CHAPTER TWELVE

Primate Biogeography and Ecology on the Sunda Shelf Islands: A Paleontological and Zooarchaeological Perspective

Terry Harrison, John Krigbaum, and Jessica Manser

ABSTRACT

Sundaland, with its complicated history of island formation and landbridge connections with mainland Southeast Asia, has figured prominently in studies of primate biogeography. The non-human primates on Sundaland are taxonomically diverse (comprising

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27 species), and they exhibit relatively high levels of provinciality and endemism. By combining archaeological and paleontological evidence, with data from molecular, paleoclimatological and paleoecological studies, it is possible to reconstruct the major zoogeographic events that took place in the formation of the present-day catarrhine primate community on the Sunda Shelf islands. It can be inferred that by the Late Pliocene the main islands of the Sunda Shelf had a primate fauna that included *Pongo pygmaeus* (Sumatra, Java and Borneo), *Hylobates* spp. of the *lar*-group (Sumatra, Mentawai Islands, Borneo, and Java), *Macaca nemestrina* (Sumatra, Mentawai Islands, Borneo, and Java), the common ancestor of the *Trachypithecus auratus/cristatus* clade (Java and Sumatra), and *Presbytis* spp. (Sumatra, Mentawai Islands, Borneo, Sumatra, and Java). Most of these taxa probably arrived during the Pretiglian cold phase, starting at ~2.8 Ma, when sea levels fell by more than 100 m. It is also likely that *Nasalis larvatus* (Borneo) and *Simias concolor* (Mentawai Islands) were already present as endemic taxa in the Late Pliocene, and that their last common ancestor had arrived in the Sunda islands by the early Pliocene. Soon after this initial period of colonization, *Hylobates* and *Presbytis* underwent rapid speciation as a consequence of vicariance and relictual survivorship, giving rise to *P. thomasi* on Sumatra, *H. klossii* and *P. potenziani* on the Mentawai Islands, *H. albibarbis, H. muelleri, P. hosei, P. frontata*, and *P. rubicunda* on Borneo, and *H. moloch* and *P. comata* on Java. During the Late Pliocene and Early Pleistocene, probably associated with a cold climate maximum at ~1.8 Ma, *Presbytis melalophos* and *P. femoralis*, along with *Macaca fascicularis*, colonized Sumatra, the Natuna Islands and Borneo from the Malay Peninsula. At about the same time, the orang-utan populations on Sumatra, Java and Borneo began to differentiate from each other. *Hylobates lar*, *H. agilis* and *H. syndactylus* extended their range from the Malay Pensinsula into Sumatra (and Java), probably during the Middle to Late Pleistocene, coincident with the arrival of *Trachypithecus cristatus* on mainland Southeast Asia. Meanwhile, *Pongo pygmaeus*, *Hylobates syndactylus* and *Macaca nemestrina* were extirpated on Java, probably as a consequence of a combination of ecological changes and the impact of early hominin incursions.

Key Words: Sundaland, zooarchaeology, paleontology, biogeography, ecology, primates

INTRODUCTION

The Sunda Shelf, with an estimated area of ~1,850,000 km^2, lies partially submerged beneath the Java Sea and the southwestern part of the South China Sea (Tjia, 1980; Hanebuth *et al.*, 2000). Sundaland is the name given to that area of the Sunda Shelf that emerged during periods of low sea level, particularly during the Quaternary, when sea levels fell by at least 120 m below present-day levels (Figure 1). It includes the Malay Peninsula, Borneo, Sumatra, Java, Bali, Palawan, the Mentawai Islands, and the smaller intervening

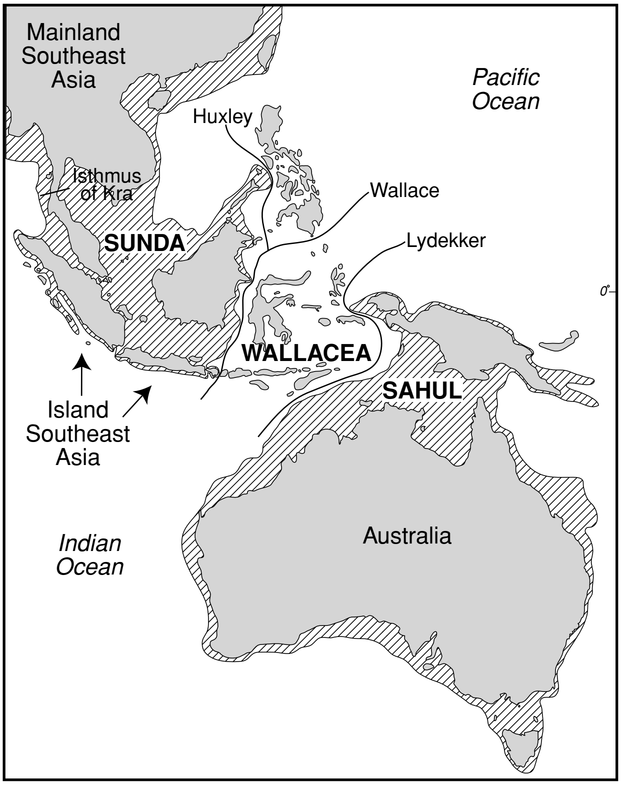

Figure 1. Map of Australasia showing extent of the Sunda and Sahul continental landmasses with Wallacea in between. Biogeographical lines of Wallace, Huxley, and Lydekker are indicated, as is the Isthmus of Kra.

islands. Periodically during the Pliocene and Pleistocene, Sundaland formed a continuous subcontinental landmass connecting Sumatra, Java, Borneo, and Palawan with the Asian mainland (Haile, 1973; Sartono, 1973; Verstappen, 1975; Tjia, 1980). The eastern boundary of Sundaland is delimited by Wallace's Line, as modified by Huxley (1868), which runs between Palawan and Luzon, Borneo and Sulawesi, and Bali and Lombok—this defines the boundary of the Oriental zoogeographic province (Huxley, 1868; Simpson, 1977). To the east is Sahulland, comprising New Guinea, Australia, and Tasmania. Its western boundary, represented by Lydekker's Line, delimits the Australasian zoogeographic province (Lydekker, 1896; Simpson, 1977).

During the Last Glacial Maximum (LGM) at ~21–18 ka, when sea levels were at their lowest, Sahulland and Sundaland continued to be separated by deep oceanic troughs. Wallacea, the region between Sahulland and Sundaland, consists of the Lesser Sunda Islands (i.e., Lombok, Sumbawa, Sumba, Flores, and Timor), Sulawesi, the Philippines (excluding Palawan), and the Moluccas (Dickerson, 1928; Scrivenor *et al.*, 1941–42; Simpson, 1977; Darlington, 1980; Groves, 1985). During the later Pleistocene glacial periods the islands of Wallacea remained unconnected to Sahulland or Sundaland (Audley-Charles, 1981; Ollier, 1985). It is possible, however, that the Philippines proper and Sulawesi may have been connected to Borneo by landbridges during the Pliocene and Early Pleistocene, when sea levels were strongly influenced by cold-climate peaks (Sartono, 1973; Heaney, 1985, 1986; Prentice and Denton, 1988; Shackleton, 1995; Moss and Wilson, 1998).

Given the position of Sundaland at the junction between two major zoogeographic provinces that straddle the Equator, and its complicated history of island formation and landbridge connections with mainland Southeast Asia, it is not surprising that the Sunda Shelf islands have figured prominently in studies of mammalian biogeography (e.g., Simpson, 1977; Heaney, 1984, 1986; Groves, 1985; Han and Sheldon, 2000; Mercer and Roth, 2003). In particular, the systematics and zoogeographic relationships of the primates on Sundaland have been extensively studied, but it is evident from recent phylogenetic analyses of the primates in the region, using various lines of evidence, that the reconstructed biogeographic history is exceedingly complicated (e.g., Brandon- Jones, 1996, 1998, 2001; Rosenblum *et al.*, 1997a, b; Morales and Melnick, 1998; Harcourt and Schwartz, 2001; Evans *et al.*, 2003). There are currently 27 species of nonhuman primates with geographic distributions that encompass Sundaland, and since these comprise more than one-third of all large mammals from the region, they represent an important faunal component. Only two of these taxa are non-catarrhine primates, *Nycticebus coucang* (slow loris) and *Tarsius bancanus* (western tarsier). The catarrhines of Sundaland are diverse (comprising 41% of all Asian catarrhine species), and they exhibit relatively high levels of provinciality and endemism (76% of the 25 species are unique to Sundaland).

We present here a study of the catarrhine primate faunas from paleontological and archaeological sites in Borneo, Sumatra, and Java. Although the fauna from these sites represents a limited database, their identification and study introduces a unique diachronic perspective on the biogeography and ecology of the Sunda Shelf islands. This analysis is of particular interest because it provides insights into prehistoric human hunting strategies and dietary preferences, and offers clues to understanding regional paleoecological change—both important factors that likely influenced the zoogeographic distribution of primates on Sundaland.

Although there appear to have been few demonstrable local extinctions on the Sunda Shelf islands during the Quaternary (*Hylobates syndactylus*, *Pongo pygmaeus* and *Macaca nemestrina* became extinct on Java; Hooijer, 1948, 1960, 1962a), climatic perturbations and the arrival of modern humans during the later Pleistocene may have had a profound impact on the primate fauna. Zooarchaeological evidence indicates that primates were extensively exploited for food, but the presumed low density of humans on the Sunda Shelf islands, and their limited technologies for hunting arboreal mammals, suggest that they had little impact on primate distributions, except at the local level (Harrison, 1996). A more important factor influencing the distribution of primate species seems to have been ecological changes caused by cooler, more seasonal climatic conditions during the Pliocene and Pleistocene, and concomitant glacio-eustatic sea level fluctuations associated with northern hemisphere glacial phases (Verstappen, 1975; Heaney, 1991; Prentice and Denton, 1988; Shackleton, 1995). These ecological changes apparently had a much more significant impact on the structure and geographic distribution of the catarrhine primate community (see Harrison, 1996, 2000).

Finally, we attempt to combine the archaeological and paleontological evidence with data from molecular, paleoclimatological, and paleoecological studies in order to recreate the major zoogeographic events that took place in the formation of the present-day catarrhine primate community on the Sunda Shelf islands. Given the limitations of the evidence available, such a scenario involves a good deal of speculation, but we believe that the analysis represents a useful first step in the development of a broader synthesis, and one that can be used as a provisional model to be reassessed as new evidence comes to light on the zoogeographic relationships and evolutionary history of Southeast Asian primates.

PALEOENVIRONMENTAL CONTEXT

The geological history of Southeast Asia has been reviewed by Katili (1975), Audley-Charles (1981, 1987), Ollier (1985), McCabe and Cole (1989), Hutchison (1989), Hall (1998, 2001), and Metcalfe (1998). The major geological processes and events that led to the formation and present-day positions of the islands and landmasses of Sundaland were completed by the Early Pliocene at ~5 Ma (Audley-Charles, 1981; Moss and Wilson, 1998; Hall, 1998). Nevertheless, Southeast Asia has continued to experience volcanic and tectonic activity (Ashton, 1972; Aldiss and Ghazali, 1984; Hall, 1998). Danau Toba in northern Sumatra is associated with the most dramatic examples of Pleistocene volcanism in the region (dated at about 840 ka, 501 ka, and 74 ka; Diehl *et al.*, 1987; Ninkovich *et al.*, 1978; Chesner *et al.*, 1991), and it presumably had a significant impact on the local ecology. The largest and most recent eruption during the Late Pleistocene dispersed ash as far as India and the Strait of Malacca (Ninkovich *et al.*, 1978; Rose and Chesner, 1987; Chesner *et al.*, 1991; Bühring and Sarnthein, 2000), and it has been implicated in a volcanic winter that may have hastened, at least regionally, the global cooling trend that followed the Odderade interstadial (Rampino *et al.*, 1988; Chesner *et al.*, 1991; Rampino and Self, 1992; Zielinski *et al.*, 1996).

During the Pliocene, global temperatures were generally warmer, with estimated maximum temperatures 3.6°C higher than at present (Dowsett *et al.*, 1992, 1996; Crowley, 1991, 1996; Sloan *et al.*, 1996). Tropical sea surface temperature estimates, based on marine microfossils, are comparable to present-day (Dowsett *et al.*, 1996; Crowley, 1996), but there is evidence of cooler conditions towards the end of the Pliocene, presumably correlated with the Pretiglian cold phase of northern latitudes dated at ~2.75 Ma (King, 1996; Ravelo *et al.*, 2004). The main Pleistocene glacial spikes occur at ~1.8 Ma, (Eburonian), ~0.92 Ma (Menapian), ~630 ka (OIS 16), ~430 ka (OIS 12), ~350 ka (OIS 10), ~140 ka (OIS 6) and ~18 ka (OIS 2) (Chappell and Shackleton, 1986; Chappell *et al.*, 1996). Average regional temperature estimates during the Pleistocene, based largely on proxy data from deep-sea cores, indicate cooler conditions by ~3–5°C on land and ~2–4°C in the seas (Petersen, 1969; Verstappen, 1975; Hope *et al.*, 1976; Rind and Peteet, 1985; Flenley, 1985; Tan, 1985; Chappell *et al.*, 1996). In particular, oxygen isotope data confirm cooler seas during glacials and interstadials, and suggest that tropical seas were ~5–6°C cooler than today (e.g., Rind and Peteet, 1985; Chappell, 1994; Stute *et al.*, 1995; Broecker, 1996; Bush and Philander, 1998; McCulloch *et al.*, 1999; Lea *et al.*, 2000). Temperatures on land and sea rose by 1–3°C during Pleistocene interglacial periods and the Holocene climatic optimum (Verstappen, 1975, 1997; Flohn, 1981; Gagan *et al.*, 1998). The Early Holocene in low latitude regions was still marked by significantly colder sea surface temperatures (~6°C cooler than at present), followed by a rapid increase in temperature up to present-day values by ~4 ka (Guilderson *et al.*, 1994; McCulloch *et al.*, 1996; Beck *et al.*, 1997).

During Pleistocene glacial phases, climatic conditions in Southeast Asia were drier and cooler than at present, with longer dry seasons and shorter wet seasons, and more pronounced seasonality (Petersen, 1969; Morley, 1982; Debaveye *et al.*, 1986; Thomas, 1987; Heaney, 1991; van der Kaars and Dam,

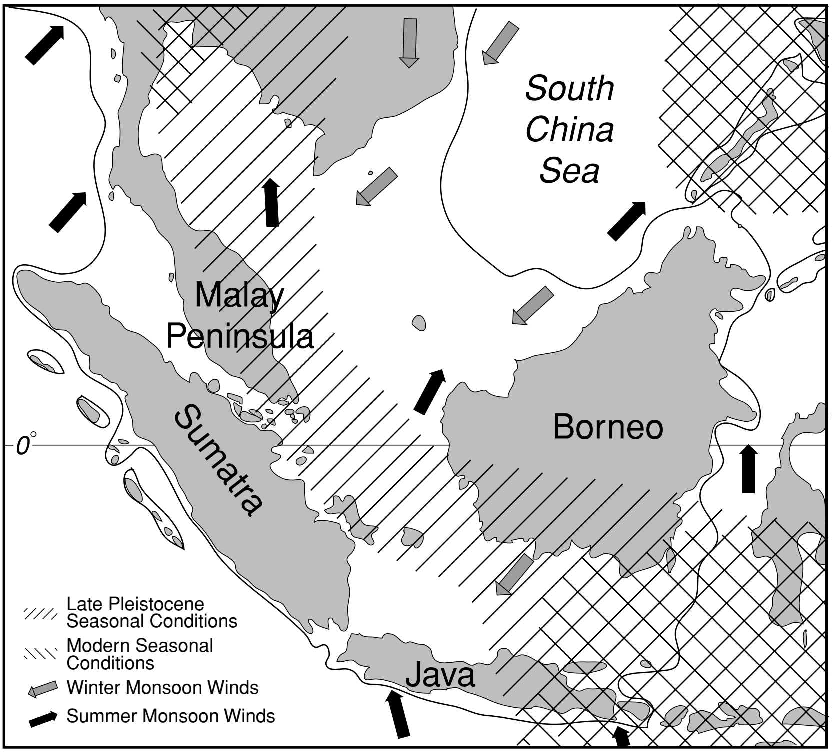

Figure 2. Late Pleistocene and present-day climate patterns in Sundaland. Late Pleistocene conditions (e.g., during the LGM) were considerably more seasonal than today. The extent of dual winter and summer monsoons (arrows) is more intense in present-day perhumid areas than in more seasonal ones. Figure adapted from Heaney (1991).

1995; Verstappen, 1997; Brandon-Jones, 1998). Despite a decrease in rainfall, Pleistocene Southeast Asia may not have been as dry as other equatorial regions (Verstappen, 1975). Rainfall increased during warm interstadials and interglacials, and again during the terminal Pleistocene, followed by alternating dry and moist periods in the Early and Middle Holocene (Flohn, 1981; Verstappen, 1997).

Palynological studies suggest that changes in vegetation in Southeast Asia during the Late Pleistocene and Holocene correlate with documented changes in temperature and precipitation. In general, during drier Pleistocene glacial periods grasslands and montane forests expanded, while tropical lowland rainforests contracted (Figure 2). Marine and terrestrial core data from Sumatra, Java, eastern Indonesia, New Guinea, and northern Australia record a decrease in forest coverage, an increase in the spread of grasslands, and an altitudinal lowering of montane vegetation zones by about 300–500 m during the LGM

(Van Andel *et al.*, 1967; Hope *et al.*, 1976; Walker and Flenley, 1979; Flenley, 1979; Maloney, 1980, 1981; Morley, 1982; Stuijts, 1983/1984; Newsome and Flenley, 1988; Stuijts *et al.*, 1988; Hope and Tulip, 1994; Haberle, 1998; van der Kaars, 1998; Kershaw *et al.*, 2001). Van der Kaars (1998) and Kershaw *et al.* (2001) suggest that pollen spectra indicate a 30–50% decline in precipitation and a reduction in mean temperatures by as much as 6–7°C. Morley and Flenley (1987) infer a dry seasonal grassland belt running southwards along the Malay Peninsula and into Java (Flohn, 1981; van der Kaars, 1991; van der Kaars and Dam, 1995). Kershaw *et al.* (2001), by contrast, contend that perhumid rainforest was only replaced by grassland in regions already experiencing some degree of seasonality, and that reduced precipitation did not have a major impact on evergreen tropical forest in core areas, such as Borneo, during the LGM. Since the exposed continental shelves appear to have been covered by rainforest in more mesic areas and by grassland, woodland, and sedgeland in drier areas, there was a net increase in the availability of tropical forest habitats on Sundaland during the LGM, although it was probably more fragmented than at present. Kershaw *et al.* (2001) do acknowledge, however, that a dry corridor may have occurred during cold phases prior to the LGM. The warmer interglacials and terminal Pleistocene experienced expansion of the core rainforest areas, generally denser vegetation cover in drier areas, and the retreat of montane vegetation zones (Flenley, 1979; Verstappen, 1975, 1997; Flohn, 1981; van der Kaars, 1991; Hope and Tulip, 1994). Mangrove forests seem to have dominated the lowland coastal areas during these periods, as it does today (Biswas, 1973).

In conjunction with the generally warmer temperatures during the Pliocene, average global sea levels are estimated to have been between 20–60 m higher than at present (Crowley, 1996; Dowsett *et al.*, 1996; Haq *et al.*, 1987; Wardlaw and Quinn, 1991). Data from deep-sea cores provide a well documented chronology for global glacio-eustatic sea level changes over the past 5 Ma (Chappell and Shackleton, 1986; Shackleton, 1987, 1995; Prentice and Denton, 1988; Chappell, 1994; Chappell *et al.*, 1996). Figure 3 outlines Late Quaternary sea level fluctuations based on d^{18}O data from the Huon Peninsula and the Sulu Sea (Chappell and Shackleton, 1986; Martinson *et al.*, 1987; Linsley, 1996; McCulloch *et al.*, 1999), and these correspond to high-resolution global estimates of sea level changes (Fairbanks, 1989; Guilderson *et al.*, 1994).

The LGM witnessed a dramatic decrease in sea level of 120–135 m (Van Andel *et al.*, 1967; Van Andel and Veevers, 1967; Yokoyama *et al.*, 2000). Lower

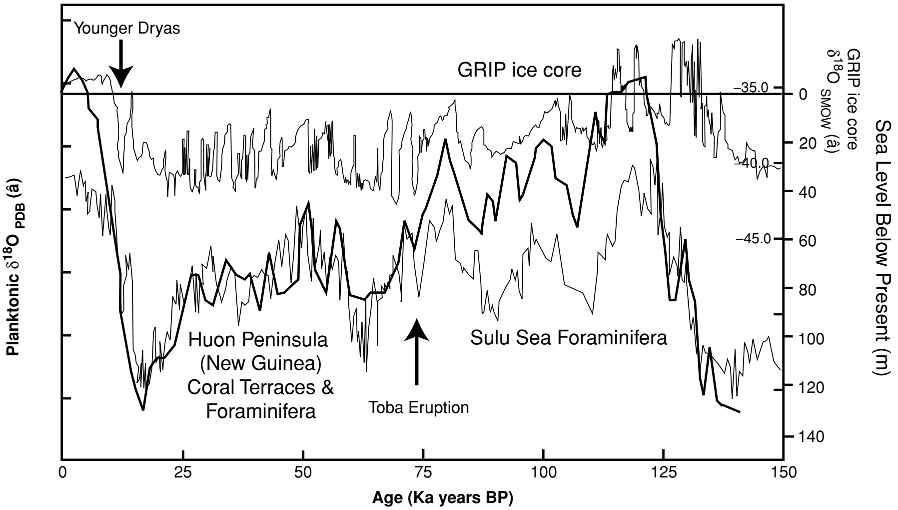

Figure 3. Late Quaternary sea level data based on Huon Peninsula (New Guinea) coral, d^{18}O (PDB) and Sulu Sea d^{18}O (SMOW). Oxygen isotope stages correspond to global climate trends. For example, OIS 2 corresponds to the Last Glacial Maximum (LGM) ~21–17 ka. Other climatic events (e.g., Toba eruption, Younger Dryas) are also noted. Figure adapted from Linsley (1996).

sea levels throughout the Plio-Pleistocene would have exposed substantial regions of the Sunda shelf (Molengraff and Weber, 1920; Fairbridge, 1953; Dobby, 1960; Petersen, 1969; Flint, 1971; Sawamura and Laming, 1974; Verstappen, 1975, 1997; Wang *et al.*, 1999; Hanebuth *et al.*, 2000; Sun *et al.*, 2000). Figure 4 depicts the exposed shelf during these periods, and shows major river systems that originated in the highlands of Borneo, Sumatra, Java, and the Malay Peninsula and transected the lowland areas (Molengraff and Weber, 1920; Umbgrove, 1938; Haile, 1973; Verstappen, 1975; Voris, 2000). In conjunction with tropical forest fragmentation, these drainage systems would probably have represented significant zoogeographic barriers to mammals, and may have contributed to increased population isolation and speciation.

The post-LGM period, up to and including the Middle Holocene, was characterized by a general trend of sea level increase (Tjia, 1970,1980; Emery *et al.*, 1971; Barham and Harris, 1983; Chappell and Shackleton, 1986; Shackleton, 1987; Edwards *et al.*, 1993; Chappell, 1994; Chappell *et al.*, 1996; Verstappen, 1997; Fleming *et al.*, 1998; Hanebuth *et al.*, 2000). A sea level curve based on sediment analysis from the Sunda Shelf documents an increase in sea level between 19–13 ka (from −114 to −64 m) (Hanebuth *et al.*, 2000).

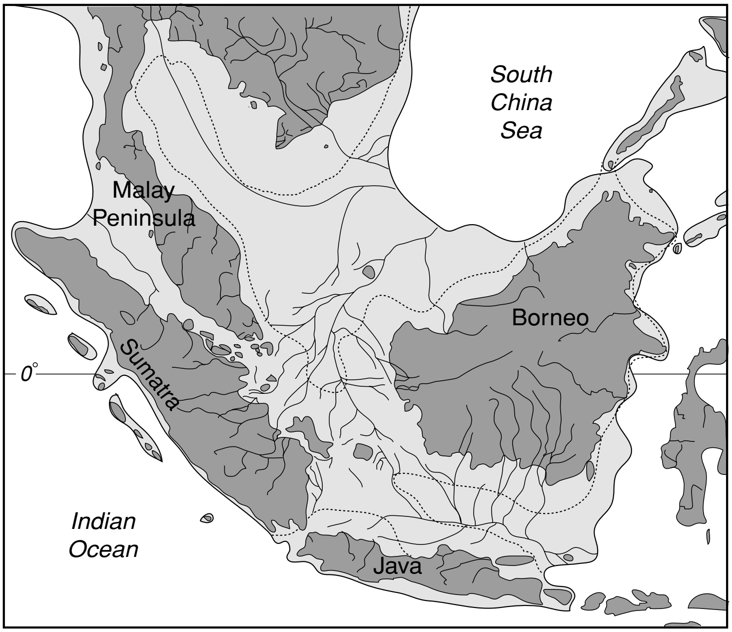

Figure 4. Map of Sundaland and adjoining islands showing paleo-river systems in relation to the 100 m isobath (solid line) and the 50 m isobath (dotted line). During low sea stands, these larger river systems were likely important zoogeographic barriers.

Average global sea levels rose to 10–20 m below present at the beginning of the Holocene (~10 ka) (Shackleton, 1987; Edwards *et al.*, 1993; Chappell, 1994; Linsley, 1996; Fleming *et al.*, 1998). During the mid-Holocene, average global sea level was at, or slightly above, present-day level (Tjia, 1970, 1977, 1984; Shackleton, 1987; Linsley, 1996; Edwards *et al.*, 1993). Sediment profiling in the Strait of Malacca confirms transgression of this area during the Holocene, reaching a maximum height of +5 m above present-day levels at ~5–4 ka (Kudrass and Schlüter, 1994). Similar estimates are inferred from cores taken off the coast of northeastern Johore on the Malay Peninsula (Nossin, 1962). Radiocarbon dating of shells and corals from cores taken from the north coast of Java indicate maximum sea level at 3,650 C^{14} yrs BP +3 m above present (Thommeret and Thommeret, 1978). Although minor fluctuations occurred throughout the Holocene, sea level reached a maximum height at ~5 ka of about 4–5 m above present level (Tjia, 1970, 1977, 1984; Verstappen, 1997), and since the mid-Holocene they have decreased to present-day levels (Tjia, 1970; Fleming *et al.*, 1998).

In summary, glacial periods in the northern hemisphere were associated in Southeast Asia with cooler and drier conditions, in which tropical forests were fragmented and seasonal woodland and savanna habitats expanded. During these glacial periods, beginning in the Late Pliocene, a belt of dry woodland and savanna probably extended southwards from the eastern side of the Malay Peninsula, through southern and eastern Borneo, to eastern Java and the Lesser Sunda Islands (Morley and Flenley, 1987; Heaney, 1991; Gathorne-Hardy *et al.*, 2002). This dry zone, with habitats largely unsuitable for arboreal primates, in conjunction with major river systems (now largely submerged under South China and Java seas), presumably provided a significant barrier to migration (Heaney, 1991; Voris, 2000). Four distinct subprovinces resulted: (1) central and northern Borneo; (2) Malay Peninsula including Sumatra; (3) Mentawai Islands; and (4) Western Java (see Figure 2). These areas probably retained tropical forest refugia with isolated and impoverished primate communities (see Brandon-Jones, 1998, 2001). A combination of relictual survivorship, vicariance, and differential recolonization resulted in distinct primate faunas in each subprovince (Table 1).

The Mentawai Islands have four catarrhine species, all of which are endemic. They are probably specialized insular members of a primate fauna that probably inhabited Sundaland during the Late Pliocene (when the Mentawai Islands were connected to Sumatra by a landbridge across the Mentawai Straits) (Samuel *et al.*, 1997). Borneo is unusual in having a high level of endemicity given its size (Table 1), but this is presumably due to its degree of isolation from other Sunda subprovinces during glacial periods, starting in the Late Pliocene. Sumatra and Java, by contrast, were more readily recolonized from mainland Southeast Asia via the Malay Peninsula (we find this scenario more plausible than Brandon-Jones' [1996, 1998, 2001] suggestion that the Mentawai Islands represented the relictual source for subsequent colonizations of Sumatra and Borneo), although Java sustained an impoverished and endemic primate fauna due to partial isolation and habitat differences.

THE ARCHAEOLOGICAL AND PALEONTOLOGICAL RECORD

Of the relatively few archaeological and paleontological localities on the major islands of Sundaland many have yielded the remains of non-human catarrhine primates. These provide an important line of evidence that helps in reconstructing the ecological and zoogeographic history of the region. A list of key localities is presented in Table 2 (see Figure 5 for locations). Unfortunately, few of the sites have been radiometrically dated; most have been correlated using

Table 1. List of extant non-human catarrhine primates on Sundaland[a]

	Malay Peninsula	Borneo	Sumatra	Mentawai Island	Java
Cercopithecidae					
Colobinae					
Presbytis comata (Javan surili)					X
Presbytis femoralis (Banded surili)[b]	X	X	X		
Presbytis frontata (White-fronted langur)		X			
Presbytis hosei (Hose's langur)		X			
Presbytis melalophos (Sumatran surili)			X		
Presbytis potenziani (Mentawai langur)				X	
Presbytis rubicunda (Maroon leaf monkey)		X			
Presbytis thomasi (Thomas's langur)			X		
Trachypithecus cristatus (Silvery lutung)	X	X	X		
Trachypithecus auratus (Javan lutung)					X
Trachypithecus obscurus (Dusky leaf monkey)	X				
Nasalis larvatus (Proboscis monkey)		X			
Simias concolor (Pig-tailed langur)				X	
Cercopithecinae					
Macaca arctoides (Stump-tailed macaque)	X				
Macaca fascicularis (Long-tailed macaque)	X	X	X		X
Macaca nemestrina (Sunda Pig-tailed macaque)	X	X	X		
Macaca pagensis (Mentawai macaque)				X	
Hylobatidae					
Hylobates agilis (Agile gibbon)	X		X		
Hylobates albibarbis (Bornean white-bearded gibbon)		X			
Hylobates lar (White-handed gibbon)	X		X		
Hylobates klossii (Kloss gibbon)				X	
Hylobates moloch (Silvery gibbon)					X
Hylobates muelleri (Müller's Bornean gibbon)		X			
Hylobates syndactylus (Siamang)	X		X		
Hominidae					
Pongo pygmaeus (Orang-utan)		X	X		
Total catarrhine species	9	11	10	4	4
Number of endemic species	0	6	2	4	3

[a] Sources: Medway (1970); Oates *et al.* (1994); Fooden (1975, 1995); Rowe (1996); Groves (2001a); Brandon-Jones *et al.* (2004). Common names after Groves (2001a).

[b] Includes *P. chrysomelas* and *P. siamensis* recognized as distinct species by Groves (2001a).

Table 2. List of archaeological and paleontological sites on Sunda Shelf islands that have yielded non-human catarrhine primates

Island	Locality	Inferred age	Key references
Borneo	Niah Cave (Sarawak)	Late Pleistocene–Early Holocene	Harrisson, 1958, 1970; Hooijer, 1960, 1961, 1962a,1962b; Medway, 1977; Harrison, 1996, 2000
	Paku Flats (Sarawak)	Late Pleistocene–Early Holocene	Everett, 1880; Harrison, 2000
	Jambusan (Sarawak)	Late Pleistocene–Early Holocene	Everett, 1880; Harrison, 2000
	Gua Sireh (Sarawak)	Early Holocene	Ipoi, 1993; Bellwood, 1997; Harrison, 2000
	Madai (Sabah)	Holocene	Bellwood, 1988; Cranbrook, 1988; Harrison, 1998, 2000
Java	Sangiran	?Late Pliocene–Middle Pleistocene	Aimi, 1981; Jablonski and Tyler, 1999
	Djetis	?Early–Middle Pleistocene	Hooijer, 1948
	Trinil	Middle Pleistocene	Hooijer, 1948, 1962a; van den Bergh *et al.*, 2001
	Bangle	Middle Pleistocene	Hooijer, 1962a
	Soember Kepoeh	Middle Pleistocene	Hooijer, 1962a
	Tegoean	Middle Pleistocene	Hooijer, 1962a
	Saradan	Middle Pleistocene	Hooijer, 1962a
	Glagahombo	Middle Pleistocene	Aimi and Aziz, 1985
	Ndangklampok	Middle Pleistocene	Aimi and Aziz, 1985
	Kali Brangkal	Middle Pleistocene	Aimi and Aziz, 1985
	Ngandong	?Late Pleistocene	Aziz, 1989; van den Bergh *et al.*, 2001
	Punung Fissures	Late Pleistocene	Hooijer, 1948; Badoux, 1959; van den Bergh *et al.*, 2001
	Wajak	Holocene	Hooijer, 1962a; van den Brink, 1982; Aziz and De Vos, 1989
	Gua Jimbe	Holocene	Hooijer, 1962a
	Gua Ketjil	Holocene	Hooijer, 1962a
	Sampung	Holocene	Dammerman, 1934
Sumatra	Lida Ayer	Late Pleistocene–Early Holocene	Dubois, 1891; Hooijer, 1948, 1962a; Harrison, 2000
	Sibrambang	Late Pleistocene–Early Holocene	Dubois, 1891; Hooijer, 1948, 1962a; Harrison, 2000
	Djambu	Late Pleistocene–Early Holocene	Dubois, 1891; Hooijer, 1948, 1962a; Harrison, 2000

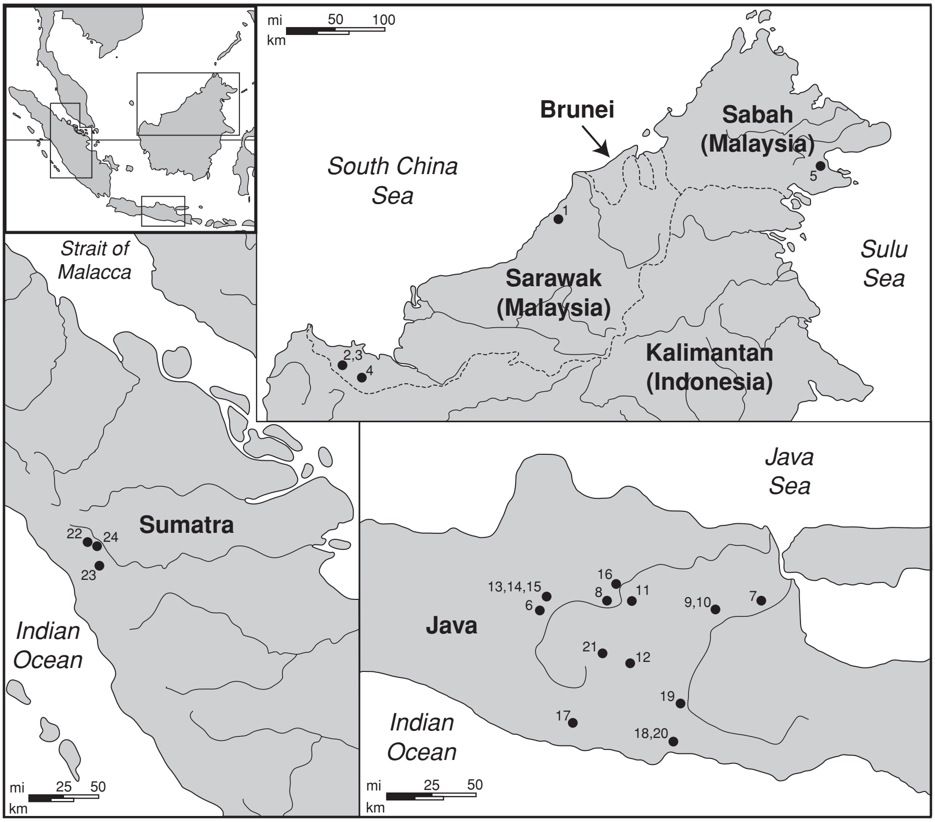

Figure 5. Map of principal Sundaic Islands showing location of sites discussed in text and listed in Table 2. Sites: 1. Niah Cave; 2. Paku Flats; 3. Jambusan; 4. Gua Sireh; 5. Madai; 6. Sangiran; 7. Djetis; 8. Trinil; 9. Bangle; 10. Soember Kepoeh; 11. Tegoean; 12. Saradan; 13. Glagahombo; 14. Ndangklampok; 15. Kali Brangkal; 16. Ngandong; 17. Punung; 18. Wajak; 19. Gua Jimbe; 20. Gua Ketjil; 21. Sampung; 22. Lida Ayer; 23. Sibrambang; 24. Djambu.

biostratigraphic data. The best series of dates is associated with Sangiran (Late Pliocene to Middle Pleistocene) and Niah Cave (Late Pleistocene to Holocene). ^{40}Ar/^{39} Ar dating of the Sangiran Dome succession has produced dates of ~0.8–1.6 Ma for the Kabuh Formation and ~1.6–2.0 Ma for the Pucangan Formation (Swisher *et al.*, 1994; Larick *et al.*, 2000). At Niah, a series of samples of charred bone and charcoal have yielded ^{14}C dates that indicate that the archaeological occupation of the site dates, more or less continuously, from older than 41,500 ± 1000 BP up to the present-day (Harrisson, 1959a; Harrison, 1996; Krigbaum, 2001). Radiocarbon dating at Gua Sireh and Madai Caves shows that occupation horizons with primates are younger than 10,500 BP (Bellwood, 1988; Ipoi, 1993; Harrison, 1998).

Of the nine genera of extant primates currently found on the Sunda Shelf islands, six are represented in the archaeological and paleontological record. Only *Tarsius*, *Nasalis*, and *Simias* are not recorded, while *Nycticebus* is known only from a few fragmentary specimens from Niah Cave in Sarawak (Medway, 1977) and from Holocene cave sites in Java (van den Bergh *et al.*, 2001). Each of the catarrhine genera known to occur—*Pongo, Hylobates, Macaca, Presbytis, and Trachypithecus*—are discussed in turn below.

Pongo

Two subspecies of orang-utan are generally distinguished—*Pongo pygmaeus pygmaeus* Linnaeus, 1760, and *Pongo pygmaeus abelii* Lesson, 1827, from Borneo and Sumatra respectively (von Koenigswald, 1982; Napier and Napier, 1985; Groves and Holthuis, 1985; Courtenay *et al.*, 1988; Groves, 1989). Recently, there has been some discussion concerning the possibility of recognizing additional subspecies or even separating the Sumatran and Bornean populations at the species level (Groves, 1986, 1989, 2001a; Courtenay *et al.*, 1988; Groves *et al.*, 1992; Rowe, 1996; Zhi *et al.*, 1996; Delgado and van Schaik, 2000; Brandon-Jones *et al.*, 2004). Certainly the two subspecies can be readily distinguished from each other based on hair color and length, distribution of facial hair, the size and shape of the throat pouches and cheek flanges in males, and various cranio-dental characteristics (MacKinnon, 1973; Groves, 1986, 2001a; Weitzel *et al.*, 1988; Courtenay *et al.*, 1988; Uchida, 1998). These morphological distinctions are supported by molecular and karyological data (Janczewski *et al.*, 1990; Ryder and Chemnick, 1993; Xu and Arnason, 1996; Zhi *et al.*, 1996; Karesh *et al.*, 1997; Rijksen and Meijaard, 1999). However, we conservatively subdivide extant orang-utans into two subspecies, and consider that the degree of morphological and molecular distinctiveness reflects the fact that these demes have been effectively isolated from one another for a considerable period of time, probably since the Early Pleistocene (Ryder and Chemnick, 1993; Zhi *et al.*, 1996; Karesh *et al.*, 1997).

The geographic range of the orang-utan is today limited to northern Sumatra and Borneo (von Koenigswald, 1982; Röhrer-Ertl, 1988; Groves, 1989, 2001a), but evidence from the paleontological and archaeological record shows that the species (or at least genus) was more widely distributed throughout Southeast Asia during the Late Quaternary. Fossil and subfossil material has been recovered from sites in southern China, Vietnam, Laos, Cambodia, Thailand, Sumatra, Java, and Borneo (Pei, 1935; Hooijer, 1948, 1961; Kahlke, 1972; Delson, 1977; Aigner, 1978; Han and Xu, 1985; Gu *et al.*, 1987; Olsen and Ciochon, 1990; Cuong, 1992; Nisbett and Ciochon, 1993; Schwartz *et al.*, 1994, 1995; Drawhorn, 1995; Tougard and Ducrocq, 1999; Bacon and Long, 2001). On mainland Southeast Asia, the remains of orang-utans have been found at Liucheng in southern China that date back to the Early Pleistocene (although de Vos [1984] has argued that the fauna also contains Middle to Late Pleistocene taxa). It also appears that the species survived until the latest Pleistocene in Vietnam (Tan, 1985; Schwartz *et al.*, 1995; Bacon and Long, 2001). The fossil record documenting the evolutionary history of orang-utans in the islands of Southeast Asia is much more scanty, however, and is restricted to occurrences on Java (the Late Pleistocene or Early Holocene Punung fissures of Gunung Kidul, and possibly also the Middle Pleistocene of Sangiran and Trinil), Sumatra (Early Holocene cave sites of Lida Ayer, Sibrambang and Djambu in the Padang Highlands) and Borneo (Late Pleistocene to Holocene of Niah Cave, Madai, Bau Caves and Gua Sireh) (Hooijer, 1948; Drawhorn, 1995; Harrison, 1996, 1998, 2000).

During the Early and Middle Pleistocene orang-utans were widely distributed throughout mainland Southeast Asia. Material from South China and Vietnam, assigned to *Pongo pygmaeus weidenreichi* (Hooijer, 1948), is ~20% larger on average in its dental dimensions than those of living orang-utans. Apparently, the geographic range of orang-utans extended onto the islands of Sundaland at this time. The oldest record of fossil orang-utans from Sundaland is probably from the Middle Pleistocene of Java. Two upper molars from Trinil, originally attributed to *Homo erectus* by Dubois (1896), have been considered by most subsequent workers to belong to *Pongo* (Hooijer, 1948). De Vos and Sondaar (1982) and de Vos (1983, 1984) argue, however, that the Trinil specimens are not orang-utans, and that this taxon is absent from the Middle Pleistocene faunas of Java, but one of us (TH) has examined the original specimens and agrees with Hooijer's (1948) assessment that the teeth most probably represent M^3 and M^4 of an orang-utan. Furthermore, von Koenigswald (1940), Widianto (1991), and Aziz and Saefudin (1996) have reported additional isolated teeth of fossil orang-utans from Middle Pleistocene sediments in the Sangiran Dome region of Java.

Dubois collected several thousand specimens of subfossil orang-utans from Early Holocene cave sites (i.e., Sibrambang, Lida Ayer, and Djambu) in the Padang Highlands of central Sumatra (Dubois, 1891; Hooijer, 1948). On the basis of their larger overall dental size (the teeth are ~15% on average larger in terms of occlusal area than those of the living subspecies [Harrison, 2000]), greater degree of canine, sexual dimorphism, and differences in the relative size of the teeth, Hooijer (1948) recognized a new subspecies—*Pongo pygmaeus palaeosumatrensis.* The small sample of orang-utan specimens from the Bau Cave sites in Sarawak (i.e., Paku Flats and Jambusan), of uncertain age, also have teeth that are comparable in size to *Pongo pygmaeus palaeosumatrensis.*

Orang-utans are found throughout the sequence at Niah Cave, and their remains are common (comprising more than 30% of non-human primate specimens) (Hooijer, 1961; Harrison, 1996, 2000). They have also been recovered from Madai Caves and Gua Sireh, but their remains are relatively much more rare than at Niah (only 9% and 3% of the primates respectively). These differences might reflect important ecological distinctions, but it is more likely that the very high frequency at Niah is due to the fact that the human occupants specialized in hunting orang-utans (Harrison, 2000). If this is so, it may account, at least in part, for the absence of orang-utans in the local environs of Niah today (apart from sporadic sightings the nearest modern day occurrence of orang-utans is more than 200 km from Niah) (Harrisson, 1959b; Reynolds, 1967; Rijksen and Meijaard, 1999).

During glacial periods, when the Sunda Shelf was exposed, orang-utans with a range that extended throughout mainland Southeast Asia as far north as southern China, were able to gain access into Sumatra, Borneo and Java. Despite intermittent land connections, however, a number of biogeographic barriers impeded free migration of orang-utans throughout the Sunda Shelf. These included major river systems that transected the present-day South China and Java seas, and a belt of drier more seasonal woodlands and grasslands that bordered the eastern edge of the Malay Peninsula, and continued onto the lowland areas between Sumatra and Borneo, through southern Kalimantan, and eastern Java and the Lesser Sunda Islands (see Figures 3 and 4; Morley and Flenley, 1987; Heaney, 1991). The population of orang-utans on the Malay Peninsula would have been easily able to colonize Sumatra during glacial times, but access to Borneo from Sumatra, presumably via the Bangka–Belitung–Karimata island chain, was more difficult because of the predominance of drier, more seasonal conditions. As a consequence of these biogeographical factors, Bornean orang-utans may have undergone a population bottleneck, as well as a greater degree of isolation and vicariance (Rijksen and Meijaard, 1999), and this has contributed to the degree of morphological and molecular separation between the two subspecies (as well as the differentiation between the individual populations on Borneo, i.e., *pygmaeus* in Sarawak and NW Kalimantan, *wurmbii* in SW Kalimantan, and *subsp. nov.* in Sabah and NE Kalimantan [see Groves, 2001a; Brandon-Jones *et al.*, 2004]). These factors also account for the unusually high level of endemism in the general primate (and broader mammalian) fauna (Table 1), despite the fact that Borneo is a relatively large island that has had frequent land connections with mainland Southeast Asia.

Hunting by humans may have been a contributing factor in the extirpation of orang-utans from south China, mainland Southeast Asia, and Java by the Early Holocene (Harrison, 1996, 1998, 2000; Delgado and van Schaik, 2000; Harrison *et al.*, 2002). The relictual populations of orang-utans survived in the perhumid tropical forests of Borneo and Sumatra until the present, probably because of several factors: (1) these populations were apparently smaller in body size and probably more committed to a fully arboreal habit than mainland orang-utans (Smith and Pilbeam, 1980; Harrison, 1996, 2000); (2) current evidence suggests that modern human hunter-gatherers were unable to exploit extensively tropical forests in Southeast Asia prior to the introduction of agriculture, because of the limited subsistence base that these ecosystems offer to obligate hunter-gatherers (Bailey *et al.*, 1989; Bailey and Headland, 1991). Thus, orang-utans were able to survive in Borneo and Sumatra because of their specialized arboreality and because of the low population densities of hominins on these islands (Harrison, 1996, 2000; Harrison *et al.*, 2002).

Hylobates

Seven species of hylobatids are currently recognized on Sundaland (Table 1). *Hylobates agilis, Hylobates lar*, and *Hylobates syndactylus* are found on both the Malay Peninsula and Sumatra, while *H. moloch* (Java), *H. klossii* (Mentawai Islands), *H. muelleri* (Borneo) and *H. albibarbis* (southwestern Borneo) are endemic species found on Sunda Shelf islands (Marshall and Sugardjito, 1986; Weitzel *et al.*, 1988; Rowe, 1996; Fleagle, 1999; Groves, 2001a; Brandon-Jones *et al.*, 2004).

Gibbons are rare at archaeological sites on the Sunda islands. At Niah, gibbons comprise only 0.5% of the total primate fauna, and they are known from just a few dental and postcranial specimens from other Early Holocene sites on Borneo (Harrison, 1998, 2000). Comparisons support Hooijer's suggestion that they are comparable in morphology and similar in size or slightly larger than extant *H. muelleri* (Hooijer, 1960, 1962a,b). Fossil gibbons are also scarce in the cave sites of similar age on Sumatra, and only a few isolated teeth have been recovered from Middle to Late Pleistocene localities in Java (Von Koenigswald, 1940; Badoux, 1959; Hooijer, 1960). Fossil and subfossil siamangs (*Hylobates syndactylus*) have been recovered from the Middle and Late Pleistocene of Java (where they are now locally extinct) and from Late Pleistocene sites on Sumatra (Von Koenigswald, 1940; Badoux, 1959; Hooijer, 1960). The specimens from Sumatra are somewhat larger than their modern counterparts, and have been assigned to a separate subspecies, *H. syndactylus subfossilis* (Hooijer, 1960).

Little about the zoogeography of gibbons and siamangs can be deduced from the current archaeological and paleontological evidence. Given the occurrence of *Hylobates* in Java during the Middle Pleistocene, they probably extended their range in the Sunda Shelf islands coincident with *Pongo* during the Pliocene, and speciated soon thereafter in their respective centers of endemicity (i.e., in Java, Borneo, and the Mentawai Islands). The underrepresentation of hylobatids in the archaeological samples is probably a reflection of the difficulty in hunting such fast-moving, upper canopy-dwelling primates, especially before the advent of bone projectile point technologies (Medway, 1959, 1977; Harrison, 1996). Given these findings, human hunting may be an important factor influencing the zoogeographic distribution of hominoids. During the Middle Pleistocene orang-utans and gibbons had similar geographic distributions in Southeast Asia, but only gibbons were able to maintain this range subsequent to the arrival of *Homo erectus* and *Homo sapiens* into the region. Humans may have been a contributing factor in the differential geographic distributions of gibbons and orang-utans, but other ecological variables may have been equally important (see Jablonski, 1998; Jablonski and Whitfort, 1999; Harcourt, 1999; Jablonski *et al.*, 2000; Harcourt and Schwartz, 2001).

Macaca

Four species of macaques occur in Sundaland, although *Macaca arctoides* is restricted to the northern limit of the region and *M. pagensis* is known only from Siberut, Sipora, and Pagai Islands in the Mentawai archipelago (Table 1).

The remaining two species, *M. nemestrina* and *M. fascicularis*, are widely distributed throughout the Sunda Shelf islands (Medway, 1970; Fooden, 1975, 1995, 2000; Brandon-Jones *et al.*, 2004). Unlike the hominoids and most colobines, *Macaca* has been able to colonize deep-water fringing islands beyond the Sunda Shelf, possibly by sweepstake dispersal, although human introductions cannot be discounted (Fooden, 1995; Heinsohn, 2001). *Macaca fascicularis* has a range that extends into the Nicobar Islands, north of the Mentawai Islands, the Lesser Sunda Islands, and the Philippines (Fooden and Albrecht, 1993; Fooden, 1995). *Macaca nemestrina* has been less successful in this regard, but a *nemestrina*-like ancestor was able to colonize Sulawesi, presumably from Borneo (Rosenblum *et al.*, 1997a; Morales and Melnick, 1998; Groves, 2001b).

Macaca fascicularis and *M. nemestrina* have been recovered from archaeological sites in Borneo dating back to the Late Pleistocene (Hooijer, 1962a,b; Harrison, 2000; Table 2). At Niah, *M. fascicularis* is much more common than *M. nemestrina* and among primates is second in abundance only to *Pongo*. Previous analyses have shown that the dental remains of long-tailed macaques are on average 13% larger than their modern conspecifics, with a gradual diminution in size through time (Harrison, 1996). A possible explanation is provided by the ecogeographic relationship between cooler climatic conditions during the Late Pleistocene and Bergmann's rule. The specimens from Niah correspond in dental size with those living in Thailand today, where annual temperatures are similar to those inferred for northern Borneo during the LGM (~5–6°C lower than at present) (Fooden and Albrecht, 1993; Harrison, 1996). All of the specimens of *Macaca nemestrina* from Niah fall within the range of modern Bornean pig-tailed macaques.

The Early Holocene sites in Sumatra have produced a large collection of macaques. By comparison to Niah and to the modern communities on Sumatra and Borneo, *M. nemestrina* is more common than *M. fascicularis*. This may be due to ecological differences, but more likely reflects differences in human hunting strategies (Harrison, 1998). Fossil macaques from Middle Pleistocene to Holocene sites on Java are all referable to *Macaca fascicularis mordax* that occurs today on Java and Bali, although the Middle Pleistocene material tends to be somewhat larger than their extant counterparts (Hooijer, 1962a; Aziz, 1989). *Macaca nemestrina* is absent from the modern primate fauna of Java, but a single specimen of this species has been recovered from the Middle Pleistocene of Sangiran (Aimi, 1981), which indicates that it did reach Java during glacial periods. Reis & Garong (2001) have recently reported the recovery of specimens of *Macaca fascicularis* from early Holocene cave sites on Palawan.

Presbytis

At least eight species of *Presbytis* occur today on the Sunda Shelf islands (Table 1), and reconstructions of their biogeographic history suggest a complex pattern of dispersal and speciation (Wilson and Wilson, 1975; Brandon-Jones, 1996, 1998, 2001). Unfortunately, the paleontological and archaeological record does not help clarify the problem, mainly because the fossil record for *Presbytis* is too sparse and the material is too fragmentary in most cases to be assigned to a particular species with any degree of confidence. Brandon-Jones (1996, 1998, 2001) has suggested that the glacial peaks during the later Pleistocene had a profound impact on the diversity and zoogeographic distribution of colobines in Sundaland. It seems more likely, however, given the morphological and taxonomic differentiation of members of this clade, and what we know about the timing of differentiation of other Southeast Asian primate species, that most of the speciation events leading to modern *Presbytis* species on the Sunda Shelf occurred deeper in time, perhaps as far back as the Pliocene or Early Pleistocene.

Presbytis is well represented at Niah, where it comprises 23% of the primate fauna. As noted above, it is difficult to assign these specimens to a species. Of the four extant species on Borneo, all but *P. frontata* occur today in the local environs of Niah (Payne *et al.*, 1985). *Presbytis rubicunda*, the maroon leaf-monkey, is the most common in the surrounding forests, but *P. hosei* and *P. femoralis* occur in the general area. Comparisons show that the material is most similar in dental morphology to *P. rubicunda* and *P. hosei*, particularly the former. The current distribution of these two species, and the relatively large size of the teeth from Niah, favor their attribution to *P. rubicunda*, although it is likely that the sample contains a mixed assemblage, including some specimens of *P. hosei*. Comparisons of dental size show that the Niah material is larger on average than all modern day species from Borneo. It would seem that *Presbytis*, like *Macaca fascicularis*, has undergone a diminution in size during the Late Pleistocene.

The colobines from Gua Sireh comprise 35% of the primate fauna. All specimens studied from that site appear to be assignable to a single species of *Presbytis*, although species identification is uncertain. The only *Presbytis* living today in western Sarawak is *P. femoralis*, and the Gua Sireh material is consistent in size and morphology with this species. *Presbytis* is also known from the Middle Pleistocene site of Soember Kepoeh in Central Java (Hooijer, 1962a), which shows that the taxon occurred east of its current distribution in the past. There are no examples of *Presbytis* from Late Pleistocene–Early Holocene sites in central Java, suggesting that local extinction had already occurred by this time. *Presbytis* is also recorded from Bau in Sarawak and from Early Holocene sites in central Sumatra, but again the specimens cannot be readily identified to species.

Trachypithecus

Two species of *Trachypithecus* are found today on the Sunda Shelf islands—*T. cristatus* on Borneo and Sumatra (as well as mainland Southeast Asia), and *T. auratus* on Java, Bali, and Lombok (Oates *et al.*, 1994; Rowe, 1996; Rosenblum *et al.*, 1997b). *Trachypithecus* is the only colobine that extends its geographic distribution beyond Wallace's Line, although there is the possibility that it was introduced on Lombok (Brandon-Jones, 1998; Heinsohn, 2001). Clearly, an important factor influencing the movement of primates between different subprovinces is their relative abilities to colonize new areas, particularly across stretches of ocean. Apart from modern humans, colobines and hominoids were apparently unable to extend their ranges beyond the Sunda Shelf, whereas macaques were able to establish themselves in the Philippines, Sulawesi, and the Lesser Sunda Islands, as far East as Timor and Flores.

Trachypithecus is well represented at Niah (comprising 13% of the primate fauna), but specimens are not found uniformly throughout the deposits. *Trachypithecus* is absent from depths greater than 60", whereas *Presbytis* is found throughout the sequence. This could indicate a change in hunting strategies or dietary preferences (Harrison, 1996). However, the appearance may coincide with the LGM when Niah was located ~200 km inland (presently, it is only ~17 km from the coast). Since *T. cristatus* prefers riverine forests, peat swamps, and mangrove, it is found mainly on the coastal plain of Borneo. It is likely that during the LGM, the human inhabitants of Niah were beyond the immediate range of *Trachypithecus*, but as sea levels rose at the end of the Pleistocene it became increasingly possible for hunters to obtain this species close to Niah.

Dental comparisons show that *Trachypithecus* from Niah is significantly larger than extant *Trachypithecus cristatus* from Borneo (Harrison, 2000). Nevertheless, the Niah material is still much smaller than fossil *Trachypithecus* from Java attributed to *T. auratus robustus* (Tegoean, Middle Pleistocene) and *T. auratus sangiranensis* (Sangiran, ? Late Pliocene—see Larick *et al.*, 2000 for a critical review of the dating), which are both larger than the modern Javan lutung (Hooijer, 1962a; Jablonski and Tyler, 1999). Given the early dates of these latter taxa, and consistent with the molecular evidence (Rosenblum *et al.*, 1997b), it can be inferred that the *T. auratus/cristatus* clade originated in Java, and later spread to Sumatra and Borneo, and eventually to the Malay Peninsula where it encountered *T. obscurus.*

SYNTHESIS AND DISCUSSION

The study of the non-human catarrhine fauna from archaeological and paleontological sites on the major islands on the Sunda Shelf provides a unique diachronic perspective on the zoogeography and ecology of Sundaland. In particular, it provides valuable insight into the significance of two major extrinsic factors that may have had a profound impact on the distribution of primates in the region: (1) the arrival of hominins since the late Pliocene or early Pleistocene (who influenced primate distributions through hunting, habitat disturbance and destruction, and the translocation of primates as "ethnotramps" [Heinsohn, 2001]); and (2) climatic perturbations associated with the onset of the major phase of glacial cycles in the northern hemisphere from the Late Pliocene onwards.

Of the seven genera of catarrhines living today on Sundaland, five are found in the archaeological and paleontological record—only *Simias* and *Nasalis* are not represented. The geographic range of *Pongo* is restricted today to northern Sumatra and Borneo, but the paleontological and archaeological evidence shows that the species was widely distributed throughout the Sunda Shelf islands, as well as on the mainland of Southeast Asia during the Pleistocene. During glacial periods, when tropical forests were fragmented and the exposed Sunda Shelf was transected by major river systems, populations of orang-utans on Borneo, Sumatra, and Java were probably isolated and severely reduced in size. It is likely that intermittent land connections between Sumatra and the Malay Peninsula permitted gene flow between orang-utan populations across the Strait of Malacca. However, the combination of a belt of drier, more seasonal woodland and grassland and major rivers separating Sumatra from Borneo during glacial times, when the two landmasses were connected, represented a major impediment to gene flow between orang-utan populations. The bottleneck and isolation that occurred in the orang-utan populations on Borneo, probably during the Early Pleistocene, is reflected in the morphological and molecular distinctiveness of the endemic subspecies and the three major populations on Borneo (Ryder and Chemnick, 1993; Xu and Arnason, 1996; Zhi *et al.*, 1996; Karesh *et al.*, 1997; Rijksen and Meijaard, 1999; Groves, 2001a). Ryder and Chemnick (1993) and Zhi *et al.* (1996) have estimated that the separation of the Sumatran and Bornean populations occurred at ∼1.5–1.7 Ma. This divergence may have been precipitated by ecological changes that accompanied the Eburonian cold phase at the start of the Early Pleistocene (at ∼1.8 Ma). Orang-utans survived on Java only until the Late Pleistocene or Early Holocene. It is possible that hunting by humans was a contributing factor in the extirpation of orang-utans from mainland Southeast Asia and Java, and that relictual populations survived on Borneo and Sumatra only because of their specialized arboreality and the low population densities of humans on these islands.

Based on current evidence from paleontological, molecular, and paleoecological studies, the following scenario is proposed to explain the present-day zoogeographic distribution of *Pongo*. During the Pliocene, orang-utans were widely distributed throughout Southeast Asia, and they probably entered Sundaland during the Pretiglian cold phase (at ∼2.7 Ma) in the Late Pliocene, when sea levels were at least 100 m below present-day levels. At the start of the Pleistocene, correlated with a major cold climate peak at ∼1.8 Ma, and associated with increased seasonality in tropical Southeast Asia, orang-utan populations became fragmented and isolated. During this period, the population on Borneo (and probably that on Java) became differentiated genetically, morphologically, and behaviorally, from the orang-utan population on Sumatra and mainland Southeast Asia (this same biogeographical pattern is mirrored in the subspecies of *Nycticebus coucang*—with *N. c. coucang* on Sumatra, Natuna, and the Malay Peninsula, *N. c. javanicus* on Java, and *N. c. menagensis* on Borneo [Brandon-Jones *et al.*, 2004]). Gene flow between the Sumatran and mainland populations probably continued throughout the Pleistocene as a consequence of intermittent landbridge connections. By the end of the Pleistocene, orang-utans had become extinct throughout mainland Southeast Asia, leaving relictual and well differentiated populations on Sumatra, Borneo, and Java. At the beginning of the Holocene, extirpation of the Javan population resulted in the present-day distribution of orang-utans.

Gibbons and siamangs are rare at archaeological or paleontological sites on the Sunda islands. Their underrepresentation at archaeological sites may be associated with the difficulty that humans experienced in hunting them prior to the advent of projectile point technologies in the Late Pleistocene (see Harrison 1996, 1998, 2000). Unfortunately, little can be deduced about their zoogeography from the limited evidence available. Given the occurrence of *Hylobates* in Java during the Middle Pleistocene, it is likely that they extended their range into Sundaland at about the same time as *Pongo* (i.e., during the Late Pliocene). The common ancestor of the *lar*-group gibbons probably colonized the major islands at this time, including Sumatra, Java, Borneo, and the Mentawai Islands, and speciated soon thereafter in their respective centers of endemism. This is consistent with recent molecular studies (Hayashi *et al.*, 1995; Hall *et al.*, 1998) that indicate that the *lar*-group diverged during the Pliocene, probably around 3.5 Ma. They may have entered the Sunda Shelf islands during a short cold phase at ∼3.4–3.6 Ma, or more likely at the start of the Pretiglian cold phase at ∼2.8 Ma, when sea levels fell by more than 50 m (Prentice and Denton, 1988), and landbridge connections were formed between mainland Southeast Asia and the major Sunda islands. Molecular evidence suggests that the subgenus *Symphalangus* diverged from the other hylobatids by ∼5–6 Ma (Hayashi *et al.*, 1995; Hall *et al.*, 1998), but their limited distribution in the Malay Peninsula and Sumatra today, their occurrence in Java during the Pleistocene, and their absence from the Mentawai Islands and Borneo, suggests that their initial range expansion from mainland Southeast Asia occurred later than the *lar*-group gibbons.

The inferred timing and pattern of colonization of the Sunda islands by *Macaca* is complex (Fooden, 1975, 1995; Eudy, 1980; Delson, 1980; Abegg & Thierry, 2002; Evans *et al.*, 2003). Unlike the hominoids and most colobines, *Macaca* has been able to colonize deep-water fringing islands beyond the Sunda Shelf. The absence of *M. fascicularis* in Sulawesi suggests that the progenitor of *M. nemestrina* may have arrived in Borneo prior to *M. fascicularis.* The occurrence of *M. pagensis* on the Mentawai islands, derived from a *M. nemestrina*-like ancestor, in the absence of *M. fascicularis*, leads to a similar conclusion (see Delson, 1980; Abegg and Thierry, 2002 for more detailed reviews). Tosi *et al.* (2003) have inferred from molecular evidence that the Sulawesi macaques separated from *M. nemestrina* at 2.6–3.0 Ma. Similarly, Roos *et al.*, (2003) have estimated a divergence of *M. pagensis* from *M. nemestrina* at 2.2. Ma (with a second migratory event into Siberut at 1.1 Ma). This suggests that *Macaca nemestrina* colonized the Sunda islands during the mid-Pliocene, possibly associated with the onset of the Pretiglian cold phase at ∼2.8 Ma (Prentice and

Denton, 1988), when sea levels dropped by more than 100 m. *Macaca fascicularis* followed, probably during the late Pliocene or early Pleistocene. Molecular data indicate that *M. fascicularis* diverged from the other members of the *fascicularis* species group at ~2.2–2.5 Ma (Tosi *et al.*, 2003), and this implies that *M. fascicularis* probably entered the Sunda islands from mainland Southeast Asia at the end of the Pretiglian cold phase at 2.3 Ma or during the Eburonian cold phase starting at ~2.0 Ma (Prentice and Denton, 1988). The later arrival of *M. fascicularis* into the region, at a time when sea level regressions were less dramatic, prevented it from colonizing deep-water fringing islands, such as Sulawesi and Mentawai Islands, even though its occurrence on numerous present-day islands shows that the species is a very successful island colonizer (Fooden, 1995; Abegg and Thierry, 2002).

Brandon-Jones (1996, 1998, 2001) has suggested that the glacial peaks during the later Pleistocene had a profound impact on the diversity and zoogeographic distribution of colobines on Sundaland. However, it seems more likely, given the morphological and taxonomic differentiation of the clade, and based on the fossil evidence available, that most of the speciation events leading to extant *Presbytis* and *Trachypithecus* species on the Sunda Shelf occurred more distant in time, probably as far back as the Pliocene and Early Pleistocene. It is suggested here that the *Trachypithecus auratus/cristatus* clade originated in Java, probably during the late Pliocene, and later spread to Sumatra, Borneo, the Natuna Islands, and the Malay Peninsula. The zoogeographic relationships of *Presbytis* spp. are complex, and much better paleontological and molecular data are needed to reconstruct their evolutionary history. Even so, the last common ancestor of *Presbytis* spp. was probably present on one of the larger Sunda Shelf islands, probably Borneo, during the Pliocene, and this gave rise to the various endemic species on Borneo, Java, Sumatra, and the Mentawai Islands, and the genus later extended its range from Sumatra onto the Malay Peninsula. Given that the evidence suggests that *Hylobates* and *Macaca* colonized the Mentawai islands during the Pretiglian cold phase at ~2.5–2.8 Ma, and that there were probably no subsequent influxes of catarrhine primates (but see Roos *et al.*, 2003 for an alternative scenario for *Macaca*), it seems that *Presbytis* (and *Simias*) were already present on the Sunda Shelf islands by mid-Pliocene times.

Hence, it can be inferred that by the Late Pliocene the main islands of the Sunda Shelf had a primate fauna that included *Pongo pygmaeus* (Sumatra, Java, and Borneo), *Hylobates* spp. of the *lar*-group (Sumatra, Mentawai Islands, Borneo, and Java), *Macaca nemestrina* (Sumatra, Mentawai Islands, Borneo, and Java), the common ancestor of the *Trachypithecus auratus/cristatus* clade (Java and Sumatra), and *Presbytis* spp. (Sumatra, Mentawai Islands, Borneo, Sumatra, and Java). Most of these taxa probably arrived during the Pretiglian cold phase, starting at ~2.8 Ma, when sea levels fell by more than 100 m, although it is conceivable that some may have arrived earlier, during a shorter cold phase at ~3.4–3.6 Ma, when sea levels declined by at least 50 m. Although supporting evidence is lacking, it is also highly probable that *Nasalis larvatus* (Borneo) and *Simias concolor* (Mentawai Islands) were already present as endemic taxa in the Late Pliocene, and that their last common ancestor had arrived in the Sunda islands by the early Pliocene. Soon after this initial period of colonization, *Hylobates* and *Presbytis* underwent rapid speciation as a consequence of vicariance and relictual survivorship, giving rise to *P. thomasi* on Sumatra, *H. klossii* and *P. potenziani* on the Mentawai Islands, *H. albibarbis, H. muelleri, P. hosei, P. frontata*, and *P. rubicunda* on Borneo, and *H. moloch* and *P. comata* on Java. During the Late Pliocene and Early Pleistocene, probably associated with the Eburonian cold climate maximum at ~1.8 Ma, *Presbytis melalophos* and *P. femoralis*, along with *Macaca fascicularis*, colonized Sumatra, the Natuna Islands, and Borneo from the Malay Peninsula. At about the same time the isolated orang-utan populations on Sumatra, Java, and Borneo were beginning to differentiate from each other. *Hylobates lar*, *H. agilis*, and *H. syndactylus* extended their range from the Malay Pensinsula into Sumatra (and Java), probably during the Middle to Late Pleistocene, coincident with the arrival of *Trachypithecus cristatus* on mainland Southeast Asia. Meanwhile, *Pongo pygmaeus*, *Hylobates syndactylus*, and *Macaca nemestrina* were extirpated on Java, probably as a consequence of a combination of ecological changes and early hominin incursions.

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