Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate

Robert J. Morley
PALYNOVA, 1 Mow Fen Road, Littleport, nr. Ely, Cambs CB6 1PY, UK

Key words: SE Asia, Tertiary, palynology, plants, dispersal, plate tectonics, climate

Abstract

Geological evidence for plant dispersals in SE Asia is reviewed by reference to both published, and previously unpublished, evidence from the time of first appearance of angiosperms until the Quaternary. It is concluded that angiosperms did not originate in the SE Asian region, but dispersed into the area from West Gondwanaland. Many African plant species dispersed into India as the Indian plate drifted past Madagascar in the Cenomanian/Turonian, and many of their descendants subsequently dispersed into SE Asia following the collision of the Indian plate with Asia in the middle Eocene. Prior to this time, the SE Asian flora appears to have developed in some degree of isolation. There is no palynological evidence for dispersals from the Australian plate in the Cretaceous, and minimal evidence for such dispersals in the Paleocene/Eocene.

The Sundanian Eocene flora stretched as far east as the South arm of Sulawesi, and subsequent to the opening of the Makassar Straits in the late Eocene, a part of this flora became stranded to the east of Wallace’s Line, and probably formed a major source for other areas to the east of Wallace’s Line of taxa of Sundanian and Asian affinity, as islands rose above sea level during the Miocene, negating the need for wholesale Miocene dispersal eastward. A small number of plant taxa have dispersed westward across Wallace’s Line since the beginning of the Miocene; at 17, 14, 9.5, 5.5 and about 1 Ma. All of the taxa involved were well adapted to dispersal, and emphasis that Wallace’s Line has been a substantial barrier to plant dispersal from the Oligocene onward.

Since the Eocene, plant dispersals to and from the Sunda region have largely been controlled by climate. The Oligocene and earliest Miocene were moisture deficient over much of the region, with ever-wet forest climates first becoming widespread at about 20 Ma in the early Miocene, subsequent to which they have repeatedly expanded and contracted. The greatest latitudinal expansion of tropical rain forests occurred at the beginning of the middle Miocene, at which time they extended northward as far as Japan. Fluctuations between wetter and drier climates became more pronounced in the Quaternary, with interglacial, high sea level periods coinciding with times of rain forest expansion, and ‘glacial’, low sea levels coincided with periods of more strongly seasonal climates, accompanied by the expansion of forests adapted to seasonal climates (such as pine forests) and savannah.

A major montane connection existed in South and East Asia through both the Tertiary and late Cretaceous, from the equator to 60°N, allowing Laurasian mountain plants to disperse to and from the equator throughout this period. The survival of representatives of many ‘primitive’ northern angiosperm families in lower montane forests within the SE Asian region is thought to be due to the continuous presence of this unbroken mountain belt, rather than an origin in SE Asia. In contrast, the New Guinea mountains were formed only in the middle Miocene, from which time many Gondwanan taxa dispersed into this area from the south. Those well adapted to dispersal, such as Podocarpus inbricatus and Phyllocladius subsequently dispersed widely into SE Asia, whereas those poorly adapted to dispersal, such as Notobopus, never reached beyond New Guinea.

Introduction

Plant geographers have long recognised that the SE Asian flora has become enriched through the dispersal of taxa from other continental regions. There is clear biogeographical evidence for the dispersal of mountain plants into the region along three trackways, from the Himalayan region, East Asia, and Ausutralasia (Steenis, 1934a,b, 1936) and also for lowland plants, especially those requiring a strong dry season, both from Asia and Australia. Proposals have also been made for massive dispersals from the Sunda region to the east of Wallace’s Line, following the mid-Miocene collision between the Australian and Sunda plates, although the scale...
of such migrations is debatable. Plant distributions have also been used to suggest that there was a pre-mid Miocene contact between Australia and SE Asia, with the suggestion that this contact was pre-Tertiary (Steenis, 1962). Claims that the angiosperms actually evolved in the SE Asian region also continue to be made, despite an absence of fossil evidence (Takhtajan, 1987).

Biogeographical hypotheses such as these can only find confirmation when they are based on a foundation of historical geology. This discussion attempts to review geological evidence for plant dispersals by examining the fossil pollen and spore record for the Tertiary (and Late Cretaceous) of the SE Asian region, paying particular attention to the times of appearance in the region of pollen types exhibiting clear affinities with other continental regions. The review is based on both published and unpublished data from both outcrops and boreholes, and uses the plate tectonic reconstruction of Hall (1995) for SE Asia and Daly et al. (1987) for the Indian plate.

Geological evidence for the dispersal of lowland plants and those of the uplands, are discussed separately, although it must be appreciated that through most of the Tertiary, it is not always easy to determine from which of these sources each pollen type is derived.

In bringing to attention names of fossil pollen, a simple convention has been followed. In cases where a fossil pollen type has been adequately described according to the botanical code, the fossil name is used, generally followed, if appropriate, by an indication of the botanical affinity of the parent plant, if this is known. In cases where a pollen type remains inadequately described according to the code, but the parent plant is known, the name of the parent plant alone is used. In cases where such a pollen type might be derived from two or more plant taxa, the taxon name is also followed by the word ‘type’.

**Initial stages of angiosperm radiation**

The current fossil record provides no evidence to suggest that angiosperms actually originated in SE Asia, as proposed by Takhtajan (1969). It is more likely that they migrated into the region. Truswell et al. (1987) dismissed the suggestion of Takhtajan (1987) that they originated on an isolated Gondwanan microcontinent, which subsequently became embedded in SE Asia, on the grounds that the earliest angiosperm pollen records discovered so far for Australia post-date those from western Gondwana by 10 Ma, and also post-date the timing of separation of such microcontinents from Gondwanaland. The oldest record for Australian monosulcate pollen is from the latest Barremian or earliest Aptian (Burger, 1991), considerably later than its first appearance in the western hemisphere. Strong evidence to suggest that angiosperms originated at tropical palaeolatitudes is provided from global plots of earliest appearances against latitude (Fig.1) which indicate parallel, slow adaptation to cooler, or more seasonal, climates at higher latitudes in both hemispheres during the course of the mid-Cretaceous. The parallel diversification of both pollen and macrofossils in the mid-Cretaceous (Hickey and Doyle, 1977) suggests that this pattern reflects the radiation of the early angiosperm flora, and not simply the development of those angiosperm groups with recognisable pollen.

Fossil evidence of the representation of the earliest angiosperms in the SE Asian region is still very meagre. In the past, this was due to the lack of studies from the region. Recent palynological analyses of thick fluvial Lower Cretaceous sediments from Thailand, ranging in age from Neocomian to Aptian, have, however, failed to yield a single angiosperm pollen grain (Racey et al., 1994), and probable Barremian sediments from the Malay peninsula have produced but a single tentative record of the chloranthaceous Clavatipollenites (Shamsuddin and Morley, 1994), among an assemblage dominated by pollen of Classopollis spp. and fern spores. Current evidence, therefore, suggests that angiosperms were much less well repre-
Fig. 2. Mid-Cretaceous migration routes along the southern shore of Tethys. *Elateropollenites africaensis* (■) is recorded from the Turonian of Irian Jaya (Bates, unpublished) and Papua New Guinea (Lowe, pers. comm., 1987), and has a Late Albian to Turonian centre of abundance in Africa and South America (outlined area). *Afropolis jardinius* exhibits an identical distribution pattern in the Cenomanian of Pakistan (●) to that seen in West Africa (IEDS, unpublished); *Constantinisporis*, *Victorisporis* and *Andresiporis* (●) are very well represented in the Turonian to Campanian of sub(palaeo)equatorial Africa, but appear in the Senonian of Madagascar (Chen 1982) and India (Venkatachala, 1974; Nandi, 1991; Morley, unpublished), also recorded rarely from the mid-Tertiary (earliest Miocene) of Java (+). Turonian palaeogeographic reconstruction by Smith *et al.* (1994).

...sented during the time of their initial radiation in the eastern tropics, compared to the western.

Some evidence is now emerging to suggest the direction of plant dispersal routes into the eastern Tethyan region in the mid and later Cretaceous. Aptian shales from the Tarim basin of China contain very rare pollen of taxa characteristic of Africa and South America, such as *Afropolis zonatus* (which has been suggested by Doyle *et al.* (1990) to be derived from probable Winteraceae). In addition, low diversities of presumed ephedroid elater-bearing pollen in the Albian of Tibet (Herngreen and Duenas Jimenez, 1990), demonstrate mid-Cretaceous dispersal along the northern Tethyan coast.

Evidence is also emerging for dispersal along the southern shore of Tethys. Unpublished records by IEDS (1995) demonstrate that some typical African/South American palynomorphs, such as *Afropolis jardinius* show a similar temporal distribution pattern within the Cenomanian of Pakistan to that seen in West Africa, suggesting dispersal via Madagascar (Fig. 2). Also, the presence of specimens of the Turonian elater-bearing pollen type *Elateroplicites africaensis* in Irian Jaya and Papua New Guinea can perhaps be explained by dispersal along the southern Tethyan shoreline, or along an island arc stretching from the India to Australia, along the leading edge of the Indian plate. Such a route would have closely paralleled the southern margin of the mid-Cretaceous equatorial low pressure zone (Barron and Washington, 1985), and warrants further consideration with respect to the dispersal of megathermal angiosperms into Australia during the mid-Cretaceous.

Late Cretaceous and early Tertiary dispersal paths

A somewhat later, very clear dispersal path eastward from Africa is shown by the distribution of the subequatorially triporate *Constantinisporis* group (Fig. 2), thought by Srivastava (1977) to reflect ancestral Palmae pollen with affinity to *Sclerosperma* (although this affinity is considered unlikely, as their exine structure is different). The *Constantinisporis* group ranges from the Turonian to Campanian in West Africa, and shows an abundance maximum in Gabon during the Turonian.
Constantinisporis has also been reported from the Senonian of Madagascar (Chen, 1978) and India (Venkatachala, 1974; Nandi, 1991; Morley, unpublished), and rarely from the mid-Tertiary of Java reflecting an important dispersal path, possibly associated with low Turonian sea levels (Haq et al., 1988), which was followed, with a high degree of probability, by many groups of tropical angiosperms, such as members of the Sapindaceae (Ham, 1990) and Myrtaceae, as well as Ctenolophon (Ctenolophonaceae), and many Palmae, including the Monocolpopollenites Palmaepollenites complex, and the Longepertites group (probably ancestral to Eugelospora), even some Normapolles (Kar and Singh, 1986; Nandi, 1991) and mammals (Krause and Maas, 1990). This dispersal path probably became severed in the later Cretaceous, during which time both flora and fauna evolved in isolation.

An examination of the Late Cretaceous distribution of Nothofagus (Nothofagaceae) pollen also helps to clarify the nature and timing of south-
ern hemisphere dispersal routes (Fig 3). The first *Nostofagus* pollen is recorded from the Santonian onward in Australia and Antarctica and from younger Cretaceous rocks of South America and New Zealand, but is absent from South Africa and India, demonstrating that the latter were well separated from Gondwanaland at the time of its initial radiation.

These data show that by the earliest Tertiary, as the Indian subcontinent was drifting close to Southern Asia and Sundaland, it bore a vegetation which contained three distinct elements: an ancient, eastern Gondwanan element, comprising gymnosperms, and perhaps some angiosperms; an African allochthonous element consisting predominantly of angiosperms of tropical west Gondwanan aspect; and, as a result of its isolation during the latest Cretaceous and earliest Tertiary, a distinct endemic element. Members of each of these groups were released into Asia following docking in the middle Eocene.

Turning now to SE Asia, the best database for the earliest Tertiary remains that of Muller (1968) from Sarawak. I have reconsidered the ages assigned to the Plateau (now Kayan) Sandstone and Pedawan Formation assemblages by Muller and believe that these need to be revised (Fig 4). His *Cicatricosisporites* zone, from the Pedawan Formation, is more likely to be Albain, and the *Araucaricites* zone, from the upper part of the Pedawan Formation, is most likely of Santonian, or possibly Turonian, age. Assemblages from the *Araucaricites* zone contain abundant *Araucaricites*, common *Epifex* and rare spores, and suggest a dry, tropical climate. Angiosperms are common, but little diversified, consisting of poorly differentiated tricolpates (*Reitricolpites vulgaris*), tricolporate (*Pisatricolporites acuticostatus*, *P. prolatus*) and trispinate pollen (*Triorites minutitior*, *T. festatus*). It has become customary to extend the range of *Myrticeae* to the *Araucaricites* zone, but only one specimen of this tiny pollen type was recorded by Muller, hardly the basis for such a range extension. None of the typical West African, Indian or Australian lower Santonian taxa was noted, suggesting that at this time, Sundaland was isolated from these regions.
Reconsideration of the assemblages from the Kayam Sandstone (Fig. 5) suggests that there is no positive evidence for a Late Cretaceous age for the lower part of this formation. It is more likely that the formation is no older than Paleocene in age, although a late Maastrichtian age cannot be wholly ruled out. Muller’s main reason for extending the age of this group into the Late Cretaceous was the common occurrence of the gymnosperm pollen type *Rugibiviscidites reductus* with regular *Classopolis* spp. in the basal section of the formation. *Rugibiviscidites reductus*, which at the time of his publication, was recorded only from the mid-Cretaceous of North America, has now been demonstrated by Song Zhichen et al. (1981) to comprise a common element in the Paleocene of China, where *Classopolis* is also common (Fig. 6), opening up the possibility of a Paleocene age for the *Rugibiviscidites zone* of Muller. This conclusion is important, since it demonstrates that there is no firm evidence for the late Cretaceous ages proposed from this region for a number of critical pollen types, such as *Nymp, Proxertites*, Salicaceae, *Ilex* and Myrtaceae. The Sarawak Paleocene pollen flora is of somewhat lower diversity than contemporaneous floras in Africa, India (Frederiksen, 1994) and Australia (Harris, 1965) and lacks both Gondwanan and African elements. A pollen record is also available for about the same time period from Irian Jaya (Fig. 7). Assemblages from equivalents of the Lower Eocene Waripi Formation (which contains evaporites, consistent with accumulation on the northern coast of Australia, within the southern sub-tropical high pressure zone), are essentially of Australian aspect, with common *Casuarina* (Casuarinaceae) pollen, *Malvastrum* (similar to *Austrodactus* and *Dissilaria*, Euphorbiaceae), Myrtaceae, some proteaceous pollen, and rare *Nothofagus*, together with a tropical shoreline element, provided by the presence of ancestral
Nypa pollen (Spinizonocolpites baculatus and S. prominatus), but, other than the widespread Nypa and Myrtaceae, with no affinities to the Kayan assemblages. Evidence therefore suggests that in the Paleocene and early Eocene, Sundaland and Irian Jaya were widely separated.

SE Asian floras following India’s collision with Asia

The Indian plate collided with the Asian plate in the middle Eocene (Daly et al., 1987). At this time, both the northern margin of the Indian plate, and the Sunda region experienced an ever-wet, equatorial climate, as reflected by the common occurrence of coals in both areas. With neither oceanic, nor climatic barriers to dispersal, many plant taxa were able to disperse into the Sunda region (Fig.8). The palynological succession through the middle and upper Eocene of Sundaland can be observed in the very rich and well preserved assemblages recorded from the Nanggulan Formation in Central Java (Takahashi, 1982; Morley, 1982; Harley and Morley, 1995; Morley et al., 1996) and Malawia Formation in South Sulawesi (see below), and an uppermost Eocene succession of coals from Mangkalihat peninsula, Kalimantan (Morley, unpublished). The ‘oldest’ middle Eocene sediments from Nanggulan contain much more diverse palynofloras than the Paleocene and lower Eocene assemblages from Sarawak, and there is good reason to believe that this increased diversity is due in considerable part to wholesale dispersal from the Indian plate, as indicated by the taxa listed in Table 1 and shown in Fig.9, all of which are derived from Paleocene or older sediments from India. Obvious Gondwanan elements in this assemblage are aff. Beaupréadites matsuokae (Plate 2.4), Palmáepollentes kutcheensis (Plate 3.1-3.2) and
Polygalacidites clarus (Plate 2.6).

Close to the middle/upper Eocene boundary, two Gondwanan gymnosperm taxa, *Dacrydium* and *Podocarpus*, appear in the Sunda region for the first time. It might be expected that these also dispersed via the Indian plate. This may have been the case for *Podocarpus*, but the oldest records of *Dacrydium* post-date the separation of India from Gondwana by 20 Ma; its oldest record is from the Santonian/Coniacian of South Australia and the Antarctic peninsula (Dettmann and Thomson, 1987). Paleocene records of *Dacrydium* are known from the Ninetyeast Ridge (Kemp and Harris, 1975), which are interpreted as due to long distance dispersal, but records from India are very rare, and dubious (e.g., Mathur (1984) from northern India). Perhaps its occurrence here was also a result of long distance dispersal, for Australia was positioned far to the south.

Two additional taxa with Indian connections appear within the latest Eocene and Oligocene. *Meyeriopollis nayarkotensis* (Plate 3.3) of unknown affinity, appears in the latest Eocene of Assam (Baksi, 1962; Handique, 1992) where it first appears at about 37 Ma (Morley, unpublished). Its first appearance in East Kalimantan is at about the same time. Striate spores referred to *Magnasiatites grandiosus*, derived from the adiantaceous aquatic fern *Ceratopteris*, appear shortly after the earliest *Meyeriopollis* specimens in the Sunda region, close to the Eocene-
Oligocene boundary, but in Assam just predate the oldest *Meyeritpollis*, which led Kar (1982) to suggest that *Ceratopteris* evolved in India before dispersing across the tropics at the beginning of the Oligocene. The rare occurrence of the otherwise upper Cretaceous pollen type *Constantinisporis cf. jacqueti* from the lowest Miocene of the Talang Akar Formation in the West Java Sea (Fig. 2, Plate 3.9) indicates that the now extinct parent plant of this taxon followed the same dispersal path.

Note that several of the immigrant taxa, such as *Gonystylus* (*Cryptopollporites cryptus*), *Ixonanthos* (Plate 1.3–1.4), *Eugeissospora* (*Quiloonipollenites* sp., Plate 2.1) and *Durio* (*Laniatipollis ovatus*, Plate 2.3) are considered ‘typical’ Maleesian taxa today, and are rare, or absent from India, having been wiped out by Neogene and Quaternary climatic changes. A similar history would explain the present distribution of Dipterocarpaceae, with rafting from Africa, and subsequent range reduction in both Africa and India. Dipterocarpaceae also have two genera in Africa (*Monotes* and *Marquesia*, subfamily Monotoideae) as well as fossils of *Dipterocarpus* (Ashton, 1982), representatives in South America (*Pakaraimaeae* and *Pseudomonotes*), Seychelles (*Valeriopitris*) and Sri Lanka, and a centre of diversity in Borneo (Ashton, 1969; Ashton and Gunatilleke, 1987).

Although today, *Eugeissospora* is endemic to Borneo and Malaysia, its pollen shows some similarities to members of the fossil genus *Longipollites* (see Frederiksen, 1949), which is recorded widely in the uppermost Cretaceous and lower Tertiary of South America, West Africa and India, raising the possibility that *Eugeissospora* may be derived from the parent taxon of this group, which is of very ancient origin, with a former pantropical distribution.

---

**Table 1.** Pollen taxa recorded from the pre-collision Tertiary of India (lower Eocene and Paleocene), but from the middle Eocene of the Sunda region.

<table>
<thead>
<tr>
<th>Family/Tribe</th>
<th>Extant taxon</th>
<th>Fossil taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proteaceae</td>
<td>aff. Beauprea</td>
<td>aff. Beaupreadites matsuokae</td>
</tr>
<tr>
<td>Palmae/Calamoideae</td>
<td>Eugeissospora</td>
<td>Quilonipollenites spp.</td>
</tr>
<tr>
<td>Palmae/Iguanurinae</td>
<td>Lepidocarachis</td>
<td><em>Laniatipollis ovatus</em></td>
</tr>
<tr>
<td>Bombacaceae/Durionaceae</td>
<td>Durio-type</td>
<td><em>Spinuliporites spinosus</em></td>
</tr>
<tr>
<td>Linaceae</td>
<td><em>Ixonanthos</em></td>
<td><em>Cryptopolporites cryptus</em></td>
</tr>
<tr>
<td>Gonystylaceae</td>
<td><em>Gonystylus</em></td>
<td><em>Reitsteinhocolpites williamsi</em></td>
</tr>
<tr>
<td>Cenolophonaceae</td>
<td><em>Cenolophon parvifolius</em></td>
<td><em>Fiftycolpites</em> spp.</td>
</tr>
<tr>
<td>Cenolophonaceae</td>
<td><em>Cenolophon</em></td>
<td><em>Polygalacitaceae claras</em></td>
</tr>
<tr>
<td>Polygalacaceae</td>
<td><em>Polygala</em> or <em>Xantibiophyllum</em></td>
<td><em>Cupanioides flaccidiformis</em></td>
</tr>
<tr>
<td>Alangiaceae</td>
<td>Indet.</td>
<td><em>Compositopollenites dilatans</em></td>
</tr>
<tr>
<td>Indet</td>
<td>Ceratopteris</td>
<td><em>Magnaspiatoris grandiosus</em></td>
</tr>
<tr>
<td>Adiantaceae</td>
<td>Indet.</td>
<td><em>Dandotiaspora laevigata</em></td>
</tr>
<tr>
<td>Indet.</td>
<td>Indet.</td>
<td><em>Constantinisporis</em> sp.</td>
</tr>
</tbody>
</table>
Mid and late Tertiary climates

The Oligocene and earliest Miocene were periods of much drier and cooler climates in the Sunda region, although obvious dry climate palynomorph indicators are few. Dry climates are inferred more from the limited representation of taxa characteristic of wet climates and the character of lithologies. The driest intervals are thought to have been in the early Oligocene and early Miocene, during which periods Gramineae pollen is also relatively common. Coniferous pollen is also a common component in many areas during this time, of which Pinus is most frequently represented, and although a background presence of montane conifer pollen clearly reflects the presence of upland areas, it is probable that maxima of Pinus reflect the widespread occurrence of seasonally dry vegetation (Ashton, 1972a) within lowland areas. Today Pinus is a common element of seasonally dry vegetation in Thailand, North Sumatra and Luzon (Whitmore, 1975), and has probably been similarly associated with such climates throughout the Tertiary.

There were few new immigrants into the Sunda region during the Oligocene, which is characterised by reduced diversities compared to the Eocene. Muller (1972) notes the earliest records of Casuarina at this time in Sarawak. Since Casuarina is absent from India, and there is no positive Indian pollen record (it first appears in the Australian fossil record well after the separation of the Indian plate from Gondwana), rafting on the Indian plate is unlikely. However, Hall (1995) suggests docking of Halmahera with New Guinea in the latest Oligocene, and the possibility of dispersal via Halmahera and the eastern Philippines should be given consideration. Such a dispersal path might also explain the recent discovery of Dacrydium guillauminii pollen within the uppermost Oligocene and lower Miocene of the West Java Sea; Dacrydium spp. producing the D. guillauminii pollen type occur today only in New Caledonia.

A major climatic change occurred in the Early Miocene (Morley and Flenley, 1987), at about 21 Ma, subsequent to which time coals were formed in many areas of the Sunda region, and taxa characteristic of peat-swamps became widespread, such as Blumeodendron, Calophyllum, Cephalomappa, Durio and Stemonurus (Fig.10).

The latest part of the early Miocene, and initial part of the Middle Miocene, coinciding with nannofossil zones NN4 and NN5, is well established as a period of globally high sea levels, based on O\textsuperscript{18} data (e.g., Miller et al., 1987), and the maximum degree of Neogene coastal onlap based on sequence stratigraphic studies (Haq et al., 1988). This interval was also a period of markedly warm and moist climatic conditions throughout a large part of SE and East Asia (Fig.10). During this short period, warm and moist paratropical conditions allowed the proliferation of diverse mangroves, and mixed warm temperate and paratropical forests, as far north as Japan, with Dacrydium, Sapotaceae, and Alangium, preserved within the Japanese Dajima Flora (Tsuda et al., 1984; Yamanoi, 1974; Yamanoi et al., 1980). The effect of this warming event was seen as far north as Korea, where pollen of warm temperate taxa, such as Alangium, are commonly recorded in the same time interval. Clearly, during this time of markedly equable climate, many species migrations may have occurred. A number of additional moist and warm episodes can be noted in East Asia, principally coinciding with periods of high sea level, but none was so pronounced as the warming phase at the early-middle Miocene boundary.

Whereas a few years ago evidence for the former expansion of seasonally dry climates in the younger Neogene and Quaternary of the Sunda region was purely conjectural, evidence for such climates is now becoming more widespread. Intermittent periods of drier climates,
Fig. 11. Summary pollen diagram from Lombok Ridge, modified from Kaas (1991). ‘Glacial’ climates, coinciding with oxygen isotope stages 2+3, 6 and 8 are characterised by abundant Gramineae pollen, but low representation of pollen of coastal plants and mangroves, and fern spores, reflecting periods of widespread savannah vegetation. ‘Interglacial’ climates, coinciding with oxygen isotope stages 4+5 and 7, are characterised by abundant pteridophyte spores, and increased pollen of coastal plants and mangroves, but greatly reduced frequencies of Gramineae pollen, reflecting periods of forest and mangrove swamp expansion during periods of wetter climates. Dates marked (□) are radiocarbon dates, other dates refer to oxygen isotope stage boundaries.

reflected by maxima of Gramineae pollen, can be observed within the uppermost middle and upper Miocene, and the Plio-Pleistocene of the South China Sea, which sometimes contain pollen of the vicariad Agialitis (Plumbaginaceae), a mangrove genus now confined to India and northern Australia, and pollen of Leguminosae. Seasonal climates in Java developed from the start of the Pliocene, indicated by the common occurrence of Gramineae (both pollen and charred cuticle) and Casuarina pollen since that time (Morley et al., 1996). Dry ‘glacial’ climates within the Quaternary are clearly illustrated in pollen diagrams from cores from south of Nusa Tenggara (Fig. 11) by Kaas (1991a). There is also evidence to suggest that Pinus savannah was widespread across the Malay peninsula during dry intervals of the Pleistocene. One sample,
collected from a probable mid-Pleistocene locality from near Subang Airport (Table 2, Fig.12), yielded abundant *Pinus* pollen (Plate 3.7-3.8) and Gramineae (Plate 3.6), together with Compositae (Plate 3.5) (Morley and Flenley, 1987). Steenis (1961) explained disjunct distributions of leguminous (papilionaceous) taxa, which require a marked dry season in Nusa Tenggara and Indochina in terms of the more extensive occurrence of drier climates during glacial periods. This hypothesis is fully borne out by the fossil record, but whether the migrations of these species occurred in the Quaternary, as suggested by Steenis, or at an earlier time, remains unanswered; Ashton (1972b) thought that Steenis’ disjunct distributions predated the evolution of the ‘dry dipterocarps’, of the Asian mainland, since these are absent from Nusa Tenggara.

### Miocene migrations

All plate tectonic reconstructions indicate that the main phase of collision between the Sundan and Australian plates was during the middle Miocene; the most clear instances of westward plant migration within the region also date from about this time.

Muller (1972) remarked on a distinct increase in abundance of Myrtaceae pollen in Sarawak within the lower part of the Miocene. He tentatively interpreted this to reflect dispersal of Myrtaceae from the east, but Martin (1982) subsequently remarked on this event, and suggested that it was due to deteriorating soil conditions. The event has now been independently calibrat

<table>
<thead>
<tr>
<th>Table 2. Palynomorphs recovered from middle Pleistocene sample 3/15 from Subang, near Kuala Lumpur, Malaysia.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinacea, <em>Pinus</em></td>
</tr>
<tr>
<td>Gramineae</td>
</tr>
<tr>
<td>Smooth fern spores</td>
</tr>
<tr>
<td>Lycopodiaceae, <em>Lycopodium cernuum</em></td>
</tr>
<tr>
<td>Cyatheaceae, <em>Cyathea</em></td>
</tr>
<tr>
<td>Cyperaceae</td>
</tr>
<tr>
<td>Pandanaeae, <em>Pandanus</em></td>
</tr>
<tr>
<td>Aquifoliaceae, <em>Ilex</em></td>
</tr>
<tr>
<td>Palmae, <em>Calamus</em></td>
</tr>
<tr>
<td>Compositae</td>
</tr>
<tr>
<td>Pteridaceae, <em>Pteridium</em></td>
</tr>
<tr>
<td>Rubiaceae, <em>Nannietia</em></td>
</tr>
<tr>
<td>Myrtaceae</td>
</tr>
<tr>
<td>Sapotaceae, <em>Palphilium</em></td>
</tr>
<tr>
<td>Blechnaceae, <em>Stenochlaena palustris</em></td>
</tr>
<tr>
<td>Hamamelidaceae, <em>Altingia excelsa</em></td>
</tr>
<tr>
<td>Gutierrezae, <em>Calophyllum</em></td>
</tr>
<tr>
<td>Podocarpaceae, <em>Dacrydium</em></td>
</tr>
<tr>
<td>Dilleniaceae, <em>Dillenia</em></td>
</tr>
<tr>
<td>Dipterocarpaceae, <em>Shorea</em></td>
</tr>
<tr>
<td>+ 42 others</td>
</tr>
</tbody>
</table>

ed in Sarawak, the Malay basin (Azmi et al., 1996) and Mahakam delta, Kalimantan (Carter and Morley, 1996) to have occurred at about 17 Ma. Such a widespread, synchronous event is unlikely to relate to changing soil factors, which will differ from area to area, and a migration from the east appears to be the most probable explanation. A number of myrtaceous genera of Australasian origin, such as *Baeckia*, *Melaleuca*, *Leptospermum*, *Rhodamnia* and *Tristaniopsis*, occur in the Sundan region, predominantly in coastal settings and on poor soils, and the increase of Myrtaceous pollen at 17 Ma may reflect immigration of these taxa when Sundaland and Australia were closely juxtaposed.

Stephanoporate echinate pollen referable to the mangrove genus *Camptostemon* (Bombacaceae) shows sudden appearances in Sarawak (Muller, 1972) and East Kalimantan (Morley, unpublished) in the middle Miocene, at about 14 Ma, and a somewhat later appearance in the Malay basin, at 10, or 9.5 Ma (Azmi et al., 1996). The sudden appearance of this pollen type coincides with times of pronounced sea level lowstand, and suggests that its parent plant immigrated from elsewhere, and, since the pollen type is not recorded to the west, derivation from the east, where the pollen record is incomplete, is most likely. *Camptostemon* is currently a common mangrove tree in New Guinea, and is now virtually extinct west of Wallace’s Line,
with rare occurrences in SE Kalimantan.

A further clear migration occurred in the earliest late Miocene, indicated by the widespread occurrence west of Wallace’s Line of spores referred to *Stenochlaena papuanus* (Fig.13, 14) derived from a climbing fern allied to the East Malesian *Stenochlaena mihet* (synonym, *S. laurifolia*) or *S. cunningii*. This species rapidly dispersed across Borneo into Java, Sumatra, and into Indochina, China (Barre de Cruz, 1982) and India (Mathur, 1984), and then suddenly disappeared from the record from the western area during the earliest Pleistocene (Morley, 1978, 1991; Caratini and Tissot, 1985). Its arrival in the Sunda region has been independently dated at about 9 Ma, in Sarawak, the Malay basin (Azmi et al., 1996) and Java (Rahardjo et al., 1994).

Within the Malay basin, the sedimentary succession demonstrates that this spore type first appears following the most pronounced sea level lowstand of the Neogene (Azmi et al., 1996), and it is proposed that migration took place during this phase of low sea level. The spore type ranges from the middle or lower Miocene in Papua New Guinea, and the parent plant is common today in New Guinea, the Moluccas and the Philippines.

Truswell et al. (1987) suggested that a number of additional Australian taxa migrated into SE Asia in the Miocene. The pollen record in SE Asia, however, cannot provide support for any of their additional suggestions. This may be due to the fact that the pollen of some of their taxa are difficult to differentiate bearing in mind the high diversity of assemblages from SE Asia, but for those which have been recorded (but are as yet unpublished), *Gardenia* (Rubiacae) and Loranthaceae are noted from the middle Eocene of Java, and thus predate Australian records, whereas pollen referable to Malvaceae, of the *Tespesia* type, shows a clear base at about 21 Ma in the lower Miocene offshore Vietnam, wholly consistent with the lower Miocene record from Australia (Morley, unpublished).

In summarising westward dispersals across Wallace’s Line, it is noteworthy that all of the taxa considered are well adapted to dispersal (ferns, small-seeded Myrtaceae and mangroves), and emphasise that Wallace’s Line remained a major barrier to plant dispersal throughout the Neogene.

**Origin of floras to the east of Wallace’s Line**

The flora to the east of Wallace’s Line as far east as Fiji is essentially ‘Malesian’, with many taxa exhibiting poor dispersal by the possession of large, heavy fruits, suggesting a continental ori-
Fig. 15. Proximity of some Sundanian and East Malesian land masses through time (data source, Hall, 1995): South Sulawesi and Sunda were joined in the middle Eocene, and shared the same flora; whereas most islands of Eastern Indonesia were not formed until the middle Miocene; Halmahara and the Philippines have a much older history, and would have borne a flora of tropical aspect throughout the Tertiary. The islands of the proto-Philippines, and Halmahera were in close proximity at a number of times during the Tertiary, especially in the late Eocene/Oligocene, and late Miocene, and the possibility of dispersal between these islands and Sunda at these times is strong. ——→ main migrations; 1) dispersals from Indian plate, c.45 Ma; 2) Myrtaceae, c.17 Ma; 3) Camptosperm, c.14 Ma; 4) Nothofagus, middle Miocene; 5) Sienochlaena milnei/cumingii, c.9.5 Ma; 6) Podocarpus (Dacrycarpus) imbricatus, 3.5 Ma; 7) Phyllocladus, c.1 Ma.

origin (Whitmore, 1973), and in trying to reconcile this with the theories of continental drift (Wegener, 1929) and plate tectonics, Diels (1934) and Steenis (1979) proposed massive migrations of Sundanian taxa eastward across Wallace’s Line at the time of collision of the Australasian and Sunda plates during the middle Miocene. Recently, Dransfield (1981) has reviewed the biogeography of palms with respect to this line, and concluded that only a few palm genera made the crossing, and that numbers were of the same order in each direction. He probably overestimated the number of dispersals, since it is likely that Calamus was already present to the east prior to the collision, based on the occurrence of Dicopogratis spp. of the Calamus type from the Eocene of Sulawesi (Plate 3.4) and the Australian Eocene (Truswell et al., 1987) and abundant occurrences in the middle Miocene of Mindoro, in the Philippines (Morley, unpublished). Also, Onosperma appears to be a relict genus, with a number of Neogene records east of its present area of distribution. Similarly, Ham (1990) concludes that the only genus of the tribe Nephelieae (Sapindaceae) to cross Wallacea from the west is Pometia, other genera having dispersed into Wallacea either from the Sunda region or from the Australian plate.

Truswell et al. (1987) could not find any evidence for such a major post-collision invasion from the Sunda region from examining the Australian pollen record. However, the sudden and widespread latest Oligocene (Truswell et al., 1985; Pocknall, 1982) or earliest Miocene (Stover and Partridge, 1973, Martin, 1978), appearance of Acacia pollen (Acaciapollenites myriosporites), and the early Miocene appearances of pollen of Morremia (Perfotricolpites digitatus), Caesalpinia type (Margocolpites vanwijheii) and spores of Sienochlaena palustris (Verricatosporites usmensis) in Australia
Tertiary plant dispersals in SE Asia

(Truswell et al., 1985, Hekel, 1972) may reflect such dispersals from the Asian plate, but may not necessarily reflect dispersals across Wallace’s Line.

Consideration of the geological history of islands east of Wallace’s Line may help explain the limited evidence for Neogene crossings, but the ‘Malezan’ aspect of the eastern flora (Fig.15). Firstly, whereas many of the islands of Eastern Indonesia may be very young, such as Seram, Irian Jaya and eastern Sulawesi, the island chains of the Philippines, and Halmahera probably included emergent areas through much of the Tertiary, and these islands are likely to have borne a tropical aspect, rather than Australian flora. Secondly, although South Sulawesi is east of Wallace’s Line, its geological affinity is with the Sunda plate; it became separated from Kalimantan in the late Eocene following the opening of the Makassar Straits (Situmorang, 1982; Hall, 1995), but at the time of separation, already bore a flora with affinities to the Eocene flora of India, Java and SE Kalimantan. Middle and upper Eocene paralic sediments from the Malawwa Formation of South Sulawesi contain abundant pollen with affinities to the Sunda region, including aff. Beaufordites matsuokae (Proteaceae, Plate 2.4), Cupanioidites flaccidiformis (Plate 2.4) of sapindaceous affinity, Dicocolpos pollis spp., from Palmae, Calamoideae (Plate 3.4), Ixoniites pollen (Plate 1.3-1.4), Laeopolis ovatus, produced by Durio (Plate 2.3), Lanagogopollis, from Anga Niru (Plate 1.1-1.2) Palmae, pollenites cutchei, from the palm subtribe Iguanurinae (Plate 3.1), Quilloniopollenites spp., indicating Eugenieca (Plate 2.1) and Retistephanocarpites williamsii, from Clenopphix, Plate 1.5-1.6, together with the taxa of indeterminate affinity Meyeropollis nayarkotensis (Plate 3.5) and Compositopollenites dilatatus (Plate 2.2).

Reconstructions by Hall (1995) for 45 to 40 Ma suggest that at these times, dispersal paths were possibly present which may have allowed elements of this flora to migrate eastward to the eastern Philippines and possibly beyond. Thirdly, recent studies by the Indonesian Riset Unggulan Terpadu (RUT) demonstrate that there is a virtually continuous pollen record through the Oligocene and Miocene in this area (N. Polhaupessy and S. Sugeng, pers. comm., 1997), suggesting that the Sundanian Paleogene flora may have persisted in South Sulawesi until the time of the Miocene collision.

The pre-collision flora to the east of Wallace’s Line, with all probability, originated from the Paleogene flora of South Sulawesi, and the islands of the Banda arc and New Guinea formed during the Middle Miocene, they probably became vegetated by floras comprising elements of both the South Sulawesi and Philippine floras, mixed with Australian rain forest elements. Such an origin is fully compatible with results of a biogeographical appraisal of the flora of Sulawesi, which suggests generic affinities firstly with New Guinea, and secondly with the Philippines and Moluccas (Balgooy, 1987).

Dispersal of mountain plants

The pollen record reveals the presence of two broad dispersal paths which have allowed mountain plants to disperse into the Sunda region during the Tertiary. The first is a long established route, along which both Laurasian conifers and north temperate broad-leaved trees have dispersed, whereas the second, much later path from Australasia, is characterised by the migration into the area of southern hemisphere podocarps. Both of these dispersal paths were first noted by Muller (1966).

Typical Laurasian elements include pollen of Pinus, Picea, Abies, Rugubivesiculites, Tsuga canadensis type, Tsuga diversifolia type, Taxodium type, and pollen of the temperate trees, Alnus, Betula, Carya, Juglans and Pterocarya, whereas the southern podocarps comprise Podocarpus (Dacrycarpus) imbricatus type and Phyllocladus hypophyllus type pollen (Fig.16).

The typical abundances of pollen from each of these sources differ in that the Laurasian elements may be extremely abundant, and in some settings may actually dominate palynomorph assemblages, whereas the southern element is invariably a minor, background component of the assemblages.

Dispersals from Asia

The Laurasian connection of Sunda with East Asia is very ancient. The presence of common Rugubivesiculites reductus and Pinus type pollen (Alisporites similis and Pinuspollenites cf. spherisaccus) in the probable Paleocene of Sarawak shows that the connection was already well established at the beginning of the Tertiary (Fig.5). There is little evidence for the representation of montane elements in the area during the Eocene, since the pollen record for this period is poor, but Laurasian montane elements,
consisting of *Pinus, Picea, Abies, Tsuga* and temperate angiosperms are abundant in the Oligocene and earliest Miocene, after which time they exhibit a gradual decline, with marked reductions in representation at about 21 Ma and 18 Ma in the early Miocene, although they occasionally return in small pulses, especially in the Plio-Pleistocene.

The Laurasian element is not abundant throughout the Sunda region, but is characteristically present in sediments within the Malay, Penyu, Vietnamese and Natuna basins, offshore Sarawak, the Gulf of Thailand and to a lesser extent, central Sumatra (Fig.17). It occurs as a background element in the lower Miocene of Mahakam Delta, but occurs only sporadically from the Java Sea basins. *Pinus* is the most abundant and widespread pollen type, followed by *Picea, Alnus* and *Tsuga*. The remaining types become progressively more common toward the Gulf of Thailand, and offshore Vietnam. Pollen of temperate taxa, including *Alnus*, is extremely common in the early Miocene and Oligocene of the intermontane basins of Thailand (Watanasak, 1988, 1990) where it occurs in association with abundant *Quercus* pollen, suggesting a vegetation similar to some modern temperate forests.

The approximate extent of the upland topography through the late Cretaceous and Tertiary of the Sunda region which bore this upland flora can be obtained through the comparison of the relative representation of elevated and lowland terrain proposed on the global palaeogeographic maps of Smith et al. (1994). The widespread representation of elevated terrain was a major feature throughout the late Cretaceous and Early Tertiary, but became reduced in the Neogene, complying closely with (but probably based partly on) the distribution of the Laurasian gymnosperm and temperate pollen (Fig.18).

The presence of a major elevated area, including Sunda with East Asia, as indicated by Smith et al. (1994) throughout the period of radiation of the angiosperms, and also through the period of global climatic deterioration since the end of the Eocene, is very important from the point of view of survival of certain primitive angiosperms in SE Asia. One of the reasons for Takhtajan (1969) suggesting that SE Asia was the birthplace of angiosperms was the occurrence of many more archaic angiosperms in the sub-montane forests of this region compared to South America or Africa. The presence of a continuous elevated area in SE Asia, stretching from the equator to over 60°N, throughout this period, is certainly responsible in a large part for the retention of archaic angiosperms in the Far Eastern tropics. Such upland latitudinal connections in the South American and African tropics are either absent, or have been intermittent.

Steenis (1936) defined two migration tracks from Asia, the Sumatra track, characterised mainly by herbaceous taxa with connections in the Himalayas, and the Luzon track, with connections with East Asia. Migrations discussed here do not appear to relate to either of these directly, but suggest that the Malay peninsula provided the main dispersal route from Asia during the Tertiary. The Sumatran track probably became established following the uplift of the Barisan mountains in the mid Miocene, whereas the Luzon track may relate more to the southerly drift of Palawan (although there is no palaeobotanical evidence available to test this suggestion), or to dispersal via Taiwan during
phases of low Pleistocene sea levels, since these areas became juxtaposed only in the latest Tertiary (Hall, 1995).

Dispersals from Australasia

*Podocarpus* sect. *Dacrycarpus* (now elevated to generic level by Luebbenfels, 1988), which produces disaccate pollen, is more or less restricted to moist, upland regions of SE Asia. It has a good pollen record in the Sunda region, which extends only over the last 3.5 Ma, since the latest phase of the Early Pliocene (Fig. 16). *P. imbricatus* is presently widespread in SE Asia, occurring throughout Sundaland, and into Indochina, and is the classic example of westward migration across Wallace’s Line. New data from Irian Jaya, and the southern Philippines, show that Wallace’s Line itself was no barrier to this species; it appears to have arrived in the Bird’s Head area of Irian Jaya only in the earliest Pliocene. Kaas (1991b) subsequently dates its earliest appearance in the Southern Philippines in the mid Pliocene, attributing its arrival there to the establishment of suitable habitats as a result of local tectonic uplift. This pollen type is particularly common in the uppermost lower Pliocene of Java (Rahardjo et al., 1994), and is recorded at identical times from offshore Sarawak/Sabah. It appears to have taken longer to reach the Malay peninsula, for its pollen is absent from the Pliocene of the Malay basin, but is present within Malay peninsula Quaternary sediments.

The pattern of migration displayed by *Podocarpus imbricatus* is followed, although to a lesser degree, by that of *Phyllocladus hypophyllus* (Fig. 16), which dispersed only as far as Borneo, where it occurs today, and where its pollen can be seen only in sediments of Quaternary age (Muller, 1966, 1972; Morley, 1978; Caratini and Tissot, 1985). It is also recorded in the southern Philippines at about the same time (Kaas, 1991b).

In Papua New Guinea and Irian Jaya, montane podocarp pollen is accompanied by that of *Nothofagus* (Khan, 1976), whose arrival in this area also appears to have been strongly controlled by the uplift of the New Guinea mountains. It first appears in the Birds Head of Irian Jaya in the late Miocene, but was never able to disperse further to the west, presumably because of its inability to disperse across water barriers. As previously noted by Muller (1972), the fossil record for southern podocarps reflects the New Guinea tract of Steenis (1936).

Anomalies

Consideration of the palynological record in relation to plate tectonics leaves remarkably few unexplained anomalies. The main anomalous distributions were previously in the Oligocene, but the late Oligocene collision of Hall (1995) may explain these. Only the record of *Dacrydium* from the upper Eocene of Java cannot be readily explained from geological evidence for past continental positions. The Paleocene occurrence of *Dacrycarpus* pollen on the Ninetyeast Ridge was explained by Kemp and Harris (1975), as due to long distance dispersal, and a similar explanation may apply here. The major ‘anomaly’ seen in the pollen flora is its uniformity over long periods of time (cf. Martin, 1982, Truswell et al., 1987). It is remarkable to realise that, despite such tectonic upheavals as witnessed in SE Asia, the pollen flora of the region reveals few changes, and regional migrations appear to be so few. Perhaps we are not looking carefully enough to see the real picture?

Conclusions

The current palynological record provides no evidence to suggest that the SE Asian region was an area of initial radiation of angiosperms. Angiosperm diversities were probably lower than in other tropical areas until the middle
Eocene, when floras were enriched by widespread migrations from the Indian plate. Since
Gondwanan elements were brought to SE Asia via the Indian plate, there is less need invoke an
earlier, Cretaceous, connection between Sunda and Gondwana in order to explain present day
plant distributions.

The Sundanian Eocene flora stretched as far east as the south arm of Sulawesi. Subsequent to
the opening of the Makassar Straits in the late Eocene, a part of the Sundanian flora became
stranded in South Sulawesi to the east of
Wallace’s Line. This area probably provided a
major source of taxa of Sundanian, and Asian
affinity, to areas to the east of Wallace’s Line, throughout the remainder of the Tertiary, negat-
ing the need for wholesale eastward dispersal
across the Makassar Straits during the Miocene.

A small number of taxa have migrated west-
ward across Wallace’s Line since the main phase
of collision of the Australian and Sunda plates
during the Miocene. Such events occurred at
about 17 Ma, with the immigration of Myrtaceae,
Campnospathus at 14 Ma, and at about 9.5 Ma, at
which time a fern, ancestral to Stenochlaena
milnei, dispersed from the East, and spread
widely across the region. All of the above are
well adapted to dispersal, and emphasise that
Wallace’s Line remained a substantial barrier to
dispersal throughout the Oligocene and Neogene. Acacia was among the taxa which
probably dispersed from the Sunda plate
(though not necessarily across Wallace’s Line) to
Australia in the latest Oligocene or earliest
Miocene.

The pre-collision East Malesian flora probably
developed on island arcs of the Palaeo-Philipp-
ines, and from the Paleogene Sundanian flora
which became stranded in South Sulawesi after
the late Eocene opening of the Makassar Straits.
It is speculated that the New Guinea flora formed as a result of the intermixing of these
floras with the Australian flora in the Miocene.

SE Asian rain forest floras successively mi-
grated northward during periods of Miocene high sea level and moist, warm climates. Their
greatest northward migration was at the early/middle Miocene boundary, when several
mangroves, and other tropical taxa, dispersed northward as far as Central Japan. Some migrations
from Australia probably took place in the
Oligocene. These include Casuarina, and Da-
crydium spp. producing the D. guillauminii
pollen type. There is a significant number of
pollen types from the mid-Tertiary of Java which
compare closely with pollen of endemic; or
characteristic extant taxa from New Caledonia.
These include Beurlaebidites matsuokae (Beau-
prea, Proteaceae), Palmaepollenites kut-
chenesis (Burretkokenia and Basseliae; Palmae)
and the Dacrydium guillauminii type.

A major montane connection existed through-
out the Tertiary, and probably late Cretaceous,
in SE Asia, from the equator, to 60°N. This
allowed Laurasian mountain plants to disperse freely to and from the equator throughout this
period. This mountain range became of much
reduced extent during the later Tertiary, espe-
cially after about 20 Ma. The proliferation of
primitive ‘northern’ angiosperm families within
lower montane forests of SE Asia, such as
Magnoliaceae, is thought to be due largely to
the continuous presence of this mountain belt,
which probably provided an unbroken succe-
sion of niches for such groups irrespective of
climatic changes at lower altitudes. Both
Magnoliaceae and Fagaceae would fall into this
category. In contrast, the Neogene convergence
of the Sunda and Australian plates, and the de-
velopment of substantial upland areas in New
Guinea, has provided niches for related southern
families (Nothofagaceae) or archaic previously
cosmopolitan families (e.g., Winteraceae)
which, during the later Tertiary, found refuge in
the southern hemisphere. In this manner, some
bihemispheric family pairs have been brought
close together in SE Asia, without requiring an
origin in this area, thus knocking a few more
ails in the coffin of the theory that angiosperms
evolved in some isolated area ‘somewhere be-
tween Assam and Fiji’.

The dispersal of Australian mountain plants,
such as Podocarpus imbricatus and Phyllo-
cladus hypophyllus, became possible as a result
of the development of suitable upland niches in both East and West Malesia, rather than the formation of continuous terrestrial connections. The SE Asian region is a vast area, and still remains very poorly studied using palynology. One safe prediction is that further detailed studies will undoubtedly bring to attention many new records, which will certainly modify, and improve, the sketchy picture of migration and dispersal outlined above.

Acknowledgements

The author is grateful to Eko Budi Lelono and Lucila Nugrahaniingsih of the Indonesian Riset Unggulan Terpadu, or RUT (an Integrated Research Team from ITB, LEMIGAS, PERTAMINA, PPPG, PPGL and UGM) formalising biostatigraphic zonation for the different provinces of Indonesia) for discussions about Eastern Indonesian palynology, and Petronas Research and Scientific Services (PRSS) for the opportunity to undertake a detailed appraisal of Malay basin palynostratigraphy. Moyra Wilson kindly provided the samples from the Malawa Formation from South Sulawesi. Tim Whitmore kindly provided many useful comments on the first draft of the manuscript, and Mary Dettmann helped in naming protaeaceous pollen and some taxa of Australian affinity.

References

Harley, M. M. and Morley, R. J., 1995. Ultrastructural studies of some fossil and extant palm pollen, and the recon-


Kaas, W. A. van der. 1991a. Palynology of eastern Indone-


Kar, R. K. and Singh, R. S. 1986. Palynology of the Creta-

Kemp, E. M. and Harris, W. K. 1975. The vegetation of Terti-


Krause, D. W. and Maas, M. C. 1990. The biogeographic origins of late Paleocene-early Eocene mammalian immi-
grants to the Western Interior of North America. Geologi-


Martin H. A. 1978. Evolution of the Australian flora and vegeta-

Martin, H. A. 1982. Changing Cenozoic barriers and the Aus-

Mathur, Y. K. 1984. Cenozoic palynofossils, vegetation, ecology and climate of the north and northwestern sub-


Morley, R. J. 1991. Tertiary stratigraphic palynology in southeast Asia: current status and new directions. Geo-

Morley, R. J. and Fenley, J. R. 1987. Late Cainozoic vegetational and environmental changes in the Malay Ar-
chipelago. In Biogeographical Evolution of the Malay Ar-
chipelago, pp. 50-59. Edited by T. C. Whitmore. Oxford Monographs on Biogeography 4, Oxford Scientific Publi-
cations.

Morley, R. J., Lelono, E, B., Nugrahaningsih L. and Nur Hasjim. 1996. LEMIGAS Tertiary palynology project: aims, progress and preliminary results from the Middle Eocene to Pliocene of Sumatra and Java. GRDC Palaeo-
tology Series, Bandung Indonesia (in press).


Muller, J. 1972. Palynological evidence for change in geomorphology, climatic and vegetation in the Mis-


ternational Symposium on Stratigraphigraphic Correlation of Southeast Asia, Bangkok, November 1994: 208.


Srivastava, S.K. 1977. Cteniophotum and Sclerosperma palaeo-

Steenis, C. G. G. J. van. 1954a. On the origin of the Malay-

Steenis, C. G. G. J. van. 1954b. On the origin of the Malay-


drought plants from Asia to Australia. Reinwardtia 5: 420-429.
Plate 1. Middle Eocene palynomorphs from Central Java and S Sulawesi, all x1000. 1-2. Lanagiospollis cf. regularis (Amanthum sect. Conostigma, Amanthaceae), S Sulawesi, Malawa Formation, sample P-04. 3-6. Drosanthus pollen (Drosanthaceae), Central Java, Nanggulan Formation, sample XIVF. 5-6: Retistephanocolpites williamsi (Cenolophoph parvifolius, Cenolophomaceae), S Sulawesi, Malawa Formation, sample P-04.
Plate 2. Middle Eocene palynomorphs from Central Java and S Sulawesi, all x1000. 1: Quilltonipollenites sp. (Eugetoeea, Palmae), S Sulawesi, Malawa Formation, sample P-04. 2: Compositopollenites dilatus (family indet.), Central Java, Nanggulan Formation, sample XIV. 3: Lagopolis ovatus (Duino type, Bombacaceae; sect. Durioneae), S Sulawesi, Malawa Formation, sample P-04. 4: aff. Bonplandiales ovatus (Bombacoideae, Bombacaceae), S Sulawesi, Malawa Formation, sample P-04. 5: Cephaloecides flaccidiformis (Sapindaceae), Central Java, Nanggulan Formation, sample XIV. 6: Polygalacites clarus (Polygalaceae; family indet.), S Sulawesi, Malawa Formation, sample P-04. 7: Danutiaspora laevisata (Pteridophyta, family indet.), S Sulawesi, Malawa Formation, sample P-04.