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# THE VEGETATION OF TERTIARY ISLANDS ON THE NINETYEAST RIDGE: PALYNOLOGICAL EVIDENCE FROM DEEP-SEA DRILLING

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# The vegetation of Tertiary Islands on the Ninetyeast Ridge: palynological evidence from deep-sea drilling.

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Pollen from deep-sea drillsites on the Ninetyeast Ridge reflects island floras that flourished in the Paleocene and Oligocene, and showed pronounced similarity to Australian and New Zealand Early Tertiary floras. Although closer to southern landmasses when emergent, these islands were truly oceanic, and their colonization occurred through long-distance dispersal mechanisms.

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Deep-sea drilling on the Ninetyeast Ridge, a linear sea-floor elevation separating the Wharton Basin on the east from the Central Indian Basin to the west, has shown the presence of shallow-water sediments at several points along the ridge crest[1,2]. At Deep Sea Drilling Project Sites 214 and 254, in the northern and southern sectors of the ridge respectively (Fig. 1), sequences of volcaniclastics, sands, clays, pebble conglomerates, and organic-rich intervals lie immediately above oceanic basement and show evidence of subaerial weathering and deposition. Among the strongest evidence for subaerial conditions is the presence of assemblages of well-preserved spores and pollen, reflecting the existence of a land vegetation of some diversity at points along the ridge crest at intervals during the Paleogene. Such vegetation is here interpreted as that of oceanic islands that were emergent along the line of the ridge from perhaps the latest Cretaceous to the late Oligocene; present fossil evidence establishes the presence of such vegetated land areas for the Paleocene and again in the Oligocene.

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Preliminary accounts of the microfloras have already been published[3,4]; this paper documents the occurrence of these pollen-rich sediments discusses the floristic composition of the vegetation they reflect, the dispersal problems faced by the island floras, and how these might have been affected by former distributions of land and sea areas. Detailed taxonomy of dispersed spores and pollen is currently being undertaken (Kemp and Harris, unpublished work).

## Tectonic setting of the Ninetyeast Ridge

The Ninetyeast Ridge extends for some 5000 km along the 90°E meridian, from 32°S to approximately 9°N, beyond which it is obscured by sedimentary cover in the Bay of Bengal. The crest of the ridge deepens progressively from south to north, and sediments immediately above oceanic basement in drillsites on the crest show an orderly pattern of age increase northwards. Similarities in sedimentary sequences at the drillsites accord with northward subsidence of the ridge throughout its history; the north to south diachronism of boundaries between shallow-water and deep-water facies has recently been demonstrated for the northern sector of the ridge[5].

A tectonic model to account for the origin of the ridge has recently been put forward[6,7], and subsequently elaborated[8]. The ridge has been interpreted as having been derived from an extrusive pile accumulating at the junction of a former active spreading centre and a north-south trending transform fault paralleling the present trace of the ridge. According to this model, volcanism was associated with motion along a transform that accommodated relative movement between the Indian and Australian plates until their fusion in the late Oligocene. The formation of both the ridge and the attached Indian plate in relatively high southern latitudes and their subsequent northward movement is supported by magnetic anomaly data[9], by the palaeomagnetism of basalts in drillsites on the ridge crest[10], and by calcareous microfossil evidence indicating warmer depositional conditions in younger strata[11].

We feel justified in regarding formerly emergent areas on the ridge crest as relatively small islands, for the configuration of the ridge places limits on the east-west dimension of such land areas, and the age differences of basal sediments from north to south does not suggest that large areas were emergent at any one time.

## Stratigraphy of sampled sites

The generalised stratigraphy of Sites 214 and 254 is shown in Fig. 2. At Site 214, well-preserved assemblages of spores and pollen were recovered from the interbedded volcaniclastics and lignites; there is no evidence for marine conditions in this sequence. These assemblages continue into overlying glauconitic carbonate silts and sands, which contain marine microfossils: dinoflagellate cysts, acritarchs, foraminifera, nannofossils and molluscs. The spore and pollen assemblages show little change throughout the entire sampled sequence, and are treated in this discussion as a single unit. Foraminifera in the glauconitic unit indicate a Paleocene age - P4 - for that unit[12]. The nannofossil zone of _Heliolithus kleinpellii_ is present in Core 37 at 337 m below the sea-floor, and the section may be as old as the _Cyclococcolithina robusta_ Zone in Core 41 at 389 m [13]. It is reasonable to extrapolate this mid-Paleocene dating down into the volcaniclastic sequence below as the microfloras are essentially the same throughout.

At Site 254, excellently preserved spores, pollen, and rare dinoflagellates were recovered from the lowest sedimentary unit. This part of the sequence consists of poorly sorted sandstone and clay, with some pebble conglomerates, and a high content of organic matter, and grades at its base into weathered olivine basalt. It has been interpreted as being derived from the subaerial weathering of a basaltic terrain, with rapid deposition of weathering products in a quiet, shallow-marine environment[11]; a lagoonal setting adjacent to vegetated highlands is perhaps represented. Mollusc fragments, foraminifera, and ostracods attest to the marine origin of the unit;

poor sorting suggests little current activity. Age estimates of the palyniferous basal unit based on calcareous microfossils are ambiguous; the firmest age control comes from the lower part of the overlying calcareous ooze unit, which has yielded middle to late Oligocene planktonic foraminifera[11]. Below this, foraminifera, ostracods, and molluscs are not stratigraphically diagnostic, and an age range of Eocene to late Oligocene has been suggested[11].

## Composition of the microfloras

At Site 214, the detailed distribution of palynomorphs over a 116-m interval has been documented[3]. Major pollen groups at this site include 15 form-species of angiosperms, 18 of pteridophytes, 4 conifers, and 3 lycopods. The dominant angiosperm pollen is referred to Arecipites, a form genus related to modern palms. Also abundant is Clavatipollenites, which has similarities to the extant New Zealand and New Caledonian genus Ascarina (Chloranthaceae). Pollen of Gunnera (as Tricolpites reticulatus) is consistently present; this form also occurs in Miocene lignites on Kerguelen. Several pollen species occur at the site in such low frequencies that a wind-blown origin cannot be discounted: included here are pollen types deriving from Nothofagus (of the brassi group), Proteaceae, Casuarinaceae, and Didymelaceae. The last-named family is presently confined to Malagasy, but similar dispersed pollen, as Schizocolpus marlinensis, occurs in Tertiary sequences in southeastern Australia[14] The remaining angiosperm pollen at the site cannot be referred to any extant genus or family.

Gymnosperm pollen at Site 214 suggests a largely podocarpaceous parentage; form species which may derive from Dacrydium, Microcachrys, Phyllocladus, and Podocarpus have been identified. Fern spores are dominated by smooth-walled trilete types of the Cyathaceae. Other families recognized include Polypodiaceae, Gleicheniaceae, and Schizaceae. Lycopod spores are not common, but three form species have been identified.

The flora represented by the pollen assemblage at Site 254 was more diverse, with, as minimum figures, 26 angiosperm species, 3 conifers, 17 ferns, 2 lycopods, and a wide variety of fungi. The most abundant of the angiosperm pollens is a complex of the form genus Rhoipites, of indeterminate affinity; comparable pollen is presently produced in a number of families, including Rutaceae, Goodeniaceae, Flacourtiacaeae, and Verbenaceae. Among forms that could be more positively identified to family level, pollen of Myrtaceae is most common. Two types were identified; one is a finely granulate form similar to that seen in such genera as Lophomyrtus, Rhodomyrtus, and related taxa; the other, with prominent processes on the grain surface, resembles no known living form. Next in abundance are pollens akin to those of living palms; generic affinity is again hard to fix, but similarities to pollen of Cocos, Jessenia, and Paralinospadix are evident.

Small, thin-walled diporate pollens identified as Moraceae/Urticaceae are common. Moraceae seems the most likely parent family for the group, but pollen of some tropical Urticaceae (e.g. Laportea) is indistinguishable. Pollen of Gunnera is again consistently present. The presence of pollen of the disjunct southern families Proteaceae and Restionaceae is of interest. Each is represented by a single form species; the Proteaceae by a type comparable to the Australian Tertiary form Proteacidites symphonemoides, and Restionaceae by the fossil form Milfordia homeopunctata, which shows marked resemblance to pollen of some extant Restio species, e.g. R. subverticillatus. Casuarinaceae is here represented in the pollen spectrum in quantities that suggest it was indigenous, rather than wind-blown; the dispersed pollen is indistinguishable from that of the division Cryptosomae. A further southern element is the form-species Cupanieidites orthoteichus, a zone fossil in Australian Early Tertiary sequences, with affinities to the tribe Cupanieae of the Sapindaceae. Angiosperm families of global distribution are represented by Compositae and Graminae, of rare occurrence, and by Loranthaceae (as Gothanipollis) and Sapotaceae. Extremely rare Nothofagus and Didymelaceae grains were noted.

Conifer pollen at Site 254 makes up some 20 percent of the pollen spectrum. In contrast to site 214, pollen of Araucariaceae is common at this site, and has been tentatively identified as that of _Araucaria_. Podocarpaceae include _Podocarpus_ and _Microcachrys_ types. The fern spore spectrum is similar to that at Site 214. Of the abundant fungal remains, only the fructifications of the epiphyllous Microthyriaceae could be firmly identified.

## Phytogeographical considerations

The plant microfossil assemblages discussed above indicate that the vegetation of these islands had much in common with the Early Tertiary vegetation of Australia, New Zealand, southernmost South America and Antarctica. Few species occurred in common with the Tertiary floras of India and the Indo-Malaysian archipelago. Of 41 form-species of pollen isolated at Site 214, 28 have been identified, or have closely similar counterparts, in the Australian Tertiary. At Site 254, 28 of the known 48 form-species occur in the Australian Tertiary, and 19 are known from the Tertiary of New Zealand. Resemblances occur within all of the plant groups present. Among the conifers, the mixture of podocarpaceous and araucarian elements is typical of the Early Tertiary of the southern continents. Among angiosperms, species lists indicate that many common forms existed between continent and island, but there are qualitative differences which lie chiefly in the extreme rarity of _Nothofagus_ pollen at the island sites, and in the poor representation of Proteaceae there, in strong contrast to Early Tertiary continental floras.

Reconstructions of the Indian Ocean for the mid-Paleocene and late Oligocene (Fig. 3) indicate that distances of the Ninetyeast Ridge islands from the southern continents were much less in the Early Tertiary in comparison with present geography, an observation which must account in part for the similarity of the island floras with those of the landmasses to the southeast. It does, however, seem likely that the sites were still truly oceanic, separated from the nearest continents by distances probably in excess of 1000 km.

The floras, therefore, must have become established through the long-distance dispersal of propagules, in the same way as has the vegetation of modern south-temperate and Subantarctic islands. The presence of possible 'stepping stone' islands would have increased the rate of biotic exchange between the Ninetyeast Ridge islands and the large Australia - Antarctica continent[15], and increased the probability of a given species making a successful passage from continent to island. Such intermediate island sites may have been present on the Kerguelen and Broken Ridges, which,according to most reconstructions, were joined in a single mass abutting the southern end of the Ninetyeast Ridge until perhaps the Eocene. The emergence of parts of Broken Ridge in the Early Tertiary is confirmed by the presence of beach gravels in the single drillsite on the feature[2], and the Kerguelen Islands were emergent at least in the late Oligocene-early Miocene, judging by the presence there of plant remains[16,17] in lignites interbedded with lavas which have recently been dated isotopically[18].

Problems in understanding the colonization of the Ninetyeast Ridge islands are related to the apparent inability of some of the modern familie represented to cross extended water gaps. Adaptations for long-distance wind and water transport are unknown in such families as Proteaceae and Restionaceae, and their present disjunct distributions are usually explained by invoking former land connections. Casuarinaceae and Myrtaceae are other families well represented on the Ninetyeast Ridge, for which there is no evidence of ability to make long ocean crossings. Araucaria, too is a genus with a modern distribution accountable in terms of previous land connections; its presence on Pacific islands such as Norfolk and New Caledonia may result from former links with Australia/New Zealand via the Lord Howe Rise[19]. The distribution of fossil Araucaria in Tertiary sediments of the Indian Ocean region, however, cannot be accounted for in a similar manner. Araucariaceae are presently unknown from countries surrounding this ocean, and most fossil records in the region are no younger than Early Cretaceous[20]. There were, however, Early Tertiary stands of Araucaria on Kerguelen[17], in addition to those on the southern end of the

Ninetyeast Ridge. The lack of Tertiary records of the taxon from nearby Western Australia (D. Hos, personal communication), and from that part of Antarctica bordering the Indian Ocean[21] makes migration pathways for these island stands difficult to trace.

The Podocarpaceae are also poorly represented today on oceanic islands, although they may have migrated to the Late Tertiary through the islands of the Indo-Malayan archipelago. Investigations of dispersal characteristics of Podocarpus fruits[22] led to the suggestion that dispersal of the group might have been achieved through the agency of frugivorous birds, but the efficiency of such a dispersal mechanism over long ocean distances remains speculative.

It is possible that the role of bird transport in the establishment of many taxa on the island sites of the Ninetyeast Ridge and Kerguelen was considerable. Birds must account for much seed transport to modern south-temperate and Subantarctic islands, although observations of actual dispersal are few[23,24]. It is perhaps significant that among the Ninetyeast Ridge microfloras there are some groups in which bird dispersal of seed is known - in addition to Podocarpus, Gunnera is another genus known to be dispersed[25] by birds, as are members of the Loranthaceae. A possible example of the establishment of Myrtaceae (Metrosideros) on shelf islands of New Zealand by migrating birds has also been recorded[24]. Moraceae is also a group with a high potential for this kind of dispersal.

Direct transport by winds and currents, and transport by biological agents are facilitated in regions of intense oceanic and atmospheric circulation, and in this context it should be noted that the islands of the Ninetyeast Ridge, when emergent, lay in the belt of circum-polar circulation. However, the intensity of this circulation at different times in the Paleogene is conjectural. In the Paleocene, with Australia-Antarctica still joined, and in the absence of a polar ice-cap, circulation in southern latitudes may have been relatively sluggish. By the Oligocene, however, an extensive ice-cap was present on Antarctica[26], and a narrow seaway had opened between Antarctica and Australia, so that the development of strong westerly winds and currents seems likely.

Comparison with modern island floras.

The reconstructions of Fig. 3 suggest that the islands of the Ninetyeast Ridge, when emergent, lay somewhat south of 40°. It is instructive, then, to compare what can be deduced of their vegetation from the pollen records with that of modern islands in comparable latitudes and similar oceanic positions. Presently, in the eastern Indian Ocean, Amsterdam and St Paul Islands lie at 37°55'S and 38°44'S, and Kerguelen at 49°30'S. The floras of these modern islands have few species; St Paul and Amsterdam presently support some 18 species of flowering plants[27, 28], a figure somewhat lower than the 26 reflected in the pollen spectrum for Site 254, which probably lay even farther south. Kerguelen presently supports about 21 flowering plant species. On the modern islands, the floras are further distinguished by a high ratio of pteridophytes to angiosperms - the occurrence of 'fern bush' communities on the more temperate of the southern oceanic islands, including Amsterdam Island, is a common feature[28].

The islands of the Ninetyeast Ridge thus seem to have supported an angiosperm flora of unusually high diversity for such high Indian Ocean latitudes, but their pteridophyte assembly was comparable in numbers to those of existing islands in the region. Even more striking than the apparently high diversity shown by the Tertiary island floras are the basic differences in floristic composition between these and the modern islands. Plants of high-latitude southern regions have been divided into 'insular' and 'continental' groups[29]; in the first category are taxa with a widespread distribution on southern oceanic islands; in the second are groups that have present ranges largely confined to the continents - the families Centrolepidaceae, Proteaceae, Restionaceae, Myrtaceae, and the genus Nothofagus have been cited as being chiefly of this distribution. Their absence from modern islands in the southern Indian Ocean is noteworthy, as is the observation that this absence occurs irrespective of the existence of apparently suitable habitats on some of these islands. Such an absence has been taken by biogeographers to indicate a lack of dispersal ability in these groups.

The fossil evidence to hand suggests that members of some of these continental families did in fact become successfully established on islands of the Ninetyeast Ridge, where pollen of Myrtaceae, Restionaceae, and Proteaceae occurs in quantities that are not suggestive of a wind-blown origin. Geological considerations dictate that establishment at these sites must have involved dispersal across significant ocean gaps, so that these groups may not always have lacked vagility. In further suggests that the current absence of the groups from southern oceanic islands is a function of the recent environmental history of those islands, all of which have been subjected, to greater or lesser degree, to late Neogene chilling.

There are presently insufficient data to assess to what extent the high diversity of the Ninetyeast Ridge floras, especially that from Site 254, was related to the area of the islands, or to the length of time during which they were emergent. Site 254 was drilled atop a broad plateau on the crest of the ridge, but it is impossible to assess the original area of emergence. There is similarly poor control on emergence time, as basalts at the base of the sequence are too weathered for isotopic dating. The lithology of the palyniferous unit, however, suggests that emergence, weathering, erosion, and deposition took place over a relatively short time span; extrapolated sedimentation rates from Site 254[12] indicate that an interval of appreciably less than 10 million years may have been involved.

Data from the two sites then, indicate the presence of vegetated islands on the crest of the Ninetyeast Ridge in the Paleocene and Oligocene. Floristic similarities of the island floras to early Tertiary floras of Australia and New Zealand can probably be related to greater proximity of the island sites to the composite southern landmass in the Early Tertiary, than at present. Nevertheless, colonization of the islands from such a continental source still required the crossing of wide ocean areas, which in many cases seems to have been effected by plant families which presently show little ability for such long-distance dispersal. This situation suggests that a measure of dispersal ability has been lost in modern representatives of these groups. The relatively high diversity shown by the fossil floras in comparison with those of modern high-latitude Indian Ocean islands is perhaps a function of climatic history, with the present species poverty being related to the rigorous conditions of the late Neogene.

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Figure 1: Sketch map of the Indian Ocean region, showing the Ninetyeast Ridge and related features, and the position of Deep Sea Drilling Project Sites 214 and 254.

Figure 2: Simplified stratigraphic columns at Sites 214 and 254, with the position of spore and pollen-bearing core samples shown on the right of the columns. Modified from von der Borch and Sclater[14], and Davies and Luyendyk[12].

Figure 3: Reconstructions of the eastern Indian Ocean for the mid-Paleocene and the late Oligocene, modified from Sclater and Fisher[7]. Position of all Deep Sea Drilling Project drillsites on the ridge crest is shown. Active centres of sea-floor spreading are shown by heavy lines. Basalts at Site 214 were being extruded approximately 60 million years BP, along a transform parallel to the trend of the Ninetyeast Ridge; the Kerguelen and Broken Ridges are shown joined. At 25 million years BP, when Site 254 was emergent, a new axis of spreading, trending northwest separated Australia-Antarctica and Broken Ridge-Kerguelen. Site 214 has been spread to the north and submerged.

Fig. 1

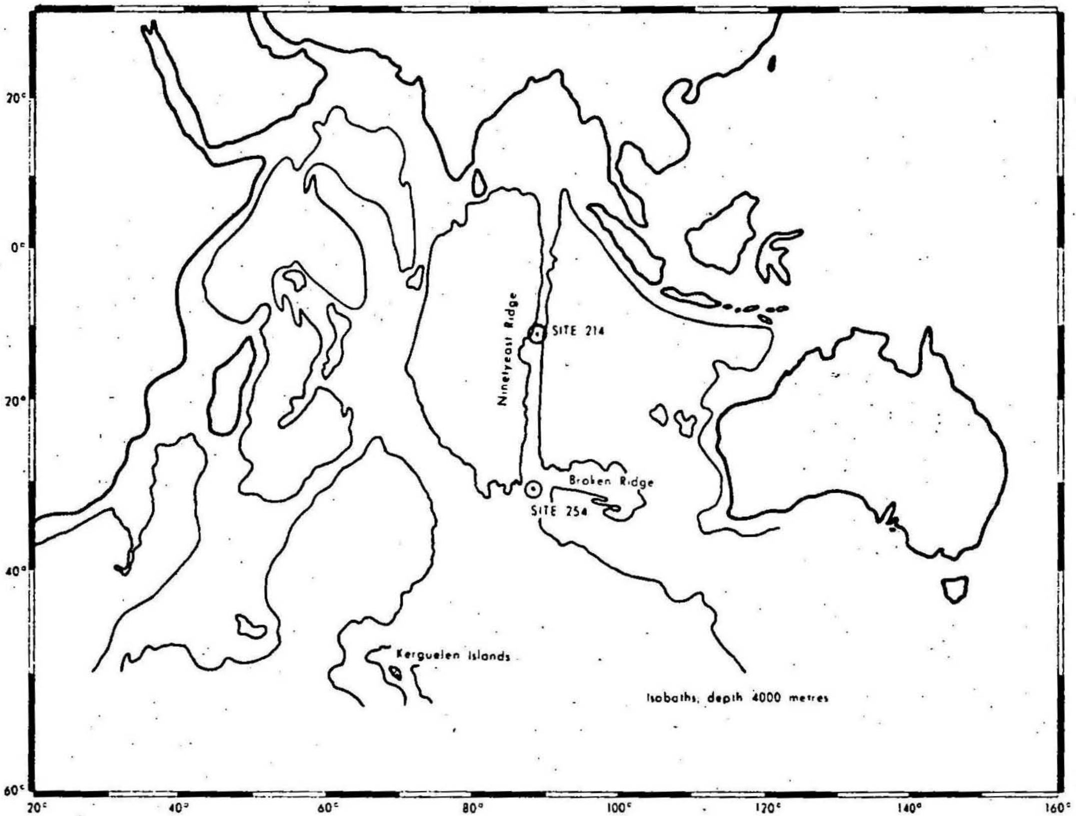

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Fig. 2

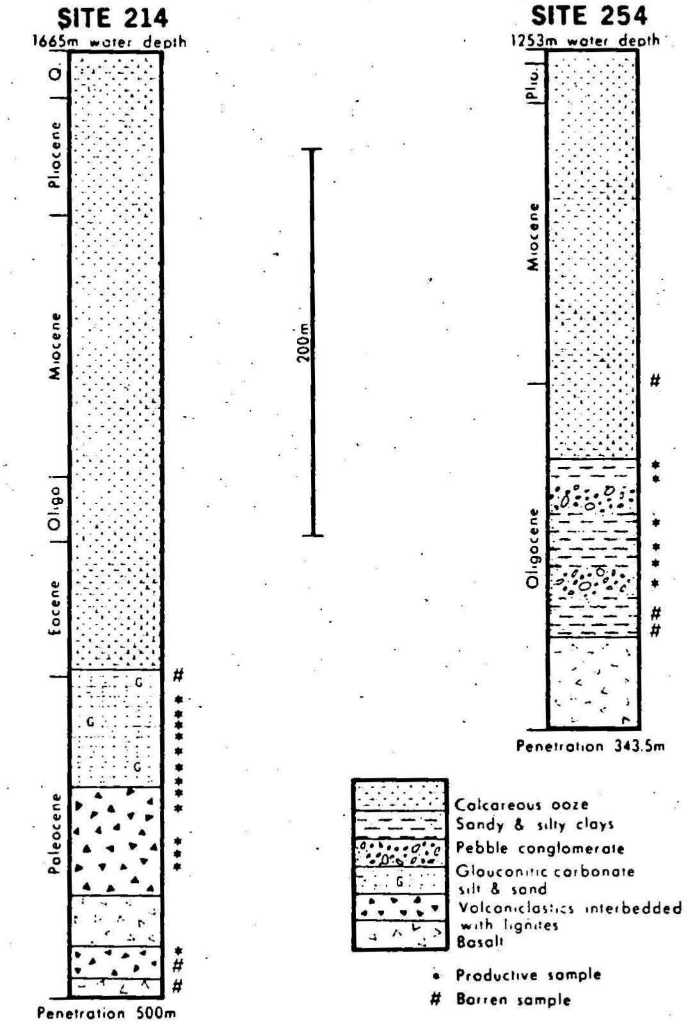
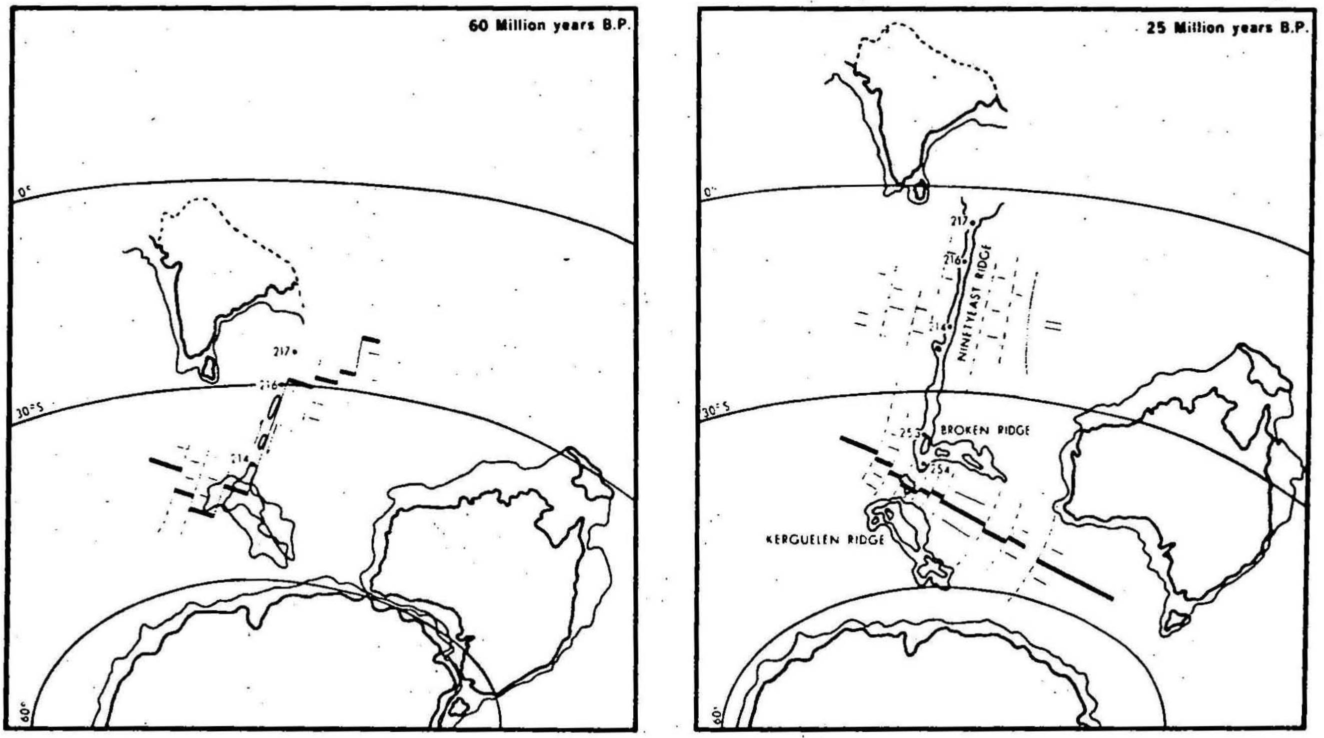

SITE 214
1665m water depth
Q
Pliocene
Miocene
Oligo
Eocene
Paleocene
Penetration 500m
200m
SITE 254
1253m water depth
Plio
Miocene
Oligocene
Penetration 343.5m
Calcareous ooze
Sandy & silty clays
Pebble conglomerate
Glauconitic carbonate silt & sand
Volcaniclastics interbedded with lignites
Basalt
• Productive sample
# Barren sample

Fig. 3



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