Biogeographic implications of the Tertiary palaeogeographic evolution of Sulawesi and Borneo

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Abstract

Sulawesi and Borneo are located in a critical position for biogeography, bordering Wallace's faunal divide and in the middle of the Indonesian archipelago, an extremely active tectonic area throughout the Tertiary. Wallace's original line now marks the western boundary of Wallacea: a biogeographic zone with a high degree of species endemism between areas with Asiatic and Australian flora and fauna. Tectonic controls have strongly influenced the distribution of depositional environments and hence the past and present distribution of terrestrial and shallow marine biota.

Palaeogeographic maps presented, using plate tectonic reconstructions as a base, illustrate the evolution of the area and highlight important features for palaeobiogeography. The Tertiary geological history of eastern Kalimantan and Sulawesi is inextricably linked to the progressive accretion of continental and oceanic material from the east, onto the eastern margin of Sundaland (Eurasian margin), and to the resultant development of volcanic arcs. This westward drift of material throughout the Tertiary, particularly that of microcontinental blocks, may have provided a potential pathway which allowed rafting or island hopping of Australian biota towards Asia and vice versa. A land bridge existed between Borneo and mainland SE Asia for much of the Tertiary, whereas the formation of the Makassar Straits in the early Tertiary isolated small land areas in Sulawesi from those in Borneo. Both of these factors resulted in strong biogeographic differences between Borneo and Sulawesi and contributed to a high degree of endemism on Sulawesi. Chains of volcanic island arcs, related to subduction along the eastern edge of Sundaland during the Tertiary, may have presented island hopping routes to and from the Philippines, Borneo and Sulawesi, and possibly Java.

Introduction

The islands of Borneo and Sulawesi are of prime importance to the biogeography and palaeobiogeography of SE Asia. Wallace's (1863) faunal divide, originally thought to delineate regions of Asiatic and Australian flora and fauna, runs between the islands of Bali and Lombok and north through the Makassar Straits, which separate the islands of Borneo and Sulawesi (Fig.1; George, 1981). This faunal divide is now taken as the western boundary of Wallacea (Dickerson, 1928), a 'transitional' area between Asiatic and Australian biotas (Whitten *et al*., 1987). Wallacea includes Sulawesi, the Moluccas and the Lesser Sunda islands as well as an extensive area of shallow sea, and its eastern margin is taken as Lydekker's line; the western boundary of the strictly Australian fauna (Fig.1). The transitional nature of biota within Wallacea is sometimes seen, for example, by the eastward increase in Australian representatives in the reptile fauna between the western and eastern boundary lines (Ziegler, 1983). However, for most organisms Wallacea does not represent a region of homogeneous biota, or a region of gradual change in species composition. In reality, Wallacea is best described as a biogeographic region, situated between areas with Asiatic and Australian floras and faunas, where organisms show a high degree of endemism (George, 1981; Whitten *et al*., 1987).

The sharp contrast in fauna between areas bordering Wallace's original line is not reflected to the same extent by the flora (George, 1981; Balgooy, 1987). There are approximately 2,300 genera of flowering plants in total in the archipelago and for most Wallace's line is unimportant, although 297 genera, including some of the palms, do reach their eastern limit there

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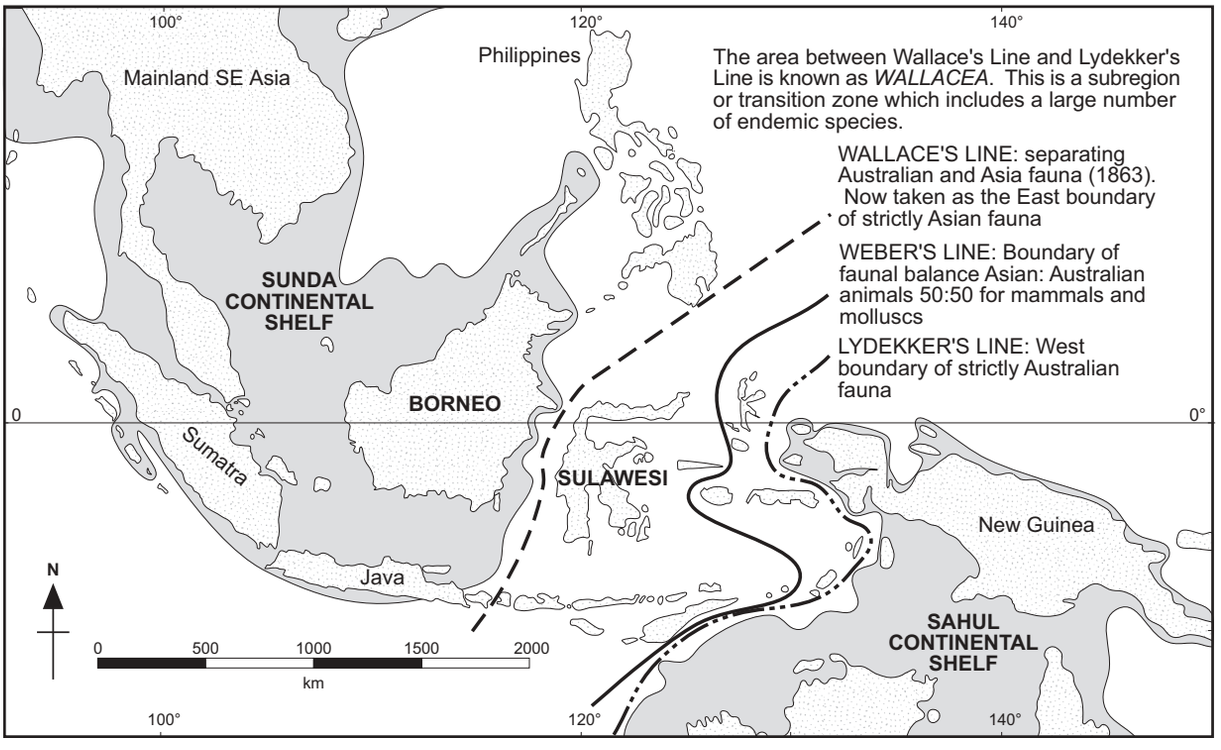

Fig. 1. Map of SE Asia showing the location of Borneo and Sulawesi in the centre of the region. The original faunal divide of Wallace (1863) is shown. Areas of continental shelves are shown in grey.

(Dransfield, 1981; George, 1981). This may be because many plants are better at overseas dispersal (Briggs, 1987), because their range is often strongly related to suitable habitats and climate (Steenis, 1979; Balgooy, 1987; Takhtajan, 1987), or because certain floral elements were present on both sides of Wallace's line before the formation of the Makassar Straits. Multiple migration pathways, via northern and austral routes, have been suggested for some groups of plants after breakup of Gondwana (Dransfield, 1981, 1987; Whitmore, 1981b; Audley-Charles, 1987; Truswell *et al.*, 1987; Morley, 1998 this volume). For certain groups of animals the Makassar Straits appear to have been a barrier to dispersal, whereas organisms such as some oriental frogs, reptiles, birds and mammals occur on both sides of Wallace's line and in some cases their range extends as far as Australia. However, overall there is still a clear faunal change across the Makassar Straits (Cranbrook, 1981; Briggs, 1987; Musser, 1987).

The SE Asian region has been an extremely active tectonic area throughout the Cenozoic, and geological and geophysical evidence indicates that considerable lateral and vertical crustal, or plate, movements have occurred in the region. During the last twenty years several plate tectonic reconstructions have been postulated for the area (Carey, 1975; Peltzer and Tapponnier, 1988; Rangin *et al.*, 1990; Daly *et al.*, 1991; Lee and Lawver, 1994, 1995; Hall, 1996). There is now a growing consensus over some of the main points of the plate tectonic evolution of the area, although details of the reconstructions and the driving mechanisms are still under dispute. The reconstructions show the movements of lithospheric plates, and it is important to realise that these do not directly correspond to regions of land and sea.

A number of workers have related biogeography to the plate tectonic evolution of SE Asia. Audley-Charles *et al.* (1981) showed SE Asia in its world-wide context and identified major plate tectonic events, evaluating their importance for biogeographers. These included the separation of India from Antarctica-Australia, the separation of Australia-New Guinea from Antarctica, the juxtaposition of India with Asia, and most recently the convergence and subsequent juxtaposition of Australia with SE Asia. The regional evolution of SE Asia and its biogeo-

graphic implications, with particular reference to Sulawesi, were reviewed by Audley-Charles (1981). The formation of the Makassar Straits, and possible temporary land links across this seaway, and the juxtaposition of different tectonic fragments in Sulawesi, particularly those in the east with Australian affinity, were identified as major influences on the biogeography across Wallace's line. The evolution and dispersal of the angiosperms were discussed in the light of plate tectonic events by Audley-Charles (1987). Burrett *et al.* (1991) related rifting of fragments away from Australia and their subsequent convergence and collision with mainland SE Asia to biogeography. All authors note the importance of superimposing palaeoenvironmental data onto plate tectonic reconstructions to provide meaningful information to biogeographers, and the actual difficulties of undertaking such a task. Audley-Charles (1987) and Hall (1998 this volume) attempted to identify areas of past land, shallow and deep sea regions from the plate tectonic evolution of SE Asia.

This paper concentrates on the Tertiary evolution of Borneo and Sulawesi and synthesises palaeoenvironmental information obtained from the geological record with plate tectonic reconstructions. Areas of land, marginal marine, shallow marine and deep marine areas are shown on plate tectonic reconstructions of Borneo and Sulawesi for the Tertiary and provide a means to examine possible migrations or dispersals in the areas bordering Wallace's line.

Present-day distribution of organisms in Borneo and Sulawesi

Borneo and Sulawesi include a variety of habitats, such as high mountainous areas, lower rolling topography and flat coastal plains. A complex interplay of factors, including physical differences in environment (altitude, soil type and slope all influenced by local geology), local and regional variations in climate as well as regional geological evolution may all influence the nature and diversity of organisms found on Borneo and Sulawesi. Today both Borneo and Sulawesi have tropical climates, although some areas of Sulawesi may experience long dry periods and a more monsoonal climate than areas in Borneo. The present-day environments of Borneo and Sulawesi are described in detail in MacKinnon *et al.* (1996) and Whitten *et al.* (1987).

The biota of Borneo at both generic and species level is similar to mainland SE Asia and other islands on the Sunda Shelf, particularly Sumatra, from which Borneo is separated by about 220 km (Fig.1). There are, however, differences and in particular Borneo has a higher number of endemic plants and animals than adjacent areas to the west. In relation to its size the fauna of Borneo is less diverse than its western neighbour Sumatra, but more of its animals are exclusive with thirty nine land animals and thirty birds being endemic to the island (Whitten and Whitten, 1992; MacKinnon *et al.*, 1996). The mammal population of Borneo, represented by 222 species of land animals, is almost identical to that of mainland Asia at family level with primates, bears, cats, squirrels and rhinos all represented. Borneo has the highest number of species of primates and tree shrews within the SE Asian region (MacKinnon *et al.*, 1996). Borneo has some 450 resident species of birds, the third highest in the region after New Guinea and Sumatra, which is a reflection of the size of the island, the diversity of available habitats and proximity to mainland Asia. Borneo is one of the richest islands on the Sunda Shelf for freshwater fish (394 species of which 149 are endemic), amphibians (at least 100) and reptiles (at least 166 species of snake, MacKinnon *et al.*, 1996). Most of the freshwater fish species of Borneo are seen in Sumatra and elsewhere in SE Asia, although again Borneo has a higher number of endemic species. Of all the vertebrate groups the primary freshwater fish most clearly demarcate Wallace's original line and there is a total absence of primary division freshwater fish in Sulawesi, although a few occur in the Philippines (Kottelat *et al.*, 1993).

Borneo has the most diverse flora of the Sunda Islands, with some 10,000-15,000 species of flowering plants of which one third are endemic (Whitten and Whitten, 1992; MacKinnon *et al.*, 1996). Invertebrate species are extremely abundant on Borneo, although accurate figures are not available for the less well known groups. Much of the flora and fauna endemic to Borneo is confined to the high mountainous areas, particularly in Sabah and Sarawak, indicating a degree of niche partitioning related to local environmental conditions and to the lateral separation of similar habitats.

On Sulawesi there is an extremely high degree of endemism amongst the fauna, particularly of the mammals. The biota of Sulawesi, particularly at a generic and higher level, shows affinities with those of both Australia and Asia, although far fewer families are represented compared with Borneo or New Guinea (Whitten *et*

al., 1987; Michaux, 1994; Holloway, 1997). Out of 127 species of indigenous mammals, 79 (62%) are endemic to Sulawesi, and this rises to 98% if the bats are excluded (Whitten *et al*., 1987). Much of the characteristic Sundaic fauna, including moles, flying lemurs, tree shrews, lorises, gibbons, pangolins, porcupines, dogs, otters, weasels, cats, elephants, tapirs, rhinoceroses and mouse-deer do not occur east of Wallace's line (Musser, 1987; Whitten *et al*., 1987), although Plio-Pleistocene elephant fossils have been found in Sulawesi (Cranbrook, 1981; Whitten *et al*., 1987; Aziz, 1994). Of the Sulawesian mammals many of the placentals have Sundaic affinities, some of the endemics, such as the anoa, have no Sundaic relatives, whereas the marsupials are clearly an Australian element (Musser, 1987; Michaux, 1994). A high degree of endemism also occurs within the indigenous amphibian (19 out of 25 species) and reptile (13 out of 40 lizard species and 15 out of 64 species of snake are endemic with one monotypic genus) populations and it is likely that more species of these groups have yet to be discovered (Whitten *et al*., 1987). About a quarter of the birds on Sulawesi (total 328) are endemic and although a dominant Sundaic influence is seen, some Australian elements also occur (Mayr, 1944; Whitten *et al*., 1987; Holmes and Phillipps, 1996; Michaux, 1996). Unlike Borneo, Sulawesi has no records of strictly freshwater fish (Cranbrook, 1981; Whitten *et al*., 1987; Kottelat *et al*., 1993). However, of the fish that live primarily in freshwater and show a little saltwater tolerance, and those with considerable marine tolerance, such as the diadromous fish, 68 species occur in Sulawesi and of these 52 are endemic (78%, compared with 38% in Borneo). Like Borneo there are 8 endemic genera (Kottelat *et al*., 1993).

The distribution of flora in Sulawesi appears to be strongly related to climatic and local physical conditions, including altitude and soil types (Whitten *et al*., 1987). Analysis of over 4000 species in 540 genera suggests that the Sulawesi flora is most closely related to other relatively dry islands in the region (Balgooy, 1987). Dransfield (1981), suggested that the paucity of palms on Sulawesi may be related to a drier Pleistocene climate. Balgooy *et al*. (1996), recognised 933 indigenous plant species on Sulawesi, and of these 112 were endemic to the island. Montane floras are similar to those in Borneo, whereas the flora of the lowlands and areas underlain by ultrabasic rocks have a strong affinity with that of New Guinea (Balgooy, 1987; Whitten *et al*., 1987). Of the non-endemic plants in Borneo, about 50% do not occur in Sulawesi (Whitten *et al*., 1987).

The invertebrate fauna of Sulawesi in general has affinities with areas to the west, but in comparison is depauperate and displays a higher degree of endemism (Gressitt, 1961; Whitten *et al*., 1987; Vane-Wright, 1991). An Australian, or in some cases a Philippine, affinity has also been recognised within some of the invertebrates, including the Lepidoptera (de Jong, 1990; Holloway, 1987, 1990, 1997) and the cicadas. The cicadas are poor dispersers, show a high degree of endemism (73 out of 77 species in Sulawesi are endemic), and a number of species are restricted to one of Sulawesi's arms or to its central part, perhaps reflecting the Tertiary geological evolution of Sulawesi (Duffels, 1990).

Data sources

The plate tectonic reconstructions of Hall (1996) are used as a template in this paper upon which to draw palaeogeographic maps. Although these reconstructions differ from many of the earlier plate tectonic reconstructions for SE Asia (Rangin *et al*., 1990; Daly *et al*., 1991; Lee and Lawver, 1994; 1995) in terms of their detail, particularly in eastern SE Asia, the Borneo-Sulawesi parts of the reconstructions do not differ significantly for the purposes of plotting palaeogeographic data.

The series of palaeogeographic maps presented here illustrates the evolution of Borneo and Sulawesi during the Cenozoic. The data used in constructing these maps were derived from fieldwork by the London University SE Asia Research Group, and an extensive literature review of the islands of Borneo and Sulawesi. These maps have been based on available geological evidence, including facies data, stratigraphic information, biostratigraphy, igneous, metamorphic, structural and palaeomagnetic data. Significant gaps exist within the data set and particularly for some of the remoter areas there is limited information. Previous attempts at palaeogeographic reconstruction have either been limited to small areas, such as hydrocarbon exploration blocks (Wain and Berod, 1989) or very generalised palaeogeographies for very long time periods (Umbgrove, 1938; Beddoes, 1980; Rose and Hartono, 1978; Weerd and Armin, 1992). As far as we know this is the first attempt to synthesise palaeographic data with plate tectonic information for the whole area of

Borneo and Sulawesi.

The most important environmental elements distinguished are land areas, including regions of mountainous topography, low lying regions of fluvial deposition, major river systems and marginal marine/deltaic systems. Areas of shallow water and deeper water, fine grained and coarser redeposited clastic and carbonate deposits were also mapped. Volcanic centres, with regions of inferred subaerial and submarine volcanism, are also shown on the reconstructions. Thus the key environments for terrestrial and marine faunas and floras are emphasised. The outlines of the present coastlines are shown on the reconstructions for reference.

Geology and tectonics of Borneo and Sulawesi

Borneo and Sulawesi are situated in a tectonically complex region between three major plates (Eurasia, Indo-Australia and Pacific/Philippine Sea). The present day setting is mirrored by the complexity of the pre-Tertiary and Tertiary geology of these two islands. Large areas of eastern Kalimantan and western Sulawesi had been accreted onto southwestern Borneo, part of the eastern margin of Sundaland, by the Cenozoic (Hall, 1996; Metcalfe, 1998 this volume). Subduction of the Indian Ocean, Philippine Sea and Molucca Sea plates has been responsible for the progressive collision and accretion of fragments of continental and oceanic crust along the eastern margin of Sundaland throughout the Cenozoic. Within this overall compressional regime a number of sedimentary basins and deep marginal basins formed along the eastern and southern margins of Sundaland as a result of Tertiary extension and subsidence.

Borneo

Borneo is bounded by three marginal basins (South China, Celebes and Sulu Seas), microcontinental fragments of south China origin to the north, and mainland SE Asia (Indochina and peninsular Malaysia) to the west (Figs.1 and 2). Borneo has been interpreted as the product of Mesozoic accretion of oceanic crustal material (ophiolite), marginal basin fill, island arc material and microcontinental fragments onto the Palaeozoic continental core of the Schwaner Mountains in the SW of the island (Fig.2; Hutchison, 1989; Metcalfe, 1998 this volume). At the beginning of the Tertiary, Borneo formed a promontory of the Sundaland craton: the stable eastern margin of the Eurasian plate (Hall, 1996; Metcalfe, 1998 this volume). East of Borneo, separating it from Sulawesi, are the deep Makassar basins (Fig.2), formed during the Paleogene (Situmorang, 1982). Two NW-SE trending fault zones, the Adang and the Sangkulirang, bound the North Makassar basin to the south and north (Fig.2). Major tracts of eastern, central and northern Borneo are covered by Tertiary sediments (Fig.2) which were deposited in fluvial, marginal-marine or marine environments. These depocentres were often laterally interconnected through intricate and narrow links (Fig.2; Pieters *et al*., 1987; Pieters and Supriatna, 1990). Tertiary sedimentation in these regions occurred contemporaneously with, and subsequent to, a period of widespread Paleogene extension and subsidence, which may have begun in the middle Eocene or earlier.

Sulawesi

Sulawesi is formed of distinct north-south trending tectonic provinces (Fig.3; Sukamto, 1975) which are thought to have been sequentially accreted onto Sundaland during the Cretaceous and Tertiary. In part due to a lack of information, and to different interpretations of the available data, the evolution and juxtaposition of fragments within Sulawesi remain highly contentious and an attempt has been made to describe different hypotheses and to evaluate how these might affect biogeographic studies.

The north and south arms of Sulawesi are composed of thick Tertiary sedimentary and volcanic sequences overlying pre-Tertiary tectonically intercalated metamorphic, ultrabasic and marine sedimentary rocks (Fig.3; Sukamto, 1975; Leeuwen, 1981). Central Sulawesi and parts of the SE arm of Sulawesi are composed of sheared metamorphic rocks and in the east there is a highly tectonised melange complex (Sukamto, 1975; Hamilton, 1979). Similarities between the pre-Tertiary rocks and dating of metamorphic rocks suggests that they were accreted onto the eastern margin of Sundaland before the Tertiary (Sukamto, 1975; Hasan, 1991; Parkinson, 1991; Wakita *et al*., 1994). The Tertiary stratigraphy of western Sulawesi is similar to that of east Kalimantan and the East Java Sea because the whole area began to subside in the early middle Eocene and a large basin formed (Weerd and Armin, 1992).

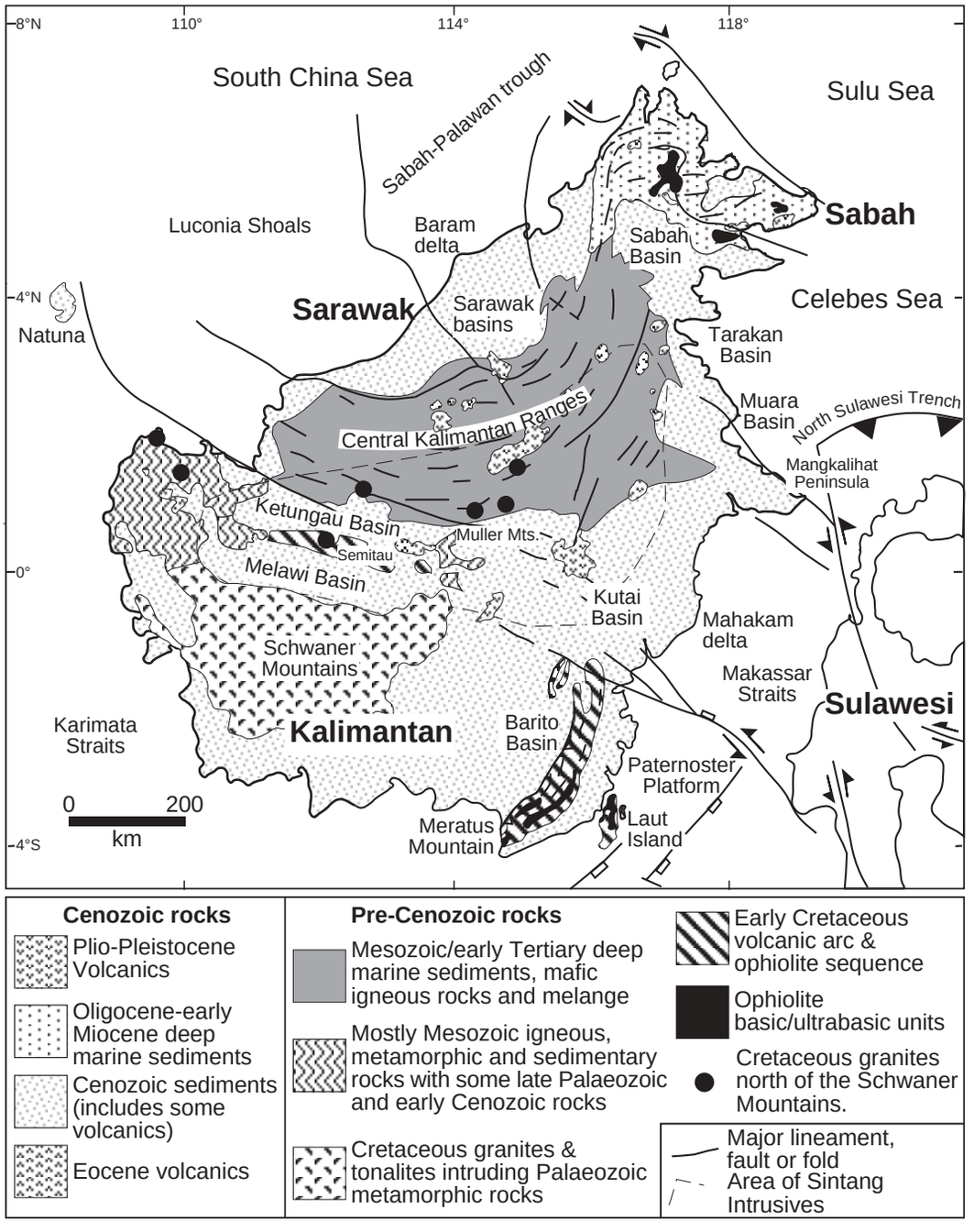

Fig.2. Simplified geological map of Borneo.

The eastern side of south Sulawesi and much of the eastern part of the east and southeast arms of Sulawesi are composed of tectonically intercalated marine sedimentary rocks and mafic and ultramafic igneous rocks (Sukamto, 1975; Silver *et al.*, 1978; Simandjuntak, 1990; Parkinson, 1991; Bergman *et al.*, 1996). These rocks are ophiolites inferred to represent oceanic lithosphere and overlying marine sediments accreted to Sulawesi. Dates varying between Cretaceous to Miocene have been obtained for the mafic and ultramafic rocks in eastern south Sulawesi (Yuwono *et al.*, 1987; Bergman *et al.*, 1996), although it is not clear which represent emplacement or deformation ages (Bergman *et al.*, 1996; Polvé *et al.*, 1997).

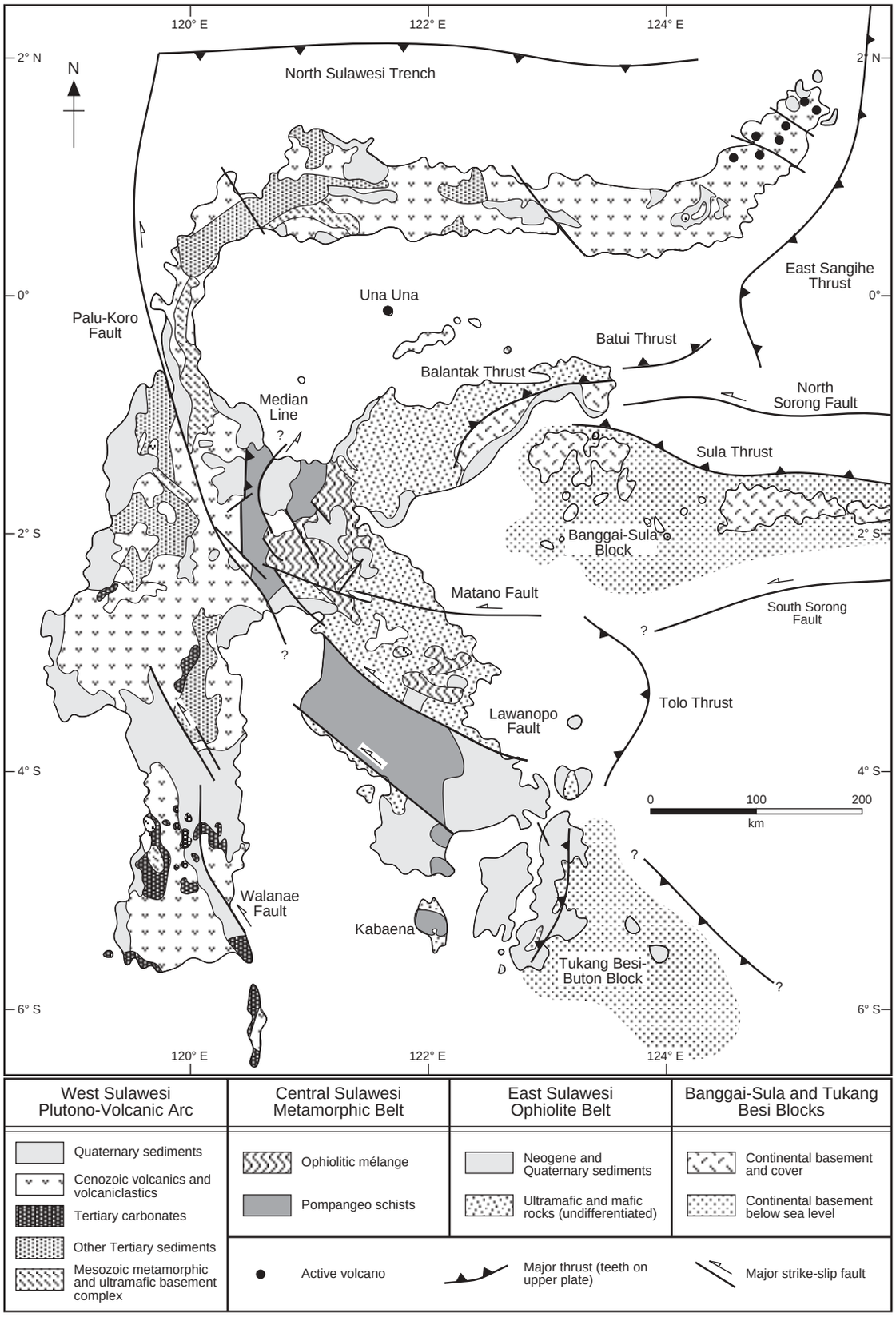

Fig.3. Simplified geological map of Sulawesi.

Central and part of southeast Sulawesi have been attached to western Sulawesi in the reconstructions. The East Sulawesi ophiolite was emplaced after the mid Oligocene. Debate on the location and origin of this oceanic crust (Parkinson, 1991; Mubroto *et al*., 1994; Monnier *et al*., 1995) need not concern biogeographers since before accretion and uplift it was situated in a deep marine setting. Palaeogene igneous lithologies in the north arm of Sulawesi may also represent part of an ophiolite sequence (Monnier *et al*., 1995), although both shallow and deep marine origins for these rocks have been inferred (Carlile *et al*., 1990).

On the islands of Buton-Tukang Besi and Banggai-Sula metamorphic and igneous lithologies of continental origin are exposed or are thought to underlie sediments of Palaeozoic and Mesozoic ages respectively. The Palaeozoic lithologies have Australian-New Guinea affinities, whereas deposition of shallow and deep marine sediments during rifting and drifting of the fragments is inferred for the Mesozoic (Audley-Charles, 1974; Hamilton, 1979; Pigram and Panggabean, 1984; Garrard *et al*., 1988) Buton is thought to have collided with eastern Sulawesi during the early (Davidson, 1991) or middle Miocene (Smith and Silver, 1991), whereas latest Miocene to early Pliocene collision with the east arm of Sulawesi is inferred for Banggai-Sula (Garrard *et al*., 1988; Davies, 1990). Fortuin *et al.* (1990) and Davidson (1991) suggested that Tukang Besi was a separate microcontinental block which was accreted to Buton in the Plio-Pleistocene, although not all authors recognise this as a separate microcontinental fragment (Smith and Silver, 1991).

Palaeogeographic maps

Eocene

During the Eocene (Figs.4 and 5) a land connection between southern Borneo and mainland SE Asia is inferred (Pupilli, 1973) which may have been present since the Jurassic (Lloyd, 1978). Little geological information is available for the Sunda Shelf, since few wells penetrate this area. A thin cover (<300 m) of Quaternary sediments is reported to overlie pre-Tertiary rocks in this area (Ben-Avraham and Emery, 1973). Although land is inferred for this area throughout much of the Tertiary, it is possible that marine sediments deposited during possible transgressions of this region may have been removed by later erosion. In the NW tip of Borneo, Maastrichtian to early Eocene fluvial/marginal marine sands were deposited within an intra-montane basin (Tate, 1991). These sediments may have been part of a larger fluvial system, fed by river systems from Indochina, supplying material to turbidites in Sarawak, Sabah and parts of Kalimantan (Fig.4) from late Cretaceous to lower Eocene times (Moss, 1998). In the early to middle Eocene deep marine turbidites in Sarawak were uplifted and deformed by the 'Sarawak orogeny' (Hutchison, 1996). Late middle Eocene shallow and deep marine sediments unconformably overlie older rocks. By the early to middle Eocene much of Borneo appears to have been emergent. Eocene (50-45 Ma) rhyolitic lavas and ash occur in three localities in Kalimantan (Heryanto *et al*., 1993; Pieters *et al*., 1993a; Suwarna *et al*., 1993; Moss *et al*., 1997).

On the reconstructions, west, central and parts of the SE arm of Sulawesi are regarded as a region of microcontinental material forming a contiguous land area during the early Paleogene. Much of mainland SE Asia, southern Borneo and western Sulawesi appears to have been emergent during the Paleocene and the early Eocene, with a distinct lack of dated sediments recorded from these periods. Geochemistry and dating of calc-alkaline rocks and interbedded sediments in eastern South Sulawesi suggests there was a volcanic arc in this area during the Paleogene (Sukamto, 1975; Leeuwen, 1981; Sukamto and Supriatna, 1982). Paleogene basic volcanics and volcaniclastic lithologies are also present in western central and northern Sulawesi, although both shallow and deep marine origins have been suggested (Trail *et al*., 1974; Carlile *et al*., 1990; Polvé *et al*., 1997).

There was widespread basin formation in middle Eocene times around the margins of Sundaland. Much of eastern Borneo, western Sulawesi, the Makassar Straits and the east Java Sea was an area of Tertiary sedimentation, in which the depositional environments varied between fluvial, deltaic, shallow marine clastic and carbonate shelves and areas of deeper water sedimentation. Evidence for Eocene extension, block-faulting and subsidence is seen on seismic lines crossing the Makassar Straits (Burollet and Salle, 1981; Situmorang, 1982; Guntoro, 1995; Bergman *et al*., 1996), and this was the time when the land connection between Borneo and Sulawesi was severed. Sea floor spreading began in the marginal oceanic basin of the Celebes Sea in the mid-Eocene (Weissel, 1980; Rangin and Silver, 1990) and may have influenced basin

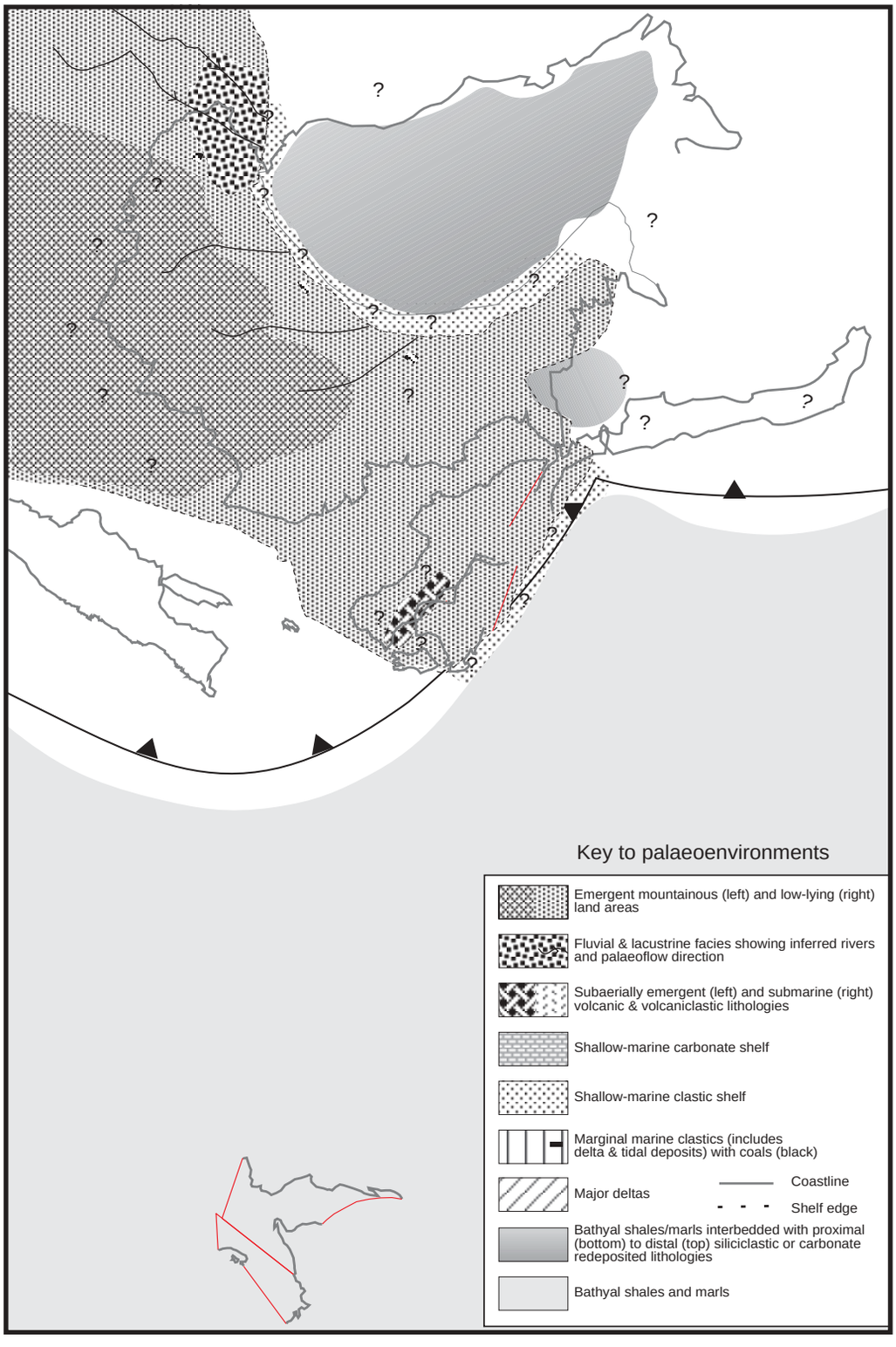

Fig.4. Palaeogeographic map for 50 Ma, early Eocene. A key to the environments is shown. Note that rivers are shown schematically for all time slices. See pages 157-164 for colour plates of Figs.4 to 9.

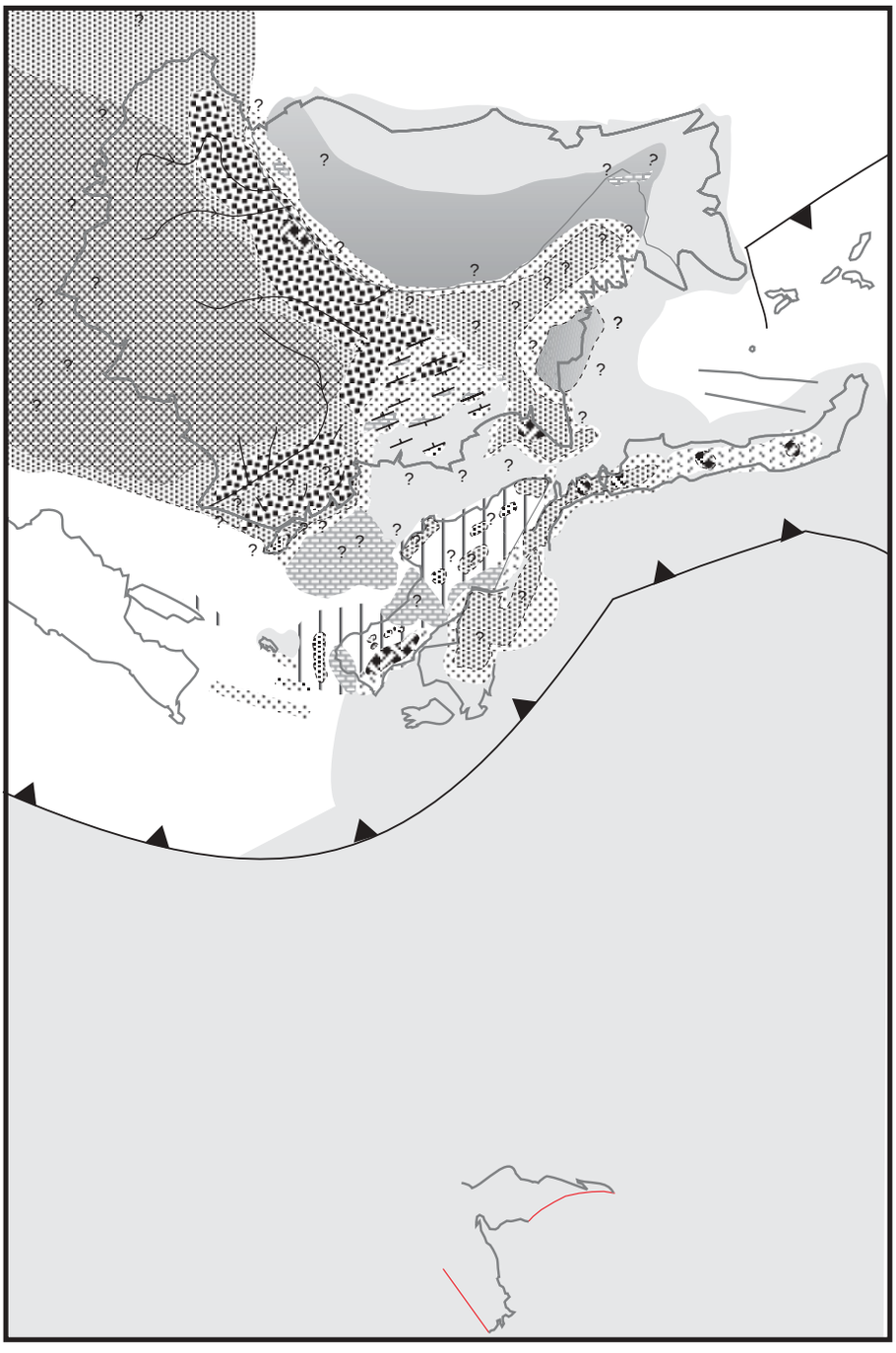

Fig.5. Palaeogeographic map for 42 Ma, middle Eocene. A key to the environments is shown in Fig.4.

initiation in Borneo and Sulawesi (Hall, 1996; Moss *et al.,* 1997). Rhyolitic volcanism, ash-falls and lava flows were partially contemporaneous with initiation of formation of the Tarakan (Netherwood and Wight, 1992) and Kutai basins (Leeuwen *et al*., 1990; Moss *et al*., 1997). Similar volcanism also occurred along the southern margin of the Mangkalihat peninsula (Sunaryo *et al*., 1988) and in the Muller Mountains (Pieters *et al*., 1993b).

In west Borneo fluvial and lacustrine sediments were deposited throughout much of the Eocene in elongate depocentres of the Melawi-Ketungau-Mandai area (Fig.2). It is in-

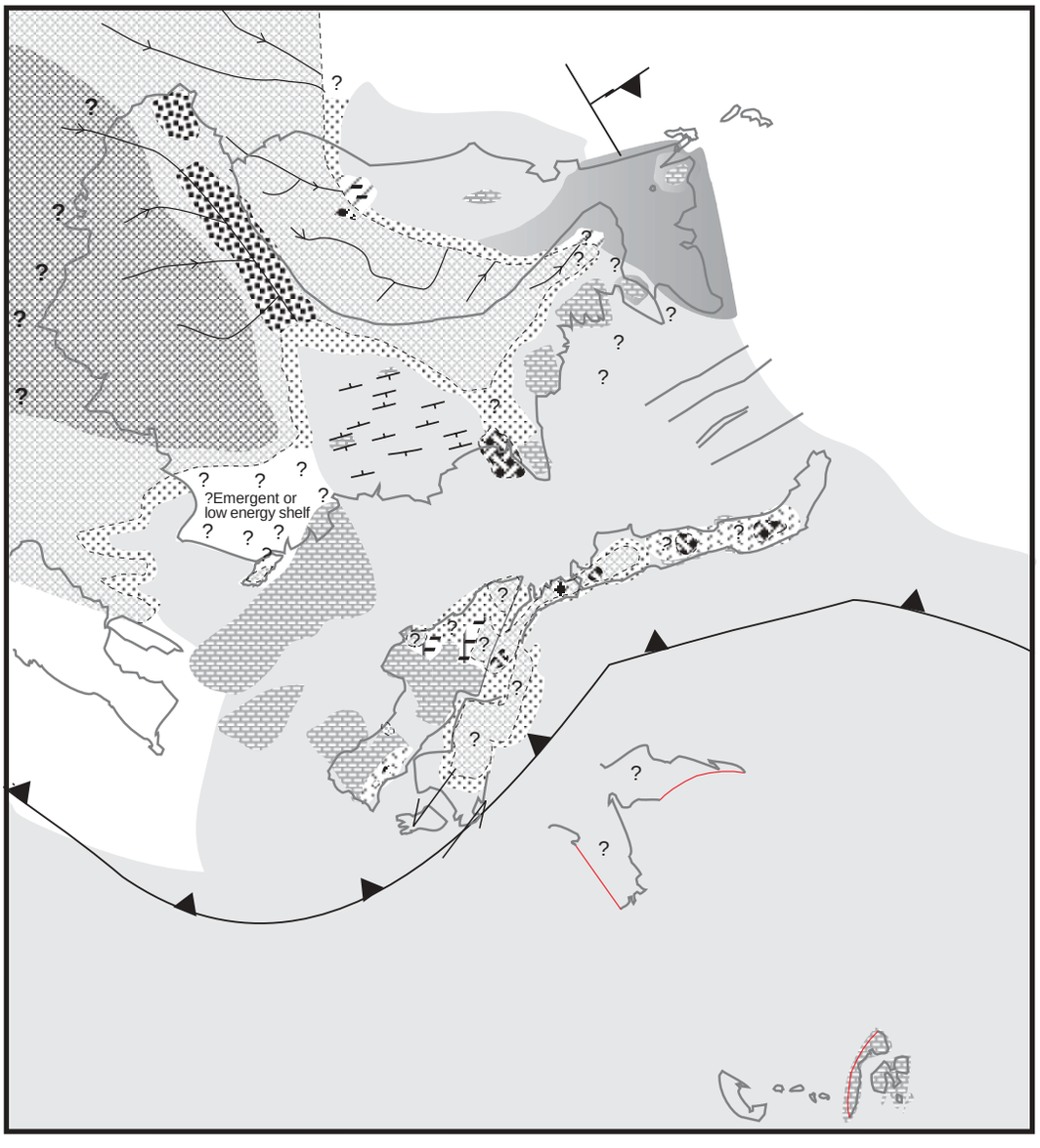

Fig.6. Palaeogeographic map for 34 Ma early Oligocene. A key to the environments is shown in Fig.4.

ferred that sediment deposited in these areas was supplied by rivers flowing from the south (Schwaner Mountains) or west (Indochina) since deep marine areas were present to the north and east. Fluvial and marginal marine sediments were also deposited in the Barito-Asem-Asem-Pasir area, although by late Eocene times shallow and deep marine clastic and carbonate sedimentation prevailed. Marginal marine lithologies with coals and intercalations of volcanic rocks occur with the Tarakan-Muara depocentres, although shallow and deeper water carbonate deposition was common by the late Eocene. By middle to late Eocene times (Moss and Finch, 1998), large parts of the Kutai depocentre and neighbouring western central Sulawesi were areas of deep, open oceanic sedimentation and this is inferred to have been the case for much of the north and south Makassar basins. Around the margins of this deep basin in the Kutai area, the northern part of the Tarakan basin and western, central and northern Sulawesi upper Eocene deltaic sands, coals and some shallow marine clastics were deposited (Kusuma and Darin, 1989; Coffield *et al.*, 1993; Moss *et al.*, 1997; Weerd and Armin, 1992). In

western south Sulawesi marginal marine clastics and coals are conformably overlain by a thick shallow marine carbonate succession (Wilson and Bosence, 1997). By late Eocene times, shallow marine carbonate sedimentation had been established over much of south Sulawesi (Wilson, 1995) and southwestern central Sulawesi (Coffield *et al*., 1993) although these areas were separated by a deep marine basinal area (Wilson and Bosence, 1996).

Oligocene

In the Oligocene (Fig.6) a land connection between Borneo and Indochina is inferred (Pupilli, 1973; Lloyd, 1978). Turbidites were deposited in Sabah in a deep marine basin. These may have been fed from major river systems of Indochina or Kalimantan. They pass laterally into shallow marine and deltaic sediments in Brunei (Tate, 1994) and at the margins of the basin in Sabah and Sarawak. There were several areas of shallow marine carbonates in this region throughout the Oligocene. During the Oligocene the Sarawak basin was progressively infilled. The west Sarawak coastline had a north-south orientation for the early Oligocene to early Miocene (Doust, 1981; Agostinelli *et al.,* 1990).

Flat-lying reflectors seen on seismic sections across much of the north and south Makassar basins suggest deep marine sedimentation occurred in a uniformly subsiding basin during the Oligocene (Situmorang, 1982; Guntoro, 1995). However, in other parts of the basin, particularly along the eastern margin of the Paternoster platform, seismic and borehole data suggests active faulting may have continued through the Oligocene and possibly into the Miocene (Situmorang, 1982; Guntoro, 1995; Wilson and Bosence, 1996). Oligocene deep marine sedimentation also occurred in much of the Kutai basin (Moss *et al*., 1997) and in some areas of western central Sulawesi. An input of volcaniclastic material is also recorded in western central Sulawesi. In the Tarakan-Muara area, the Mangkalihat peninsula, Barito basin, offshore southern Barito and in South Sulawesi extensive shallow water carbonate platforms developed or continued to accumulate sediment during the Oligocene, while deeper water marls were deposited in adjacent areas (Fig.6; Bransden and Matthews, 1992; Bishop, 1980; Armin *et al*., 1987; Netherwood and Wight, 1992; Saller *et al*., 1992, 1993; Supriatna *et al*., 1993; Weerd and Armin, 1992; Weerd *et al*., 1987; Wilson, 1995).

The mainly fluviatile west Kalimantan basin (Melawi-Ketungau-Mandai area) had begun to diminish in size or had already been infilled by the early Oligocene (Fig.6). Seismic data and fission track dating of derived apatite grains suggest that the Semitau ridge began to rise in the early Oligocene (Moss *et al*., 1997) and this uplift would have favoured erosion rather than deposition in this area. Deltaic and pro-delta environments appear in the western part of the Kutai basin toward the end of the Oligocene (Weerd and Armin, 1992; Tanean *et al*., 1996; Moss *et al*., 1997, 1998). This is thought to be related to uplift and erosion of the central ranges of Borneo at the end of the Oligocene which supplied sediment towards the Makassar Straits.

Tectonically disrupted ophiolitic rocks (Simandjuntak, 1986) comprising much of the east and SE arms of Sulawesi represent oceanic crust and overlying deep marine sediments. Metamorphic ages of 28-32 Ma obtained from at the base of the East Sulawesi ophiolite (Parkinson, 1991) suggest the ophiolites were detached in an oceanic setting at this time and emplaced later. The progressive emplacement of the ophiolitic sequence would have resulted in the development of more extensive land areas in Sulawesi.

The microcontinental blocks of Banggai-Sula, Buton and Tukang Besi, although drifting westwards towards Sulawesi, had yet to be accreted onto Sulawesi. These blocks rifted from the Australian-New Guinea continent during the late Mesozoic (Audley-Charles, 1974; Hamilton, 1979; Pigram and Panggabean, 1984; Garrard *et al*., 1988; Davidson, 1991). During the Cenozoic, some were areas of shallow marine sedimentation (Garrard *et al*., 1988; Smith and Silver, 1991; Davidson, 1991) and may have become emergent.

Miocene

During the Miocene (Figs.7 and 8) a switch in sedimentation style from extensive carbonate shelves to deltaic deposition and progradation occurred on the eastern side of Borneo, particularly in the Tarakan-Muara and Barito basins (Achmad and Samuel, 1984; Netherwood and Wight, 1992; Weerd and Armin, 1992; Siemers *et al*., 1992; Carter and Morley, 1996; Stuart *et al*., 1996). The predominance of deltaic sedimentation around the northern and eastern parts of Borneo, particularly the extremely deep Kutai

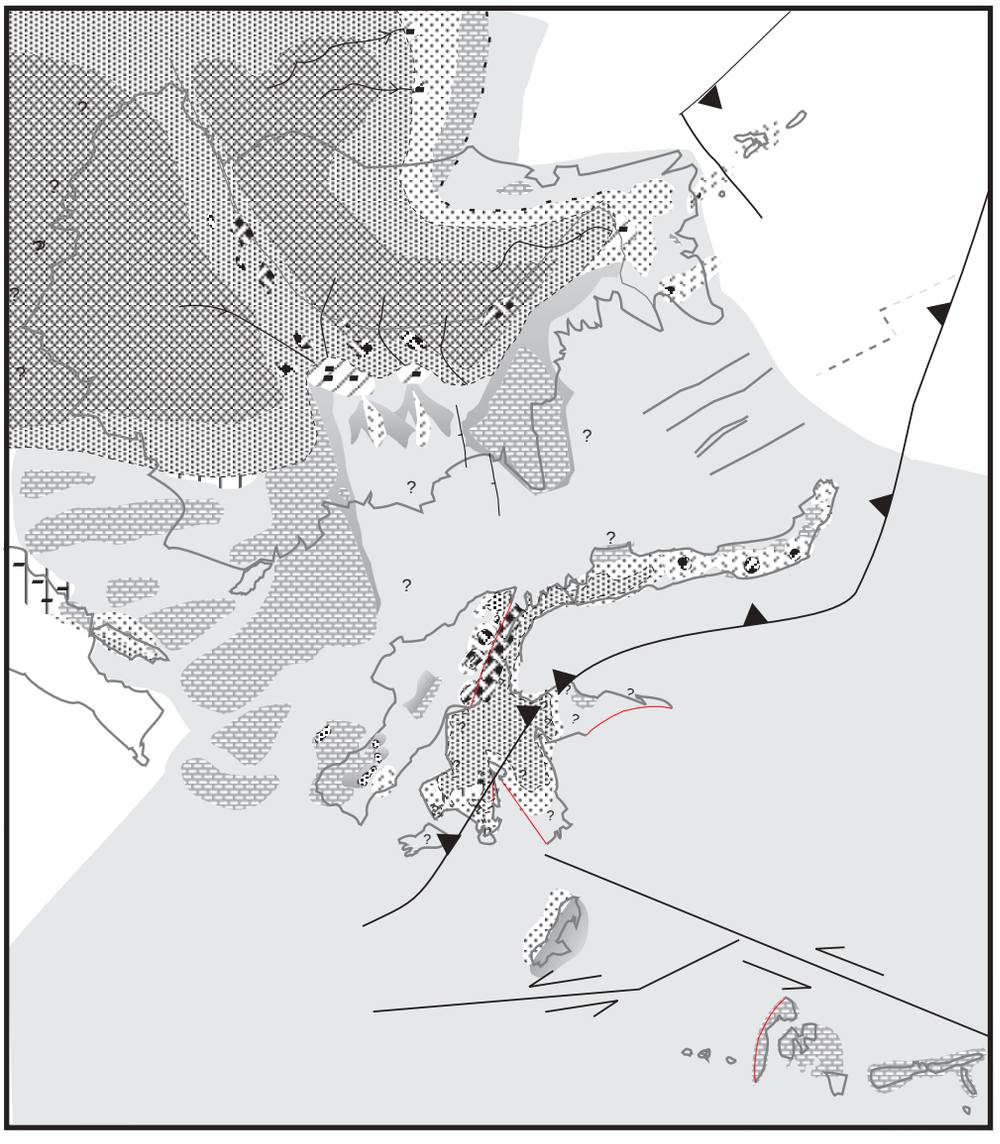

Fig.7. Palaeogeographic map for 21 Ma, early Miocene. A key to the environments is shown in Fig.4.

basin, suggests that most of the major river systems were draining into these areas. Abundant detritus was supplied from the uplift and denudation of the centre of the island and coeval volcanism (Tanean *et al.,* 1996; Moss *et al.*, 1997, 1998). By the end of the Miocene the drainage system within Borneo was similar to the present-day. The Mahakam delta had prograded to near its present-day position by the late Miocene (Addison *et al.*, 1983; Land and Jones, 1987) and siliciclastic marginal marine and deltaic deposition predominated in this area. The Makassar Straits remained a deep water basin separating Sulawesi from Kalimantan, although as the land area increased in eastern Borneo due to the progradation of deltas, the distance across this seaway was progressively reduced.

A large area of carbonate deposition developed during the middle to late Miocene in the Luconia Shoals area, which was distant from areas of coastal siliciclastic deposition in Sarawak (Doust, 1981; Agostinelli *et al.*, 1990; Rice-Oxley, 1991). By the end of the Miocene the palaeo-Baram delta had begun to prograde to the NW, and the coastline had adopted an orientation similar to its present-day NE-SW orientation (Doust, 1981; Agostinelli *et al.,* 1991). In Sabah, shallow marine to marginal marine

Fig.8. Palaeogeographic map for 8 Ma late Miocene. A key to the environments is shown in Fig.4.

sediments were deposited (Tjia *et al.*, 1990; Clennell, 1992). Volcanic arc activity occurred in the Sulu and Cagayan arcs during the Miocene (Rangin *et al.*, 1990) and this probably resulted in emergent chains of volcanic islands. During the late Miocene to the Pleistocene, basalts and trachy-andesites were extruded in central Borneo (Moss *et al.,* 1997, 1998).

Shallow marine carbonate deposition continued on high blocks in southern and western central Sulawesi until the middle Miocene, surrounded by deep marine sedimentation (Wilson, 1995). The East Sulawesi ophiolite had been accreted onto western Sulawesi, and it is inferred that land areas were emergent in central Sulawesi during at least part of the Miocene as a result of this collision. In the north arm of Sulawesi island arc basalts were erupted during the Oligocene and Miocene. They are interbedded with shallow marine carbonate deposits, and volcanic islands are inferred to have been emergent. Between the middle Miocene through to the earliest Pliocene a volcanic arc developed along the length of western Sulawesi (Yuwono *et al.*, 1987; Bergman *et al.*, 1996).

The microcontinental blocks of Banggai-Sula and Buton-Tukang Besi were accreted onto eastern Sulawesi during the Miocene or earliest Pliocene. The inferred timing of collision of the various fragments onto eastern Sulawesi varies depending on the author. On Buton, obduction of ophiolitic material and the reworking of pre-Miocene strata into clastic deposits has been related to early to middle Miocene collision with SE Sulawesi (Fortuin *et al.*, 1989; Smith and Silver, 1991; Davidson, 1991). Prior to collision, deep marine sediments were deposited on Buton, although uplift and thrusting associated with collision would have created emergent land areas in the middle Miocene. Pliocene block faulting on Buton, which created contemporaneous areas of deep and shallow marine sedimentation, may have been related to collision of Tukang Besi (Fortuin *et al.*, 1989; Davidson, 1991). Eocene to middle Miocene limestones present on Banggai-Sula indicate shallow water depositional environments, possibly locally emergent, prior to collision in the lat-

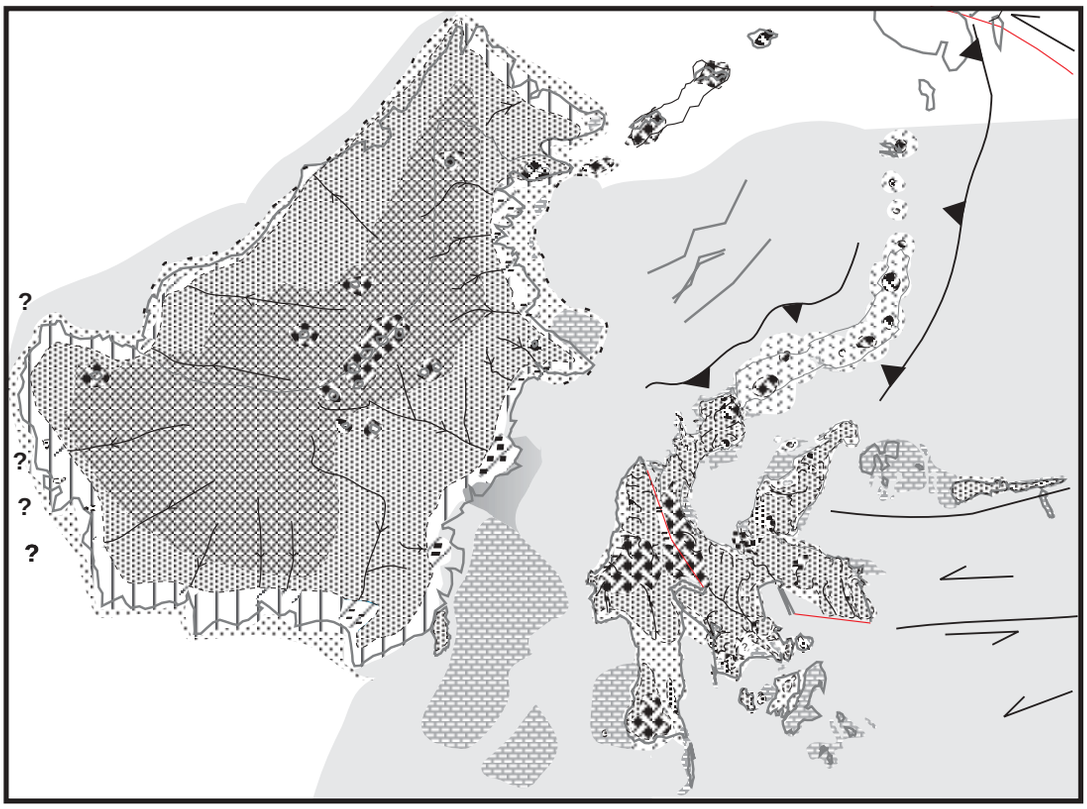

Fig.9. Palaeogeographic map for 4 Ma, early Pliocene. A key to the environments is shown in Fig.4.

est Miocene to early Pliocene (Garrard *et al.*, 1988; Davies, 1990). More extensive land areas would have formed after collision.

Pliocene-Recent

By the Pliocene (Fig.9) the coastlines of both Borneo and Sulawesi were similar to the present. Major shallow water carbonate areas persisted on the east and west sides of the Makassar Straits. The coastline of Borneo was dominated by deltaic and marginal marine depositional environments. The Mahakam river carries a large sediment volume which is deposited mainly in the delta and deltaic progradation occurred throughout the Pliocene and continues at the present day. At some point in the latest Miocene or Pliocene Borneo lost its land connection to mainland Indochina (Lloyd, 1978). Possible events responsible include reorganisation of plates, the end of a late Miocene glaciation, and/or global sea level changes in the late Miocene. The present-day Karimata Strait did not form until 7000 years ago, shown by the presence of a drowned Pleistocene river drainage system on the Sunda Shelf (Umbgrove, 1938). The Pleistocene river drainage system recognised by Umbgrove (1938) across the Sunda Shelf is related to a sea level lowstand during a glacial period.

The final juxtaposition of the fragments that comprise Sulawesi occurred between the Pliocene and the present. Although most authors infer that internal rotation and juxtaposition was achieved via a system of linked strike-slip faults and thrusts, the linkage and displacements along faults is still contentious. The Pliocene reconstruction shown is based on matching palaeoenvironments and assuming reasonable strike-slip displacements along major faults and some internal deformation of blocks within Sulawesi. Collisions and subduction east of Sulawesi caused transpression during the Neogene and Quaternary which resulted in uplift of extensive areas in Sulawesi and caused rapid uplift of a number of high mountain areas, particularly in central Sulawesi (Bergman *et al.*, 1996). The transpressive regime also resulted in extension and subsidence in other areas. Bone

Bay separates the south and SE arms of Sulawesi is suggested to have developed as an extensional feature in the late Oligocene (Davies, 1992). Seismic data suggests that the form of Bone Bay was then further modified during the Miocene/Pliocene by transpressive and transtensional movements (Davies, 1992; Guntoro, 1995). The nature of Quaternary sediments and historic legends suggest that until quite recently a seaway separated the south arm from the rest of Sulawesi (Bemmelen, 1949; Sartono, 1982).

Igneous activity continued in western Sulawesi until the Pliocene and Pleistocene and is similar in nature to the late Miocene volcanics in the same area (Yuwono *et al*., 1987; Bergman *et al*., 1996). Along the north arm of Sulawesi, Miocene to Pliocene volcanism is related to south-dipping subduction of the Celebes Sea oceanic crust under the north arm of Sulawesi (Carlile *et al*., 1990). A string of active Quaternary to Recent volcanoes dominate the Sangihe Islands and the eastern part of the Minahasa region, and are related to west-dipping subduction under this area.

Implications for palaeobiogeography and biogeography

Important elements of the palaeogeographic reconstructions for biogeographers are the extent of land areas and island chains, the timing and nature of material accreted onto the margin of the Sundaland craton and the distribution of different environments through time and space. The reconstructions show that the spatial and temporal distribution of land areas and habitats differed considerably during the Tertiary from those seen today in the Sulawesi-Borneo area.

Land migration of terrestrial organisms between Borneo, mainland SE Asia and some of the Sunda Islands, such as Sumatra, would have been possible throughout much of the Tertiary, since at least a transitory land connection is inferred to have existed between these areas until the Plio/Pleistocene. The marked similarity between the flora and fauna of Borneo and mainland SE Asia can be accounted for by the existence of this land bridge during the Tertiary. As noted earlier there is little information on the geology of the Sunda Shelf and evidence for marine incursions, perhaps associated with Cenozoic global sea level changes (Haq *et al.,* 1987; 1988), may have been overlooked or removed by later erosion.

The Paleogene formation of the Makassar Straits, at a period when other basins were forming around the margins of the Sundaland craton, was one of the most important geological events to affect the biogeography of Borneo and Sulawesi. Western Sulawesi was accreted to eastern Borneo in the late Cretaceous, forming a continuous land area probably during part of the Paleocene and the early Eocene. During this period, prior to the formation of the Makassar Straits, the interchange of terrestrial biota between Borneo and western Sulawesi could have occurred unhindered across a continuous land bridge. However, the actual movement of organisms would have depended on habitat availability and dispersal rates of organisms across a land bridge which may have existed for as little as ten million years. Palynological evidence from the middle to upper Eocene Malawa Formation in South Sulawesi suggests that diverse angiosperms with Laurasian affinity were established in South Sulawesi prior to the rifting of the Makassar Straits (Morley, 1998 this volume). Distribution patterns and fossil evidence for some groups of plants (Truswell *et al*., 1987), such as some of the palms, the families of Magnoliaceae/Winteraceae and the genera *Fagus*/*Nothofagus*, have been used to infer various dispersal pathways via northern and austral routes after the breakup of Gondwana, with an ancient Gondwana origin being implicit (Dransfield, 1981; Whitmore, 1981b).

Subsidence resulting in the formation of the Makassar Straits and surrounding Tertiary basinal areas would have progressively increased the spatial separation of emergent land areas in Borneo and western Sulawesi from the Eocene to the Oligocene. Extensive shallow water carbonate platforms developed in South Sulawesi, SE Kalimantan and the Mangkalihat peninsula during the Tertiary. Although it is possible that small areas of these platforms were emergent, subsidence rates in the region were quite high and that any such islands would have been limited in size and only emergent for short periods of time.

Palaeogeographic information indicates that there were only small land areas in western Sulawesi between the middle Eocene and middle Miocene, and that for the most part western Sulawesi was isolated from major clastic input. However, a volcanic arc, part of which may have been emergent, is inferred to have extended down the east side of western Sulawesi into southern Java. The formation of the Makassar Straits and resultant isolation of local-

ised, small land areas in western Sulawesi goes some way towards explaining the affinities at generic and higher level of Sulawesi's terrestrial biota with those of Borneo and mainland SE Asia, and the high degree of endemism amongst Sulawesi's fauna and flora at species level (Musser, 1987; Holloway, 1987). Musser (1987) noted that the non-volant mammals of Sulawesi have ancient origins and that because the fauna is an unbalanced, depauperate one (40% of species are bats) typical of oceanic islands, origin is believed to have been across sea.

Rivers supplying clastic material derived from the erosion of the central part of Borneo beginning in the Oligocene resulted in the progradation of large delta systems into northern and eastern Borneo. Sedimentation in the Kutai basin and Makassar Straits progressively reduced the distance between Borneo and Sulawesi to the present 200 km across the Makassar Straits. A compressive regime, which developed in the area in the middle to late Miocene and continues to the present day, resulted in uplift or reduced subsidence rates in the Makassar Straits region compared with the Paleogene. Eustatic sea level changes, with magnitudes of tens of metres, related to fluctuations in the size of the polar ice sheets have been recorded during the Plio-Pleistocene. This, together with the compressive regime, suggests that part of the shallow water areas separating Borneo and Sulawesi may have become emergent during the later part of the Neogene with only a narrow seaway remaining where deep water channels now occur. If such a situation developed, and assuming favourable conditions occurred, migration of terrestrial organisms would have been facilitated, particularly during the Plio-Pleistocene, whereas the migration of marine organisms may have been hindered. On the basis of palynological data Morley (1998 this volume) suggested that during the Neogene only a few plant taxa were able to disperse across the Makassar Straits, and it is likely that those that did were well adapted to dispersal.

A number of authors (Duffels, 1990; Musser, 1987; Balgooy, 1987) have noted that the flora and fauna of the south arm of Sulawesi is different from the rest of Sulawesi. For much of the Tertiary South Sulawesi was below sea level and it was probably only in the Pliocene when island areas in South Sulawesi became connected with those in central Sulawesi. Giant tortoise, elephant, stegodont and pig fossils have been found in Pleistocene deposits in South Sulawesi, but not in the rest of Sulawesi. It is not clear whether these animals were restricted to South Sulawesi (Musser, 1987) and only migrated into the area during the later part of the Neogene during periods of low sea level and emergence of more extensive land areas bordering a narrow seaway in the Makassar Straits. Today South Sulawesi has a dry climate compared with other areas in Sulawesi, and there are mostly limestones or volcanic rocks in this area. The climate and soil type, as well as palaeobiogeographic separation of this area, would all have influenced the flora and therefore to some degree the fauna of this area (Balgooy, 1987).

Volcanic arcs were important as potential land bridges and island hopping routes for organisms during the Tertiary. They are inferred to have existed along the north arm of Sulawesi and the eastern side of west Sulawesi, perhaps extending down through Java from the Eocene until the late Oligocene. During the Neogene a volcanic arc occurred along the north arm of Sulawesi and possible island chain connections may have existed to the Philippines. During the Miocene, the Sulu and Cagayan volcanic island chain may have formed an island hopping route for organisms between the northeast tip of Borneo and parts of the Philippines.

The nature and timing of material accreted onto western Sulawesi is of considerable importance for potential migrations of terrestrial organisms with Australian affinities. The East Sulawesi ophiolite, which now comprises much of the east and southeast arms of Sulawesi, formed in a deep marine area and this area would not have been subaerially emergent until its accretion onto western Sulawesi. Therefore the East Sulawesi ophiolite could not have formed a potential 'raft' for the dispersal of terrestrial organisms.

In comparison, parts of the microcontinental fragments which make up the Banggai-Sula and Buton-Tukang Besi islands, which were accreted onto eastern Sulawesi in the Miocene or Pliocene would have been islands or shallow water areas during their drift towards Sulawesi during the Tertiary. These microcontinental blocks were rifted from the margins of the Australian-New Guinea continent in the late Mesozoic, and land bridges would have been severed at this time. The stratigraphy of these microcontinental blocks indicates that the blocks subsided and became areas of deep marine sedimentation from the late Jurassic to Cretaceous. Therefore, although parts of these areas became emergent in the Tertiary, Australian affinity fauna and flora could not have been

'rafted' on these microcontinental blocks. However, during the Tertiary, the Australian continent drifted steadily northwards and some microcontinental blocks between the Australian and Sundaland cratons became emergent as islands. These blocks, some of which were accreted onto Sulawesi in the Miocene or Pliocene, may then have rafted or acted as an island hopping routes for Australian organisms, such as some of the marsupials, to colonise Sulawesi. Palms have a large fruit, suggesting long-distance dispersal might be limited and Dransfield (1981, 1987) noted that the disjunction of Papuasian and Sundaland palms occurred between Sulawesi and the Moluccas, consistent with relatively recent (Miocene) juxtaposition. Another possible island hopping route for Australian fauna to reach Sulawesi may have been via the Philippines and along the Sangihe volcanic arc. Palaeomagnetic evidence suggests that India rifted away from the Gondwanaland supercontinent at about 140 Ma, whereas Australia-New Guinea separated from Antarctica between 110-90 Ma. It may be possible that organisms, particularly some of the flora, which had evolved prior to these two separation events, were present in both India and Australia, and that after the interaction of these areas with the Sundaland craton that migrations could have occurred from both east and west into the Malay archipelago.

The wind and current direction as well as the distribution of land masses and their local climates during the Tertiary would have affected the distribution and migration of both terrestrial and marine biota. Although, in general, Borneo has a wetter climate than Sulawesi, both have tropical monsoonal climates and are affected by winds from the east and west at opposing times of the year, depending on when low and high pressure zones develop over the adjacent continental land masses of Australia and mainland SE Asia. These strong monsoonal winds would help to distribute wind blown biota east-west between some of the closer islands in the archipelago today. Although it is difficult to infer past wind directions and strengths, it would seem likely that during the Tertiary, since the Australian land mass was further to the south, the effects of one of the monsoons would have been less than today (Whitmore, 1981a). There is a growing amount of evidence that Indonesia, and particularly Borneo (from the pollen record), was more strongly seasonal during the late Tertiary and middle Pleistocene than today (Whitmore, 1981a; Morley and Flenley, 1987). This would have favoured the migration of savannah plants and animals across the area between mainland SE Asia, Borneo and other islands on the Sunda Shelf (Morley and Flenley, 1987). Cooler conditions during glacial periods and lowered sea levels exposing more land areas (Whitmore, 1981) in the late Tertiary and Quaternary would have encouraged animals to move southwards over land bridges to Borneo. Also during glacial maxima, montane vegetation zones would have been lower (Hope, 1996) providing 'stepping stones' for the migration of montane and temperate taxa (Whitmore, 1981a; Morley and Flenley, 1987).

Today the current directions and strengths around Borneo and Sulawesi vary depending on the prevailing wind directions. Surface currents in the East Java Sea flow predominantly east or west at opposing times of year, whilst those in the Makassar Straits are predominantly south directed and around the rest of the Sulawesi coastline more variable. The deep water channels in the Makassar Straits form a pathway for waters from the Celebes Sea, through the East Java Sea to the Indian Ocean, principally through the Lombok Straits. During the Tertiary, the land areas of Borneo and Sulawesi would have been smaller than today and currents would have been less constrained, but still controlled by prevailing wind directions. The dispersal of marine organisms, especially those with a planktonic larval stage, such as corals or molluscs, would have been unhindered throughout the Tertiary and partly controlled by prevailing wind and current directions and the availability and spacing of suitable habits. Whitmore (1981a) noted that sea level fluctuations would alter current patterns in the region and thereby affect climates, with periods of more seasonal climates occurring during glacial periods when sea levels were lowered.

Conclusions

Borneo and Sulawesi, bordering Wallace's original line of faunal divide, are of prime importance to biogeographers, since these islands occur at the 'mixing zone' or area of overlap between Asian and Australian biota. Borneo and Sulawesi are located in the midst of a convergent zone of three major plates, and the tectonic evolution of the area, together with the climate and local factors, strongly influenced the past and present day distribution of fauna and flora.

The main palaeogeographic changes in the

Borneo-Sulawesi region and their implications for biogeography are:

1. A continuous land connection between Borneo and mainland SE Asia may have existed throughout much of the Tertiary and would have allowed fairly unhindered migration of terrestrial biota.
2. Western Sulawesi had been accreted to eastern Borneo by the late Cretaceous, and by the early Eocene there were continuous land areas in the Schwaner Mountains, NW Kalimantan, the Mangkalihat peninsula and parts of western Sulawesi. The dispersal of certain flora and fauna between Borneo and western Sulawesi could have occurred at this time.
3. Extension in the Makassar Straits region and the formation of surrounding Tertiary basinal areas in the Paleogene resulted in the progressive separation of locally emergent land or volcanic areas in western Sulawesi and Borneo, and this isolation may have contributed to the high degree of species endemism on Sulawesi.
4. The East Sulawesi ophiolite was accreted onto Sulawesi during or after the late Oligocene and resulted in the formation of more extensive land areas in Sulawesi. Since the ophiolite formed in a deep marine setting it would not have acted as a potential raft for biota.
5. Microcontinental fragments accreted onto eastern Sulawesi in the Miocene to Pleistocene may have been emergent as they drifted towards Sulawesi and allowed island hopping or rafting for biota of Australian affinity.
6. Island hopping routes for the dispersal of organisms between Borneo-Sulawesi and the Philippines may have existed along volcanic arcs, such as the long-lived North Sulawesi arc, the Sulu and Sangihe arcs, and the Cagayan arc.
7. The uplift and subsequent erosion of Borneo since the late Oligocene and the emergence of more extensive land areas in Sulawesi led to the progressive reduction in width of the Makassar Straits. This may have facilitated the interchange of biota during the later part of the Tertiary, particularly during periods of relative sea level lows when large areas of shallow marine shelves may have become emergent.
8. Although Borneo and western Sulawesi remained in near tropical latitudes throughout the Tertiary, the wide variety of micro-environments shown by the palaeogeographic maps would have led to niche partitioning. This partially explains the higher number of endemic species in Borneo compared with Sumatra, which otherwise does show a marked similarity in fauna and flora with Borneo.

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