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THE BIOGEOGRAPHICAL EVOLUTION AND PHYLOGENY OF THE GENUS *PRESBYTIS*. MEIJAARD, E. AND GROVES, C.P.

Key words: primate, biogeography, craniometrics, phylogeny, *Presbytis*, metachromism, distribution, South-East Asia, Sundaland

Abstract

The genus *Presbytis* is more or less confined to Sundaland, and, within this region, the distribution of its species is partly a result of changes in geography, sea levels, and vegetation during the Pleistocene (and perhaps of the Late Pliocene) and partly of present-day soils and vegetation. We use the molecular cladogram of ZAIN, the phylogenetic insights of BRANDON-JONES, and our own craniometric analysis to elucidate the past patterns of vicariance, dispersal, and range contraction and expansion.

Introduction

In this paper, we examine the biogeography of *Presbytis*, a genus of leaf monkey (Colobinae) confined to Sundaland, i.e., the Malay peninsula (including peninsular Thailand) and the western Indo-Malay archipelago (Sumatra, Java, Borneo, the Natuna Islands, the Riau Islands, and the Mentawai Islands) (see Figure 1). Although in the seminal work of NAPIER and NAPIER (1967) leaf monkeys now belonging to other genera were placed in the genus *Presbytis* and only five species (*P. agyula*, *P. melalophos*, *P. frontatus* [sic], *P. rubicundus* [sic] and *P. potenziani*) were recognized in the group now under consideration, the group has become more and more speciose as understanding has grown. GROVES (2001) has produced a working taxonomy (here reproduced as far as is necessary in Table 1) with explanations of how it differs from those of earlier authors, in particular, the important contributions of BRANDON-JONES (1977, 1996a,b,c, 1998) and AIMI and his colleagues (AIMI and BAKAR, 1996; AIMI et al., 1986), as follows:

- Sumatran/Malay peninsular *P. femoralis* is now universally regarded as a species distinct from *P. melalophos*.
- BRANDON-JONES (op cit.) has recognized *P. siamensis* as a further Sumatran/Malay species.
- GROVES (2001) separates Bornean *P. chrysomelas* from *P. femoralis*.
- The species formerly called *Presbytis agyula* [a name which does not in fact refer to a leaf monkey but to a macaque (NAPIER and GROVES, 1983)] has been broken up. POOCOCK (1935), AIMI and BAKAR (1996) and GROVES (1970) have separated Sumatran *P. thomasi* and Bornean *P. hosei* from Javan *P. comata*. BRANDON-JONES (1996b) did not recognize this separation, and continued to refer all three to a single species, *Presbytis comata*.
- On the other hand, BRANDON-JONES (1995) separated *P. fredericcae* from *P. comata* as a distinct species; NIJMAN (1997), however, showed that the two grade insensibly into each other over a wide area.

We may mention that work on the genus continues, and it is far from certain that the number of valid species is at a maximum; in particular, we are of the opinion that *P. hosei sabana* and *P. h. canterus* should be regarded as separate species from *P. hosei*.

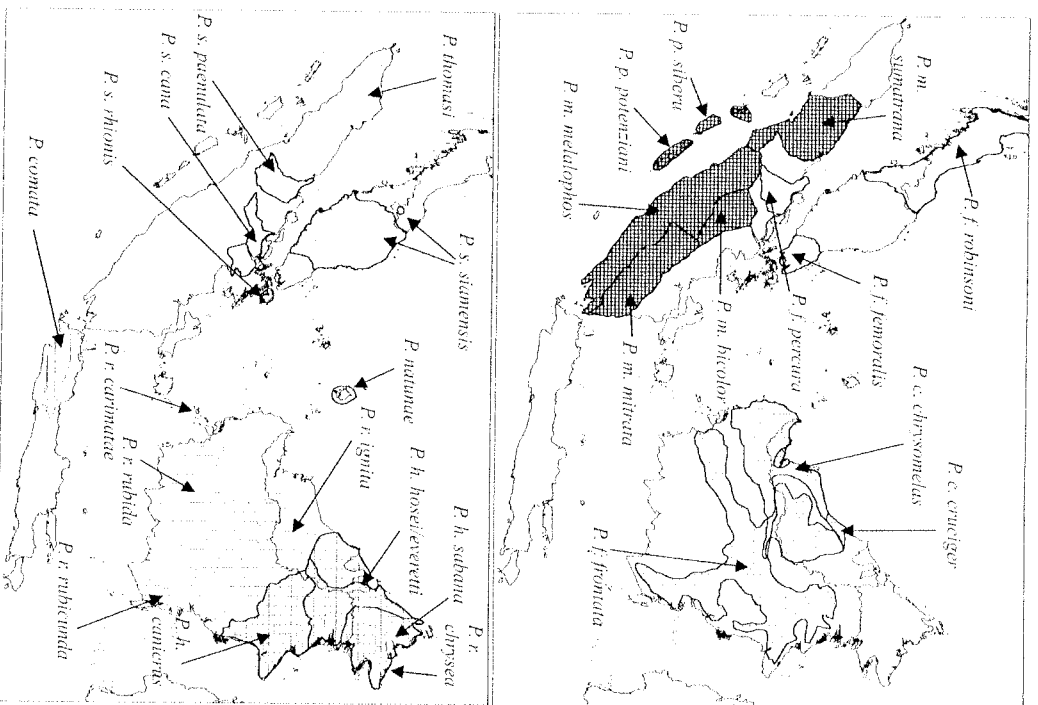


Fig. 1: Distribution of *Presbytis* species, according to GROVES' (2001) taxonomy.

Table 1: Post-1977 Taxonomic Arrangements of the Genus *Presbytis*.

GROVES, 2001	BRANDON-JONES, 1977, 1996a, b, c	AIMI et al., 1986; AMI and BAKAR, 1996	Distribution
<i>P. melalophos melalophos</i>			W. Sumatra
<i>P. m. bicolor</i>			C. Sumatra
<i>P. m. sumatrana</i>			N.W. Sumatra, Batu Is.
<i>P. m. mitrata</i>			S. Sumatra
<i>P. femoralis femoralis</i>			Johor
<i>P. f. robinsoni</i>			N. Malay peninsula
<i>P. f. percura</i>			E.C. Sumatra
<i>P. n. natuna</i>			Bunguran I.
<i>P. chrysomelas</i> (2 subsp.)			N. coast Borneo
<i>P. siamensis siamensis</i>			Peninsular Malaysia
<i>P. s. thionis</i>			Bintang I.
<i>P. s. canu</i>			Kundur I., E.C. Sumatra
<i>P. s. puenulata</i>			E.C. Sumatra
<i>P. fontata</i>			C. & E Borneo
<i>P. comata comata</i>			W. Java
<i>P. comata fredericæ</i>	Distinct sp.		C. Java
<i>P. thomasi</i>	Subsp. of <i>P. comata</i>		Far N. Sumatra
<i>P. hosei hosei</i>			N.E. Sarawak coast
<i>P. h. everetti</i>			Inland Sarawak, W. Sabah
<i>P. h. sabana</i>			Sabah
<i>P. h. canterus</i>			E. Kalimantan
<i>P. rubicunda</i> (6 subsp.)			Borneo, Karimata Is.
<i>P. potenziati</i> (2 subsp.)			Mentawai Is.

Phylogenetic Relationships

BRANDON-JONES (1977) proposed a set of evolutionary relationships among *Presbytis* species based mostly on coat coloration (Figure 2a). He suggested that the most primitive form of *Presbytis* is *P. potenziati* from the Mentawai Islands, off western Sumatra, with dark coloration, followed by the intermediate forms, *comata*,

thomasi, and *hosei* (which he united in a single species, *P. comata*), and culminating in the most derived forms, *P. melalophos femoralis*, *frontata*, and *rubicunda*, with red/brown coloration. Among the "derived" forms, BRANDON-JONES (1996b) proposed a special affinity between *P. melalophos* and *P. rubicunda* because of similarities in behavior. Based on head pattern, BRANDON-JONES further proposed that *P. rubicunda* derived from *P. siamensis*. He also suggested a close evolutionary affinity between *P. frontata* and *P. comata sabana*, based on shared external cephalic structures. BRANDON-JONES (1996c) provided the following hypothesis for the evolution of *Presbytis comata*. During the late Middle Pleistocene the species was continuously distributed across Borneo and Sumatra. *Presbytis* was initially contracted to the Mentawai Islands by a severe glaciation at 190 thousand years (Kyr) ago. At this time, neither the Mentawai endemic *P. potenziანი* nor its descendant *P. comata* had colonized Borneo, and *P. comata* evolved from *P. potenziანი* after this glacial period. The next glacial period restricted *P. comata* to several glacial refugia, including one in north Borneo, in approximately the same area as the present-day distribution range of what he referred to as *P. comata everetti* (i.e., western Sabah and eastern Sarawak). The three peripheral Bornean subspecies of *P. comata* (*hosei*, *canterus*, and *sabana*) appear to represent the first stage of extra-refugial dispersal. BRANDON-JONES also hypothesized a glacial refugium in northern Sumatra, from which populations dispersed. One branch (*P. melalophos*) dispersed as far as the southern tip of the island, and another emigrated to the Malay Peninsula and north-west Borneo. The only possible instance of sympatry resulted from a reverse dispersal of *P. siamensis* from the Malay Peninsula (BRANDON-JONES, 1996c). To allow for the interstadial dispersal from Sumatra to Borneo, BRANDON-JONES hypothesized an eastward current that carried rafts of floating vegetation between the two islands.

Melding BRANDON-JONES's model of color evolution with the principle of metachromism of HERSHKOVITZ (1967; 1977), GROVES (1989) proposed a centrifugal speciation hypothesis for the genus. He saw black - gray - red/brown as increasingly centrally evolved and dispersing out to replace the more plesiomorphic colors, so that the primitive black *P. potenziანი* remains only on the Mentawai Islands, the grey *P. comata*, *P. thomasi*, and *P. hosei* are in Java, northern Sumatra and northeastern Borneo, respectively. The remaining species, all red or brown, are central in distribution (spoiling this is a tendency for the apomorphic ones to revert to black in some areas: *P. melalophos sumatrana*, *P. femoralis chrysomelas*).

AIMI and colleagues (AIMI and BAKAR, 1996; AIMI et al., 1986) considered the taxonomy of the genus in Sumatra, recognizing three species distinguished alike by characters of pelage, skull and vocalization. In this model, *P. melalophos* is the sister species to a clade containing *P. femoralis* plus *P. thomasi*. They effectively completed the metachromatic progression by describing a new subspecies, *P. melalophos bicolor*, the whitest, and so, in the Hershkovitzian scheme, most apomorphic of all in the central Sumatran highlands.

ZAIN (2001) used various molecular techniques, including mtDNA markers (ND3, ND4L, ND4, and HRNAs), paternal Y-chromosome markers (TSPY and SRY), and biparental autosomal markers (IRBP intron-3), to investigate phylogenetic relationships among several (but not all) *Presbytis* species (Figure 2b). He also used the DIVA program (see RONQUIST, 1997) to reconstruct the possible ancestral distribution

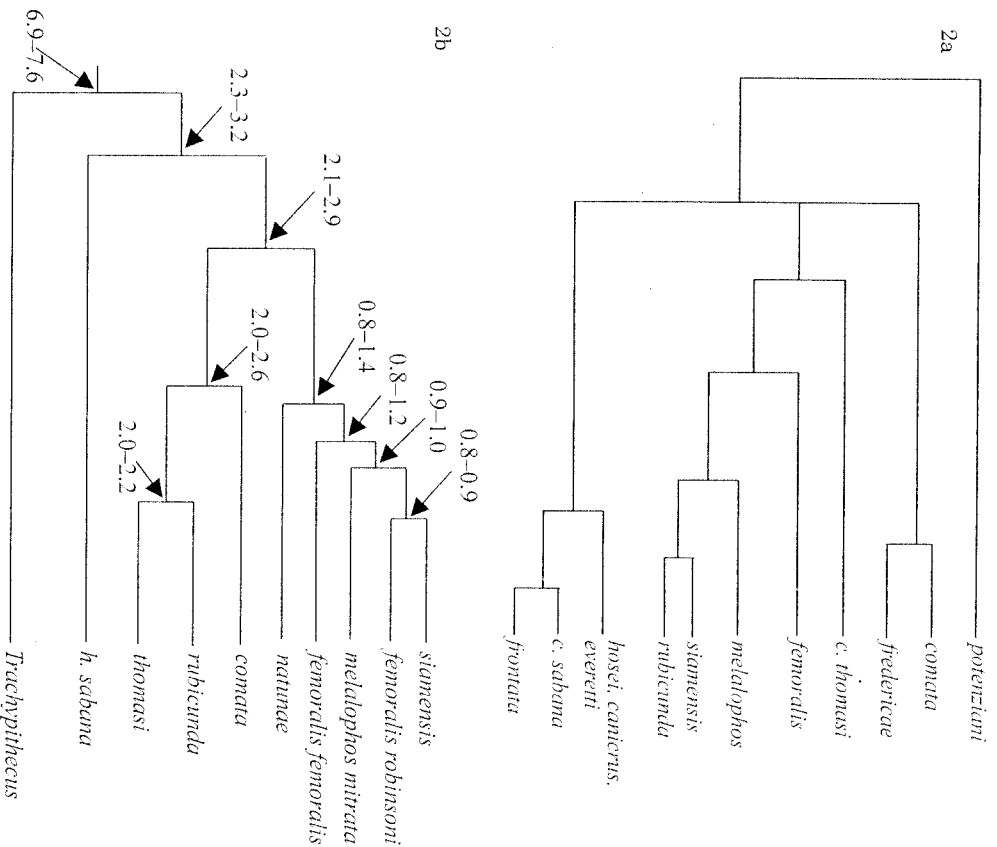


Fig. 2. Phylogeny of *Presbytis*, after (a) BRANDON-JONES, 1996a, b, and (b) ZAIN, 2001. Note that, strictly speaking, BRANDON-JONES regards some living taxa as unchanged ancestors of others, but in (a) they have here been represented as sister taxa for comparison with ZAIN's phylogeny. In (b), the subspecific names used by ZAIN have where appropriate been changed to specific names as in Table 1 and in the text. Numbers in (b) refer to estimated divergence times between clades [after Fig. 3.10 in ZAIN (2001)]. Taxa not included in this research were: *femoralis perwira*, Sumatran *siamensis* subspp., *frontata*, *potenziანი*, *h. hosei* and *everetti*, and *canterus*.

- tribution of the genus *Presbytis*. ZAIN's main conclusions, relevant to this research, were that:
- *P. comata*, *P. thomasi*, and *P. hosei* are separate entities and do not belong to the same species as suggested by CHASEN (1940), HOOLJER (1962), and recently restated by BRANDON-JONES (1996a).
 - *P. rubicunda* and *P. melalophos* (including *P. siamensis*) are not closely related. Instead, *P. rubicunda* groups closely with a clade containing *P. thomasi* and *P. comata*, a result that is strongly supported by high bootstrap values.
 - The ancestral *Presbytis* underwent two cladogenic events on Borneo. The first split separated into *hosei* and a clade containing all other *Presbytis*. This second clade underwent a further cladogenic subdivision into a *melalophos*-like group and a *comata*/*thomasi*/*rubicunda* clade.

The chain of evolutionary events suggested by ZAIN (2001) involves a dispersal pattern starting on Borneo, moving west to the Malay Peninsula and Sumatra, and south to Java. This is exactly opposite to the direction of events proposed by BRANDON-JONES (1996a), whose ancestral species moved from the Mentawai Islands to the east via Sumatra [note, however, that ZAIN (2001) did not study *P. potenziani* from the Mentawai Islands]. ZAIN (2001) estimated that the divergence time among *Presbytis* species ranged from 3.2 to 0.8 Ma; although, *P. potenziani* was probably the species that first diverged from the other *Presbytis* (BRANDON-JONES, 1996a, and also see below), and *Presbytis* evolution thus started earlier.

One of us (EM) has investigated the palaeoenvironments of the SE Asian region in the Late Tertiary to Late Quaternary (MEIJAARD, 2003a) and has also worked extensively on the distribution of Bornean primates (e.g., MEIJAARD and NIJMAN, 2000; MEIJAARD and NIJMAN, 2003). Furthermore, we statistically analyzed measurements on 277 colobine skulls which provided additional insight into the phylogenetic relationships within *Presbytis*. These craniometric data will be published elsewhere. In this paper, we use our palaeoenvironmental reconstructions and combine them with our latest biogeographic and taxonomic insights to test which of the above biogeographical scenarios is more parsimonious with our data.

Palaeoenvironmental reconstructions

ZHANG et al. (1993) suggested that Asian colobines migrated into Sundaland during the Late Pliocene or Early Pleistocene; the earlier part of the time span fits the divergence times estimated by ZAIN (2001). They migrated from Africa to India and dispersed into southern India, Burma, Malaya and Sundaland. It is possible that, at the same time, another migratory route existed along the northern bank of the Tethys Sea in southern Tibet via Yunnan into Vietnam and, finally, toward the east around the Sichuan Basin. For colobines, that may have meant that there were two important centers of radiation, one being Sundaland and the other being the Heng Duan mountain region (ZHANG et al., 1993). The split between *Nasalis* and *Presbytis* occurred approximately 5 Myr ago, according to SARICH (1970), after which *Simias* and *Nasalis* split. ZAIN (2001), however, estimated an earlier split, 6.7–7.4 Myr ago, between *Nasalis* and *Presbytis*, based on a ceropithecine-colobine divergence of 10–11 Myr [DELSON, personal communication, quoted in ZAIN

(2001)]. Presumably, this split occurred in Sundaland, whereas the mainland Asian colobines diverged in the other center of radiation (ZHANG et al., 1993).

If the *Presbytis* group, indeed, entered Sundaland at the end of the Miocene or in the Early Pliocene, they would have followed a route along the Malay Peninsula into what is now Borneo, and possibly Sumatra (see below). Java became disconnected from this landmass after the Early Pliocene, and dispersal to Java could only have occurred across sea water (Figures 3 and 4). The proto-Kapuas River could have been a barrier between the northern and southern part of Sundaland, although no evidence concerning this is presently available.

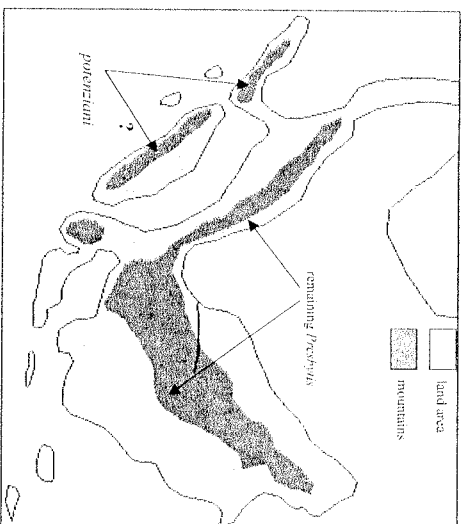


Fig. 3: Land distribution during the Late Miocene–Early Pliocene.

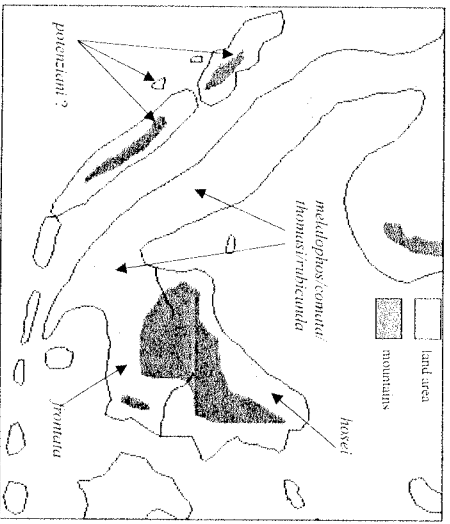


Fig. 4: Land distribution in the Late Pliocene–Early Pleistocene.

A land connection between Borneo and western Java probably existed in the Late Miocene-Early Pliocene (ca. 7–5 Myr ago) (MEIJAARD, 2003a), but it is unlikely that leaf monkeys had already entered Sundaland at that time. The first time that *Presbytis* monkeys could have migrated to Java would have been in the Early-Middle Pleistocene, as is also suggested by fossil finds of *Presbytis aygula* (= *comata*) (HOOLJER, 1962) and other similar-sized monkeys of the genera *Micaca* and *Trachypitheus* (e.g., van den BERGH, 1999; JABLONSKI and TYLER, 1999, but note that LARICK et al. (2000), suggested that this happened much later, in the Middle-Late Pleistocene). This land connection between Borneo/Alalaya and Java probably disappeared after the Middle Pleistocene (see van BEMMELLEN, 1970), which would have isolated the species on Java. The arrival of a new Late Pleistocene fauna on Java as shown in the fossils of the Punung fissures (e.g., BADOUX, 1959) indicated that by approximately 80–60 Kyr ago Java had once more become connected to the rest of Sundaland. It is unclear whether this fauna originated from Borneo or from Sumatra, or from both, but the species composition (including *Capricornis sumatraensis*, *Hylobates syndactylus*, *Elephas maximus*, and *Sus scrofa vittatus*) strongly suggests a land link between Sumatra and Java. All of these species now occur in Sumatra but not in Borneo; *Elephas maximus* is thought to be a recent arrival on Borneo (MEDWAY, 1977).

It is unclear for how long Sumatra remained an island. The Asahan Arch, a land bridge between the Malay Peninsula and northern Sumatra (see Figure 3), may have existed until the Late Miocene or Early Pliocene (MEIJAARD, 2003a), but it is unclear whether this predated the arrival of *Presbytis* in Sundaland or not. It could be that *Presbytis* arrived on Sumatra as early as the Late Miocene-Early Pliocene, and did not survive (see below), whereas "modern" species arrived on Sumatra only during the Middle-Late or Late Pleistocene, presumably when a land connection with the Malay Peninsula and Java was established. There are also indications that northern Sumatra remained an island separate from southern Sumatra during much of the Pleistocene (MEIJAARD, 2003a), and, possibly, *P. thomasi* evolved on this isolated northern island.

The Mentawai Islands probably became sub-aerial in the Pliocene (see SAMUEL et al., 1997), when the island arc was uplifted. Presumably, this led to increased sedimentation in the seas between the islands and the mainland, and it is unclear whether and when the islands were connected to Sumatra. Siberut, Sipura, and the Pagai Islands are presently all separated from Sumatra by seas < 100 m deep, and it is therefore likely that low sea-levels during the Late Pleistocene would have connected the islands to the mainland. This is also indicated by the mammalian faunas on these islands which appear to be a mixture of endemic species and ones that are much more widespread in Sundaland (e.g., MEIJAARD, 2003b). Still, the relative paucity of common Sundaland species in the southern Mentawai Islands suggests that if a last glacial maximum (LGM) land connection existed between these islands and mainland Sumatra, it probably still posed a considerable ecological barrier, limiting the dispersal of terrestrial mammals to and from these islands.

The question of when Borneo first became an island is of considerable importance to the evolution of leaf monkeys. Borneo had for a very long time been part of the Asian mainland through its connection with the Malay Peninsula. LLOYD (1978 cited in WILSON and MOSS, 1999) suggested that Borneo lost its connection to the

mainland during the latest Miocene or Pliocene, which was possibly caused by global sea-level changes and/or plate readjustments (WILSON and MOSS, 1999), but EM's reconstruction indicates that this may have happened later. Also, because the seas between Borneo and Malaya would probably have been shallow, they would have been greatly influenced by glacially induced sea-level changes.

Fossil record

The fossil record for the colobines in island South-East Asia is relatively poor. On Java, HOOLJER (1962) tentatively identified some Middle Pleistocene remains as *Presbytis*, which he considered to be identical to *P. aygula* (= *P. comata*). On Borneo, there is a relatively large sample of cranio-dental remains from the Niah Cave area in north-east Sarawak. According to HARRISON (2000) this material, which dates back to the Late Pleistocene, definitely does not include *P. femoralis* (= *P. chrysomelas*), and is most similar to *P. rubicunda* and *P. hosei*. The colobines from Guna Streh, a Holocene deposit in western Sarawak, appear to be assignable to a single species of *Presbytis*, which is presumably *P. chrysomelas* (HARRISON, 2000). In Sumatra, HOOLJER (1962) described *Presbytis* remains from the Late Pleistocene cave deposits of Lida Air in Central Sumatra, but he could not determine their specific identity.

Phylogenetic reconstruction based on craniometrics

In addition to the data by BRANDON-JONES (1996a, b) and ZAIN (2001), we obtained further phylogenetic data by statistically analyzing measurements on 277 colobine skulls including all the *Presbytis* species and *Trachypitheus cristatus* and *T. obscurus* as outgroups (MEIJAARD and GROVES, unpublished data). First, we obtained unstandardized canonical discriminant functions evaluated at group means, which provided the input in a dissimilarity matrix based on the square root of the squared Euclidean distance between species. Dendrograms were constructed using MEGA version 2.1 (KUMAR et al., 2001). The resulting Neighbour-Joining tree, rooted at the split between *Trachypitheus* and *Presbytis* (Figure 5), indicated

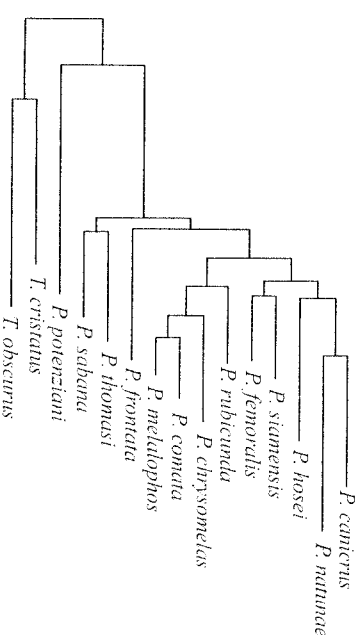


Fig. 5: Phylogenetic tree based on craniometrical dissimilarities between *Presbytis* species (MEIJAARD and GROVES, unpublished data).

that initially *P. potenziani* and the other *Presbytis* diverged, which is in accordance with BRANDON-JONES [1999, note that ZAIN (2001) did not include *potenziani* in his analysis]. From this point onwards, our phylogenetic reconstruction deviates from that of BRANDON-JONES by splitting a clade containing *sabana* (but not *hosei* and *canturus*) and *thomasi* from the other *Presbytis*. Interestingly, ZAIN, who only used samples from *sabana* and not other taxa in the *hosei* group, also proposed an early divergence of *sabana* (note, however, that we only measured 2 *sabana* skulls and that the early split of this species does not have statistically significant support). Our data also support the earlier mentioned hypothesis that *canturus* should be considered a species distinct from *hosei* and *sabana*, which is primarily based on the significantly longer palate in *canturus* together with a relatively short cranium.

Discussion

Based on the existing information, we attempt to reconstruct how leaf monkeys could have dispersed through and evolved in the region. It appears that they initially arrived from the Asian mainland probably sometime during the Late Miocene–Pliocene. Considering the early divergence of *potenziani*, hypothesized by BRANDON-JONES and supported by our craniometric data, the ancestral *potenziani* probably entered Sumatra across the Asahan Arch (Figure 3), which shortly afterwards became submerged, cutting off connections between Malay/Borneo and Sumatra. *P. potenziani* evolved on Sumatra and spread to the Mentawai Islands during the Pliocene–Pleistocene. Why the species became extinct on mainland Sumatra is unclear. It may either have been displaced by a later *Presbytis* species, or, maybe, its habitat temporarily disappeared during one of the many Pleistocene glacials. None of the phylogenetic reconstructions supports a sister species relationship between *potenziani* and *thomasi*, although WILSON and WILSON (1977), who compared *Presbytis* vocalizations, suggested that the two may be subspecifically related. Still, it is unlikely that *potenziani* and *thomasi* arose vicariantly when the Mentawai Islands and Sumatra became disconnected.

In Borneo/Malaya, several million years later, a split probably occurred between *sabana* (with or without the other species from the *hosei*-group) and *frontata*. We hypothesize that this split happened at the start of the Pleistocene and was caused by the development of the Mahakam River. SMIT-SIBINGA (1953) stated that, ca. 2 Myr ago, the Mahakam River came into being, because of uplift in the central Borneo region, and that this river initially flowed into the very large Kutai Lake (of which the present lakes are only remnants). Together with the Kapuas River in west Borneo, this could have divided Borneo into 2 distinct regions.

Sometime during the Pliocene or Pleistocene the separation of Borneo from the Malay Peninsula would have provided a mechanism for the divergence between the *siamensis/femorals/melalophos/chrysomelas* group and the remaining Bornean *Presbytis* species. *P. comata* would subsequently have migrated to Java across an Early–Middle Pleistocene land bridge, but it is unclear whether this land bridge was only connected to the Malay Peninsula or whether there was also a direct link to Borneo. ZAIN's (2001) data and our craniometric analysis support a close relationship between the Javan *comata* and the Bornean *rubicunda*. Although there is limited

concordance between the 3 phylogenetic models regarding the relationships between *thomasi*, *comata*, and *rubicunda*, ZAIN's data strongly suggest that the 3 species form a monophyletic clade. We speculate that an ancestral species on the southern Malay Peninsula, or on the peninsula's extension along the Riau/Lingga Archipelagos and Bangka and Belitung Islands, crossed to Sumatra, Java, and Borneo during an Early–Middle Pleistocene glacial period. It remains unclear where and for how long these land connections between Malaya, Java, Sumatra, and Borneo existed. During the Early–Middle Pleistocene, the following situation may have existed:

- In northern Borneo, the *hosei*-group occurred, separated by the Kapuas and Mahakam Rivers from the *frontata*-ancestor.
- In southwest Borneo, *rubicunda* lived.
- On Java, *comata* occurred.
- On most of Sumatra, *thomasi*—*potenziani* having by then been isolated on the Mentawai Islands, whereas the *melalophos*-group (including *siamensis*, *femorals*, and *natauae*) occurred on the Malay Peninsula and its southern extension to the Riau, Lingga, Bangka, and Belitung areas (see Figure 6).

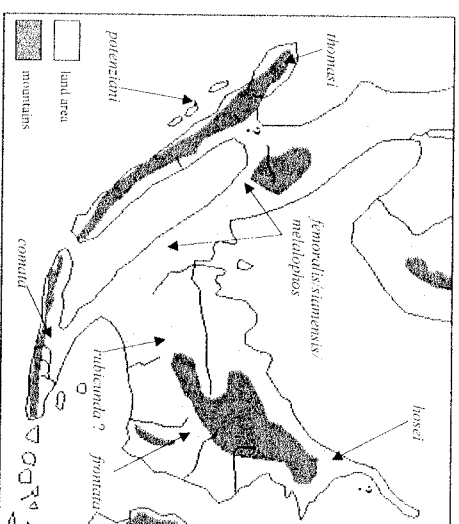


Fig. 6: Land distribution during an Early–Middle Pleistocene period of low sea-levels.

Assuming that ZAIN's (2001) divergence times are approximately correct, speciation in the *melalophos*-group happened during the Middle Pleistocene, sometime between 1.4 and 0.8 Myr ago. Van den BERGH et al. (1996) suggested that a regime of moderate sea-level fluctuation mode had existed since 2.4 Myr BP but that this changed dramatically to high amplitude fluctuations during the Middle–Late Pleistocene (app. 800 Kyr ago). Minimum sea levels dropped to 170 meter below the present-day levels. These much lower sea-levels could have provided opportunities for dispersal of the *melalophos*-group into Borneo and Sumatra, which, after sea-levels rose, would have isolated them in those areas (Figure 7).

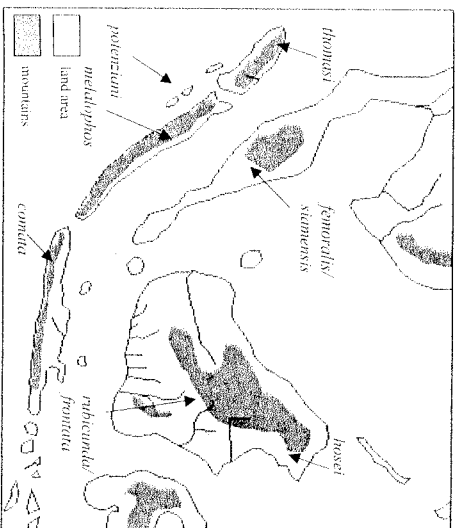


Fig. 7: Land distribution during a Middle Pleistocene period of high sea-levels.

The 3 phylogenetic models do not agree on the relationships between *metulophos*, *femorals*, *stamensis*, and *natunae*, and the speciation model for this group remains unclear. Considering that *metulophos* occurs exclusively on Sumatra, evidently its evolution was the direct result of the dispersal of its ancestor from Malaya to Sumatra during a period of low sea-levels, after which it was isolated again when sea-levels rose. On Sumatra, *metulophos* would have encountered *thomasi*, unless the latter species was already isolated in north Sumatra (north of the Sibolga area), which EM thinks may have been an island for much of the Pleistocene.

Interestingly, ZAIN (2001) estimated that *natunae* diverged from the rest of the *metulophos*-group between 1.4 and 0.8 Myr ago, which suggests that its ancestor dispersed from Malaya to the Bunguran Island area (to which *natunae* is now restricted) or that it evolved elsewhere as an isolated population, before being restricted to the Bunguran Island area after the LGM. We do not have an explanation for the divergence between *femorals* and *stamensis*, which presumably occurred on the Malay Peninsula and its southern extension. During periods of low sea-level, large rivers may have dissected this narrow land area, especially in the more eroded southern parts (where now only small island groups remain), and possibly the two species became isolated by one of these rivers.

Having provided a working model for speciation within *Presbytis*, we will now try to find an explanation for some of the peculiar distribution patterns, and the subspeciation within the group. Firstly, there is the unusual situation of general sympatry between the Bornean species (Figure 1, Table 2): *P. rubicunda* is sympatric with each of the others, and locally there is marginal sympatry between pairs of others, whereas on Sumatra and in Malaysia, the species occur almost completely allopatrically. BRANDON-JONES (1996b) ascribed this to different climatic histories of Pleistocene refugia in the two islands. We suggest that it relates, rather, to present-day ecology.

Table 2: Sympatric Species of Two Dietary Guilds in Borneo and Sumatra.

Borneo	
folivores/granivores	Frugivores
Colobines	Cercopithecine + Hylobatids
N. Kalimantan and E. Sarawak	Sabah: W. Sarawak + most of Kalimantan
<i>N. larvatus</i>	<i>N. larvatus</i>
<i>P. rubicunda</i>	<i>P. rubicunda</i>
<i>P. hosoi</i> or <i>conicus</i>	<i>P. sabana</i> or <i>frontata</i> or <i>chrysomelas</i>
<i>P. frontata</i> or <i>chrysomelas</i>	<i>T. cristatus</i>
<i>T. cristatus</i>	
Sumatra	
<i>Presbytis</i> sp.	<i>M. fascicularis</i>
<i>T. cristatus</i>	<i>M. nemusina</i>
	<i>H. lar</i> or <i>gillis</i>
	<i>Symphalangus syndactylus</i>

The higher population density (and correlated behavioral differences) of orangutans (*Pongo* spp.) in Sumatra compared to Borneo has been interpreted as springing from Sumatra's greater soil fertility, and consequent higher biotic productivity (DELGADO and van SCHAIK, 2000). In Africa, trees in forests growing on poor soils have leaves with highly developed toxic defenses against predation, and the arboreal primates that are most diverse and most abundant are those able to detoxify them, such as many colobines. It is in such forests that specialized leaf eaters and seed predators (e.g., most *Presbytis*) predominate in the poorest soils of all. On the other hand, on better soils, there is a greater diversity of trees with fleshy fruits, and all monkey taxa are more frugivorous than their vicarants in regions of poorer soil. In the richer regions of West-Central Africa, colobines, primarily folivorous, are absent altogether, with the exception of *Colobus guereza*, which at Makokou is actually predominantly a frugivore (GAUTIER-HION, 1984; GAUTIER-HION et al., 1985).

Dipterocarps form an even higher proportion of the canopy in Borneo than in Sumatra. Borneo or Java (WHITMORE, 1975, especially pp. 182-185). The fact that *hosoi*, *sabana*, and *conicus* occur sympatrically with *rubicunda*, and partly with *frontata* and *chrysomelas*, and *rubicunda* is sympatric with each of the others, suggests that there are three ecologically distinct groups. MITCHELL (1994) suggested that where *hosoi* (that is, the species from the *P. hosoi* group) is sympatric with *rubicunda*, the former may be found more often in the upper canopy and emergents of a forest while *rubicunda* is more often found lower down. *P. hosoi* is primarily folivorous (MITCHELL, 1994; RODMAN, 1978), whereas *rubicunda* is mixed granivorous, frugivorous, and folivorous (DAVIES, 1984), or even mostly seed or fruit eating (van SCHAIK et al., 1992). Such considerable ecological differences indicate that the species are also genetically rather distinct, an assumption which is supported by ZAIN's (2001) data. We therefore hypothesize that the poorer soils of Bor-

neo have permitted colobines to specialize in narrow feeding niches, where they experience limited competition from their closest relatives. On Sumatra, on the other hand, there is ecological scope for only a single folivore-granivore specialist, there is considerable competition for the same resources, and species tend to remain allopatric. Clearly, this hypothesis requires further testing.

Further, unusual distribution patterns that require an explanation are found in Sumatra. Firstly, it is remarkable that *Presbytis* is absent from Bangka and Belitung, and the south-east coast of Sumatra, although a large number of other tropical forest species occur in these areas. MEIJAARD (2003b) found evidence that, during the LGM, several areas in Sundaland were too dry to retain a closed forest cover (see Figure 8). Although EM found no such evidence for the Bangka, Belitung, and south-east Sumatra areas, others (e.g., HEANEY, 1991, see Figure 8) have included these areas in the dry zone. This could explain why *Presbytis* species did not occur in these 3 areas during the LGM, and we hypothesize that they did not manage to re-invade after climatic conditions improved.

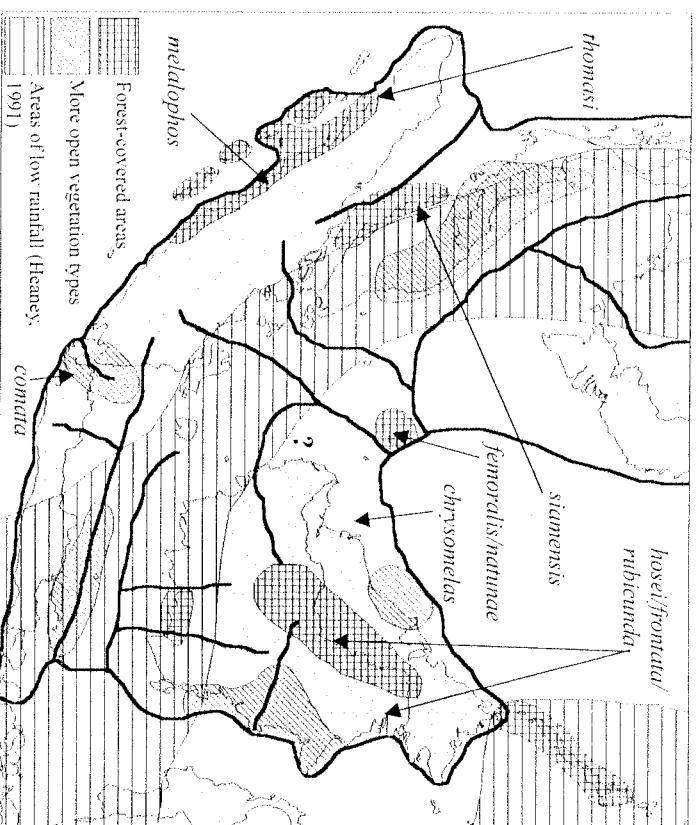


Fig. 8. Land distribution during the Last Glacial Maximum, including wet and dry zones (after MEIJAARD, 2003b).

Figure 8 also provides an explanation for the curious distribution patterns of *P. f. percura*, *P. s. penulata*, and *P. s. comata* (see Figure 1). Because of the existence of drier vegetation types during the LGM that were unsuitable for *Presbytis*, species would have retreated into wet forest refugia. Figure 8 shows that such refugia existed near the mouth of the Molengraaff River (hereafter named Bunguran refugium) and on the west side of the mountains of Malaya (west Malay refugium). MEIJAARD's hypothesis is supported by CRANBROOK (2000), who stated that "the faunal list from 40+ Kyr in Sarawak does not support BRANDON-JONES's (1998) postulate that, from 80 Ka, conditions of cold and aridity eliminated forest habitat suitable for leaf monkeys and orangutans". CRANBROOK does, however, suggest that, during the LGM, lower montane forest could have vegetated the entire present lowland area of Borneo, as indicated by the fossil finds at sea-level of montane mammals such as Lesser Gymnure (*Hylomyx sullus*) and Ferret Badger (*Melogale persomata*). If such temperature sensitivity is a key factor, then for long periods during the LGM, the rich flora of the lowland mixed dipterocarp forest formations must have been confined to extreme lowland elevations, perhaps in river valley refugia or on the maritime periphery. On good soils, forest patches could have attained high stature. There must have been a variety of evergreen trees, with a sufficiently extended fruiting season, to support large frugivore primates (orang-utan), as well as a perennial leaf cover to feed the folivorous leaf monkeys.

If we assume that *femoralis* retreated to the Bunguran refugium, and *siamensis* to the west Malay one, then after the climatic amelioration, when sea-levels started to rise, *femoralis* could have migrated west following the courses of the main rivers, which would have led them northwest towards central Malaya and southern Thailand, and west-southwest towards their present-day Sumatran ranges. *P. siamensis*, on the other hand, could have stayed in the west Malay refugium, but presumably found an opportunity to reach eastern Sumatra, directly opposite its Malayan range. *P. femoralis*, on its return to Sumatra, drove a wedge in the *siamensis* population. ZAIN's (2001) data show that this may not be the full story, as he found that *P. femoralis femoralis* and *P. f. robinsoni* diverged during the Middle Pleistocene, ca. 750 Kyr before the LGM, while also suggesting that *femoralis* is not monophyletic relative to *melalophos* and *siamensis*. This could mean that *P. f. robinsoni*, from the northern Malay Peninsula, is specifically distinct from *P. femoralis femoralis* and *P. f. percura*. Further taxonomic and phylogenetic work is needed before we can really test the above hypothesis.

For *P. chrysomelas*, a similar scenario can be developed, with the species retreating towards the Bunguran refugium during the LGM (note that there are no pre-Holocene fossils of this species on mainland Borneo), after which it reinvented Borneo from the west. *P. chrysomelas* largely displaces both *frontata* and *rubicunda* in the lowlands of Sarawak (BANKS, 1934; NIJMAN and MEIJAARD, in preparation), whereas in east Borneo, where *chrysomelas* is absent, *frontata* and *rubicunda* are found at low elevations. This suggests that *chrysomelas* occupied the exposed Sunda Shelf during the LGM, and when sea-levels started to rise it moved into western Borneo, thereby displacing *frontata* and *rubicunda*, especially in swamp areas.

Conclusion

In this paper we have attempted to merge information from a variety of sources, including genetics, morphological studies, and palaeoenvironmental reconstructions, to improve our understanding of the evolution of *Presbytis* leaf monkeys in the Sundatic Region. We think that our model is in general agreement with the existing data, although many hiatuses remain in our knowledge. Further work is needed on the phylogeny of the genus, especially addressing *potenziani*, *fontata*, the *hosi-* group, and *chrysomelas*, while also more research is needed to provide more accurate palaeoenvironmental maps.

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