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.

Deep-sea drilling on the Ninetyeast Ridge has shown the presence of shallow-water sediments at several points along the ridge crest[1,2]. At DSDP 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 well-preserved spores and pollen, reflecting the existence of a land vegetation of some diversity at points along the ridge crest during the Paleogene. Such vegetation is here interpreted as that of oceanic islands that were emergent along 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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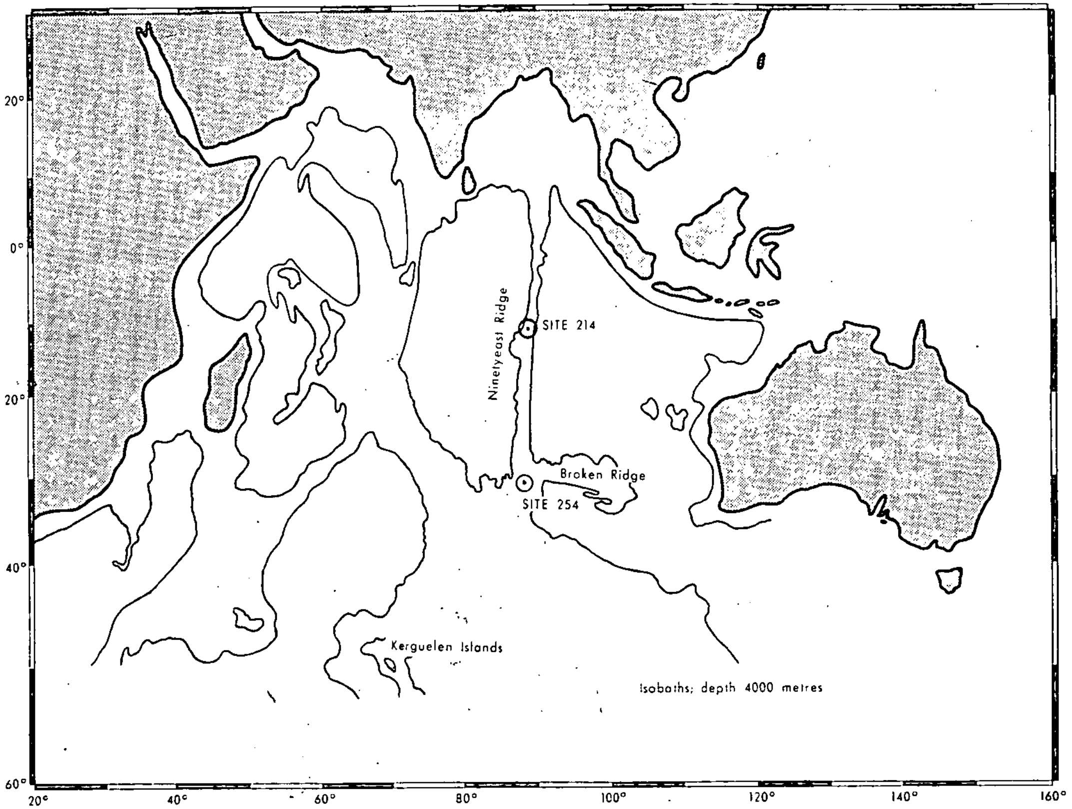
Fig. 1. Location of DSDP Sites 214 & 254
Ninetyeast Ridge, Indian Ocean.


20°
0°
20°
40°
60°
20°
40°
60°
80°
100°
120°
140°
160°
Ninetyeast Ridge
SITE 214
Broken Ridge
SITE 254
Kerguelen Islands
Isobaths; depth 4000 metres

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 the influence of former distributions of land and sea areas on these. Detailed taxonomy of dispersed spores and pollen is currently being undertaken (Kemp and Harris, unpublished work).

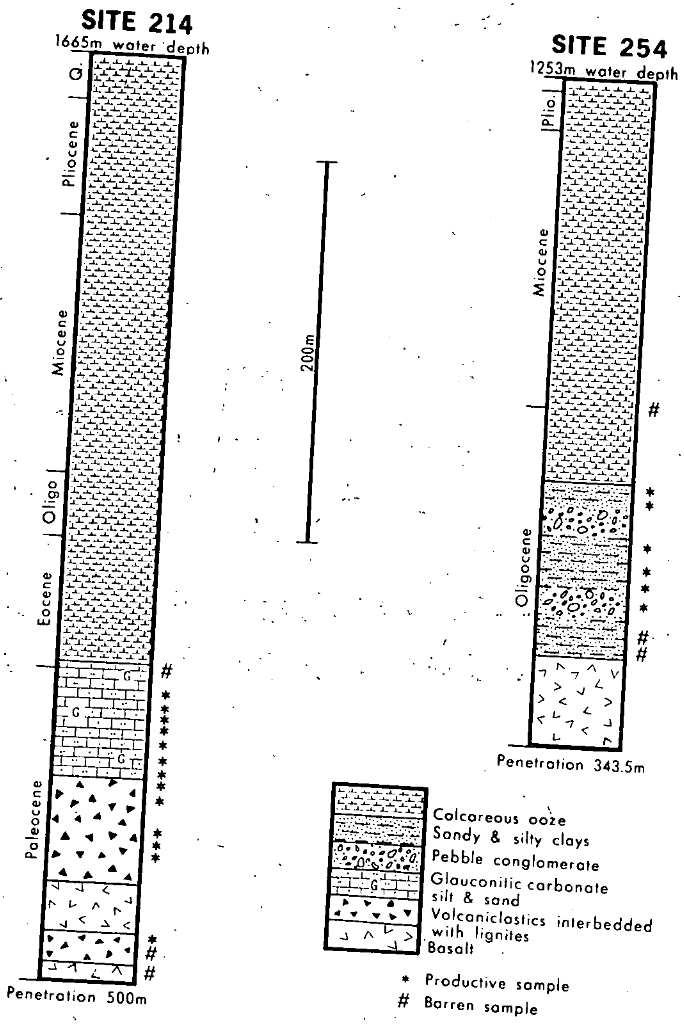
Tectonic setting of the Ninetyeast Ridge

The Ninetyeast Ridge extends for some 5000 km along the 90°E meridian, from 32°S to at least 9°N. The ridge crest deepens progressively from south to north, and sediments immediately above oceanic basement in crestal drillsites increase in age northwards. Similarities in sedimentary sequences at the drillsites accord with northward subsidence of the ridge throughout its history; the north to south diachronism of shallow and deep-water facies boundaries has recently been documented for its northern sector[5].

The ridge has been interpreted[6,7] as having formed from an extrusive pile accumulating at the junction of a former active spreading centre and a north-south trending transform fault parallel to the present ridge. According to this model, volcanism was associated with motion along a transform accommodating 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[8], by the palaeomagnetism of basalts in drillsites[9], and by calcareous microfossils indicating warming of depositional conditions in younger strata[10].

Formerly emergent areas on the ridge crest are likely to have been relatively small islands, as the configuration of the ridge places limits on their east-west dimension, and the age differences of basal sediments from

Fig. 2. Generalized stratigraphic columns of DSDP Sites 214 & 254.


SITE 214
1665m water depth
Q
Pliocene
Miocene
Oligo
Eocene
Paleocene
G
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

north to south precludes the emergence of large areas 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 spores and pollen were recovered from interbedded volaniclastics and lignites; this sequence is non-marine. These assemblages continue into overlying glauconitic carbonate silts and sands which contain dinoflagellate cysts, acritarchs, foraminifera, nannofossils and molluscs. Foraminifera in the glauconitic unit indicate a Paleocene age - P4[11]; the nannofossil zone of *Heliolithus kleinpelli* is present at 337 m below the sea-floor, and the section may be as old as the *Cyclococcolithina robusta* Zone at 389 m[12]. This mid-Paleocene dating is extrapolated down into the volcaniclastic sequence below as the spore and pollen assemblages are essentially the same throughout.

At Site 254, excellently preserved spores and pollen occur abundantly in the lowest sedimentary unit. This consists of poorly sorted sandstone and clay, some pebble conglomerates, has a high content of organic matter, and grades downwards into weathered olivine basalt. It possibly originates from the subaerial weathering of a basaltic terrain, with rapid deposition of weathering products in a quiet, shallow marine environment[10]; a lagoonal setting adjacent to vegetated highlands is perhaps represented. Age estimates of the palyniferous basal unit are ambiguous; the firmest control comes from the lower part of the overlying calcareous ooze unit, which has yielded middle to late Oligocene planktonic foraminifera[10]. Below this, foraminifera, ostracods and molluscs are not stratigraphically diagnostic, and an age range of Eocene to late Oligocene has been suggested[10].

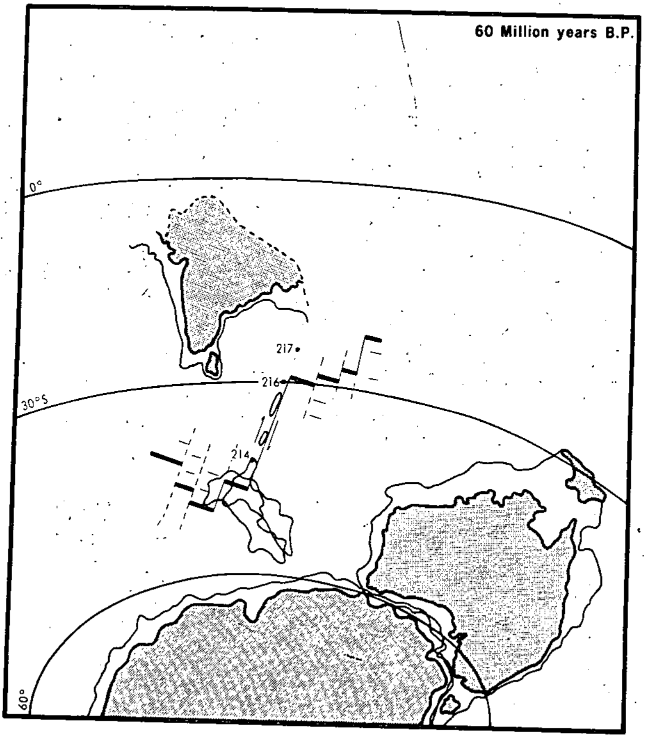
Composition of the microfloras

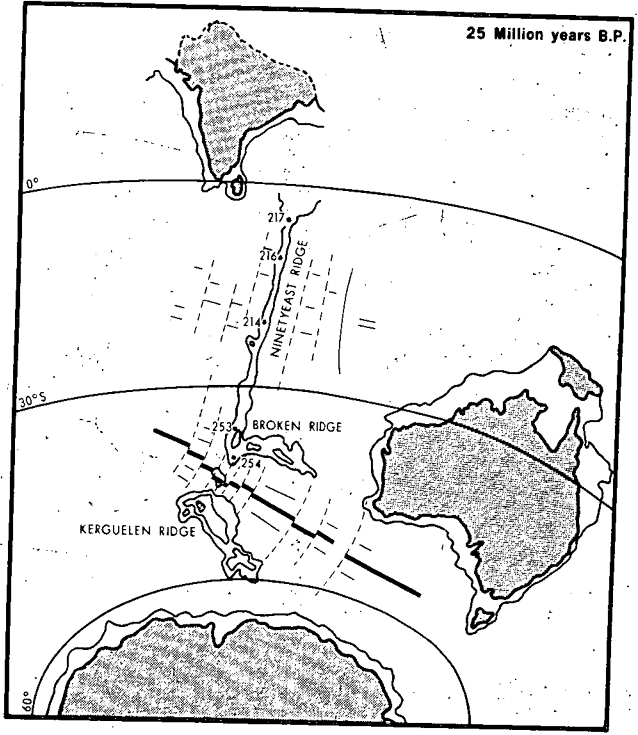
Form-species of angiospermous and gymnospermous origin present at the two sites are listed in Table 1. At Site 214, the major pollen groups include 15 form-species of angiosperms, 18 pteridophytes, 4 conifers and 3 lycopod

Table 1 - Form species of angiospermous
and gymnospermous origin present at
DSDP Sites 214 & 254.

Palynological form-species	Probable botanical affinity	DSDP Site 214	DSDP Site 254
Angiosperms			
Arecipites cf.*waitakiensis* (McIntyre)	Palmae		X
Arecipites sp.	Palmae	X	
Australopollis *obscurus* (Harris)	unknown	X	
Clavatipollenites *hughesii* Couper	Chloranthaceae (*Ascarina*?)	X	X
Cupanieidites *orthoteichus* Cookson & Pike	Sapindaceae (Cupanieae)		X
Echiperiporites sp.	unknown		X
Gothanipollis cf.*gothani* Krutzsch	Loranthaceae		X
Haloragacidites cf.*harrisii* (Couper)	Casuarinaceae (*Casuarina*)	X	X
Milfordia *homeopunctata* (McIntyre)	Restionaceae (*Restio*?)		X
Myrtaceidites cf.*mesonesus* Cookson & Pike	Myrtaceae		X
Myrtaceidites spp.	Myrtaceae	X	X
Proteacidites cf.*symphonemoides* Cookson	Proteaceae		X
Proteacidites sp.	Proteaceae	X	
Nothofagidites spp.	Fagaceae (*Nothofagus*)	X	X
Psilotricolporites sp.	unknown		X
Psilodiporites cf.*redundantis* Guzman	Moraceae/Urticaceae		X
Polycolpites sp.	unknown		X
Sapotaceoidaepollenites *rotundus* Harris	Sapotaceae		X
Sparganiaceaepollenites sp.	Sparganiaceae		X
Spinizonocolpites *prominatus* (McIntyre)	Palmae		X
Schizocolpus *marlinensis* Stover	Didymelaceae (*Didymeles*?)	X	X
Striatricolporites sp.	unknown		X
Tricolpites *reticulatus* Cookson	Gunneraceae (*Gunnera*)	X	X
Tricolpites spp.	unknown	X	X
Tricolporites spp.	unknown	X	X
Tubulifloridites cf.*antipodica* Cookson	Compositae (Tubuliflorae)		X
Tubulifloridites sp.	Compositae?	X	
Gymnosperms			
Araucariacites *australis* Cookson	Araucariaceae (*Araucaria*?)		X
Lygistepollenites *florinii* (Cookson & Pike)	Podocarpaceae (cf.*Dacrydium*)	X	
Microcachryidites *antarcticus* Cookson	Podocarpaceae (cf.*Microcachrys*	X	X
Podocarpidites spp.	Podocarpaceae	X	X

Fig. 3. Reconstructions at 60 & 29 Million years B.P of eastern Indian Ocean.


60 Million years B.P.
0°
217
216
30°S
214
60°


25 Million years B.P.
0°
217
216
214
NINETYEAST RIDGE
30°S
253
BROKEN RIDGE
254
KERGUELEN RIDGE
60°

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 Tertiary floras of India and 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 plant groups. Among conifers, the mixture of podocarpaceous and araucarian elements is typical of the southern hemisphere Early Tertiary. Among angiosperms, species lists indicate that many common forms existed between continent and island, but qualitative differences lie in the extreme rarity of <u>Nothofagus</u> pollen at the island sites, and in the poor representation of Proteaceae there.

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, which must account in part for the similarity of the island floras with those of the landmasses to the southeast. Islands which mig have been emergent in the late Cretaceous would have been even closer to the continents. 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, as has the vegetation of modern south temperate and subantarctic islands. Possible intermediate island sites, acting as biotic 'stepping-stones' between the southern continents and the ridge islands may have been present along the formerly joined Broken and Kerguelen Ridges; beach gravels in a drillsite on Broken Ridge confirm that parts of it were emergent in the Early Tertiary[2], and the Kerguelen islands have possibly been emergent since the Oligocene[13].

Problems in understanding the colonization of the Ninetyeast Ridge islands relate to the apparent inability of some of the modern families represented to cross extended water gaps. Adaptations for long-distance wind and water transport are unknown in Casuarinaceae and Myrtaceae, and the present disjunct distributions of these and other southern families such as Proteaceae and Restionaceae are usually explained by invoking former land connections. Araucaria, too, has a modern distribution in the Pacific accountable in terms of previous land connections[14]. Migration pathways to the Early Tertiary Araucaria stands in the Indian Ocean, on Kerguelen[15,16] and on the Ninetyeast Ridge islands, however, are more difficult to trace, and there are no Tertiary records from countries bordering that ocean. Podocarpaceae is another family poorly represented today on oceanic islands, although migration may have occurred through Indo-Malayan archipelagic islands in the late Tertiary.

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. The intensity of this circulation must have varied through the Paleogene; in the Paleocene, with Australia-Antarctica still joined, and in the absence of a polar ice-cap, circulation may have been relatively sluggish. By the Oligocene, however, in the wake of the opening of a seaway between Australia and Antarctica, and the development of an Antarctic icecap[17], strong westerly winds and currents seem likely.

Bird transport may have been significant in the establishment of many taxa on the Ninetyeast Ridge and Kerguelen sites. Birds must presently account for much seed transport to south temperate and sub-antarctic islands, although direct observations are few. Among the Ninetyeast Ridge microfloras there are some groups in which bird dispersal of seed is known – Gunnera, for instance and members of the Loranthaceae are known to be dispersed by birds, and transport of *Podocarpus* fruits by frugivorous birds has been suggested[19], although the efficiency of such a dispersal mechanism over long ocean distances remains speculative. Moraceae, too, is a group with a high potential for this kind of dispersal and a possible example of the establishment of Myrtaceae (*Metrosideros*) on New Zealand shelf islands by migrating birds has been documented[20].

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°. 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[21,22], 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. Modern island 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[22]. On spore evidence the pteridophyte assembly of the fossil islands appears comparable to those of the modern ones.

Even more striking than the apparently high diversity shown by the Tertiary island floras are 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[23]; in the first category are taxa with a widespread distribution on southern oceanic islands; in the second are groups presently largely confined to the continents - the fam- Centrolepidaceae, Proteaceae, Restionaceae, Myrtaceae, and the genus *Nothofagus* have been cited as being chiefly of this distribution. These groups are absent from modern islands in the southern Indian Ocean in spite 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.

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, Proteaceae, and that of Podocarpaceae and Araucariaceae 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. It further suggests that their current absence from southern oceanic islands reflects the recent environmental history of those islands, all of which have been subjected, to greater or lesser degree, to late Neogene chilling.

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