

Pre-glacial Bornean primate impoverishment and Wallace's line

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Abstract

Leaf monkeys (*Semnopithecus*, subgenus *Trachypithecus*) and lorises (*Loris* and *Nycticebus*) are both geographically disjunct between southern India and SE Asia, with endemic representatives in eastern Indochina. These parallels appear to result from restriction to, and re-expansion from, rainforest glacial refugia in southern India, northeast Indochina and west Java. Sureli (*Presbytis*) and gibbon (*Hylobates*) distributions reveal further refugia in north Borneo, north Sumatra and the Mentawai Islands. Modern Sumatran primate distribution was moulded by at least two cold dry glacial periods. The earlier one 190,000 years ago eliminated all Sumatran primate habitats whereas, after recolonization, the later one 80,000 years ago left a north Sumatran rainforest refugium. Not only did the Mentawai Islands provide a reservoir for the recolonization of Sumatra, but indirectly for an interglacial invasion of Borneo which, like Sulawesi, had previously been outside the range of *Presbytis* and gibbons. Bornean primate zoogeography indicates that before the first arid period there may have been fewer than four primate species on Borneo. Most of the present twelve or thirteen Bornean primate species rafted there interglacially or post-glacially from Sumatra. Pre-glacial Bornean primate impoverishment is primarily attributed to a suspected south coastal dry zone which would have inhibited or precluded colonization. Colonization of islands further east must generally have bypassed Borneo via Java or the Philippines. The Bornean climatic barrier presented a more severe impediment to faunal exchange across Wallace's line than did the sea depth along its course. Such climatic barriers, whose influences waxed and waned with the glacial cycles, would have affected most SE Asian islands and were the prime inhibitor of faunal and floral exchange between the Oriental and the Australasian regions.

Introduction

SE Asia has a rich primate fauna, comprising orang-utans (*Pongo*), gibbons (*Hylobates*), colo-

bine monkeys (*Nasalis*, *Pygathrix*, *Presbytis* and *Semnopithecus*, subgenus *Trachypithecus*), macaques (*Macaca*), loris (*Nycticebus*) and tarsiers (*Tarsius*). Twelve (or thirteen if the presence of *Hylobates agilis* is accepted) primate species occur on the island of Borneo. And yet, despite the presence of suitable habitats, only the macaques on Sulawesi and the Lesser Sunda Islands and, to a much lesser extent, the leaf monkeys on Lombok (purportedly by human introduction), have crossed Wallace's line.

The effectiveness as a faunal barrier of this most widely-adopted division of the Oriental from the Australasian zoogeographic region, is generally attributed to the depth of the sea channel extending from the Bali-Lombok Strait, between Borneo and Sulawesi, to the east of the Philippines. The deep Makassar Strait remained a sea barrier when the Sunda and Sahul shelves were exposed during glacial sea-level depressions. Huxley's line coincides approximately with the eastern edge of the Sunda shelf, and Lydekker's line with the western edge of the Sahul shelf. These later variations on the division have been regarded as clear-cut faunal boundaries enclosing a transitional zone.

However, major recolonization of the volcanic Krakatau archipelago, 12 km away from the next nearest island, has occurred in only a matter of decades (Smith, 1943; Thornton, 1996). No convincing explanation has been offered as to how a sea barrier such as the Bali-Lombok Strait, little more than three times as wide, could have inhibited colonization for millennia. Floating islands capable of transporting a

viable sample of flora and fauna have been reliably reported. Even if these crossed a strait only once a century, their impact on floral and faunal exchange between the two land masses would have been significant. Conditions favouring such rafting would have been enhanced during periods of climatic change (see the discussion below).

The inference (Brandon-Jones, 1996a) that during the glaciations Asian rainforest was reduced by drought to a few scattered pockets of distribution provides a more plausible explanation for these biogeographic barriers. Not only could rainforest communities on such islands as the Philippines and Sulawesi, have been entirely eliminated, leaving only severely degraded forest or no forest at all, but the recession of rainforest from some coastal areas, would have seriously impaired the ability of rainforest to disperse by rafting. Contraction and expansion of rainforest distribution has been the prime mediator of present primate species diversity on Borneo (Brandon-Jones, 1996b), in sharp contrast to the probable presence there, demonstrated in this paper, of only two primate species before the penultimate glaciation. If such a faunal turnover can be established for Borneo, seemingly in the heart of the Asian moist rainforest, extending such analysis to other Indo-Pacific islands should produce further insights into the effects of climate change on floral and faunal migration and diversity.

Glacial effects on Asian primate distribution

Both the pied leaf monkeys (*Semnopithecus auratus*, *S. francoisi*, *S. batinbensis*, *S. laotum*, *S. delacouri* and *S. johnii*) of Java (Indonesia), northeast Indochina and southern India (Brandon-Jones, 1995), and the grizzled surelis (*Presbytis comata*) of Java, north Sumatra and north Borneo (Brandon-Jones, 1993, 1996a, b) display a tripartite disjunction. Brandon-Jones (1996a) inferred that the once continuous sub-continental Indian, Chinese and SE Asian rainforest was fragmented by a glacial drought 190,000 years ago. It subsequently re-expanded, although probably not to its former extent, only to contract again during a second, less severe drought 80,000 years ago. Asian colobine monkey zoogeography suggests that these droughts eliminated all but a few small pockets of rainforest. Such rainforest refugia survived in north Sumatra, the Mentawai Islands (off west Sumatra), north Borneo, west Java, northeast

Indochina and southern India (Brandon-Jones, 1993, 1995, 1996a, b, 1997). Some of these refugia are located at one thousand metres or more in altitude, but most are areas which would have remained sea-bound, either as promontories or islands, or are coastal areas which retained a maritime climate during desiccative glacial sea-level depressions.

The dual contraction and re-expansion of the rainforest led to the fracturing of the distribution of the pied leaf monkeys from continuity between Java, northeast Indochina and southern India, to survival in those areas alone (Fig.1; Brandon-Jones, 1995). The prosimian loris has a parallel distribution, with an endemic representative, *Nycticebus pygmaeus*, in eastern Indochina (Fig.2). This suggests a similar history of disjunction and partial recolonization. In both cases recolonization has been northward, undoubtedly from Java in the case of the leaf monkeys, and probably so in the case of the loris. Gibbon (*Hylobates*) distribution is similar, but without an outlying population in southern India. Recolonization has been extensive but incomplete. At least four primate genera (*Hylobates*, *Presbytis*, *Semnopithecus* and *Macaca*) have added Borneo to their pre-glacial distribution, but others (*Pongo*, *Nasalis* and *Pygathrix*) have undergone little or no post-glacial dispersal.

The Mentawai archipelago is the key to interpreting the biogeography of Sumatra and Borneo. Ancestors of its endemic primates (*Hylobates klossii*, *Nasalis concolor*, *Presbytis potenziანი* and *Macaca pagensis*) must formerly have existed on Sumatra, but no longer occur there. The ebony leaf monkey (*Semnopithecus auratus*) can only have reached Java by way of Sumatra, from which it is also now absent. *Presbytis potenziანი* is sister-taxon to *P. comata* of north Sumatra, north Borneo and west Java (Brandon-Jones, 1993). An ancestral taxon similar to *P. potenziანი* is presumed to have been the initial coloniser of SE Asia. *Hylobates klossii* and the gibbons of Java and (with some variation) north Borneo, are chromatically monomorphic, unlike those of the Malay peninsula and Sumatra. *H. 'lar' vestitus* of north Sumatra is replaced in southern Sumatra by the polymorphic *H. agilis*. The call of the south Bornean gibbon (whose specific allocation, like that of *H. 'lar' vestitus*, remains debatable) is virtually identical to that of *H. agilis* (Geissmann, 1995). This indicates a geographic relationship between the Mentawai Islands gibbon and other gibbons analogous to that between *P. potenziანი* and *P. comata*. *H. klossii* today is suggested to be mor-

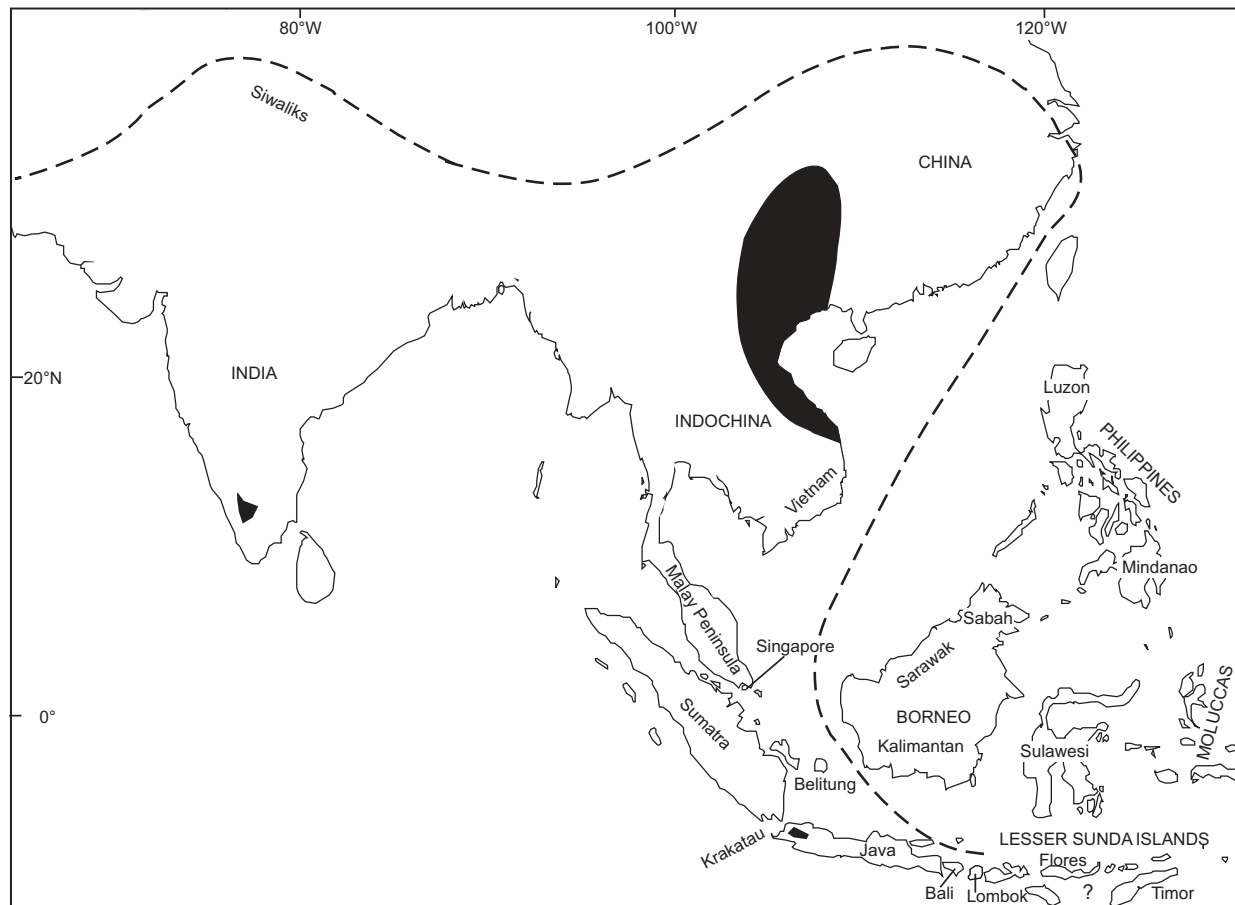


Fig. 1. The glacial refugial distribution of the pied leaf monkeys (*Semnopithecus auratus*, *S. francoisi*, *S. batinbensis*, *S. laotum*, *S. delacouri* and *S. johnii*) after deforestation 190,000 years ago, with an estimate (dashed line) of their distribution before that date.

phologically conservative, descended directly from the Mentawai progenitor of most, if not all other extant gibbons, except for the concolor gibbons and the siamang. Brandon-Jones (1993, 1996a) inferred that all Sumatran primates (and Sumatran primate habitats) disappeared during the earlier glacial drought, persisting only on the Mentawai Islands, whose maritime climate protected it from the desiccating effect of the glacial emergence of the Sunda shelf.

During the interglacial, *Presbytis comata* diverged from *P. potenziani*, and *Hylobates lar* vestitus, *H. muelleri* and *H. moloch* diverged from *H. klossii*, as moist rainforest recolonisation of Sumatra, Java and southern Borneo facilitated dispersal from the Mentawai Islands. *Pongo* reinvaded Sumatra, probably from Borneo, but possibly from Indochina. During the later, and lesser drought, rainforest area contracted less than during the previous dry period, enabling these recolonisers to survive in north Sumatra,

north Borneo and west Java. The absence of *Nasalis*, and of endemic subspecies of *Semnopithecus* and *Macaca* in the Sumatran refugium, which sustained the more moist rainforest-associated *Pongo*, *Hylobates* and *Presbytis*, indicates that two deforestations occurred. After the second dry period, independent evolution of brownish species occurred on Sumatra (*P. femoralis*), Borneo (*P. frontata*) and Java (*P. fredericae*) from the populations of *Presbytis comata* within those islands. *P. femoralis* dispersed to Borneo. Two reddish species, the Sumatran *P. melalophos*, and the Bornean *P. rubicunda* are the end-products of chromatic successions from black, through grey, then brown to red, and in some cases to albinistic, which characterise colobine post-glacial dispersal (Brandon-Jones, 1996b). Each stage in the succession was probably correlated with a phase of rainforest regeneration. This suggests that climatic remission was punctuated, rather

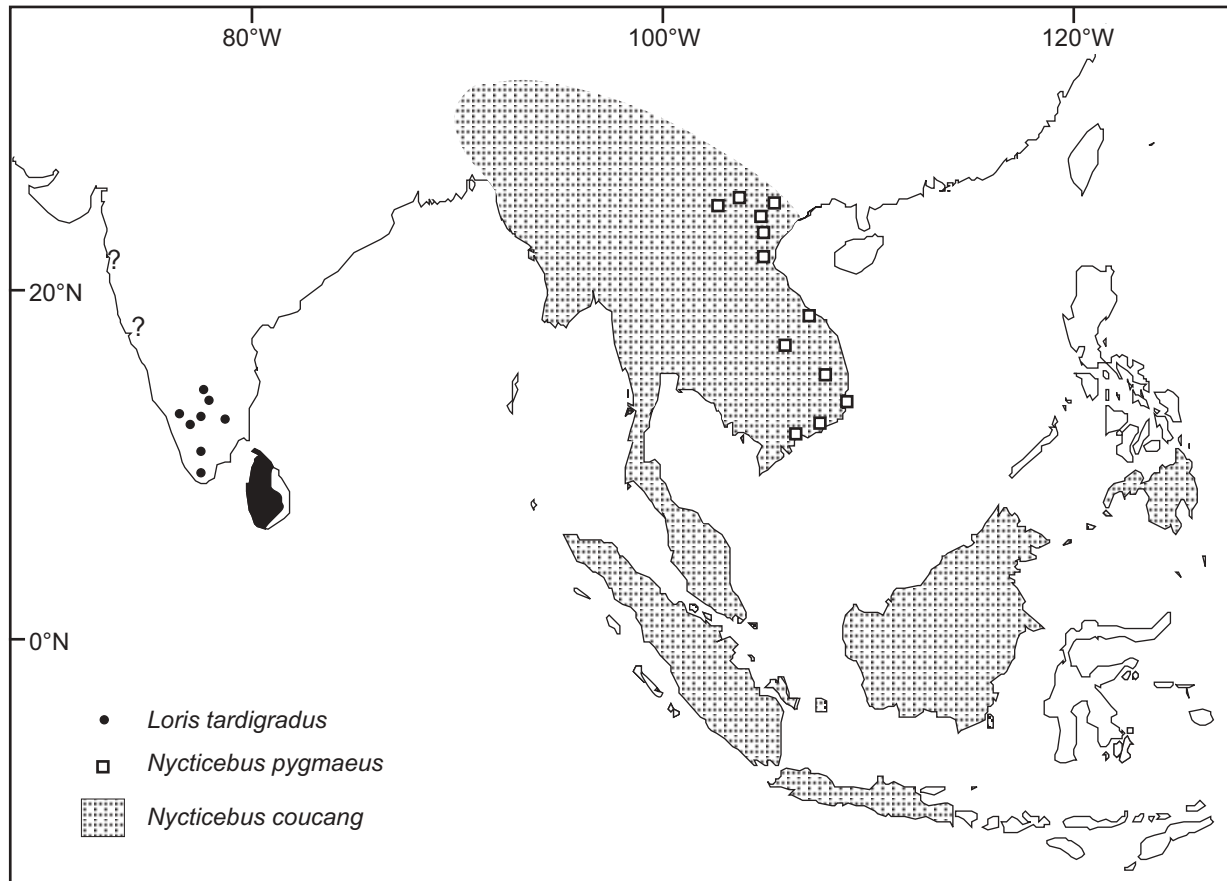


Fig.2. The geographic distribution of the lorises (*Loris* and *Nycticebus*).

than continuous.

The endemic Mentawai Islands macaque, *Macaca pagensis*, is closely related to the pigtailed macaque, *M. nemestrina*. Externally however, the population on Siberut (the northernmost Mentawai island) is more similar to other members of its species group, such as the lion-tailed macaque, *M. silenus*, isolated in southern India, and the Sulawesi macaque, *M. tonkeana*. These Siberut, Sulawesi and south Indian macaques probably also have a glacially-fragmented distribution (Fig.3; Brandon-Jones, 1998). The distribution of *Macaca nemestrina* dwindles to a narrow corridor as it enters Meghalaya, India (Fooden, 1975; Biswas and Diengdoh, 1978), indicating it is a northward-dispersing species, yet to colonize Java and north Vietnam. The northern subspecies is paler in pelage colour which, by Hershkovitz's (1968) principles of metachromism, supports this interpretation. Although it had an earlier common ancestor with the Sulawesi species, its most recent common ancestor was probably

with the macaque of the two southernmost Mentawai islands.

Dating the deforestations

The silvered leaf monkey, *Semnopithecus cristatus* has reached islands such as Belitung and Serasan, and the long-tailed macaque, *Macaca fascicularis* many more. Their failure to colonize the Mentawai Islands seems to reflect a shortage of time rather than ability, and indicates that their geographic radiations occurred recently. *S. auratus* (a close relative of *S. cristatus*) evidently did not spread from Java between the two arid periods, suggesting this interval was short. *S. cristatus*, *Macaca fascicularis* and *M. nemestrina* are unrepresented by endemic taxa in the north Bornean refugium and thus appear to have been absent from Borneo until after the second arid period. Subfossil evidence from Niah Cave in northwest Borneo indicates the presence there of *Macaca*

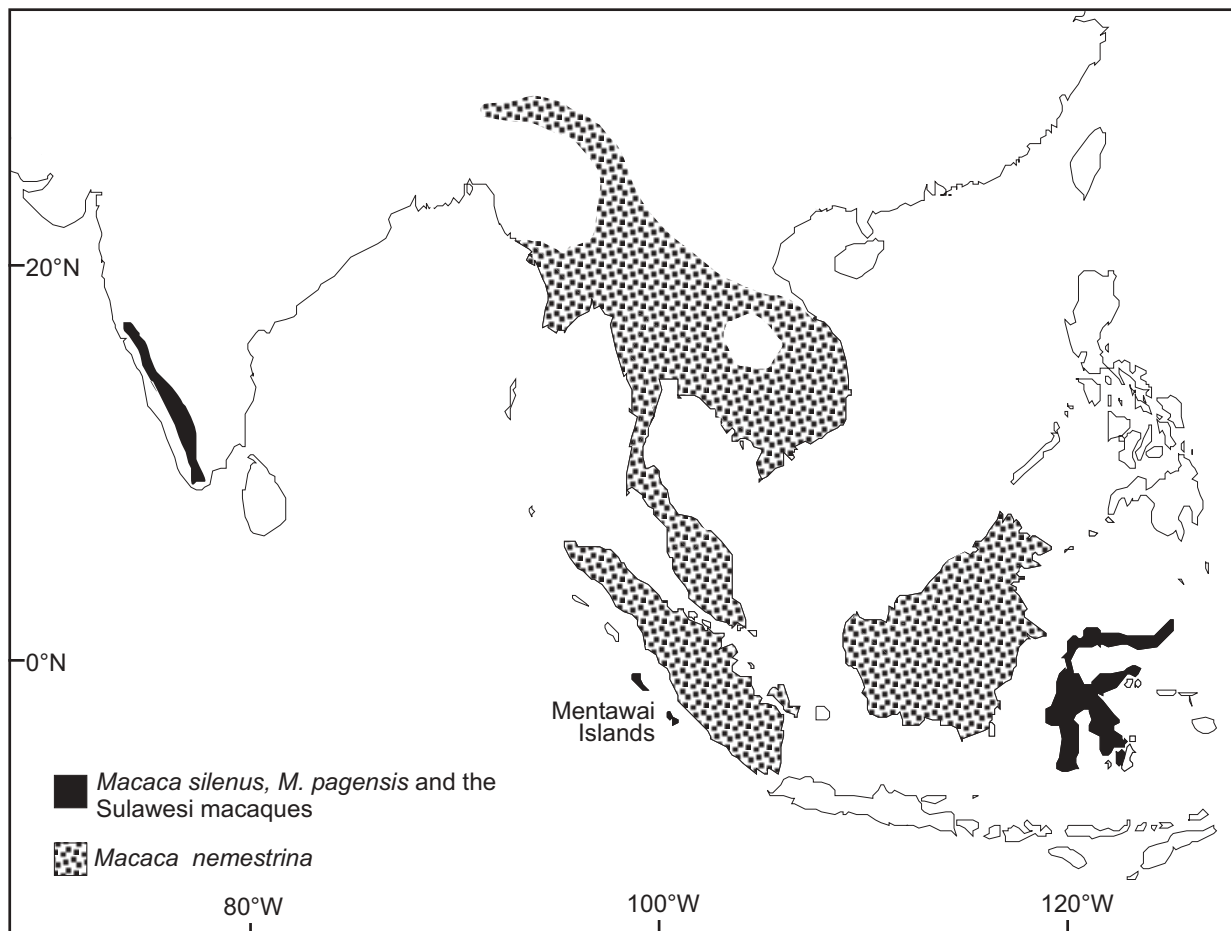


Fig.3. The geographic distribution of the *Macaca silenus* species group.

before the most recent glacial maximum (Brandon-Jones, 1996a). The two most recent glacial maxima at about 135,000 and 21-22,000 years ago, are indistinguishable in severity. Instead, they were preceded by a fluctuating, but persistent, temperature decline and succeeded by a rapid temperature increase. Neither of the two most recent glaciations included a cold period preceded by a significantly colder one (Martinson *et al.*, 1987). The more abrupt onset of the earlier glaciation seems the only relevant difference between the two glaciations. At the end of each interglacial, precipitation or temperature seems to have suddenly dropped below a critical threshold for widespread forest maintenance, and this threshold was not re-attained until the beginning of the subsequent interglacial. In the penultimate glaciation, this threshold was broken more abruptly, and the succeeding interstadials offered little remission. The deforestations appear to have occurred

quite rapidly as the interglacials ended about 190,000 and 80,000 years ago (Brandon-Jones, 1996a), and the appearance of *Macaca* on Borneo before the most recent glacial maximum, indicates that some reafforestation had occurred by then.

An Indonesian deep-sea core, about 850 km NNW of Australia, yielded grass pollen associated with low sea-level dry glacial periods at 190,000-130,000 years and 38,000-12,000 years ago. Interglacial periods supported woodland/fern vegetation (Kaars, 1991). During the Middle Pleistocene, pine-grassland savannah similar to the open woodlands of Thailand and Luzon (Philippines) occupied areas now characterised by lowland rainforest near Kuala Lumpur, Malaysia (Batchelor, in Morley and Flenley, 1987). Palaeosol development in the intramontane Bandung basin, west Java, indicated an anomalously dry climate at the end of the penultimate glaciation about 135,000 years ago, followed by

very warm and humid interglacial conditions from 126,000 to 81,000 years ago (Kaars and Dam, 1995).

At the advent of the last glacial period, about 81,000 years ago, freshwater swamp forest on the Bandung plain was replaced by an open grass-and-sedge-dominated swamp vegetation, indicating a considerably drier climate. A similar climate from 81,000 to 74,000 years ago in the adjacent mountains, is suggested by the strong decline in *Asplenium* ferns. Their resurgence from 74,000 to 47,000 years ago, indicates a return to slightly warmer conditions. Inferred depression of montane vegetation zones and fern scarcity from 47,000 to about 20,000 years ago, suggest distinctly cooler and possibly drier climatic conditions in the Bandung area (Kaars and Dam, 1995). The survival at Niah until about 40,000 years ago of a giant pangolin, otherwise known only from the Middle Pleistocene of Java, conveys some impression of the then prevalent conditions. The tall termite mounds necessary to sustain this extinct species, almost a metre longer than the largest living pangolin, are now characteristic of savannah areas. Its Middle Pleistocene contemporaries, the hippopotamus, antelope, cattle, chital and other deer are all obligate grazers. The terrestrial predators of that era, which include hyenas, three genera of dogs, sabre-toothed 'cats', possibly two 'tigers', a leopard, leopard cat and civets, accord with this impression of a plains community. Data from Niah Cave, the Tabon Cave in the Philippines, and the Ngoum Rock shelter in Vietnam, indicate a cool dry period from 32,000 to 23,000 years ago. The end of this period was even colder, producing a rubble layer in the Ngoum Rock shelter, and probably explaining the scarcity of monkeys and arboreal squirrels at Niah about 19,000 years ago, and the disappearance from this locality almost at sea-level, of two mammal genera, *Hylomys* and *Melogale*, now exclusively montane. This latter drought probably coincided with the most recent glacial maximum when west Javan temperatures fell by 4-7°C. A synchronous dry period occurred in Africa and South America. Since 23,000 years ago the climate moderated, producing a stalagmitic floor in the Tabon Cave (Brandon-Jones, 1996a).

The Javan Quaternary fossil and climate record

Recent clarification, and improved dating, of the Javan fossil mammal record reveals several

faunal successions, and has been interpreted to indicate rainforest existence on the island for only 80,000 years. Evidence is absent for mammals on Java before the first major sea level recession at 2.4 Ma. This suggests that before that time, Java may have been largely submerged. The Ci Saat and Trinil faunas of 1.2 and 0.9 Ma respectively, which mark the first appearance there of *Homo erectus*, were preceded by the oldest recognizable fauna, the Upper Pliocene Satir fauna at 2-1.5 Ma. This fauna included *Geochelone atlas*, which persisted until at least 1.2 Ma, after the first immigration of *Stegodon* to Java, implying a more protracted faunal turnover than had been thought. The distribution of this giant tortoise at some time extended from Java to the Siwaliks in north India, and further undermines the concept of rainforest stability. Between the impoverished Satir and the Ci Saat faunal stage, both *Tetralophodon bumiajuensis* and *Hexaprotodon simplex* were replaced by the new immigrants, *Stegodon* and *Hexaprotodon sivalensis*.

A major faunal immigration, the Kedung Brubus fauna, with the greatest abundance of medium to large-sized mammals, indicating relatively open and dry conditions, coincided with a marked sea-level depression at 0.8 Ma. Of its maximum number of 25 species, ten are new records, five of which are probably SE Asian mainland immigrants (*Rhinoceros unicornis*, *Tapirus indicus*, *Manis palaeojavanica*, *Hyaena brevirostris* and *Lutrogale palaeoleptonyx*). Most taxa from the Trinil fauna persist in the Kedung Brubus fauna, and extinctions were negligible. Large bovids dominate both faunas, but with double the number of megaherbivores (eight against four) in the latter fauna. Palynological results from the Sangiran area (with the exception of an anomalous meter section whose abundance of spores and *Podocarpus* tree pollen indicates increased humidity) are poor in tree pollen and spores, but rich in herbaceous plant pollen. Little change, other than a slight impoverishment, is evident in the imprecisely dated Ngandong fauna.

The earliest evidence of both tropical rainforest and *Homo sapiens* derives from the Upper Pleistocene Punung fauna, probably correlated with the warm interglacial from 125,000 years ago onwards. Seventeen Kedung Brubus taxa had disappeared, with ten replacements. These replacements include large numbers of primates such as *Pongo* and *Hylobates*, indicating a major environmental change to humid conditions. The presence of *Homo sapiens*, suggests an age less

than 110,000 years. Bergh *et al.* (1996) dated this fauna to 60-80,000 years, based on its similarity with the Jambu and Lida Ajer Sumatran cave faunas, for which aspartic acid racemization dating gave ages of 60-70,000 years and 80,000 years respectively. The invasion probably occurred between 80-110,000 years during the later part of the interglacial. Multiple extinctions with limited replacement, are demonstrated by the Holocene fossil cave faunas, such as Wajak, Sampung and Hoekgrot. *Pongo* is absent from this composite cave fauna, and probably disappeared from Java during the last glacial.

Variations in oxygen isotope levels from benthic and tropical planktonic foraminifera suggest that from about 2.8 Ma to 2.4 Ma ice volumes and sea levels fluctuated, with an overall increase in the former and a decrease in the latter, culminating at about 2.4 Ma in the first major glaciation. Sea level fluctuations then moderated, remaining constant until 0.8 Ma, with a mean of about 70 m below present day level (PDL), and lowest sea levels at about 100 m below PDL. Although insensitive to short-term fluctuations, the one global Pleistocene low sea level event detected by seismostratigraphy commenced at 0.8 Ma when sea levels were apparently exceptionally low for long enough to register on many seismic profiles. Sea level fluctuations then abruptly increased in amplitude, averaging about 90 m below PDL, with sea levels falling as low as 170 m below PDL. This fluctuation mode persisted until recent times (Bergh *et al.*, 1996).

Rainforest dispersal by island hopping

The correlation between glacial landmass emergence and aridity, refutes the notion that rainforest could readily have dispersed across the exposed Sunda and Sahul shelves. Conditions favourable to dispersal returned only when the sea re-attained its interglacial level. This implies that SE Asian rainforest has perhaps permanently been disjunct or insular in distribution, and has dispersed across sea barriers. Extensive areas of grassland or desert on the other hand, would pose insurmountable barriers. The presence of *Presbytis femoralis*, but not *Semnopithecus obscurus*, for example on Singapore, suggests the absence of an overland rainforest connection even between Singapore and peninsular Malaysia, although the dispersal route of *P. femoralis* probably brought it within range of Singapore earlier than did the dispersal route of

S. obscurus. Such distributional differences tend to confirm that, when exposed, Sundaland was inimical to rainforest dispersal. This would suggest it was predominantly grassland-encompassed desert, perhaps comparable to the dry zone in present-day north Burma.

If marine rainforest dispersal seems implausible, a reliable account exists of a floating island with unusually tall nipa palms being mistaken for a three-masted vessel. The same report tells of a pirate marooned on the bank of a hostile river when his companions were forced to make a hurried embarkation. On seeing a small island floating to the sea, he swam to it and for many days subsisted on its palm fruits. These islands are created by floods undermining the matted roots of riverside nipas (St. John, 1862, pp. 16-17). Natural rafts, sometimes carrying living mammals, have been recorded over a hundred miles off the mouths of tropical rivers, such as the Ganges, the Amazon, the Zaire and the Orinoco (Matthew, 1915, p. 206). Such rafts are likely to have been much more frequent during the post-glacial period of vegetational succession, when primary rainforest gradually reestablished itself at the expense of lower canopy vegetation. Under-storey vegetation, steadily dying off as it became shaded out, would have been increasingly vulnerable to the action of river spates.

Needless to say however, the odds are stacked against successful rafting. Ironically, the better the swimmer the less likely an animal is to cross a strait, because it will have less reluctance about deserting a raft and a greater ability to resist wind and currents. This is probably a major factor in the endemism of the ably swimming proboscis monkey on Borneo, and the absence from Borneo of the tiger which occurs on Sumatra, Java and Bali. To succeed, the raft must offer ample food and protection from the elements, and the animal must be pregnant or accompanied by a member of the opposite sex. These undoubtedly rare coincidences have encouraged the belief that the deep sea channels which remained as barriers when the Sunda and Sahul shelves were exposed were sufficient to have created Wallace's line and other such faunal divides. This ignores the most important consideration that, for successful rafting, landfall must be accompanied by an appropriate climate. Rainforest flora and fauna on a raft will not flourish on arrival unless the raft lodges at a locality with adequate precipitation and temperature.

The deep sea channels were undoubtedly sig-

nificant in maintaining localised maritime climates when these disappeared elsewhere but, compared to climatological barriers, they were relatively trivial in impeding dispersal. The longevity of the potential dispersal route between Asia and Australia is demonstrated by the presumably Asian origin (other than of those introduced by man) of the New Guinea and Australian rats (Muridae), which are now almost exclusively either endemic species, endemic genera or even endemic subfamilies (Simpson, 1977, p. 115). These successful dispersers are comparatively well able to cope with a range of climates, and perhaps exceptionally adept at survival on the inimical conditions of a raft.

Pre-glacial Bornean primate impoverishment

Although lingering on in Vietnam until about 23,000 years ago (Ha Van Tan, 1985), and formerly occurring in China (Kahlke, 1973) and Java, the main stronghold of the orang-utan appears to be Borneo. This suggests the existence there of both orangs and their rainforest habitat before the first deforestation. Establishing the presence of rainforest on Borneo may seem superfluous but, before this deforestation, the only primate undoubtedly present was the endemic proboscis monkey, *Nasalis larvatus*. Its anatomy, and that of its only close relative, *Nasalis concolor*, on the Mentawai Islands, is that of a predominantly terrestrial monkey, and is very reminiscent of macaques. The genus evidently evolved in forest-woodland (Brandon-Jones, 1996a). Its natural habitat must intermittently have been overwhelmed by mangrove and rainforest. The proboscis monkey remained on Borneo only because its island distribution prevented it from following the climatic and geographic recession of its native vegetation. Even in isolation, this is clear evidence of former extensive areas of open woodland on Borneo. Nevertheless, the fact that the proboscis monkey and the orang-utan have not reclaimed central Sarawak suggests that, at glacial extremes, most of the open woodland disappeared, leaving the two primate species with a very localised distribution in north (and perhaps west) Borneo.

Presbytis and *Hylobates* are represented in the Bornean refugium by the second-wave colonizers, *Presbytis comata* and *Hylobates muelleri*, but not by the initial colonizing ancestors of *P. potenziani* and *H. klossii*. Having established the probability of rainforest there dur-

ing the first dry period, the absence of these initial colonizing species implies their genera were then absent, otherwise they would be expected to persist in Borneo, cohabiting with their descendent congeners. Such areas of sympatric distribution in Borneo do exist for both sureli species and gibbon species (see Brandon-Jones, 1996b; Mather, 1992). It is possible that the tarsier was also absent and survived the first arid period only on Sulawesi, where its vertical clinging and leaping adaptation would have equipped it well for survival in shrub vegetation, even if rainforest disappeared. Despite Simpson's (1977) reservations, this accords with Groves' (1976) view that Sulawesi might have been a centre of origin for the tarsier. The loris may have survived only in Java, Indochina and southern India. Thus there is the distinct possibility that, until 190,000 years ago at the earlier deforestation, or even until 135,000 years ago at the penultimate glacial maximum, there were only two primate species on Borneo. This does not establish that Bornean rainforest is necessarily of similar age, but it implies that gibbons, a family endemic to Asia, are latecomers to Borneo.

Modern Bornean primate diversity

How then do we account for the present primate diversity on Borneo? Probably the first arrivals after the orang-utan and the proboscis monkey, were *Presbytis comata* and *Hylobates muelleri*, which reached Borneo between the deforestations. It is possible that the loris and the tarsier also invaded during this interval, but more probable that, with the macaques and silvered leaf monkey, they did not arrive until after the second deforestation. The white-fronted sureli, *Presbytis frontata* diverged *in situ* from *P. comata sabana* after the latter event. Its other Bornean congeners, *P. femoralis* (directly) and *P. rubicunda* (indirectly), diverged from *P. comata thomasi* on Sumatra (Brandon-Jones, 1996b). If the south Bornean gibbon is a subspecies of *Hylobates agilis*, it was another Sumatran immigrant to arrive on Borneo since the second deforestation, otherwise it presumably evolved *in situ* from *H. muelleri*. All the extraneous primates evidently rafted to Borneo, because of the unavailability of suitable habitats for dispersal across Sundaland. *P. femoralis* and *P. rubicunda* seem to confirm this by their allopatric distribution in Kalimantan, compared to their sympatric distribution in Sarawak, Borneo. This geographic variation in sympatry is virtually ir-

reconcilable with the concept of prolonged rainforest stability. It is readily explained by inferring recent arrival in separate localities on the west coast (the only other island occupied by *P. rubicunda* is Karimata which it presumably colonized *en route*), followed by parallel eastward dispersal, which was more extensive or rapid in *P. rubicunda*. If rainforest had existed in central Sundaland, the two species would surely have become sympatric much further westward than they do. As predicted by Hershkovitz's (1968) principles of meta-chromism, pelage colour in both *P. rubicunda* in north Borneo, and *P. melalophos* in south Sumatra, dilutes to a pale colour.

Borneo as a dispersal barrier

It is possible that primate impoverishment on Borneo, before the first deforestation, was simply due to an arid coastal climate which prevented rafted rainforest from establishing itself. This is supported by Stresemann's (1939) conclusion that grassland widespread in SE Asia during the Pliocene persists in south Borneo, and by the apparent entire extirpation and replacement during the Pleistocene of the south-west Bornean freshwater fish fauna (Brandon-Jones, 1996a). By restricting animal and plant colonization of south Borneo the dry zone responsible would have diminished its potential as an intermediate route to Sulawesi. Virtually all the 183 butterfly genera on Sulawesi are Asian, with no special link to Borneo. A set of younger patterns based on the distribution of the 470 species (200 of which are regional endemics) links Sulawesi to the Philippines, Lesser Sunda Islands and especially the Moluccas, in addition to Asia (Vane-Wright, 1991). This circum-Bornean faunal zone is also reflected in Hooijer's (1975) suggestion that Sulawesi, Flores, Timor and intervening small islands had Pleistocene geographic continuity as 'Stegoland'. The proposition of such broad land connections across waters now nearly 3000 metres deep is geologically tenuous and is rendered superfluous by the presence of indistinguishable large Pleistocene stegodonts on Mindanao (in the Philippines) and on Java (Simpson, 1977, p. 113). The possibility of a physical connection of the latter islands with the others is almost negligible. Although Groves (1976) believed that mammal migration between Sulawesi and the Philippines was insignificant, the stegodont dispersal between these islands must have crossed sea barriers.

Sulawesi organisms with Indomalayan affinities evidently circumvented Borneo, via Java or the Philippines, many of their ancestors along the route, being eliminated by subsequent glacial drought.

The climatic origin of Wallacea

Simpson (1977, p. 117) concluded that Huxley's line, which approximately coincides with the eastern edge of the Sunda shelf, and Lydekker's line, which roughly corresponds to the western edge of the Sahul shelf, are clear-cut faunal boundaries separated by an unstable zone, now often termed Wallacea. He declined to categorize the intermediate zone as transitional, in order to encourage further research on its biogeography. The possibility that this unstable zone was at least partly created by climatic barriers was appreciated as early as 1845 (Müller, 1846). Lincoln (1975) concluded that Wallace's line was primarily an ecological division, with the Lesser Sunda Islands to the east of the line being drier and smaller with an impoverished but dominantly Oriental avifauna. Smith (1943, p. 140) remarked that the Philippines, Sulawesi and the Lesser Sunda Islands, as compared to Borneo, Java and Sumatra, "are notable for the absence of large mammals, not because they could not have reached them, but because they could not survive upon them if they got there". Pleistocene mammals contradict this. "The former presence of somewhat diverse proboscideans on islands between the Huxley and Lydekker Lines remains a puzzling fact that must be taken into account... The large stegodonts, ubiquitous where any Pleistocene mammals are known, surely were not all victims in the first generation of occupants" (Simpson, 1977, p. 113). Perhaps these elephant-like mammals thrived during relatively dry glacial periods of extensive grassland, and died out during excessive aridity when much of it turned to desert. As the climate changed their island distribution would have, as with the proboscis monkey, curtailed their ability to follow their preferred habitat.

Australasian organisms spreading northwards would have experienced a similar series of advances and local extinctions on their precarious 'stepping-stone' route to Asia. Relatively few of them, such as the Sulawesi phalangers, have successfully negotiated the climatic adversities (and perhaps superior competition) intermittently intervening to obstruct their passage. Islands along the route have varied (according

to their size, topography and geographic situation) in their ability to sustain varying grades of vegetation for varying periods of time. Many species presumably had precursors eliminated from islands behind them on the route, and possibly their descendants from islands ahead of them. Steenis (1935, p. 404) for example, noted that Mount Kinabalu in Sabah, Borneo, is far richer than Timor in Australian temperate plants. Hence the need for caution in inferring dispersal routes from existing distributions. A species' absence can be as informative as its presence. The net result has been an ebb and flow of dispersal correlated with the glacial cycles. Wallace's line and other faunal divides such as Müller's and Weber's, may therefore mark only the approximate midpoint between two or more rainforest glacial refugia in Australasia and SE Asia.

Conclusions

Asian primate distribution indicates that most Asian rainforest was eliminated by glacial drought. Sumatran primate distribution indicates that this occurred at least twice, and that the most recent deforestation was less drastic than its predecessor. The two deforestations appear correlated with the terminations of the two most recent interglacial periods. The Javan fossil record suggests that before these interglacials, conditions generally favoured open country animals. The correlation between landmass emergence and aridity implies that SE Asian rainforest dispersal, successfully negotiated sea barriers. Indications that southwest Borneo had a prolonged arid climate which would have prevented rafted rainforest from establishing itself, provides an explanation for the apparent necessity for most fauna to bypass it on their route to islands further east. The contrast between evident pre-glacial Bornean primate impoverishment and its present primate diversity, provides a model for the effects of climate change on SE Asian island biogeography, and demonstrates how such effects could have restricted faunal and floral interchange between Australasia and SE Asia.

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