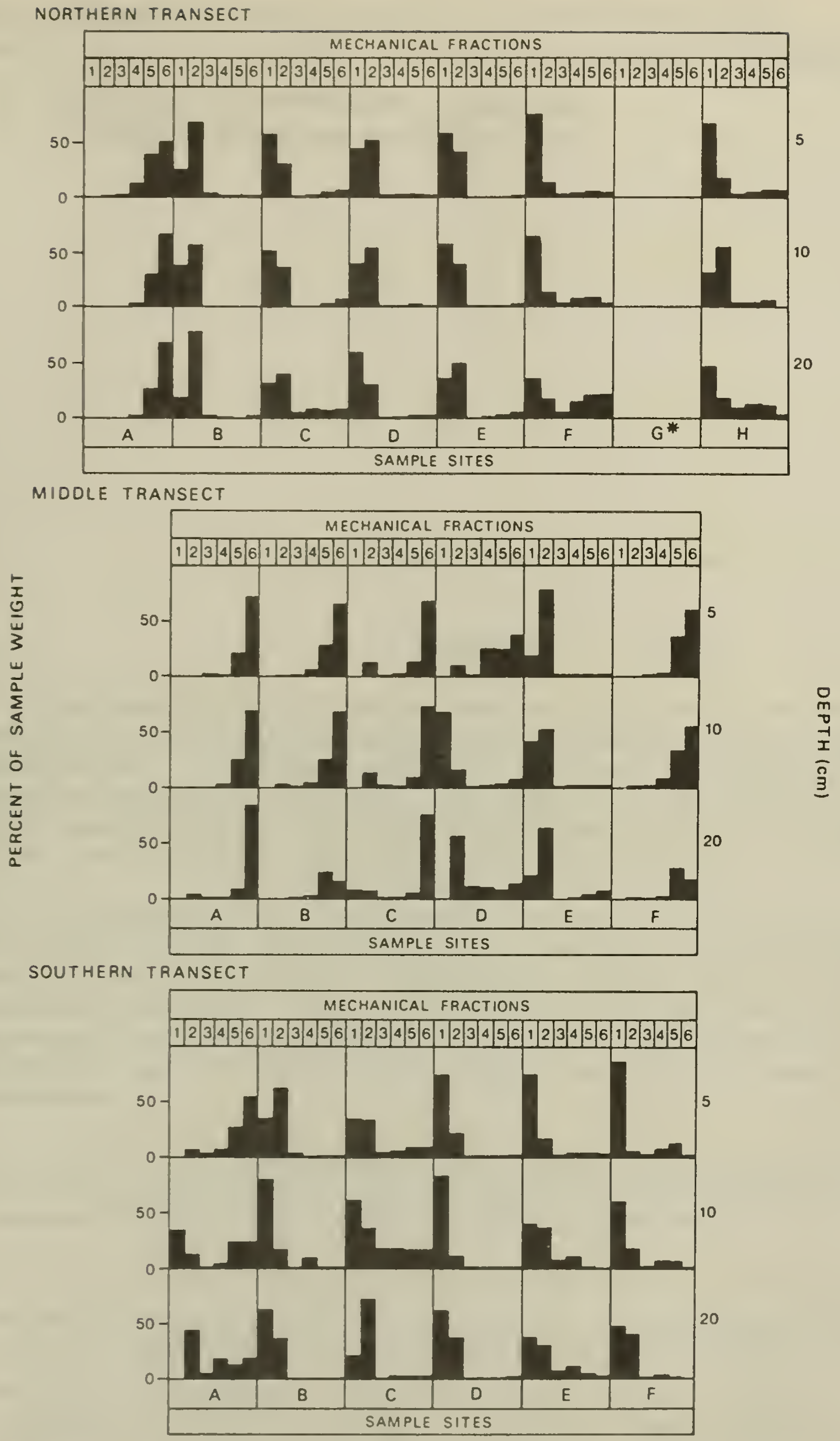


Fig. 6. Total Phosphate and Nitrogen levels, together with percentage organic matter in the soils from three transects.



NORTHERN TRANSECT

MIDDLE TRANSECT

SOUTHERN TRANSECT

Fig. 7. Mechanical fractions of the transect soils. The asterisks denote those samples composed entirely of organic Mangrove peat.

THE TERRESTRIAL VEGETATION OF AN INDIAN OCEAN CORAL ISLAND: WILINGILI, ADDU ATOLL, MALDIVE ISLANDS

II. A LIMITED QUANTITATIVE ANALYSIS OF THE VEGETATION DISTRIBUTION

by D.McC. Newbery[1] and R.A. Spicer[2]

ABSTRACT

The distribution of the vegetation of Wilingili was assessed by measurement of 45 species and 51 soil variables at each of twenty chosen sites. Principal components analysis (PCA) was used to identify the main gradients of the vegetation, the component scores being correlated with the floristic and environmental variables to detect associations between these variables.

Two gradients were identified. Firstly, a mid-island lagoon to sea shore gradient of decreasing sandiness and increasing sodium along which a change from coconut communities, through bush to strand vegetation was seen. The second, a north to south gradient represented changes from bush to forest accompanied by increasing iron, phosphorus and nitrogen with decreasing sandiness, magnesium and carbonate.

A simple model relating the main types of vegetation, the position of the gradients and an approximate realisation to the successional development of the island is discussed.

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INTRODUCTION

The general features of the vegetation on Wilingili have been described in the previous paper, in which an identifiable lagoon-to sea-shore gradient was studied. Here, we adopt an alternative approach by sampling the vegetation over all the island with a view to the recognition of the main floristic and environmental gradients illustrated by the use of ordination techniques.

The data collected are not extensive and so the application of numerical multivariate techniques and their interpretation will be limited. This paper, we hope, will serve as an introduction to the, as yet, little studied topic of the ecology of terrestrial coral island vegetation.

METHODS

Vegetation and soil measurements of stand sites

Twenty subjectively chosen sites, hereafter referred to as stand sites, were studied in detail with the primary aim being to record the major vegetation types present on the island, and secondly to investigate the possible occurrence of a longitudinal gradient from the southern tip to the northern head of the island (Fig. 1). Furthermore four stand sites (numbers 2, 3, 4 and 5; Fig. 1) were included to show the stages in the common phenomenon of coconut grove regeneration after disturbance, which was super-imposed on the more natural vegetation of the island. This disturbance was chiefly the result of bush clearing and of trampling. On field observation all stand sites, with the possible exception of site 11, could be considered as members of a continuum, rather than distinct groups of differing vegetation.

At each site a 10 m by 10 m area square was pegged out with string and within it more strings laid to subdivide the area into 100 1 m by 1 m quadrats. Thirty five of these quadrats were randomly selected, and in each, the presence or absence of each species was noted, so that on summation for each stand site a local frequency estimate for each species was attained, as a score out of thirty-five. These data, referred to as the floristic variables matrix, appear in Table 1. Fig. 1 shows the relative position of each site on the island.

A soil pit was dug in the central area of each stand site, in a similar manner to transect soil pits (described in the previous paper). Soil pH was recorded *in situ* at each of the three depths, 5, 10 and 20 cm depth (Table 2, col.1). Soil samples of approximately 150 grammes wet weight were also taken at each of these depths in each stand site.

Chemical analysis of soils

On return to England the soil samples were air dried in the laboratory. It had been necessary to store the soils wet in the field.

Because of the somewhat unusual nature of the 'soil' a mechanical fraction scale had to be specially devised. The six fractions, MF/1/X...MF/6/x where x is the depth collected, correspond to the following particle sizes: 1, >20 mm; 2, 20-3.35 mm; 3, 3.35-2.0 mm; 4, 2.0-1.0 mm; 5, 1.0-0.5 mm; 6, <0.5 mm. Each sample was sieved and the mechanical fractions recorded as percentages of the total air dry weight. It will be noted that for site 11, each fraction, because of the peaty nature, was given an equal value of 16.7%.

After the six weeks storage of the soils, wet, and in an anaerobic state, total elemental analysis seemed an appropriate measure of the nutrient status of the soil rather than an analysis for the exchangeable fraction. This former measure of soil nutrients has been successfully employed in previous studies of vegetation whose scale was comparable to that of Wilingili (e.g. Austin, Ashton and Greig-Smith, 1972).

The soil sample was subdivided and a portion (approx. 20 g.) milled in a Glen Creston Sample Mixer Mill (M280) using tungsten carbide balls.

Two digests were prepared: (a) nitric and perchloric acids (4:1 mixture), with two replicates of each sample, and (b) sulphuric acid and hydrogen peroxide. These were made up to 10 per cent acid solution for analysis.

Iron, copper, calcium and magnesium were determined by atomic absorption spectroscopy using digests (a). These digests were also analysed for potassium and sodium by flame emission spectroscopy.

The organic matter content of the soils was determined by loss on ignition at 375°C (Ball 1964) with subsequent subtraction for air dried soil moisture. Samples of pure calcium carbonate heated to this temperature lost no weight, indicating that organic matter losses were not confounded by any losses in carbonate from the samples. This method was preferable to a wet oxidation procedure, which in agreement with Orphanos (1973) was found to be unsuitable for such carbonate rich soils. Carbonate itself was assessed gravimetrically by the method of Bauer, Beckett and Bie (1973).

Phosphate (in the nitric: perchloric acid digests) was estimated by the molybdenum blue and total nitrogen (in the sulphuric acid: peroxide digests), by the alkaline-phenol reaction on a Technicon Auto Analyzer. The results of the analyses are summarised in Table 2 as the means of each variable over the three depths sampled. Variables for each of the three depths constitute the environmental variables matrix (51 variables).

NUMERICAL ANALYSIS

The raw data matrices to be considered in the ensuing analysis are:

(i) Matrix X, the floristic variables matrix, Table 1 (45 spp.), and,
(ii) Matrix Y, the environmental variables matrix (51 variables) a condensed form of which appears as Table 2.

Principal components analysis (PCA) was employed in a numerical analysis of the data, to elucidate those floristic and environmental variables most important in the distribution of, or rather changes in, the vegetation of the island. The method of analysis was Q-type and used the weighted similarity coefficient of Orloci (1966). Classification techniques have not been employed in the work reported here. Computer programmes were written in Fortran lV by Dr. A.J. Morton and one of us (D.McC. N.).

Stand Ordinations

Standardisation for stands (to zero mean and unit variance for each stand) was supplied to matrix X, resulting in matrix A_1. PCA of A_1 provided a stand ordination based on floristic variables (Fig. 2). Matrix B, the result of standardisation of Matrix Y (to zero mean and unit variance for each environmental variable) was also subjected to PCA giving a second stand ordination, this being based on environmental variables (Fig. 3).

Floristic and environmental variables ordinations

Matrix X was then standardised for species (each to zero mean and unit variance) giving matrix A_2 the transpose of which, A_2^T, was subjected to PCA with the production of a species ordination (Fig. 4).

Transposition of matrix B, to B^T and subsequent PCA of B^T produced an ordination of environmental variables (Fig. 5).

Table 3 shows the percentage variance removed by each of the first three components in the four ordinations.

Correlation analysis

To investigate which floristic and environmental variables were associated in the distribution of the vegetation, a correlation procedure was adopted (Flenley 1968, Burden and Randerson 1972).

Considering the principal components removed in the stand ordinations of matrix A_1, each vector of component scores (*sensu* Gittins 1969):

$$C_v \quad (1, 2 \ldots 20),\ x = 1, 2, 3$$

was correlated with each vector of floristic variables (i.e. species)

$$F_y \quad (1, 2 \ldots 20),\ y = 1, 2 \ldots 45$$

and each vector of environmental variables,

$$E_z = (1, 2 \ldots 20),\ z = 1, 2 \ldots 51$$

The following different correlations were performed for each pair of vectors:

C.v. (i) Fy, (ii) Ez, and (iii) $\log_e$ (Ez) with the Pearson product moment correlation coefficient, and,
C.v. (iv) Ez applying the Spearman Rank correlation coefficient (Siegel 1961)

Methods (iii) and (iv) were included to cover the possibility of non-linear relationships suggested by the work of Austin and Noy-Meir (1971).

As a criterion, with which to summarise the results usefully and concisely, those correlation coefficients with statistical significance of $P<0.05$ were selected. Table 4 presents such a summary of a correlation analysis, based on the component scores of the PCA of matrix A_1.

DISCUSSION

Methodology

In the preliminary analysis of the data matrices X and Y, a number of principal component analyses (PCAs) were performed on different arrangements of the data. Far be it from the purpose of this paper to present a full discussion of the comparison of the different methods. This has been adequately done by a number of authors, more recently by Whittaker (1973). However, for this particular and somewhat unusual set of data, the reasons for the final adoption of standardisations, used in the above section, will be outlined briefly.

The stand ordination, from a PCA based on unstandardised floristic variables (not illustrated), resulted in the formation of a group of species poor sites (stand sites 6-12 inclusive, Table 1). This was not advantageous to interpretation especially as those sites contained important species which featured in other sites. The effect of standardisation for stands was to spread out these species poor sites across the ordination (Fig. 2), to give truer realization to the position of site 11, and to enable the possible detection of gradient along the length of the island.

Treatment of matrix Y, the environmental variables, to produce a stand ordination, was achieved most efficiently by standardisation for the variables. Straight ordination and an ordination based on logarithmic transformation of matrix Y proved unsatisfactory.

For the species ordination, standardisation for each species was essential, as in its absence, or with only standardisation for stands, all rare species were clumped at the ordinations origin with failure to dissect out the main vegetation types. Ordination of the environmental variables was again best performed with standardisation for each species.

Correlation analysis were applied to the component scores of most of the alternative PCAs mentioned immediately above. Only that analysis, using the component scores from PCA of matrix A_1, provided an intelligible interpretation of the data and the results of which were further supported by those environmental variable ordinations finally adopted. It was felt that this correlation procedure was relevant only to the component scores of the PCA matrix A_1 as matrix X was based on a complete set of floristic data. On the other hand, matrix Y obviously lacks many variables of the environment, since those actually measured had inevitably been selected by circumstance and intuition based on some postulate of their importance. A correlation analysis procedure based on the component scores of the PCA of matrix B did, in fact, lead to very spurious conclusions which neither matched the other correlation analysis in Table 4, nor complemented the groupings of variables inferred by the ordinations. This latter-mentioned correlation analysis procedure is not illustrated and will not be referred to further

Interrelations of floristic and environmental variables

Stand ordinations, from the PCA of matrix A_1 (Fig. 2), and from the PCA of matrix B (Fig. 3) do not suggest any grouping of sites, though sites which are geographically close (Fig. 1) tend to lie near one another on the ordinations and sites 11 and 19 are separated from the rest, for example sites 15, 17 and 19 and sites 2, 3 and 4 in Fig. 2. In general terms axis I (Fig. 3) and axis III (Fig. 3) tend to separate out the sites, with the northerly ones at one end and the southerly ones at the other end. The stand ordination of the environmental variables also illustrates the difference of sites 11 and 19 from the other sites.

More immediate information is to be gained from an examination of the variables ordinations. From the scatter of points on the species ordination (Fig. 4) it is evident that some species are highly associated as groups A, B and C. These groups have not been delimited by a quantitative method such as classification, as this was considered unnecessary for such a small body of data, but seek only to help visual interpretation. Groups A, B and C contain the following species, consistent in three dimensions:

A: *Cyperus ligularis, Psilotum nudum, Oplismenus imbecilis, Fimbristylis cymosa, Cladium jamaicense* and *Euphorbia indica.*
B: *Kalanchoe pinnata, Nephrolepis hirsutula, Colocasia esculenta, Neisosperma oppositifolia, Laportea interrupta* and *Ficus benghalensis.*
C: *Portulaca tuberosa, Sida humilis, Launaea pinnatifida, Lepturus repens* and an unknown species (No. 34, Table 1).

Examination of the third axis Fig. 4b, c reveals four more groups separated from the central mass of points in Fig. 4a. These groups D to F include:

D: *Ipomoea macrantha, Vernonia cinerea* and *Eragrostis tenella*
E: *Guettarda speciosa, Pemphis acidula, Rhizophora mucronata* and *Tournefortia argentea.*
F: *Carica papaya, Polyscias guilfoylei, Achyranthes aspera* and unknown species (no. 39, Table 1).
G: *Passiflora suberosa, Morinda citrifolia, Asplenium nidus* and *Hernandia peltata.*

Group A includes essentially those species which recolonise disturbed coconut groves in the north of the island (sites 2-5) whilst B contains those species of the wetter central forest close to the encampment (such as site 18). The two main species of disturbed areas are *Thuarea involuta* (no. 3) in the heavily trampled parts of the island and *Wedelia biflora* (no. 19),a weed-like species inhabiting disturbed cleared ground. (Fig. 5b, c). Group C on the other hand includes those species recognised from the scrub sites (sites 13 and 14) together with *Cassytha filiformis* (No. 7).

The forest sites are the four groups D to F plus other species. The arrangement of these groups presents a successional picture from the shrubs and small trees in D, (related to the species of group C) to the mature hardwood forest sites of group G. Group G species are found in such sites as 15, 17 and 19 amongst the main species, *Pisonia grandis* and *Passiflora suberosa.* Group E, again, are intermediary forest sites but drier, typified by site 15 and associated with the pawpaw, *Carica papaya.* Lastly, group F, may be identified by mid-island scrub, including the most common bush on the island, *Guettarda speciosa,* and the mangrove, *Rhizophora mucronata.*

The remaining species, so far not discussed, are probably, in terms of biomass the most important, having associations with two or more species groups between which they lie. *Cocos nucifera* (no. 5), the coconut, for instance, in Fig. 5b, lies between groups A, B, C, D, and E as it shares a distribution among all those sites whose species constitute these five groups, (with the exception of the mangrove). The strand plants, *Scaevola taccada* and *Suriana maritima* (nos. 1 and 41) lie close to the other members of group E, especially *Pemphis acidula* (no. 13), which shares a strand and inland scrub habit, and *Apluda mutica* (no. 10). *Pandanus* sp. (no. 8) and *Hibiscus tiliaceus* (no. 4) cannot easily be placed with any group in particular owing to a somewhat general habit.

The environmental variables ordination, Fig. 5, of which only the first two axes are illustrated, characterises by observation four main groups P, Q, R, and S with the remaining seven variables loosely comprising a group referred to as T.

The five groups consist of the following variables:

P: MF/5 (5, 10, 20), MF/6 (5, 10, 20), Mg (5, 10, 20).
Q: pH (5, 10, 20), Ca (5, 10, 20), CO_3 (5, 10, 20).
R: MF/1 (5, 10, 20), MF/2 (5, 10, 20), MF/4 (5), Fe (10, 20), Cu (10), Phos (5, 10, 20).
S: MF/3 (5), Na (5, 10, 20), K (5, 10, 20), N (5, 10, 20), C (5, 10, 20)
T: MF/3 (10, 20), MF/4 (10, 20), Fe (5), Cu (5, 20).
(Note that the figures in parenthesis denote depth in cm at which the measurement of the variable was made).

The following points of interest may be made:

(i) that the third principal component essentially separates out group R into mechanical fraction sizes 1 and 2 at one end and phosphorus and iron at the other, hence solving the apparently anomalous group R associations.

(ii) Group Q associations are obvious, that is rise in pH with calcium carbonate content, whilst group P illustrates the high magnesium content of fine-grained soils.

(iii) The cationic (monovalent) status is well associated with the organic matter constituents carbon and nitrogen, which together operate as a functional colloidal structure in the matrix of coral blocks which is resistant to leaching of potassium.

Having identified the main groups of variables present, attention may now be returned to the stand ordinations and more particularly to their component scores used in the correlation analysis mentioned above.

Considering the component scores of the stand ordination based on the PCA of matrix A_1, component 1 (Table 4) associates an increase in *Scaevola taccada* and *Pemphis acidula* and a decrease in *Cocos nucifera, Portulaca suberosa* and species of group A with increasing percentage of large particles and sodium. On axis 2, *Pemphis acidula* increase and *Scaevola taccada, Cassytha filiformis* and *Guettarda speciosa* decrease is associated with increase in percentage intermediate particle size. Component 3 associates, increase in *Pisonia grandis* and species of group G and decrease in *Apluda mutica* and *Cassytha filiformis*, with increase in the percentage of large particles, iron, phosphate and nitrogen and decrease in the percentage of small particles, magnesium and carbonate.

With a view to the interpretation of Table 4 the following points are relevant. Firstly, that correlations of environmental variables tend to complement each other. For example where percentage of large particles increases, that of small particles decreases, and those variables that are highly associated in Fig. 5 tend to correlate the scores of the same component together, (Component 3, Table 4). Secondly, species that occur together in the species ordination, such as those of groups A and G, correlate with the scores of the same component; and thirdly, measurement of a variable at three depths acts as a crude form of replication and where two or three of the depth-replicates correlate with an axis simultaneously, the case for an association with that component is strengthened.

As yet meteorological data have not featured in the interpretation of the distribution of vegetation. Spicer & Newbery (1978) have indicated that the exposure at the centre of the island is approximately half that at the shores. With no estimate of exposure at each of the stand sites, a crude measure of shelter (the inverse of exposure) can be taken as the shortest distance from each site to the sea. These distances were correlated with the components of the stand ordination based on matrix A_1. The correlation of shelter with component 1($-r$, $P < 0.01$) agrees with the other variables associated with this component. That is, a short distance inland, i.e. from the beaches, the exposure is high and the sodium deposition great (mainly in the form of sea spray) and it is here that the strand plants *Scaevola taccada* and *Pemphis acidula* survive.

The vegetation system

Successional evaluation of vegetation is normally not possible in many ecosystems without records stretching over a long time period yet in those systems in which the changing geography leads to the quick, continuous formation of new land from the sea an approximate realisation of the processes of colonisation and succession may be found at any one time. The island of Wilingili is a prime example illustrating the successional stages as a longitudinal gradient from the bare coral at the southern tip of the island (Fig. 1) to the mature forest of the northern central region. Indeed, many factors of disturbance are to be found superimposed upon this general picture of the vegetation, such as the encouragement of coconut groves on the lagoon side of the island. On the seaward side the introduction of brackish water systems, in the form of swamps and ponds, influences the system in other ways. Despite these, and other smaller complications a general trend in the development of soils and vegetation can be traced up the central 'spine' of Wilingili, especially, in its southern half. Furthermore, implications of lagoon sea gradients must be borne in mind

(Spicer & Newbery 1978) though these tend to operate in a more pronounced fashion nearer the shores.

For the purposes of the present discussion it is desirable to consider five, rather theoretical, vegetation types. (i) sparse coral strand vegetation, (ii) bush-small tree vegetation, (iii) coconut communities, (iv) forest, and (v) swamp. Amplification of these types to the real situation can be realised by reference to the species ordination (Fig. 4 and above text) of major species and species groups A to G.

The environmental variables may also be summarised into: (i) soil particle size variables (which to some degree also represent drainage properties of the soils), and (ii) organic matter variables, subsidiary to, and related, to which are pH and cationic status.

Returning to the vegetation model, Fig. 6, a number of gradients may be supposed to exist. The correlation analysis procedure, Table 4, has selected and demonstrated the two most prominent in the data.

These are:

Gradient 1: The change in vegetation from strand plants *Pemphis acidula* and *Scaevola taccada* to coconut communities, mainly of *Cocos nucifera* and *Portulaca suberosa* is accompanied by a decrease in percentage of large particles (and increases in small particles) and decrease in sodium. This gradient essentially operates mid island from the 'rocky' sea-ward beach to the sandy lagoon side of the island (Fig. 1 and 6), and is represented by component 1 (Fig. 2 and Table 4) of the stand ordination of floristic parameters. Component 2 (Fig. 2 and Table 4) is partly coincident with component 1 indicating a slight gradient from strand to bush vegetation but probably operating further south down the island beyond the limit of coconuts.

Gradient 2: This represents the change in vegetation from bush-small tree vegetation to *Pisonia grandis* dominated forest in the north, and is accompanied by a decrease in sandiness (small particles) and magnesium carbonate with an increase in larger particles, iron, phosphorus and nitrogen. It is necessary to include within this rather major and composite gradient those changes from bushy recolonising sites. Because of decreasing sandiness it seems that this gradient will operate to the lagoon side of the island and touching these disturbed sites as indicated in Fig. 6. The gradient is significantly supported by correlation of variables with component 3 of the stand ordination (Fig. 2 and Table 4).

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Table 1. Local Frequency estimates of each species at each of the stand sites.

		STAND SITE NUMBER																			
	SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*Scaevola taccada*	30		1		29	7	31	20	29	10				8		31			5	3
2	*Boerhavia diffusa*	5				2					8				4		6		3		
3	*Thuarea involuta*										21				32			6	27		
4	*Hibiscus tiliaceus*	1			6																28
5	*Cocos nucifera*	10	10	34	26	13			3	1				14	7	16	15		17		17
6	*Passiflora suberosa*	9		11	2	5								22		35	13	24		32	14
7	*Cassytha filiformis*	20	20			25					12			34	35						
8	*Pandanus* sp.	18			2									1							
9	*Guettarda speciosa*	8		3	1	20	1	2	18	14	19			1	15	30	20			6	2
10	*Apluda mutica*	26	35	34	27	9					1										
11	*Ipomoea macrantha*	13		3							7				13	3					
12	*Portulaca suberosa*	2												2							
13	*Pemphis acidula*						18	31	8		18	10	35								
14	*Sida humilis*			6										30	5						
15	*Morinda citrifolia*									10						5	10	28		12	
16	*Neisosperma oppositifolia*														3	2			11		
17	*Asplenium nidus*				2				1							3		24			
18	*Tournefortia argentea*							7													
19	*Wedelia biflora*		34	6		16									14				24	20	7
20	*Cyperus ligularis*			3	16	2													2		1
21	*Pisonia grandis*															19		35	1	12	
22	*Carica papaya*															5					
23	*Rhizophora mucronata*									35											
24	*Psilotum nudum*			6	6																
25	*Oplismenus imbecilis*			8	29															1	25

Table 1. (continued)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
26	*Kalanchoe pinnata*																		30		
27	*Nephrolepis hirsutula*																		7		
28	*Colocasia esculenta*																		15		
29	*Digitaria horizontalis*			2	18									18	19						
30	*Fimbristylis cymosa*				21																
31	*Cladium jamaicense*				4																
32	*Launaea pinnatifida*													17							
33	*Tacca leontopetaloides*																				17
34	*													3							
35	*Polyscias guilfoylei*																			24	
36	*Euphorbia indica*			3	3																
37	*Vernonia cinerea*														3						
38	*Laportea interrupta*																		4		
39	*																	7		27	
40	*Eragrostis tenella*			2											6						
41	*Suriana maritima*								7												
42	*Lepturus repens*								12					18							
43	*Achyranthes aspera*															1					
44	*Hernandia peltata*																	2			
45	*Ficus benghalensis*																		12		

* Indicates insufficient plant material collected for identification.

Table 2. Environmental measurements for each of the 20 stand sites.

Each value in the table represents the mean of 3 measurements (i.e. at the 3 depths 5, 10 and 20 cm).

	pH	MECHANICAL FRACTION %						TOTAL CONC. CATIONS mg/100g SOIL						TOTAL ANION CONC. mg/100g Soil			%
SITE		1	2	3	4	5	6	Fe	Na 10^2	Mg 10^3	K	Ca 10^4	Cu	P 10^2	CO$_3$ 10^3	N 10^2	Org. Mat.
1	8.23	0.0	1.2	2.8	11.3	52.2	33.3	14.9	7.41	1.01	35.0	2.93	0.89	0.32	42.2	1.03	2.81
2	8.60	0.0	5.1	2.5	4.4	39.9	49.2	11.6	8.09	1.06	36.1	2.68	1.05	0.19	47.1	0.66	3.39
3	8.17	0.0	4.6	2.2	6.8	37.1	48.9	6.7	8.22	1.33	36.0	3.24	0.99	0.14	44.8	0.54	2.91
4	8.10	0.0	12.9	14.2	34.4	28.3	8.6	7.8	7.64	1.03	38.9	2.84	1.34	0.21	46.4	1.17	4.37
5	8.20	0.0	1.3	1.3	5.7	43.6	47.9	10.6	8.14	1.05	37.2	2.82	1.09	0.22	46.6	1.00	4.60
6	8.13	42.8	26.4	4.8	7.9	11.2	7.0	6.8	8.23	1.36	33.6	2.80	0.79	0.16	44.7	0.31	2.78
7	7.97	38.0	31.9	4.1	18.2	7.5	0.2	7.9	9.41	1.26	36.1	3.24	0.79	0.17	47.2	0.31	3.40
8	8.17	13.4	40.8	8.4	12.3	16.1	8.6	10.4	8.07	2.08	35.4	3.19	0.80	0.27	45.4	0.58	4.45
9	8.50	65.2	31.6	1.7	0.8	0.4	0.2	6.1	9.32	0.85	34.2	3.10	1.08	0.29	45.4	0.84	3.94
10	8.20	21.1	60.5	4.1	3.4	6.3	4.3	7.2	9.76	0.58	34.9	2.98	1.38	0.18	42.5	1.00	4.06
11	6.80	16.7	16.7	16.7	16.7	16.7	16.7	9.6	32.34	1.26	206.7	0.22	1.25	0.88	1.2	14.46	52.72
12	8.03	36.2	15.5	7.2	23.6	12.8	5.8	8.9	10.04	1.17	40.6	3.11	0.86	0.31	43.8	0.93	4.27
13	8.37	24.6	22.4	3.9	4.2	10.6	33.8	5.8	7.30	1.31	34.8	2.70	0.97	0.27	44.5	1.00	4.43
14	8.50	12.3	2.4	0.1	1.7	38.4	43.7	8.4	7.94	0.76	36.0	2.73	1.25	0.29	43.8	1.01	4.15
15	7.77	59.8	28.0	2.7	1.9	2.8	4.5	13.7	8.83	0.17	37.7	2.72	1.17	13.30	37.0	2.13	5.15
16	8.40	23.4	15.0	1.4	1.3	2.9	55.3	6.4	8.07	1.10	36.2	2.69	0.65	0.36	42.3	1.14	4.89
17	8.33	37.4	54.7	0.9	1.3	2.0	1.6	8.7	8.40	0.39	35.6	2.65	0.91	6.31	38.1	1.93	4.73
18	8.00	9.9	56.9	11.6	11.8	5.9	2.7	12.0	7.43	0.74	36.4	2.71	1.15	2.88	39.4	3.19	8.41
19	7.93	34.3	12.1	3.6	18.3	17.1	12.8	22.9	4.68	0.32	36.8	2.27	1.38	27.36	23.7	7.34	18.90
20	8.30	0.0	5.0	0.9	14.2	40.5	39.6	10.2	7.14	0.35	35.6	2.91	0.95	1.54	39.2	1.64	3.75

Table 3. Percentage variation removed by principal components for the four ordinations.

PCA	Matrix	Component			Total
		1	2	3	
Stands	A_1	21.3	15.4	13.7	50.4
Stands	B	38.6	18.2	14.2	71.0
Floristic variables	A_2'	16.3	14.5	12.5	43.3
Environmental variables	B'	37.7	18.7	14.5	70.9

Table 4. Floristic (F) and environmental (E) variables correlation with the first three principal component of PCA matrix A_1, using parametric tests unless otherwise indicated.

		-r		+r	
COMPONENT 1	F	C. nucifera	***	S. taccada	*
		P. suberosa	*	P. acidula	***
		A. mutica	*		
		W. biflora	*		
		P. nudum	*		
		O. imbecilis	*		
		E. indica	*		
	E	MF/5/5	**	MF/1/5	***
		MF/6/5	* (pt**)	MF/2/5	NS (np *)
		Cu/5	**	MF/1/10	*
				Na/5	NS (np *)
				Na/10	NS (np *)
				Na/20	NS (np *)
				Mg/20	*
				N/5	NS (pt *)
COMPONENT 2	F	S. taccada	**	P. acidula	*
		C. filiformis	*		
		G. speciosa	**		
	E	MF/6/5	*	MF/3/5	*
		pH/10	*	MF/4/5	NS (pt*, np*)
		pH/20	**	MF/3/10	*
				MF/4/10	*
				MF/3/20	*
				MF/4/20	*
				Na/10	ns (pt*)
				K/10	NS (np*)
COMPONENT 3	F	C. filiformis	*	P. suberosa	***
		A. mutica	*	M. citrifolia	***
				P. grandis	***
				A. iridus	**
				M. peltata	*
	E	MF/5/5	* (np**)	MF/1/5	NS (np*)
		MF/5/10	* (np**)	MF/1/10	*
		MF/6/10	*	MF/2/10	NS (np*)
		MF/3/20	**	MF/1/20	***
		Mg/5	NS (pt**)	MF/2/20	Ns (pt*, np*)
		Mg/10	NS (pt**)	Fe/10	*
		Mg/20	NS (pt**)	Fe/20	*
		Carb/5	*	Phos/5	***
		Carb/10	NS (np*)	Phos/10	***
		Carb/20	Ns (np*)	Phos/20	***
				N/5	NS (np*)
				N/10	NS (np*)

+r, positive correlation; -r, negative correlation; NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; np, non-parametric test applied; pt, parametric (logarithmic) transformation of variables used.

It should be noted that the following notation has been adopted: where (1) the correlation coefficient by method (ii, see text) failed to reach significance, whilst that from methods (iii) and/or (iv) did, or (2), that significance was reached in all three cases with that of (iii) and/or (iv) being greater, these facts are quoted as such with the probability levels for methods (iii) and/or (iv) in parenthesis.

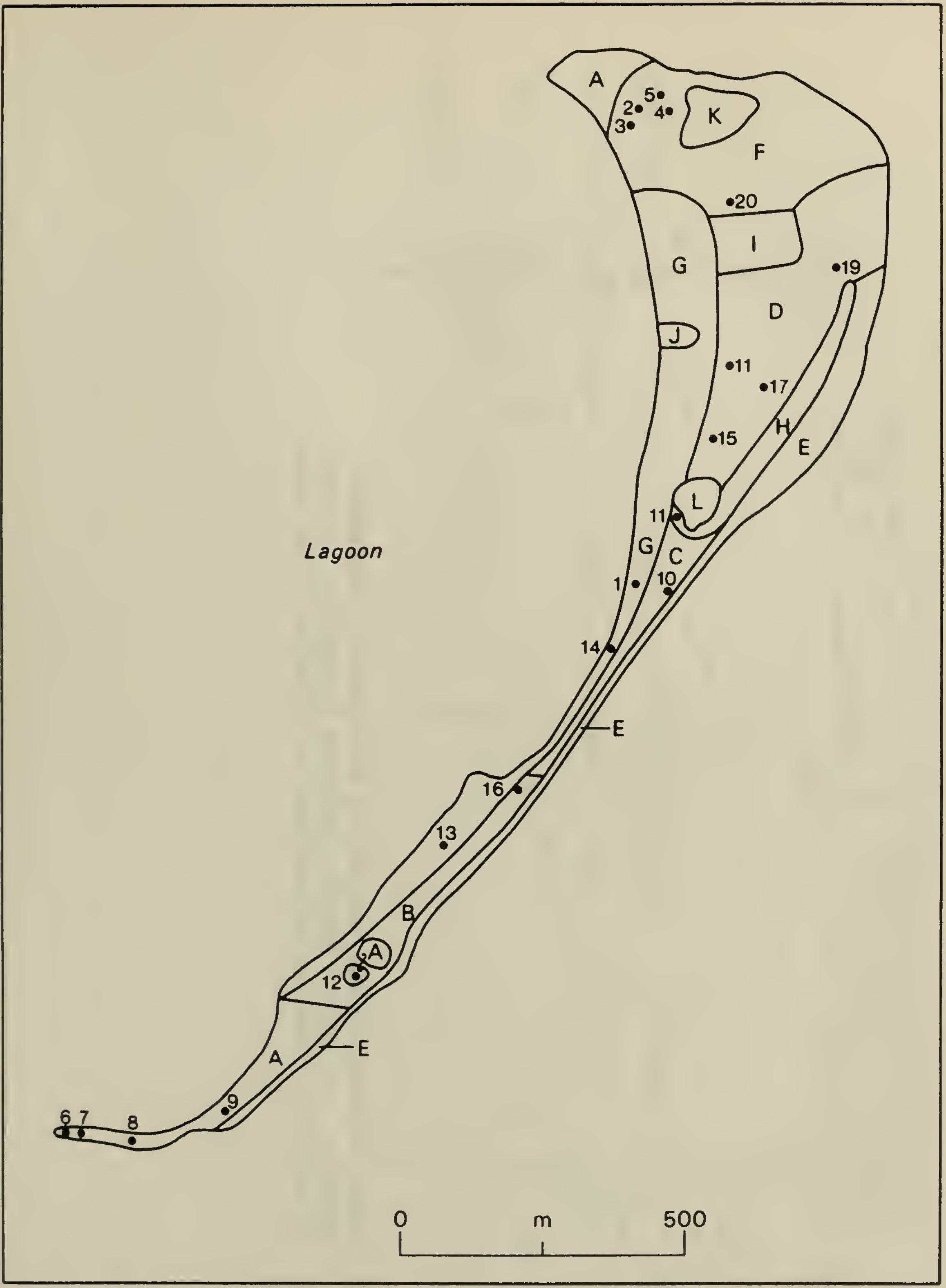

Fig. 1. Map of Wilingili indicating the positions of the stand sites with respect to island geography and general vegetation types. A, Sparse vegetation, *Pemphis acidula* and *Scaevola taccada*; B, Bush vegetation; C, small trees and shrubs; D, central *Pisonia grandis* hardwood forest; E, Strand *Pemphis acidula;* F, Northern *Pandanus*-coconut forest; G, *Cocos nucifera* groves; H, mangrove swamp; I, 'semi-cultivated' area; J, native huts; K, sea-water pond; L, brackish water pond; M, dried out ponds.

Fig. 2. Stand ordination plots from PCA on the floristic variables matrix A. (a) axes I and II; (b) axes I and III; (c) axes II and III. Numbered points refer to individual stand sites.

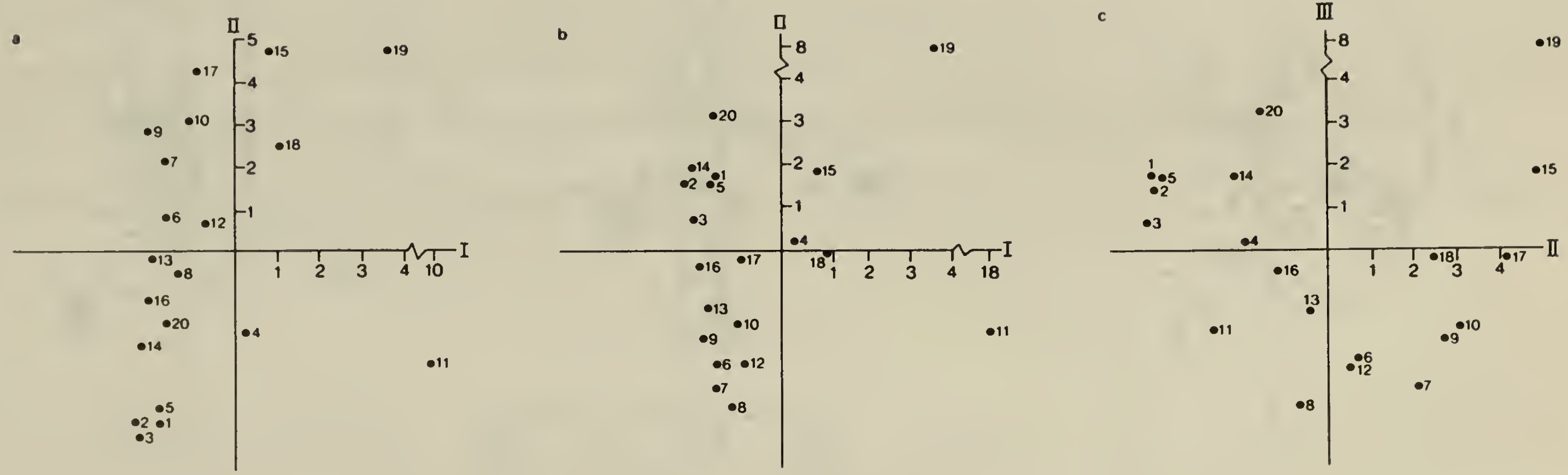

Fig. 3. Stand ordination plots from PCA on the environmental variables matrix B. (a) axes I and II; (b) axes I and III; (c) axes II and III. Numbered points refer to individual stand sites. The scale depicted in (a) also applies to (b) and (c).

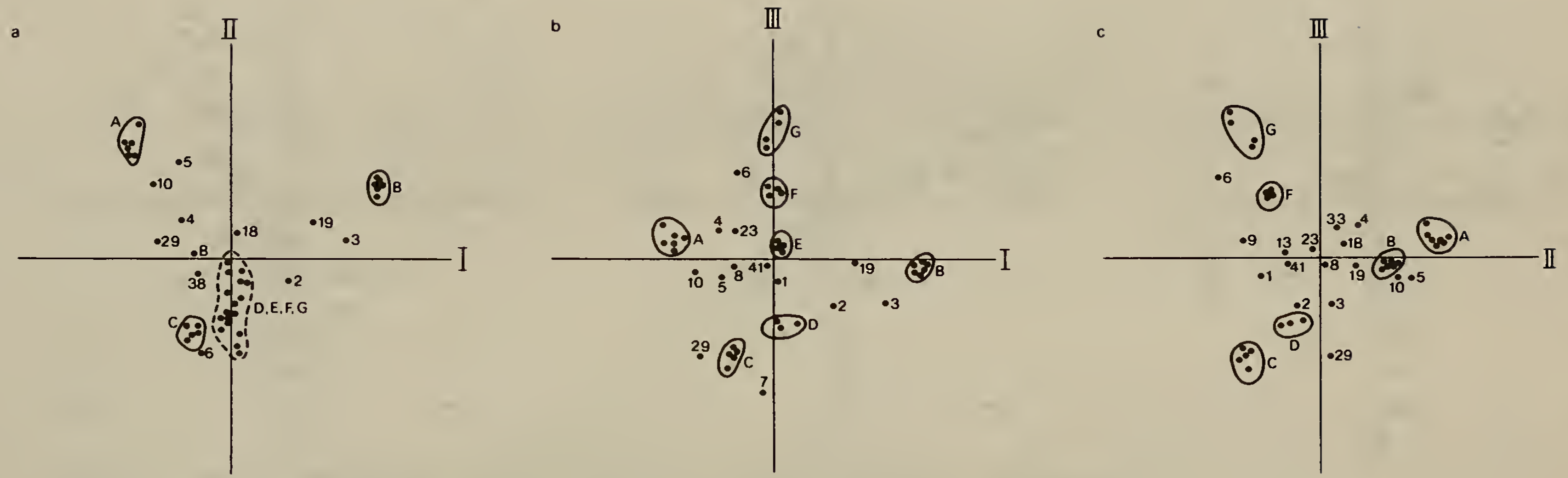

Fig. 4. Floristic variables ordination plots from PCA of matrix $A_2^{\bar{\prime}}$. (a) axes I and II; (b) axes I and III; (c) axes II and III. For content of species groups A to G see text, other numbered points refer to individual species recorded in the left hand side of Table 1.

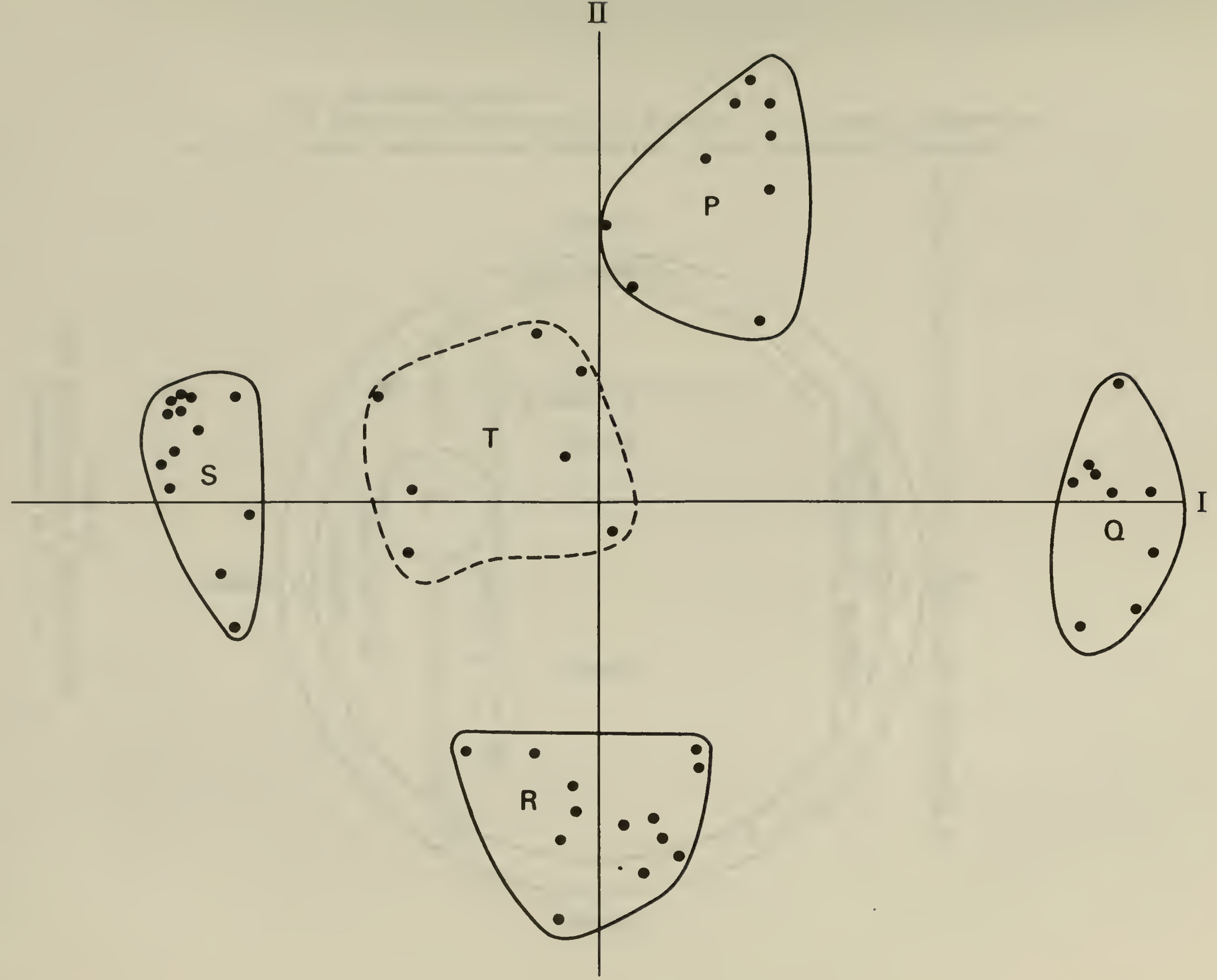

Fig. 5. Environmental variables ordination from PCA of matrix $B^{\bar{\prime}}$. For explanation of groupings of the variables see text.

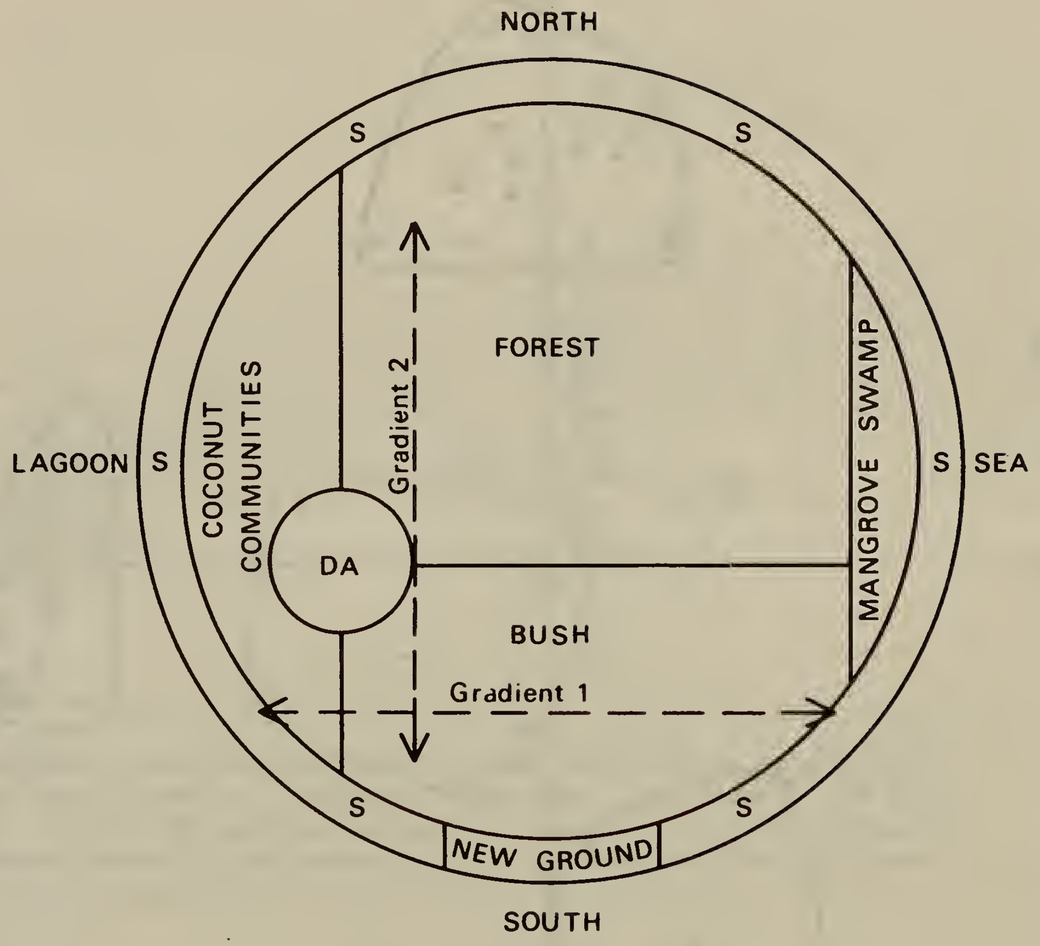

Fig. 6. Simple model of the vegetation illustrating the positions at which the main gradients operate. S, strand vegetation; DA, disturbed areas.

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A SALINE LAGOON ON CAYO SAL, WESTERN VENEZUELA

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A SALINE LAGOON ON CAYO SAL, WESTERN VENEZUELA

By Malcolm P. Weiss [1]

INTRODUCTION

Cayo Sal, the largest of a group of small coralgal (i.e., a framework of corals and coralline algae) keys off Chichiriviche, Estado Falcón, contains an enclosed hypersaline lagoon, La Salina (Figs. 1, 2). Although atoll-like in plan view, Cayo Sal rests on the shallow (<20 m) continental shelf and is not an atoll in the fullest sense (Bryan, 1953a, 1953b). During field investigation of the keys, marine sediments, and pollution by unbridled coastal development (Weiss *et al.*, in press; Weiss and Goddard, 1977), some shallow cores were taken in La Salina. This report results from the the study of those cores and the geology of Cayo Sal.

Gypsum is formed and preserved in La Salina, and halite is generated seasonally. Peat buried beneath the lagoon sediments suggests that sea level has risen about 1.5 m in the last 2700 years. Conditions of hypersalinity and the consequent sediments are in some respects similar to those in a lagoon on Gran Roque, an island in the Los Roques group (Sonnenfeld, 1973), as will be seen. The sedimentary record and morphology of Cayo Sal suggest that both were disrupted by hurricane or tsunami about 500 years ago.

CAYO SAL

Cayo Sal is an islet (10°56.7' N. Lat.; 68°15.6' W. Long.), in the form of a completely closed curve, resting on a growing coralgal reef platform, and surrounding an entirely enclosed lagoon, La Salina (Fig. 2). The reef platform, i.e., that part less than 2 m deep, extends 1.8 km in an east-west direction, 1.13 km north-south, and has an area of 0.94 km^2. The area enclosed by the seashore of Cayo Sal, including both land and lagoon, is 0.63 km^2, with maximum east-west extent of 1.25 km and north-south extent of 0.83 km. These values do not vary significantly with tide stage because the tidal range is less than 0.5 m.

The area of La Salina varies seasonally (Fig. 2). Apparent extremes recorded in aerial photographs (Fig. 3) compare closely with traces of strandlines on the ground, and show the surface area of La Salina ranges between 0.33 and 0.37 km^2. These values are for recent dry-and-wet seasonal extremes and for annual differences of the last quarter-century, the period of adequate records.

Cayo Sal is formed largely of skeletal carbonate sand. Windblown sand and silt, and mud brought by occasional floods of stream water over the nearshore waters provide only traces of terrigenous

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material to the key. The island apparently began as a patch reef growing on a high spot of the drowned alluvial plain of the Tocuyo River (Weiss *et al.*, in press).

The major elements of the coral community are typical for the Caribbean: *Acropora palmata* (Lamarck) in the surf zone is buttressed by *Montastrea annularis* (Ellis and Solander) and species of *Diploria* below, and *Acropora cervicornis* (Lamarck) occurs in protected nooks, at the lee ends of the reef and along the break in slope of the sediment apron on the southwest side. Species of *Porites* also occur, especially in El Huequito, and also with *Siderastrea* in the *Thalassia-Halimeda* community on the shallow apron of skeletal mud and sand west of the island. The inner part of the reef flat is mostly barren of corals and calcareous green algae, but paved by crusts of coralline algae or littered with algae-encrusted skeletal debris. A more widespread coral community is developed in El Huequito (Fig. 2), and most of the remainder of that bay floor is of skeletal sand and rubble.

The reef platform is not much larger than the island, except for the wide flat at the northeast corner. The morphology of the area, both in plan and in profile, suggests that El Huequito (Fig. 2) could have been formed if sediments of the former northeast corner of the island were moved southwestward by storm(s), filling that corner of La Salina, while exposing older reef-flat material to renewed colonization by corals. The low sandy barrier between La Salina and El Huequito has just a few small trees and little scrub, which seem to be migrating from the ends of the barrier. Even so, such an event cannot have been recent, if it indeed occurred; local people have no knowledge or stories of such an event and the floor of El Huequito, although shallow, has a large community of *Acropora palmata, Porites furcata* Lamarck, and *Diploria sp.* Their sizes suggest several decades of growth, based on an assumed rate of about 5 cm/yr for *A. palmata.*

The land is asymmetrical in profile at most sections, with highest elevations closer to the sea than to the lagoon. It is made mostly of skeletal sand but locally of coral chunks--up to 1.3 m long (Fig. 2). Most is stabilized by scrub growth, including sea grape and red mangrove. It has changed little in the quarter-century for which maps and air photos are available, except for some recent grading and introduction of palm trees on the inhabited western end and southwestern side (Weiss and Goddard, 1977). Accumulation of skeletal debris tends to enlarge the island by addition to its margin, but some is thrown across the island and spread into La Salina as splays of skeletal debris.

LA SALINA

A wet-season stage is shown in Figure 3A, and a dry season stage in Figure 3B. In September, 1972, the lagoon was indistinguishable from that pictured in 3B.

Bathymetry

Neither precise nor numerous depth measurements are available.

The deepest part is northeast of the center, where it was about 0.5 m deep during relatively high water in mid-November, 1972. Depth at the same place during maximum flooding (highest shore features) in recent years must have been of the order of 1 m. The bottom slopes gently from all shores into the shallow basin. The soft, slimy bottom makes "depth" an uncertain measurement; a smelly, red and black organic slime covers the bottom especially in the NE and NW quadrants. The area between high-water and low-water marks (Fig. 2) is a sort of "littoral zone." It is 60-100 m wide in the SSE quadrant and only 15-20 m wide in the NE quadrant.

When the water in La Salina is low, two small ponds become separated from the major body of water near its northwest corner (Fig. 2). The smaller of these is a low place in a sinuous channel a few meters wide that extends from La Salina almost to the sea. Although the channel held a few puddles and soggy spots in November of 1972, it is overgrown with brush and closed by the low berm at the beach. It clearly has not functioned as a water conduit for some years, but may again before long, however, for the small bay just to the north is undergoing vigorous erosion. The shore there was formerly protected by a line of beachrock (Fig. 2), but it has been breached and waves are rapidly removing the unconsolidated sand of that part of the island and sweeping it westward past the northwest point of the island. These little ponds contained brackish water during three separate visits. They are somewhat protected by vegetation from wind and sun, and thus can and do stand slightly higher than La Salina and up to 0.3 m above sea level, depending upon the tides.

Some parts of the lagoon bottom are highly reflective when the water is low (Fig. 3B). October, 1969, aerial photos show areas of the bottom that are reflective. These patches are mostly skeletal sand, and they include most of the "littoral zone" and irregular splays that reach from the east side nearly to the middle of the lagoon. Proximal parts of two such splays form wide "tongues" in the "littoral" zone in the southeast quadrant of La Salina (Fig. 2).

Hydrography

The level of La Salina was observed in September and measured once each in October, November, and December of 1972, thus covering the tail of the dry season and most of the wet season (Weiss *et al.*, in press). The level ranged from 24 cm above to 31 cm below the sea surface at the times of measurement (made at different stages of the tide). The difference between the observed extreme levels of the lagoon itself is 41 cm, significantly larger than the local tidal range of 25-30 cm. Differences would surely be somewhat greater if the lowest levels of the salt-forming dry seasons could be compared with these data. The changes of level each year arise from the fact that the ratio of precipitation to evaporation is strongly skewed in time. Records are fairly complete for the immediate region back to the mid-1950's (Table 1), about the same period for which maps exist. They show that nearly half of the annual precipitation occurs in the months of October-December, on the average, and similarly, that about 60 percent occurs from September through January.

Evaporation data are available from a station 50 km farther southeast and show a rather uniform rate through each month of the year (Table 1). Data assembled by Lahey (1958) suggest that evaporation is more uniform regionally than is precipitation. At Cayo Sal the evaporation/precipitation ratio is very high during a dry season from later winter to early fall, and low during the late fall and winter. Using mean values for the months of the year (Weiss *et al.*, in press), evaporation for October-December is 40% of rainfall, and 115% for the other nine months of the year.

Fluctuation of the level of La Salina would be greater than it is if precipitation and evaporation were the only inputs and outputs from the lagoon. Because the island is formed of unconsolidated skeletal sand and gravelly sand, percolation to or from the sea occurs readily, depending upon the relative level of La Salina and stage of the tide. This percolation, although widespread, is slow and diffuse where the subaerial material is widest. The narrow barrier of skeletal sand between El Huequito and La Salina (Fig. 2), however, has a number of seeps on the southwest side; sea water bleeds slowly from these when the tide is higher than La Salina and runs in rills down the slope into the warmer water of the lagoon. The seeps support slimy red mats, probably soft algae similar to those on the nearby bottom of La Salina. No evidence of reverse flow from La Salina to the sea was observed, but surf would obscure any outlets on the seaward side. Extreme levels of flooding or drying of the lagoon are thus moderated by phreatic connection with the sea.

During periods between abundant and deficient precipitation the level of the lagoon must be in nearly hydrostatic equilibrium with the sea, and therefore gains or loses little salt from or to it. During the wet months, the lagoon will stand high, have a lesser salinity than at other times of the year, and produce a net seaward flow of groundwater. During the much longer dry season the lagoon will stand low and gain water of normal salinity by percolation; persistent evaporation will raise the salinity in La Salina to levels that percipitate halite and gypsum. The occurrence of halite is seasonal and requires salinity ≥ 270 °/oo. Gypsum persists and becomes part of the sedimentary fill of the lagoon. Local people gather salt each season for commercial purposes, and say that fall rains "spoil the salt."

Measurements of some of the water properties were made by Sr. Pablo Almeida between 1000 and 1100 hours local time on December 19, 1972, in the midst of that rainy season; the level of La Salina was 0.3 m below the sea at that time. Water temperature ranged from 29.1°C. close to the edge of the lagoon to 29.8°C. in the body of the lagoon. This compares with 27.9°C. in the nearby open sea at the same time. Salinity ranged from 161.9 to 165.7 °/oo in La Salina (Fig. 2) but was 36.6 °/oo at one meter depth in the open sea windward of Cayo Sal. The lowest lagoon value was from warm water toward the windward shore (Fig. 2, Sta. 3). Stations in mid-lagoon or toward the leeward side showed values of 164.5 °/oo or more. These facts and rafts or floes of salt crystals seen floating in the leeward sector of La Salina in September suggest a slow movement of surface water to leeward; salt crystals may be induced on the lagoon bottom by a compensatory underflow to windward, rather like that reported from Los Roques by Hudec and Sonnenfeld (1974).

SEDIMENTS

Mud is rather more abundant than sand on the lagoon floor today, except close to the shore and in the skeletal-sand splays. Autochthonous substances are, in decreasing abundance, gypsum (Fig. 4), mollusc shells (mostly snails) and debris (Fig. 5), and cemented carbonate crusts (Fig. 6). Halite is conspicuous, but only during the dry season. The microflora of the water and the soft red algae locally on the bottom do not contribute significantly to the sediments. The allochthonous substances are mostly skeletal particles thrown over the island by storm waves (Fig. 7); as sand and mud sizes prevail over minor skeletal gravel it is probable that most of the contribution comes from the island itself or the beaches, rather than directly from the reef. Peat, plant shreds and minute unidentified capsules, probably of plant origin (see appendix) come from the key; only the peat is significant (Fig. 8). Carbonate peloids (small ovoidal pellets of carbonate mud, but not known to be fecal in origin) are common, and probably are both autochthonous and allochthonous. Traces of siliceous sand and mud occur, and are believed to be wind-borne.

Halite. Although halite is a negligible constituent of the lagoon sediments, it is formed in abundance each dry season. During a traverse in September, 1972, the late part of the dry season, a great deal of salt was observed. Salt rafts, formed of small crystals aggregated into sheets a few millimeters thick and up to several square meters in area, lay cracked, overthrust and jumbled against the lee shore. Others were seen in open water, where they form and then sail to leeward. A few piles of salt sagged on the lagoon shore, remnants of salt-gathering earlier that season. Hopper crystals (hollow, square pyramids, stepped both inside and out) were widespread on the lagoon floor. Their abundance and coverage change with the season; hopper crystals covered the bottom to within about 50 m of the shore in mid-October, but were gone a month later. Hoppers were as large as 3 cm on an edge of the square base of the hollow pyramid, but most were smaller. Hypersaline pore water filled the upper few centimeters of lagoon sediments, based on the amount of NaCl in dried samples. This is an appropriate condition for the late stage of the dessicating season, but probably changes through the seasons. For convenience, and to avoid the complication of different porosities in the samples, the ratios of mineral fractions are reported herein on an NaCl-free basis.

Gypsum. The principal evaporite mineral other than halite is gypsum. The amount in the sediments ranges from 0-70 per cent, and its abundance is inversely proportional to that of total carbonates. This relative abundance is also expressed areally, for gypsum is scarce or absent close to shore where skeletal material is abundant and where rainfall and runoff reduce the salinity of the marginal shallows. Most of the gypsum occurs as small, loose crystals--"seed gypsum"--in the fine sand to silt size-range and poorly sorted. Some crystals of granule size also occur. Where gypsum is abundant the beds have a granular, sandy look (Fig. 4). Stubby prisms and polyhedral discoids, like the smaller ones illustrated by Illing *et al.* (1965, figs. 5a, 5b, respectively), are the common crystal forms; blades are less numerous. The deposits and crystals are like those beneath Lake Marion, near Cape Spencer of the Yorke Peninsula, South Australia.

The abundance discoids are similar in form and crystallography to the much larger ones described by Merritt (1935, fig. 1), are milky or frosty looking, and most have convexly curved crystal faces. These qualities duplicate those of similar crystals of a variety of sizes, all reported from hypersaline environments (Masson, 1955; Eardley and Stringham, 1952; Shearman, 1966; p. 210; Illing *et al.*, 1965; Dunham, 1972, figs. III-64 and III-67). The curved faces of the crystals in La Salina confirm the suggestion of Deicha (1946) that NaCl concentration "poisons" the gypsum crystals and distorts their crystallography. Cody (1976, fig. 7) has produced similar crystals experimentally in saline gels, although he ascribes most of the discoidal grains to corrosion *in situ*. The countless individual euhedral-to-subhedral crystals in La Salina must have grown, rather than be the corroded remnants of larger grains.

Many discoid crystals have ragged edges and are pierced with grooves or cavities. The holes may be imperfections or may have held particles of other minerals, for calcite, dolomite and traces of halite are still enclosed in some gypsum grains. Colored zones and inclusions, probably organic stains or particles, are seen in transmitted light.

The second most abundant type of gypsum crystal in La Salina sediments is stubby prisms with 4-6 faces and blunt terminations. These are limpid and have flat, clear faces; if very short they look like little cut jewels. Cody (1976, fig. 4) grew some of this type, but most of his prisms were much more elongated. Analogous crystals of larger size occur in wet parts of Qatar sabkhas (Illing *et al.*, 1965, p. 95, fig. 5a). They report (p. 95) "...white, fine, sugary gypsum..." associated with halite in dry parts of sabkhas; the crystal form is not given. Similar porous layers of masses of prismatic and discoidal gypsum crystals formed on the floor of La Salina from time to time in the Holocene. Apparently the prismatic type contains no halite or carbonate impurities. It's possible that the clear prismatic crystals form when halite is not crystallizing, and that the cloudy discoid crystals with inclusions and curved faces form during the dry season, and perhaps after burial as well.

Although the great bulk of the gypsum is unconsolidated, small masses of intergrown crystals do occur (Fig. 6A, 6F) and some is cemented into the carbonate grapestone and crusts (Fig. 6B). The patchy clumps of gypsum seen on inter- and supratidal flats (sabkhas) bordering the Persian Gulf (Illing *et al.*, 1965, fig. 6c) were not observed at La Salina, nor even the cementing of carbonate laminae by gypsum, as on Bonaire (Lucia, 1968, fig. 10c). Dense pavements of elongate prismatic gypsum crystals, 20-30 cm long and packed with their lengths arranged vertically, do not occur. Such pavements are conspicuous in the younger deposits of the sulfate lakes near Cape Spencer, South Australia, where part of the CaO came from ground water drainage (C. von der Borch, personal communication, 1975), and the NaCl salinity must thereby have been lower than it is in La Salina.

Molluscs. The significant autochthonous biogenic mineral particles are whole or broken shells of small snails. Shells of dead cerithids litter the shore by the thousands at the end of the dry season. They contribute to sediment near the shore, but less so in mid-lagoon (Table 2). These molluscs are seasonal--*i.e.*, they flourish when salinity is suitable for them. A number of other species and a few clams are contained in the stratigraphic record (Table 2, Fig. 5), but only a few occur in the youngest layers of each core. Fossils other than molluscs occur in only trivial volumes, see below.

Carbonate-cemented Crusts. Away from the organic slime in the northern part of the lagoon, the bottom is of rather firmly packed granular material--skeletal and gypsum grains and peloids. Small masses of grapestone are common, but thin, brittle plates and chips (1-3 cm dia.) enclosing many grains are more conspicuous (Fig. 6B-E). Although traces of organic matter are entrapped in these bits of crust, very few samples have textures suggestive of algal laminites, or more than two superposed laminae, so they are not stromatolites. The crusts are porous to dense, no more than a few millimeters thick, and break easily. Some are pierced with small holes. The crusts appear related to the lacy carbonate crusts reported by Lucia (1968) from the Pekelmeer on Bonaire, but those are subaerial, more persistent, more porous, and much thicker. The grains cemented into these thin crusts may be any of the autochthonous carbonates (Mg-calcite, aragonite, dolomite), the allochthonous carbonates (Mg-calcite, aragonite), gypsum, or pieces of older crust or grapestone of these same kinds. Two types (A and B) are recognized by macroscopic characters.

A) Fresh-looking, pale yellowish gray, porous, easily broken crusts (Fig. 6C) occur on the lagoon floor at all sites sampled. Enclosed in them are grains of older carbonates (peloids, and some coated peloids and fossils--Fig. 6G, 6H), lithic grains of old crust (Fig. 6I), gypsum crystals and clusters (Fig. 6F), and pisoliths (Fig. 6J). Ostracodes and small forams are common; snails are few because most are larger than the thickness of the crusts. A few quartz grains (Fig. 6I) and rare collophane occur too. X-ray analysis of fresh material shows it to be mostly aragonite and Mg-calcite in ratios of 5/1 to 2/1. Thin sections show microspar lining or filling intergranular pores and holes in fossils, and cementing grains at points of contact (Fig. 6F-J). These bits of crust are sedimentary grains of both aragonite and Mg-calcite, partially lithified by a contemporaneous micritic Mg-calcite and some aragonite druse.

B) Dull, gray to dark gray, generally denser, sometimes etched chips of crust, otherwise similar to (A), are taken to be older examples of that same sort (Fig. 6D, 6E). These dark chips occur scattered throughout the cores; the few on the lagoon floor probably have been displaced from older layers and redeposited. The older aggregates are mineralogically more heterogeneous than the fresh ones, for all X-rayed contain some dolomite. Aragonite is less abundant than in the "fresher" crusts, and one from Unit 3K is of dolomite with only traces of aragonite and Mg-calcite. A sample from Unit 3D is obscurely laminated and composed of weakly dolomitized skeletal sand of Mg-calcite. "Dolomites" contain 40-48 mol percent $MgCO_3$, and are thus protodolomite (i.e., poorly crystallized, Mg-deficient dolomite).

Several samples of calcite from both fresh and old crusts and grapestone were measured for Mg content by the method of Neumann (1965). The mode mol percent of $MgCO_3$ ranges from 5.4 to 7.6, but only one is over 5.8.

These aggregates are petrographically very like crusts of the Pekelmeer (Lucia, 1968, figs. 17, 18) except that "pisoliths" (Fig. 6J) are smaller (*ca.* 0.5 mm) in La Salina. Multiple stages of irregular growth prevail in these also, and some have double nuclei. Except for size they seem homologous with those of Bonaire, are only locally abundant and nowhere dominant. To call them oölites because of their size would mislead the reader. Cemented peloidal aggregates (older crust) are reworked and redeposited (Fig. 6I). The mineralogy and textures compare closely with the diagenetic features of the "hypersaline field" of the Shark Bay sublittoral (Logan, 1974). Hypersaline water sinks through a mesh of mostly carbonate grains there and at La Salina. Hudec and Sonnenfeld (1974) credit efficient absorption of incident solar energy for elevated temperatures (> 40°C.) in another hypersaline lagoon and believe the heat enhances the diagenesis therein. A similar effect may occur seasonally in La Salina. One particularly dense, smooth, ivory-colored, presumably young, sample from the top unit of Core 6 (Fig. 9) is aragonite, with minor, subequal amounts of Mg-calcite and protodolomite; it is homogeneous and the minor constituents are not distinct.

In summary, fresh or reworked grains of aragonite and Mg-calcite accumulate and may be cemented by the same minerals; with time the aragonite inverts or is replaced, and dolomitization may occur. Dolomitized material is not uniformly associated with gypsum, but most units that contain some protodolomite contain some gypsum.

Organic Materials. Traces ($\leq$ 2%) of impalpable brownish-black macerated tissue is mixed with fine clay in some units, especially those close to the peats or to the present lagoon floor. The unidentified plant capsules (see appendix), peaty clumps and a few chips of wood (probably mangrove) make up 1-12% of some units (Fig. 5). The large organic fraction in unit 6A (Fig. 9) is of algae with perhaps some additions from the nearby habitations.

Layers of compact peat occur at the bottom of Core 3 and within Core 4 (Fig. 8, 9). The thickness of gravelly skeletal sand stopped the corer at other sites. Because both peats are quite similar, only Core 3-Bed L was analyzed, by R.H. Tschudy, and filed as U.S.G.S. paleobotanical locality D5038. According to Dr. Tschudy, the peat is decomposed organic matter containing many fungal hyphae, some rootlets, and the algae *Tetraporina* sp. and *Pediastrum (?)*. Pollen is not abundant, but those of *Rhizophora* (probably *R. mangle*), Chenopods and Myrtaceae occur; spores of several ferns also occur. Calcareous fossils that may have occurred were destroyed by the acidity of the peat, but no siliceous fossils occur either. Microforaminifera and dinoflagellate cysts indicate a marine influence, as do the algae, according to Tschudy, and the presence of so few pollen types suggests little diversity of vegetation in a community dominated by mangroves. This is the case for modern red mangrove communities in this region, and the ancient community is considered to have been dominated similarly by red mangrove. Like deposits of similar age have been described from Columbia by Cohen and Wiedemann (1973).

Allochthonous Skeletal Carbonates. Most of the lagoon sediment is muddy skeletal sand and gravel (Fig. 5, 7, 8); except for the grapestone and patchy crusts discussed above it is not consolidated. The particles are the debris of the reef flats, ocean beaches and the island itself: gravel is mostly of *Porites* and clam shells; sand is mostly *Halimeda* and snail fragments, ostracodes, peloids, and coated grains; mud is largely algal, plus micrite bored from coarser fragments. Quite recent aprons of this material lie along the southwestern shore of La Salina, north of Sites 1 and 2, and exemplify the main mode of lagoon filling.

These materials are Mg-calcite and aragonite. Although the skeletal sand is friable, some weakly cemented grapestone clumps occur. The grapestone is dolomitized to various degrees in the older beds; mol percentage of $MgCO_3$ ranges from 40-44%.

Siliceous Materials. Terrigenous minerals are the smallest inorganic fractions of all the samples, ≤ 1 percent in most samples, and as high as 4 percent in a very few (NaCl-free basis). Most of these grains are rounded and subrounded fine quartz sand (Fig. 6H); a few rock fragments also occur. Clays occur in trivial amounts so were not analyzed. They are surely of the same species found on the sea bottom nearby (Weiss *et al.*, in press): mostly chlorite and kaolinite, with some illite and traces of pyrophyllite.

The coarser materials and some clays are eolian; clay is also brought by the occasional spread of muddy fresh water over the coastal waters, following severe inland storms.

Fossils. Major skeletal fractions such as *Porites* and *Halimeda* have already been mentioned. These, along with minor amounts of echinoid spines, serpulid tubes and crustose coralline algae, reflect the prevailing reef-flat and grass-bed communities around the island. Grains of these types occur throughout most cores, but are scarce to absent in the highly gypsiferous beds (Fig. 9). Ostracodes are abundant in the modern sediment and calcareous older layers, but are less numerous in the gypsiferous layers. Foraminifera occur in all cores and most beds, but are much less numerous than the ostracodes, particularly in the gypsum sands; the forams may well have lived in the lagoon (Murray, 1970). Fragments of bone and crustaceans are trivial. Pulmonate snails occur only in the older layers at two sites (Table 2).

The rather numerous molluscs were identified, and their occurrence is given in Table 2. Of the many types found in the cores, only 5 occur in the youngest stratigraphic units (Table 2). All identifiable genera are typical of Late Cenozoic and Holocene brackish or shallow marine environments (Weisbord, 1962). Their diminishing abundance with time points to a progressive "poisoning" of the lagoon by increased salinity, just as does the development of gypsum.

STRATIGRAPHY

The cores on which this study is based were obtained with a driven steel pipe of 6.5 cm ID. Measurements of penetration depth and length of "rise" of core into the pipe were made each time before the core and barrel were withdrawn. All cores were compressed considerably, to as little as 50-60 percent of depth of penetration. The unit-thicknesses illustrated (Fig. 9) are all "restored," *i.e.,* increased from their recovered length by the factor necessary to expand the total length of core recovered to the actual depth of penetration. The amounts of linear compaction are compatible with experimental ranges given by Emery and Hülsemann (1964). Although they report that compaction is of uniform magnitude throughout the lengths of short cores, the different facies and textures of La Salina cores may not have compacted uniformly. Core lengths illustrated and discussed here are believed to be real; the thicknesses of several units in each core may have been distorted mutually by this extrapolation process, but none are thick enough to vitiate the geological conclusions.

The sedimentary record in La Salina is rather disorderly because thin, local fan-shaped wedges of skeletal-peloidal sandy mud have invaded the margins of the lagoon from time to time. These become markedly finer in texture towards the lagoon, from muddy gravel to mud or sand, in short distances from the edge of the lagoon. Their breadth is small with respect to the spacing between cores, which hinders correlations. Facies in mid-lagoon may also be of small extent; *e.g.,* Core 5B contains a unit of skeletal debris with peat (5B-C) which is only just recognizable in Core 5A, only 30 meters farther north (Fig. 2, 9). The peat in Core 4 lies 37 cm below the floor of the lagoon, whereas that in Core 3 is 123 cm deep; they have radiocarbon ages of 2980 and 2690 years, respectively (Fig. 9). Part of the section of Core 4 is believed to be overturned, as explained below.

Radiocarbon dates have been obtained from certain of the units. Most confidence is placed in those from the peat layers (3L and 4C) because (1) the peats are relatively thin, and (2) ages of carbonate units are doubtless the medians of broad spectra of maximum ages of grains. Given the patchy deposition of skeletal material, absolute ages might be the best correlation tool; sedimentation rates, however, were erratic in both space and time so that no correlative ties are suggested in Figure 9.

Ages of dated units are posted in Figure 9, and considered to be the age of the mid-point of each unit. Measurements, made by Dennis Coleman of the Illinois Geological Survey, are as follows:

Unit	Radiocarbon Years B.P.	B.C. Years A.D.	
2C	3170 ± 75	1220	
2E	3770 ± 100	1820	
3L	2690 ± 75	740	
4B part A	440 ± 75		1510
part B	540 ± 75		1410
4C	2980 ± 120	1030	
4D	767 ± 75		1183
5A-B	950 ± 75		1000
5A-C	2820 ± 75	870	

Approximate average rates of sedimentation can be computed from the ages and stratigraphic intervals between the mid-points of dated units. For older intervals, the rate from Unit 2E to 2C is 0.09 cm/yr near the lagoon margin and 0.02 cm/yr from 5A-D to 5A-B in mid-lagoon. For younger intervals (up to the lagoon floor) the rate is 0.02 cm/yr for both Units 2C and 5A-B. The average rate from 3L to the surface is 0.05 cm/yr, but the interval is so thick the value is unreliable. The rate from 4B to the surface is the same, but the abnormal history of Unit 4B (see below) requires this value be ignored.

Normal Succession. The stratic succession in La Salina records a history of lagoonal sedimentation, but one with a marked change from normal marine to hypersaline conditions. Peat and skeletal-peloidal carbonates are the older sediments, the carbonates having been brought mostly from the island and seaward beaches by storms. The main body of sediment, continuing to the present day, is of carbonates with gypsum. The gypsum, together with modern-day seasonal halite, records the deterioration of circulation and onset of hypersaline conditions. This began about 2700 years B.P., and terminated the accumulation of red mangrove peat 3L.

Red mangrove will grow in waters ranging from normally saline to fresh, but establishment of seedlings is favored by initial salinity approaching that of normal sea water (Stern and Voigt, 1959). Although no work has been done on the tolerance levels of mature plants, hypersaline environments appear to be unfavorable. Red mangrove cannot pioneer or expand under hypersaline conditions, however, for seedlings are deterred by salinities 140% of normal, *i.e.,* about $50^{\circ}/_{\circ\circ}$ (Bowman, 1917, pp. 631, 671). Thus, the mangrove community must have deteriorated even before conditions had become suitable for the accumulation of gypsum.

A tenuous link to the sea has existed at the northwest corner of

La Salina in more recent times, through the small pond (Fig. 2) and channel described earlier. It is possible that this was the site of the 2700-year-old connection to the sea. Gypsum is sparse in Core 6, the nearest sample site, and the acid-resistant residues contain more quartz sand and silt than other cores. The amount of quartz increases upward, to about 4 percent of the salt-free solids. Eolian transport may have brought some, but the muddy fresh water that overspreads coastal waters and surrounds the keys several times each year (Weiss *et al.*, in press) could have brought fine clastics from the mainland by intermittent flooding of this channel. The increase of quartz upward in Core 6 is, by this hypothesis, compatible with rising sea level postulated for the last 2500-3000 years. The amount of quartz is less than that in modern bottom sediments near Cayo Sal, and it comes largely from such lenses of muddy flood water (Weiss *et al.*, in press).

Overturned Succession. The age relations in Core 4 are anomalous, for an old peat lies on apparently much younger carbonate sediment. Peat 4C has two sharp contacts, is of age similar to peat 3L, and lies 86 cm higher (top-to-top) than Unit 3L. Peat 4C is "too high"--at a stratic level too young for its age of 2980 years (Fig. 9). However uncertain the dates on carbonate units may be, the dates of peats are good. Because of its anomalous stratic position, Unit 4C is shown bounded by unconformities (Fig. 9).

The abnormal form of the northeastern quadrant of Cayo Sal reef platform was touched on earlier. El Huequito (Fig. 2) has the shape of a segment of a circle centered at the northeast corner of the reef platform. It is separated from La Salina by a narrow, low berm of skeletal sand that is lower and quite different from the coral cobble material to the west and east of it (Fig. 2). That berm is poorly vegetated, especially by comparison to other parts of the island, and its height and profile suggest it was formed by the surf in the bay, as though an open gap may have been closed progressively by surf and by growth of low sand spits from both sides of the bay.

One hypothesis to explain the topographic and geographic aspects of El Huequito, and the stratic and chronic aspects of Core 4, is that La Salina once included the area of El Huequito, and that catastrophic destruction of the northeast corner of Cayo Sal made several changes in quick succession:

i) displaced the unconsolidated material of the northeast corner of the island without displacing much of the coarse coralgal rubble to right and left (Fig. 2)(if it was indeed already there);

ii) tore up an old mat of peat from below the lagoon floor, rafted it southwestward and redeposited it as Unit 4C. (About 5% of Unit 5B-C and basal 5B-B is shreds and clots of peat, possibly part of this same redeposited mat of peat.);

iii) spread mineral debris from lagoonal and supratidal deposits over the floor of El Huequito and part of La Salina (?Units 4A, 4B?);

iv) and left El Huequito open to the sea and exposed to colonization by corals.

Considerable relocation of fine materials must also have occurred throughout the lagoon, but these cannot now be distinguished with confidence. The hypersaline condition of La Salina was moderated until separation of El Huequito from La Salina once again established hypersalinity in the lagoon.

The event must have occurred after 770 B.P. and before 500 B.P. Unit 4D is thick (Fig. 9) and the upper part is certainly much younger than 770 years, but by how much cannot be even guessed (it may even include some carbonate redeposited along with the peat). In historic terms this occurred between 1180 and 1450 A.D., probably closer to the later date.

Subsequent to this supposed event, corals became established in El Huequito, and surf filled the breach into the lagoon by building a sandy beach and berm along the southwest margin of the bay, perhaps where the storm-laid debris was heaped highest. Plant succession is still in early stages on this berm.

Such a catastrophic event ought to have left other evidences of its occurrence. Damage *has* occurred on the northeast quadrants of neighboring islands (Weiss *et al.*, in press), but no means of estimating dates is at hand. The northeast quadrant of the reef edge of Cayo Peraza (Fig. 1) was broken sometime before 1950, the date of earliest air photos. This allowed heavier surf to reach the island and displace loose sand from behind protective rims of beachrock (themselves having radiocarbon ages of zero years). The reef flat on the northeast quadrant of Cayo de Los Muertos (Fig. 1) is littered with *Acropora palmata* displaced from the reef front. The platform north of Cayo Borracho (Fig. 1) has larger areas of coral rubble than of living coral, despite being a favorable site with regard to depth, clarity, and circulation. Each of these examples seems "modern" in aspect, for debris thrown onto a reef flat probably cannot endure boring and solution more than a few decades. These additional examples do little more than show that spectacularly destructive waves have struck this coast from the northeast. It remains to consider their sources and frequency.

HURRICANES AND TSUNAMIS

Destructive waves from hurricane or seismic events--or surges associated with either--might do the job, but neither sort of catastrophe is common in the southern Caribbean. Further, historical records of natural events are almost non-existent for this part of rural Venezuela.

Hurricanes

Hurricanes are not known to originate in the central part of the Caribbean--*i.e.*, between Colombia-Venezuela and Jamaica-Hispaniola (Dunn, 1956). Further, only four (1802, 1877, 1892, 1933) have passed along or across Venezuela's Caribbean coast in nearly 500 years

(Tannehill, 1950). Those spawned in the major source area (off Martinique-Barbados-Trinidad) cross the Caribbean on a westward track, but almost without exception they twist slowly to the right (Garriott, 1900; Fassig, 1913; Mitchell, 1924; Dunn and Miller, 1964) so as to swing away from Venezuela and Colombia. This fact, plus the concentration of wind power in the right front quadrant of each advancing storm, protects coastal Venezuela and the waters out to the Dutch A-B-C islands from all but those storms that are abnormally far to the south. Tropical storms of sub-hurricane intensity are less restricted (Colón, 1953), but also less damaging; their incidence and tracks are less thoroughly known, particularly in the pre-20th Century records.

Hurricane records of differing precision are available from 1493 to the present. It is clear that most of those originating near or passing through this part of the Caribbean Sea pass the meridian of Chichiriviche (68°15') at latitudes of 14° or more North (Tannehill, 1950; Dunn and Miller, 1964), and that those abnormally far south for this longitude pass south of 13° North Latitude. Between the 13° parallel and the coast at Chichiriviche is a distance of about 230 kms. The frequency of those hurricanes known to have crossed the 68° meridian south of 13° N. Lat. is a reasonable guide to the frequency of major storms that may have damaged the coast of western Venezuela directly or created spectacular storm surges (Table 3). The hurricanes that passed closest to Venezuela are starred in Table 3. According to the National Hurricane Center, storms this far south are *usually* not as intense as elsewhere, although these very rare events *may* also have been abnormally violent (P. J. Hebert, personal communication, 1976). Major damage to the coast of western Venezuela might thus be expected to have occurred as a result of hurricanes once every 100 years.

Tsunamis

Tsunamis or seiches are on record back to 1530 A.D. (Berninghausen, 1969), but only five are known to have damaged Venezuela. Three (1530, 1853, 1929) severely damaged Cumaná, on the north coast of Venezuela 440 km ESE of Chichiriviche. Damaging waves not known to have been associated with earthquakes--probably storm surges according to Berninghausen (1969)--were recorded "from Venezuela" in 1543 and on the coast 160 km west of Chichiriviche in 1955. None of these occurrences suggests itself as the cause of damage to Cayo Sal, but they illustrate destructive waves that occasionally strike the Venezuelan coast, and none coincided with any of the hurricanes listed in Table 3.

The average rate of destructive wave attack in this area since 1493, whether from hurricanes or tsunamis, is two per century. Even so, no historical incident can be correlated with the formation of El Huequito and the abnormal stratigraphy of Core 4 in La Salina. Not only was that pre-Columbian (if the radiocarbon dates on carbonates can be trusted), but records of catastrophic events of this sort that affected the more rural parts of that long coastline, especially in older times, are poor. Chichiriviche, for example, had no highway access until the early 1960's.

GEOLOGIC HISTORY

The old peat in Core 3 (Unit 3L) lies 123 cm below the floor of the lagoon and is 17 cm thick; it broke clean at the bottom of the core, so the in-place peat must be thicker than the 17 cm recovered. The top of the peat is 1.49 m below "local" mean sea level (the median position between high and low water, according to observations and local sources). No tide gauges exist near here; the closest is a La Guaira, 160 km to the east.

The depth of the lagoon 2500-3000 years ago cannot be known, but its bottom at Core 3 (Fig. 2) cannot have been higher than 1.49 m below present mean sea level. At that time the lagoon must have been either (a) of fresh to brackish water and slightly supratidal, or (b) connected by a channel(s) to the sea and intertidal. Separation of the lagoon from the sea now is only by the wave-built carbonate-sand island, a common condition for shallow coral banks, so cause "b" seems more likely. The present lagoon is intertidal-to-supratidal, permanently hypersaline, and connected regularly to the sea only by the shallow phreatic zone under the island. The change from either "a" or "b" to the present configuration requires that a relative rise of sea level, of about 1.5 m, have occurred in the last 2600-2700 radiocarbon years. Free connection to the sea must have been closed off during this time, possibly by shore processes of the rising sea--the remobilization of stable sediment and closing of channel(s) by longshore transport.

Independent evidence of a rise of this magnitude is to be found on the mainland just a few kilometers away. Two drowned terraces occur in the Golfete de Guare, near Chichiriviche (Weiss, 1973). The Golfete is an abandoned sinuous channel of the Tocuyo River, the master stream of the alluvial lowland of eastern Falcón State. Near the mouth of the Golfete the edge of the deeper and older terrace is 5.2 m below modern sea level, and suggests that sea level had been rising intermittently even prior to 2700 years ago. The younger terrace edge is 1.8 m deep, and of the right order to correlate in vertical extent with the evidence from the sediments of La Salina.

Evidence for comparable rise or Late Holocene sea level comes also from other areas. Wiedemann (1973) found a red mangrove peat 2430 radiocarbon years old buried beneath sediments of a large coastal lagoon in Colombia. His site "a" (Wiedemann, 1973, fig. 5, table 1) is close to the coast, and records a relative rise of sea level of about 2 m in 2300 years. This is a change of the same order of magnitude as that recorded here from Venezuela, but the sites are 460 km apart and the coincidence cannot support a claim of eustatic change alone.

Scholl *et al.* (1969) recently revised the eustatic rise curve for Florida; the rise there has been almost exactly 1 m in the same period of 2700 radiocarbon years. Peats from a wider geographic range, including Bermuda and Louisiana, were the basis for a steady eustatic rate developed by Redfield (1967) for the last 4000 years. Over 2700 years, that rate gives a value of 2 m. Clearly, the relative rise of sea level at Chichiriviche has been at least partly eustatic in nature.

The similarity of the vertical intervals cited from other studies, and the mostly low-lying Late Tertiary terrain of this part of the Venezuelan coast strongly suggest that the rise has been mostly or wholly eustatic.

CONCLUSION

La Salina had normal or brackish salinity 2700-2900 radiocarbon years ago, and accumulated red mangrove peat. Sea level was 1.5-1.8 m lower than at present. About 2600-2700 years ago the connection from the lagoon to the sea was interrupted as shore processes of the rising sea disturbed old beach and island deposits, and longshore transport made a new configuration of the supratidal sediment. The lagoon became, and remains, hypersaline; abundant gypsum crystallized and is preserved in the sedimentary fill. Halite forms and redissolves seasonally, so is not part of the geologic record. Sea-level rises of this magnitude and rate are attested to by drowned terraces on the nearby mainland and by buried peats in Colombia. Similarity of this rise to the eustatic values for the western Atlantic and Gulf of Mexico suggests that it is itself mostly eustatic in nature.

Between 1180 and 1450 A.D., probably closer to the latter, a tsunami or severe storm surge struck the northeast quadrant of the island, turning part of the old lagoon into a bay. At the same time a buried peat was reexposed and resedimented at an anomalous (higher) elevation, within carbonate sediments younger than itself. The salinity of the lagoon became normal, temporarily, until closure of the gap cut off circulation once more. The incomplete plant succession on the part of the island between the bay and lagoon suggests that that deposit is young, or has been unstable since becoming subaerial. Coral growth in the bay is recent. Both facts point to a catastrophe in historic times, but none is recorded in the archives of Venezuelan coastal disasters. An event in the early 15th Century is therefore a best estimate of the occurrence.

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Table 1. PRECIPITATION & EVAPORATION*

Precipitation (1954-1969)

	Annual Total in Millimeters	Percent of Annual in O, N, and D	Percent of Annual in Sept.-Jan.
Minimum Annual	560	20	35
Maximum Annual	1900	75	90
Mean Annual	1160	47	62

Evaporation (1950-1970)

	Minimum	Maximum	Mean
Monthly Averages (mm)	71 (Nov)	84 (Mar/Apr)	77.3
Annual Totals (mm)	-----	-----	927.0

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*Condensed from Weiss *et al.* (in press).

Table 2. MOLLUSC OCCURRENCES

CORES	2					3				4				5A + 5B					6					Present in
FOSSILS / UNITS	A	B	C	D	E	A	J	K	L *	A	B	C *	D	A	B	C	D	E	A	B	C	D	E	top units
GASTOPODS																								
Arene (Marevalvata) sp.		o	o																					
Tricolia bella					o		●	●		o			o		o	●	+	o				o	+	X
Smaragdia viridis viridimaris			o																				o	
Rissoina cf. R. bryerea			o					o																
Zebina browniana							o	o					o		o	o	+	o			o	o	o	
Teinostoma (Idioraphe) sp.					o																			
Teinostoma (Pseudorotella) sp.					o																			
Caecum (Micranellum) regulare					o																			
Caecum (Meioceras) nitidum					o																			
Cerithium variable	●	o	+				o			o				o	o	o	o	●					+	X

CORES	2					3				4				5A + 5B					6					Present in
FOSSILS / UNITS	A	B	C	D	E	A	J	K	L *	A	B	C *	D	A	B	C	D	E	A	B	C	D	E	top units
Cerithium sp.	o	o				●	o	o		o	o		o		o		o		o			+	●	X
Bittium (Bittiolum) varium		o		o	o			o		o			o	o		o	o		o					X
Alaba incerta			o														o						o	
Alabina cerithidioides				o	+			o					o		+	o	●				o	●	●	
Cerithiopsis sp.																							o	
Balcis conoidea			o																				+	
Columbella mercatoria					o												o							
Anachis cf. A. obesa				o																				
Mitrella sp.								o										o					o	
Oliva (Minioliva) cf. perplexa			o	o	●												o	o					+	
Granula lavalleeana		o	o	o	o		o									o	●	o					+	
Bulla umbilicata					o																		o	
Haminoea aff. H. petiti				o	o																			
Turbonilla sp.					o								o				o				o	o		
Unidentified pulmonates				o	o																		o	

CORES	2					3								4				5A + 5B					6					Present in
FOSSILS / UNITS	A	B	C	D	E	A					J	K	L *	A	B	C *	D	A	B	C	D	E	A	B	C	D	E	top units
PELECYPODS																												
Arcopsis adamsi			o															o									o	X
Brachiodontes sp.																				o								
Codakia costata				o																							o	
Gouldia cerina				o																	o							
Number of groups represented	3	6	10	9	14	1	-	-	-	-	6	7	-	5	2	-	8	4	7	8	16	9	3	1	4	8	24	5

o = 3 or fewer   ● = 4-5   + = more numerous   * Peat beds: no calcareous fossils; see text

Table 3. HURRICANE RECORD FOR

SOUTHERN CARIBBEAN SEA

1493-1801 - none known to have affected Venezuela (Garriott, 1900)

*1802 (Sept. 16) - Cumaná, Venezuela (10-11°N.; 64-65°W.)(Garriott, 1900)

1831 (June 23-27) - passed from Trinidad to north of Curaçao (Redfield, 1846)

Three other 19th-Century hurricanes crossed or came near to Trinidad, and may have had abnormally southerly courses like that of 1831. Their tracks subsequent to the dates and localities tabulated below are not known (Garriott, 1900), which suggests that they swept WNW across the open Caribbean.

Oct. 18, 1809 - Trinidad

Aug. 12, 1810 - Trinidad; Barbados

Oct. 10, 1847 - Tobago; Trinidad

*1877 (Sept. 21-Oct. 5) - storm apparently moved toward NW, and passed south of Curacao on the 23rd. (Garriott, 1900; Tannehill, 1950)

1886 (Aug. 16-28) - passed from Grenada and by Curaçao at about 13°N. (Fassig, 1913)

*1892 (Oct. 6-15) - passed from east of Tobago across Isla Margarita, passed about 30' (35 miles) north of Chichiriviche, and crossed the Paraguaná and Guajira peninsulas (Mitchell, 1924)

*1933 (June 27-July 6) - originated in the Atlantic, passed between Trinidad and the mainland of Venezuela, across the gulfs of Paria and Cariaco, and then across Bonaire and north of Curaçao. This is the only hurricane of record known to have passed south of Trinidad (Tannehill, 1950), although its track suggests that the Sept., 1877 storm may have had a similar course.

*Paths approached the mainland most closely, and are most likely to have affected the Chichiriviche area severely.

APPENDIX

"Seed"-like or "fruit"-like fossils, found in some of the mineral layers of the cores described above and referred to as "plant-capsules" on page 8, have been the subject of much interest, and as yet have not been identified, except to the extent that they seem to be of plant origin. They have been shown to neo-botanists and paleo-botanists, to entomologists, to bryozoologists, to malacologists. None of these would hazard a guess, except to suggest one of the other, totally different, groups of organisms.

I had no hesitation, at first glance at detached material, about calling them Ruppia maritima L. fruits, which would have been quite likely, considering the saline habitat. They were stalked, small asymmetrically ovoid beaked black objects. Closer examination of several dozens of specimens showed that this was not even a close possibility. The "fruits" were borne on a very slender branching "inflorescence", but mostly detached or on single capillary branches, occurred singly, in pairs, threes, and, in one example, decussately 4 together, united by their bases at two slightly different levels. The "fruits" are dehiscent dorsally by a trap-door-like arrangement, opening from below. The individual "fruits" are 1-2 mm long, somewhat laterally compressed, asymmetric, with a slender beak. On each side, just below the beak, is a thin spot, becoming an opening, giving the impression of two eyes. Well preserved examples are blackish, smooth. When somewhat weathered the surface is roughish and slightly brownish or purplish. All that were broken open were empty or had matrix inside. One already opened when found has a mass of small bodies that might be seeds or could be mineral grains.

We have as yet no clue to the identity of these fossils.

F. R. Fosberg

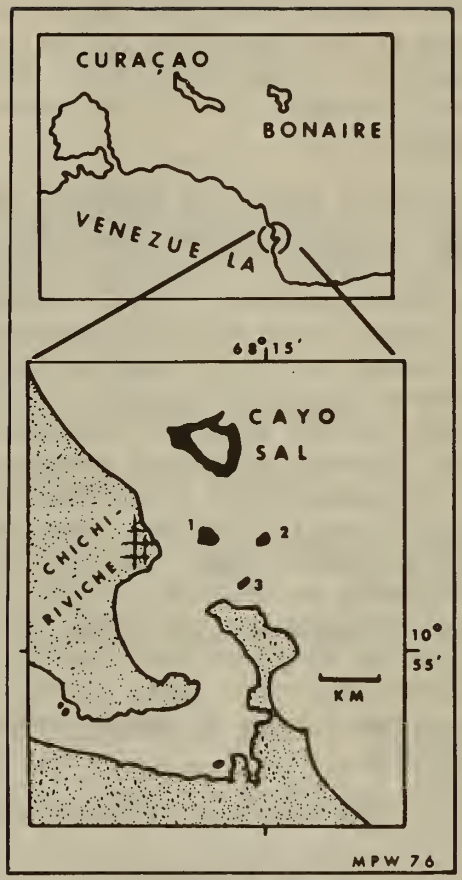


Fig. 1. Index Map. Cayo Sal is named; smaller cays are (1) Cayo de Los Muertos, (2) Cayo Peraza, (3) Cayo Pelón. Cayo Borracho (not shown) lies 3 km NNE of Cayo Sal.

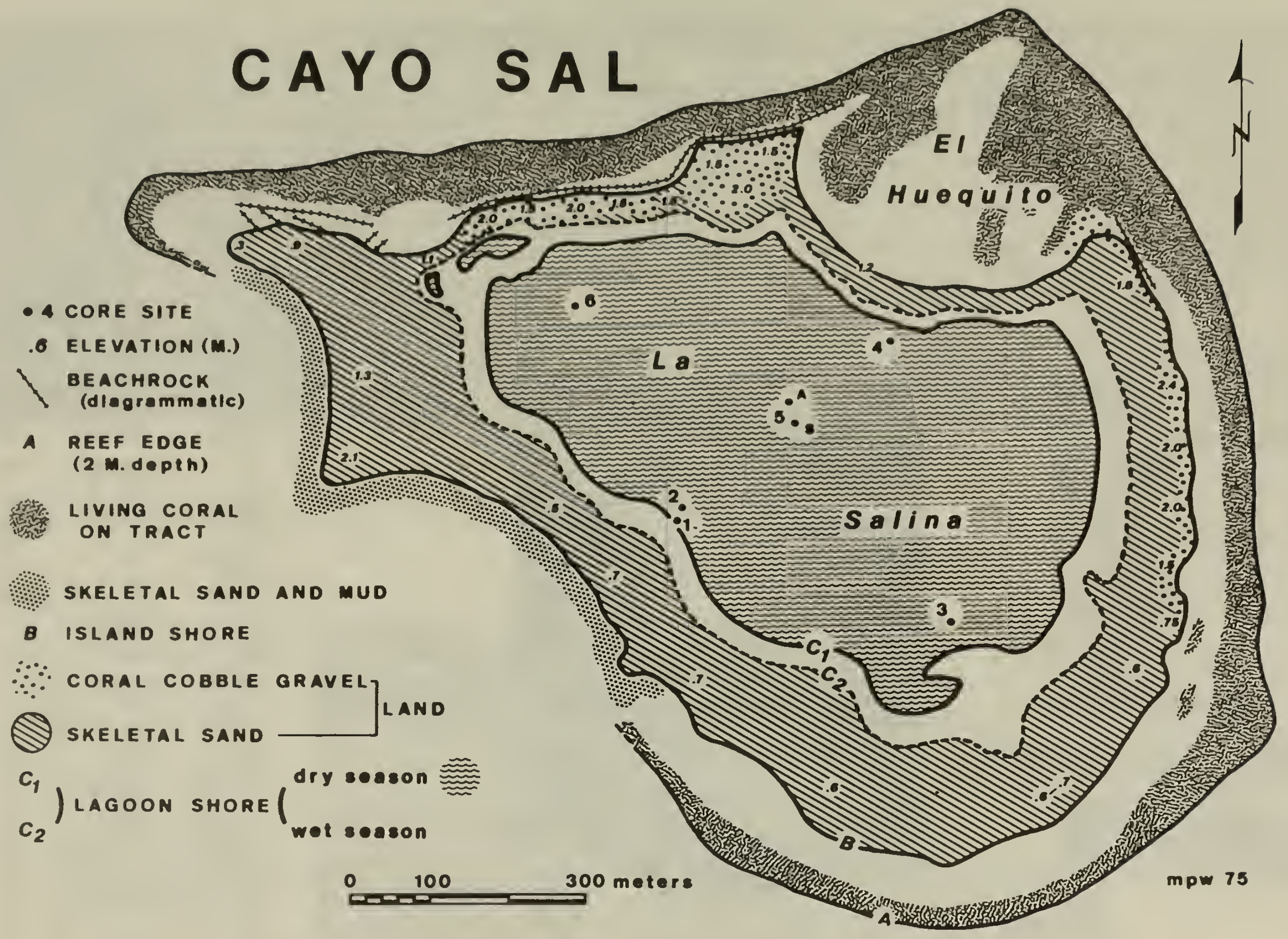


Fig. 2. Map of Cayo Sal, including island platform, reef tract, island, and lagoon (La Salina) with core locations. Compare with aerial photos in Figs. 3A and B.

Fig. 3. A) Aerial photo of Cayo Sal taken during high stage of La Salina in winter of 1950-51. (Frame 241D, mission C-12, 1950-51)

B) Aerial photo of Cayo Sal taken during low stage of La Salina on May 6, 1965. (Frame 371, mission 020124, 1964-65)

(Published by authorization of Cartografía Nacional, M.O.P., Venezuela.)

Fig. 4. Gypsiferous units in Core 3, showing Beds G-J (cf. Fig. 8). H, I and J are more than half seed gypsum. Lighter laminae are highest in gypsum; darkest ones have conspicuous slime of clay and organic residues. Bar of 2 cm measures dry, compacted thickness.

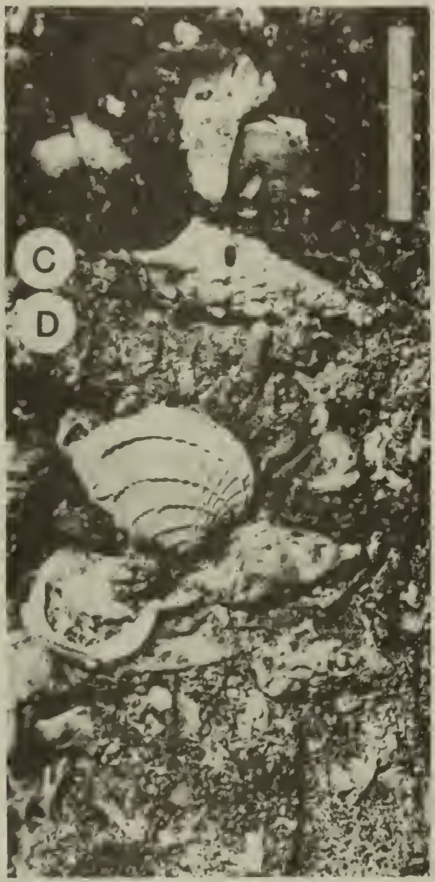


Fig. 5. Shells and scraps in older part of Core 5B. Bed C has skeletal sand and mud and a little peat that colors it conspicuously; the matrix of D is less well sorted and has less organic material (cf. Fig. 8). Bar of 2 cm measures dry, compacted thickness.

Figure 6 (facing)

A) Piece of gypsum crust, calcined and whitened during drying, from lagoon floor near Core 5B.

B) Crust of mixed gypsum and carbonate, from same sample as A.

C) Pale, "fresh" carbonate crust (Type A), from same sample as A.

D) Dark, "old" carbonate crust (Type B), from same sample as A, with intergrown gypsum rosette.

E) Darkened carbonate crust (Type B), from same sample as A.

F) Thin section of isolated gypsum rosette from same sample as A, cross-polarized light. Matrix is aragonite with some Mg-calcite and a trace of dolomite.

G-H) Two thin sections of peloidal-skeletal carbonate crusts from Core 2, Unit A, cross-polarized light. Crusts consist of aragonite, some Mg-calcite and a trace of dolomite, and are cemented by micrite and microspar, G) Peloids, with ostracodes and mollusc fragments, packed more tightly than in many grapestone and crust fragments. H) Peloids and skeletal grains, but more porous and with more conspicuous microspar.

I) Thin section of a druse-and-microspar cemented peloidal carbonate crust (Type A) containing older peloidal lithic grains (dark patches) as clasts, cross-polarized light. Bright spot against convex curve of larger lithic grain is quartz. Crust is of aragonite with some Mg-calcite; from Core 6, Unit A.

J) Thin section of pisolith of drusy aragonite with at least 5 generations of acicular druse, enclosed in porous fresh crust of cemented peloids, cross-polarized light. Crust is of aragonite with some Mg-calcite and a trace of dolomite; from lagoon floor near Core 5B.

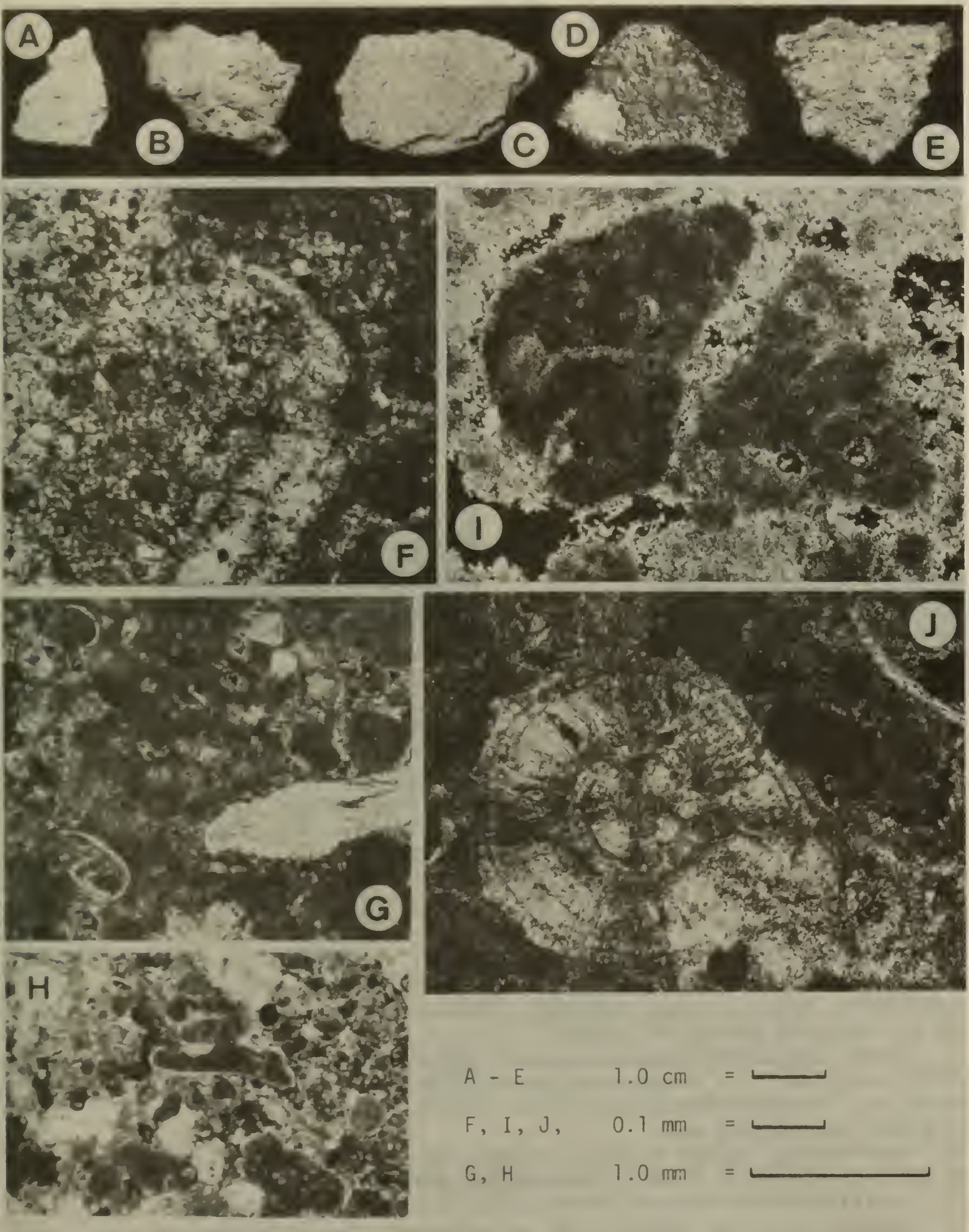
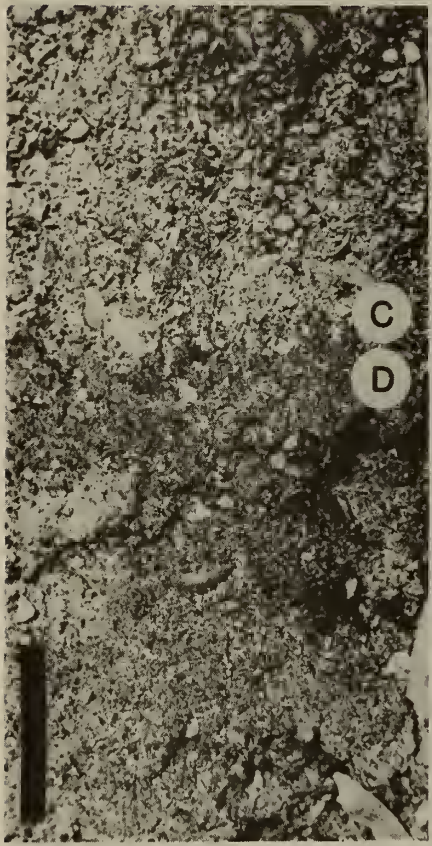


Fig. 6 - Cemented aggregates of gypsum and carbonate grains.

Fig. 7. Skeletal debris, mostly allochthonous, in Core 2. Bed C (above) has very little residue, but D has some peaty shreds and blebs (cf. Fig. 8). Bar of 2 cm measures dry, compacted thickness.



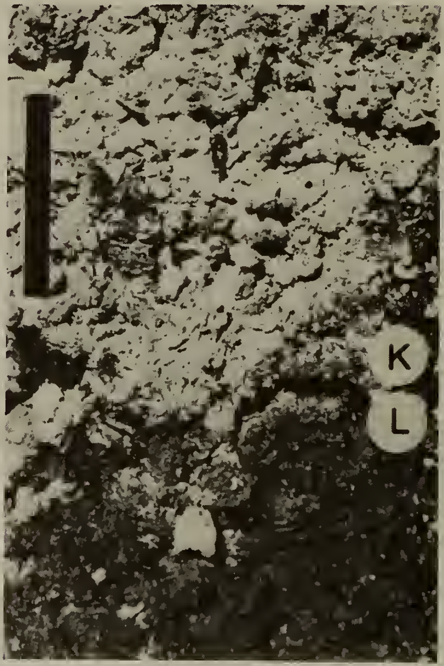


Fig 8. Beds K and L of Core 3 (cf. Fig. 9). Skeletal-peloidal debris with very little gypsum lies over a mangrove peat of 2690 ± 75 radiocarbon years that contains trivial amounts of mineral matter. Bar of 2 cm measures dry, compacted thickness.

Explanation for Figure 9 (facing)

CARBONATE is mostly skeletal and peloidal. GYPSUM is seed gypsum of sand and silt size. Organic material typcially exceeds quartz-plus-clay in acid-resistant RESIDUES. PEAT occurs as compact masses and as scattered shreds and blebs.

Three sedimentary structures are distinguished: SKELETAL--in which gross debris is conspicuous; MASSIVE--having a uniform, compact structure; LAMINATED--like massive but with color/textural bands such as gypsum and organic mud.

The textural ratios of the particles, grains and skeletal shards in the beds are given as MUD $\gtrless$ SAND-plus-granules.

Stratigraphic units are lettered from the lagoon floor down.

Radiocarbon dates refer to the units between the boundaries indicated.

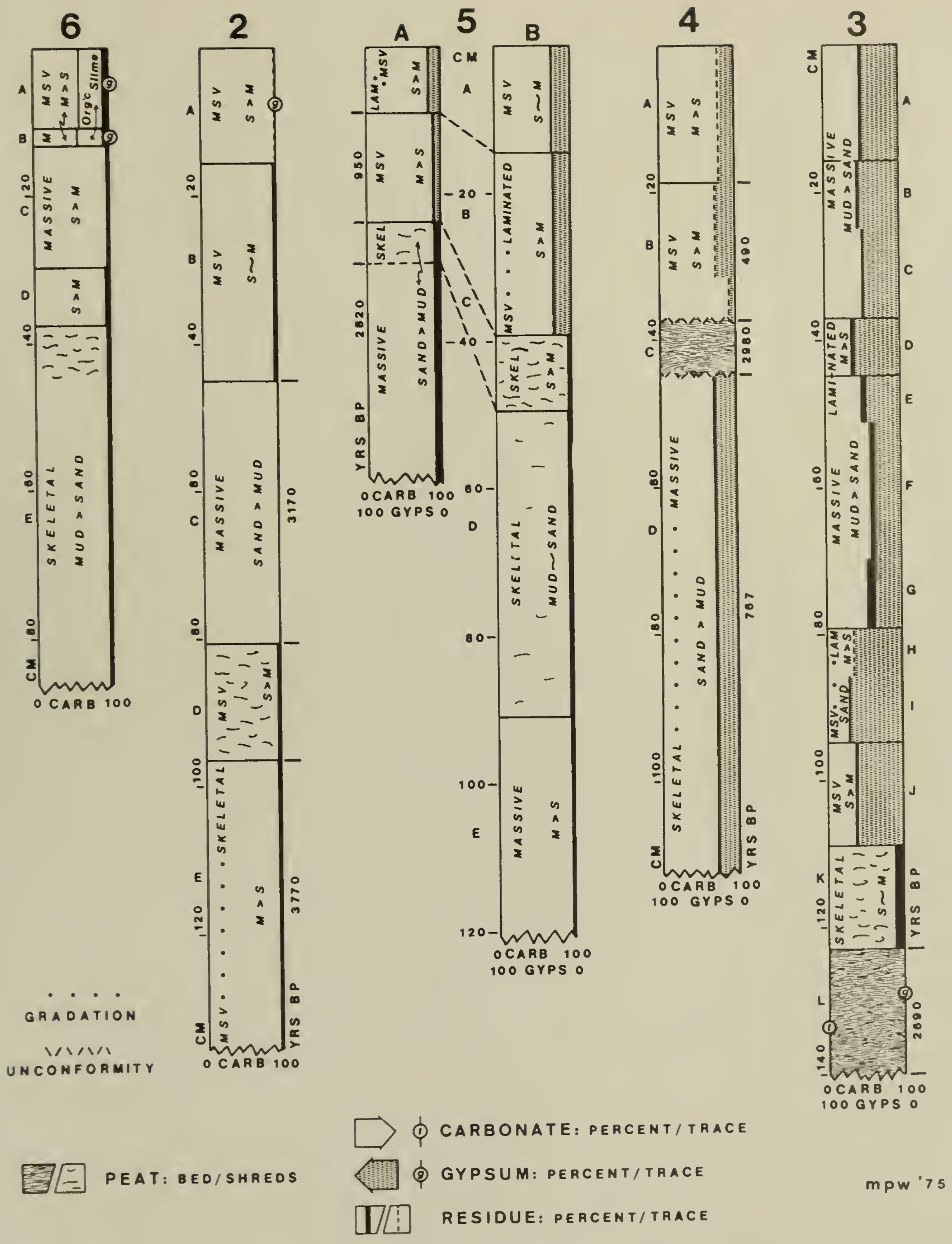


Fig. 9. Graphic logs of the cores arrayed with their tops (the lagoon floor) on a common line.

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