PLEISTOCENE ZOOGEOGRAPHIC EVOLUTION OF JAVA (INDONESIA) AND GLACIO-EUSTATIC SEA LEVEL FLUCTUATIONS: A BACKGROUND FOR THE PRESENCE OF *HOMO*

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ABSTRACT

The faunal succession of the Quaternary hominid-bearing deposits of Java has recently become increasingly well-dated. An attempt is being made to correlate major faunal events, including the first occurrences of Homo erectus *and* Homo sapiens, *with global eustatic sea level fluctuations and climatic changes. So far there is no proof for the presence of mammals on Java at 2.4 myr, when the first marked glacio-eustatic sea level lowerings are thought to have occurred. The Satir fauna is the oldest recognizable faunal unit on Java. This fauna has an age of between 2 myr and 1.5 myr and indicates island conditions. Java gradually emerged due to tectonic and volcanic processes during this period. Hominids are still lacking at this stage. Fairly isolated conditions seem to have continued until around 0.8 myr, as suggested by the unbalanced character of the Ci Saat and Trinil faunas, with ages of 1.2 and 0.9 myr respectively.* Homo erectus *was able to reach Java during this time interval. A major faunal immigration event, leading to a maximum number of medium to large-sized mammals, is represented by the Kedung Brubus faunal stage, corresponding with a marked lowering of eustatic sea level at 0.8 myr. Relatively open and dry conditions prevailed at this stage. Another major faunal turnover event is recorded in the Late Pleistocene Punung fauna, which represents the first tropical rainforest fauna on Java and includes* Homo sapiens. *This drastic environmental change and faunal migration was probably induced by the penultimate glaciation at 135 kyr and the subsequent warm phase from 125 kyr onwards (oxygen-isotopic stages 6 and 5). The Punung fauna was probably established on Java between 110 and 70 kyr when the sea level was fluctuating between 40 and 65 m below present-day sea level, thus permitting overland dispersal to Java, in combination with more warm and humid conditions as compared to the foregoing faunal stages and the glacial maximum at 135 kyr. Between the Late Pleistocene Punung faunal stage and the Holocene faunal stage (as represented by several fossil cave faunas like Wajak, Sampung, Hoekgrot) a large number of extinctions is recorded, while replacement by new immigrations during the last glacial maximum appears to have been limited. The extinctions were probably caused by a number of climatic factors, possibly in combination with habitat alteration by* Homo sapiens.

INTRODUCTION

During the 1980s a new biostratigraphic scheme was established for Java (de Vos *et al.* 1982; Sondaar 1984) to replace the classical biozonation for Java of von Koenigswald (1933, 1934), which was based on mixed faunas. The new mammal faunal succession has recently been roughly dated (Watanabe and Kadar 1985; Leinders *et al.* 1985). It runs from old to young: Satir fauna (1.5 myr) – Ci Saat fauna (1.2 myr) – Trinil Haupt-Knochenschicht Fauna (1 myr; the Trinil H.K. fauna only includes species derived from this layer, see de Vos *et al.*, (1982)) – Kedung Brubus fauna (0.8 myr) – Ngandong fauna (date uncertain) – Punung Fauna (last interglacial period) – Wajak fauna (Holocene). This faunal succession is characterized by an increasing exchange of faunal elements
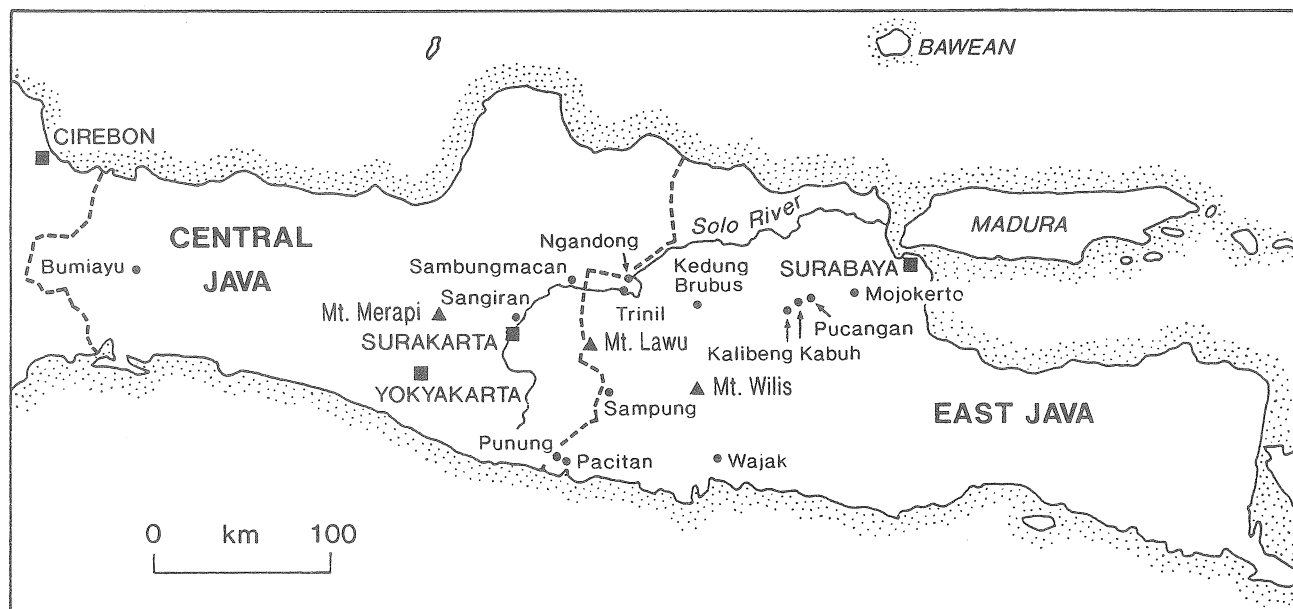
Figure 1: Map of Central and East Java showing localities mentioned in the text.

with the Southeast Asian continent since the Early Pleistocene.

Homo erectus material from Java has been found at different stratigraphic levels in association with distinct faunal units. This material can be divided on morphological characteristics into distinct groupings. The Trinil holotype skullcap and the Sangiran skull *Pithecanthropus* II were found in levels associated with the Trinil fauna. The mandible from Kedung Brubus and the Sangiran skull *Pithecanthropus* VIII were found in layers associated with a Kedung Brubus fauna whereas the Solo Man fossils were associated with the Ngandong fauna. In this paper we will try to refine the biostratigraphic succession by including recent information on fossil finds and dating techniques and consider the zoogeography of Java in the light of global eustatic sea level fluctuations.

NEW FOSSIL FINDS AND DATING RESULTS

Satir Fauna

For the older faunal stages proposed by Sondaar (1984), the Satir and Ci Saat faunas were given an age of 1.5 myr and 1.2 myr respectively by Leinders *et al.* (1985), based on faunal correlations between the type faunas from the Bumiayu Area in west Central Java (Figure 1) and fossil assemblages originating from excavations in the "black clays" in the Sangiran area (Aimi and Aziz 1985), which

have been absolutely dated by means of fission-track dating on widely recognizable tuff layers. Excavation number 8 at the base of the Kali Glagah Series near Bumiayu (van der Maarel 1932) was taken as one of the type localities for the Satir fauna as proposed by Sondaar (1984). This locality has yielded several remains of *Tetralophodon bumiajuensis* as figured by van der Maarel (1932). This species is also known from Sangiran, although it is very rare there and no exact stratigraphic position is known for the *Tetralophodon* fossils originating from the Sangiran area. By analysing the fluorine content of a *Tetralophodon bumiajuensis* mandible originating from the Sangiran area and comparing it with fluorine data from excavated fossils from several stratigraphic levels, as reported by Matsu'ura *et al.* (1985), Leinders *et al.* (1985) were able to show that it must originate from the "black clays"[1]. Together with *Hexaprotodon simplex, T. bumiajuensis* is characteristic of the Satir fauna, for which Leinders *et al.* (1985) propose an age of 1.5 myr. Paleomagnetic evidence from the Kali Glagah series in Bumiayu (F. Sémah 1986) suggests that the base of the Kali Glagah series, including the level of excavation number 8 of van der Maarel (1932), antedates the Olduvai Event. Therefore the first occurrence of the Satir fauna might well be older than the 1.5 myr originally proposed by Leinders *et al.* (1985), sug-

8

gesting that the first mammalian colonization of the western part of Java occurred during the Late Pliocene at around 2 myr.

Geochelone atlas

Another important aspect to note is the occurrence of *Geochelone atlas* in the Sangiran area. The fluorine content of a *Geochelone* fossil originating from the Sangiran area was also compared with the fluorine data of Matsu'ura *et al.* (1982, 1985). Based on these comparisons it was concluded that this giant tortoise was equivalent in age with the Satir fauna from the type localities near Bumiayu (Sondaar 1984; Leinders *et al.* 1985). The exact stratigraphic position of *Geochelone* in the Sangiran area remained unknown, however.

The excavation of trench I near Bukuran, 1.5 km ESE of Sangiran (Kadar *et al.* 1985), carried out by the Indonesian-Japanese team between 1977 and 1979, reportedly yielded remains of a turtle (Aimi and Aziz 1985; 157). However, the fossils, which are erroneously indicated as turtle in this paper, actually represent the plastron fragments of a giant tortoise according to Aziz, who joined the excavation. The Bukuran excavation trenches are stratigraphically placed in the upper part of the Sangiran Formation (=Pucangan Formation) just above tuff layer T9 and about 10 m below tuff layer 10. The latter is well dated by means of fission-track dating (Suzuki *et al.* 1985) and has an age of 1.16±0.24 myr. This information suggests that *Geochelone* continues up to this age and might still be present in a fauna intermediate to the Satir and Ci Saat faunas of Sondaar (1984). The presence of a giant tortoise at around 1.2 myr is an indirect indication that *Homo erectus* was not in Java at that time. Giant tortoises are an easy prey for hunter-gatherers and rapidly became extinct on islands where humans settled (Sondaar 1981; van den Bergh *et al.* this volume).

Ages of the Trinil and Kedung Brubus Faunas

Recent paleomagnetic results in the Sangiran area (Hyodo *et al.* 1992, 1993) were successful in removing secondary magnetic overprints that hampered previous paleomagnetic interpretations (Shimizu *et al.* 1985). As a result the Jaramillo normal event is now clearly shown to occur just below the "Grenzbank" in the Sangiran area. The fossil fauna from the "Grenzbank" can be correlated with the Trinil H.K. faunal stage (Leinders *et al.* 1985). This suggests that the Trinil H.K. fauna, which lacks the genera *Elephas, Tapirus* and *Hyaena*, has an age of around 0.9 myr, slightly younger than the 1 myr originally proposed by Leinders *et al.*(1985). Recent fossil

finds in combination with paleomagnetic results from the Kaliuter sections, 15 km north of the Sangiran Dome (Djubiantono 1992) are in agreement with this interpretation. The fossil-bearing conglomerate at Kedung Cumpleng along the Kaliuter, which is correlated with the Jaramillo event, includes *Stegodon* but has not yielded any *Elephas* remains. The fossil assemblage possibly agrees with the Trinil H.K. fauna, while the younger excavation at Pancuran, correlated with the Brunhes Epoch, has yielded *Elephas*, and should either correlate with the Kedung Brubus or Ngandong faunal stage. Detailed study of the fossil vertebrate material from the Kaliuter sections, which comprises *in situ* material, could further improve the mammalian stratigraphical succession.

Ages of the Ngandong and Punung Faunas

Absolute dating of the Ngandong fauna is still problematic. Bartstra *et al.* (1988) give a preliminary U-series age of 50 to 100 kyr for fossil bone samples collected from an excavation in a terrace remnant located at the original site where the Geological Survey of the East Indies in 1931-1932 carried out their excavations (Oppenoorth 1932, 1936). This site yielded the famous Solo Man skulls. As they state, the reported age should be considered a minimum. Indeed this age seems much too young, as the faunal composition of the Ngandong fauna is very similar to that of the Kedung Brubus fauna (though many taxa, including *Homo erectus*, differ on subspecies level; see de Vos *et al.* 1994). Both faunas are characteristic of an open woodland environment (Sondaar 1984). The Ngandong fauna should be younger than the Kedung Brubus fauna but older than the Punung fauna (de Vos 1982), the latter being characteristic of a tropical rainforest environment which must have invaded Java during the Late Pleistocene. The Punung fauna is here considered to have an age of between 80 kyr and 60 kyr, based on the faunal similarity between it and the faunas from the Sumatran caves of Jambu and Lida Ajer, for which aspartic acid racemization dating gives ages of 60-70 kyr and 80 kyr respectively (Skelton and de Vos, in preparation).

A few U-series ages obtained from fossil bone samples originating from other Solo terrace remnants near Matar and Tapan (Bartstra *et al.* 1988) seem to provide a better age for the Ngandong fauna. They are 165(+30/-23) kyr for a bone sample from Matar and 190(+40/-30) kyr for a Tapan bone sample. Possibly the bone samples from their excavation at Ngandong did not come from the original site of the Solo Man skulls, which is located

south of the Ngandong River and not north of it, as is indicated in Figure 3 of Bartstra *et al.* (1988: 331).

Finally, the Wajak fauna and faunal remains from several other caves on Java (Sampung, Goa Jimbe, Hoekgrot) are of Holocene date (Shutler *et al.* 1994; Storm 1992 a and b).

It should be noticed here that the recent absolute ages for two hominid sites on Java published by Swisher *et al.* (1994) are still a matter of debate. They claim that *Homo rectus* was already present on Java at 1.81±0.04 myr based on ^{40}Ar/^{39}Ar laser-incremental heating analysis on minerals from the supposed finding locality of the Mojokerto child. They also present another date of 1.66±0.04 myr for a site near Sangiran, where in the late 1970s two hominid specimens were recovered during the digging of an irrigation canal (S27 and S31). De Vos and Sondaar (1994) point out that these ages contradict with existing data on the detailed stratigraphy in combination with paleomagnetic data and fission-track ages (Suzuki *et al.* 1985; Hyodo *et al.* 1993). They suggest that the mineral samples dated by Swisher *et al.* (1994) might have been reworked from older strata, as they were obtained from fluvial deposits. There are also uncertainties about whether the dated samples correspond with the original layers from which the skull material originated. On a detailed geological map of the central part of the Sangiran Dome (Itihara *et al.* 1985: Figure 6), the location of S27 is indicated with "H" (at the time of publication S27 had not yet been given an official code). This location is only 70 m northwest of a major fault and inside an area of a major landslide. A short section was measured within this landslide (section S61 in Figure 9 of Itihara *et al.* 1985), showing the position of S27 to correspond with the uppermost part of the Sangiran Formation just half a meter below a gravelly sandstone layer interpreted to represent the "Grenzbank". If a dating sample had been taken only 25 m west of the hominid finding location and outside the landslide zone, it would probably represent an older stratigraphic level of the Sangiran Formation. Although we do not question the Ar/Ar dating method used by Swisher *et al.* (1994), we argue that they do not present adequate information on the sampled horizons and do not explain the discrepancies between their ages and paleomagnetic and fission-track dating results obtained by others. For the moment we cannot accept the absolute dates presented by them until more accurate information on the sampled horizons is presented.

The faunal succession of Java then becomes:
- Wajak fauna   Holocene
- Punung fauna   c. 60-80 kyr
- Ngandong fauna   Late Middle Pleistocene?
- Kedung Brubus: c. 0.8-0.7 myr
- Trinil H.K. fauna: c. 0.9 myr
- Ci Saat fauna: c. 1.2-1 myr
- Satir fauna: c. 1.5-2 myr

The so-called Ci Julang (old spelling: Tji Djoelang) fauna of supposedly Late Pliocene age originally proposed by von Koenigswald (1933) is left out here, because it has been pointed out that it is based on inaccurate data (Sondaar *et al.* 1983; Sondaar 1984; Braches and Shutler 1984). The same applies to the Ci Sande fauna of von Koenigswald (1933, 1934), which was based only on a single molar of a supposed *Aceratherium*. This molar was later shown to belong to *Rhinoceros sondaicus* (Hooijer 1946; Aimi and Sudijono 1979).

There are still some considerable gaps in our knowledge of the faunal succession as shown above and there remains much work to be done. Excavations in single horizons at fossil rich sites should be carried out in combination with absolute dating methods. For example, the large-scale excavation at Ngebung (Sémah *et al.* 1992), where *in situ* remains of fossil mammals and stone artefacts have been found in layers correlated with the "Kabuh" Formation (= Bapang Formation in the new lithostratigraphic scheme developed for the Sangiran Area; IJJST 1992), could help to fill in the gap between the Kedung Brubus and Ngandong faunal stages. The lower reaches of the time interval under consideration represent a relatively large timespan for which limited data are available at present. An example of this is the recent discovery of a complete *Stegodon* mandible from a level stratigraphically several meters below the Bukuran excavation site already mentioned in relation to the occurrence of *Geochelone*. This *Stegodon* mandible shows several primitive aspects and can be attributed to *Stegodon* cf. *elephantoides* (van den Bergh *et al.*, in prep.). Previously, all *Stegodon* material from Java was attributed to *Stegodon trigonocephalus* MARTIN by Hooijer (1955). The Bukuran mandible is distinctively more primitive, having an elongated symphysis, rather thick enamel (4.2-6.5 mm, average 5.4 mm) and only 9 or 10 lamellae in the M3 as compared to 11 to 14 lamellae in *S. trigonocephalus*. The new find shows that within this genus there has been considerable change in Java, either by new immigration or local evolution. Another example is the recent finding of a pygmy *Stegodon* mandible from Sambungmacan, which is thought to represent an Early Pleistocene island fauna (Aziz and van den Bergh, in prep.). This island fauna perhaps evolved independently from the island fauna represented by the Satir fauna, the latter lacking *Stegodon*, or it may be of different age.

GLACIO-EUSTATIC SEA LEVEL FLUCTUATIONS

A method often used for quantifying eustatic sea level fluctuations calculates total ice volumes from $\delta^{18}O$ variations recorded in foraminifera from deep sea cores. Interpretations of these $\delta^{18}O$ curves are still conflicting, basically because of the difficulty in distinguishing between the two variables that influence the $\delta^{18}O$ change; ocean temperature and ice volume change. Vrba *et al.* (1990) have summarized several possible interpretations. One interpretation uses $\delta^{18}O$ fluctuations of benthic foraminifera and assumes that the deep sea ocean temperature has remained constant and thus that the benthic $\delta^{18}O$ fluctuations primarily represent ice volume changes. This assumption has been questioned by Chappell and Shackleton (1986). By comparing ice volume calculations derived from the benthic $\delta^{18}O$ composite with sea level curves derived from dated uplifted coral terraces, discrepancies were found that should be explained by a varying abyssal ocean temperature.

An alternative interpretation assumes that the surface temperature in tropical regions remained constant and thus that the $\delta^{18}O$ composite derived from tropical planktonic foraminifera mainly represents ice volume changes (Prentice and Denton 1988). Also, this method shows discrepancies with sea level records from uplifted terraces, probably because the tropical surface temperature may also have varied. The planktonic $\delta^{18}O$ record may also have been affected by differences in surface salinity and changing seasonal growth and depth habitats (Chappell and Shackleton 1986). These problems in the interpretation of the oxygen isotope composites remain to be resolved. However, so far the oxygen isotope record can be regarded as the best indicator for global climatic conditions, as has been shown by the high resolution correlation between this record and variations in the earth's orbital geometry (orbital tuning concept, Martinson *et al.* 1987).

In the following section we will use the planktonic $\delta^{18}O$ derived glacio-eustatic sea level chart of Prentice and Denton (1988) (Figure 2), assuming that this chart at least gives a rough indication of magnitudes and frequencies of global sea level fluctuations. The record runs from 6 myr to recent and thus includes the time span of interest, the interval during which terrestrial mammal faunas are recorded on Java from about 2 myr onwards.

From around 2.8 myr to 2.4 myr there seems to have been a fluctuating increase in ice volume leading to a fluctuating but general lower sea level during this interval with a culmination at around 2.4 myr. However, some fundamental problems still exist in interpreting Pliocene
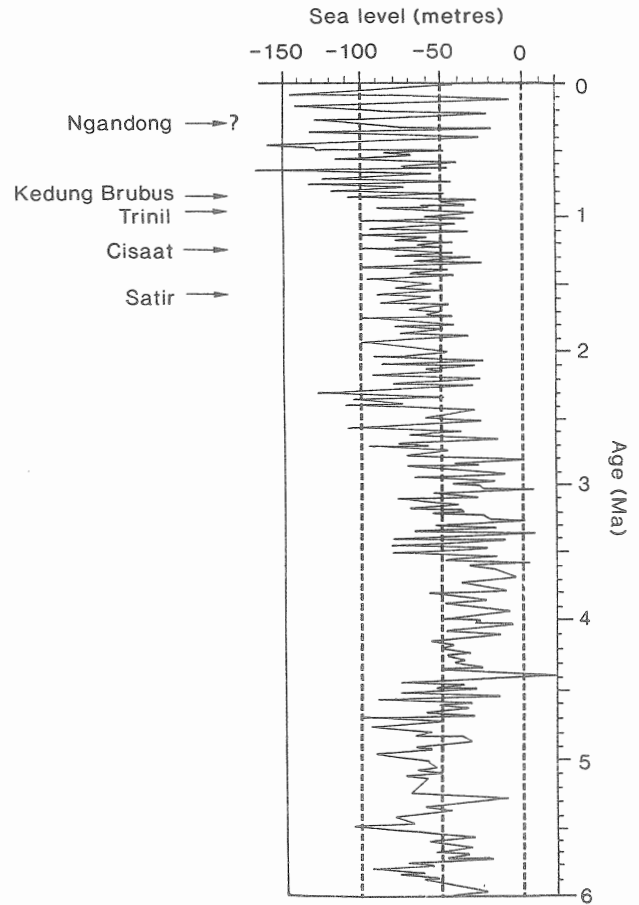

Figure 2: Glacio-eustatic sea level chart for the last 6 million years as calculated from the oxygen isotope composite derived from tropical shallow water dwelling planktonic foraminifera (after Prentice and Denton (1988). The early and middle Pleistocene Javanese faunal stages are also indicated.

ice-volume changes as derived from oxygen isotope records (Vrba 1990). After 2.4 myr the sea level, as deduced from ice volume, shows moderate fluctuations, with a mean of around 70 m below present day level (PDL) and lowest sea levels at around 100 m below PDL. This fluctuation mode seems to have remained constant until 0.8 myr. It is during this period that there is evidence for the first mammalian colonization of Java. At 0.8 myr the mode of sea level fluctuation changed drastically to high amplitude fluctuations with minimum sea levels down to 170 m below PDL and an average sea level of around 90 m below PDL. This fluctuation mode continued up to recent times.

Besides the $\delta^{18}O$ derived glacio-eustatic sea level charts there is another important tool in detecting global
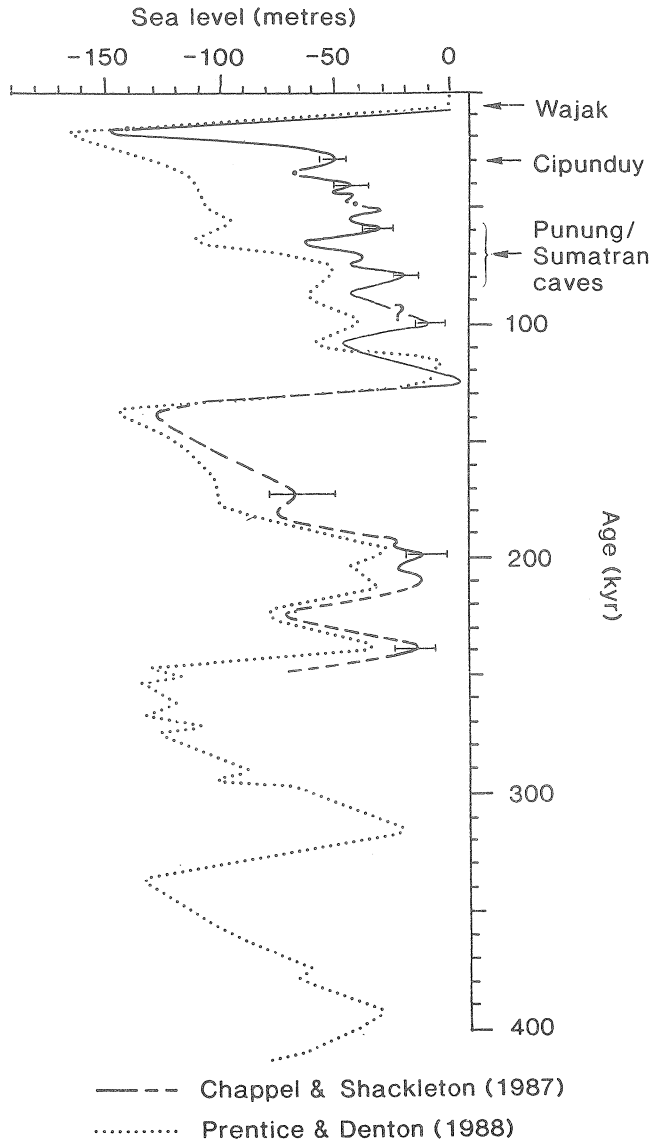
Figure 3: Sea level chart for the late Pleistocene-Holocene based on dated raised coral reefs in the Huon Peninsula, Papua New Guinea (after Chappell and Shackleton 1986). For comparison also shown is the sea level chart of Prentice and Denton (1988). The Sumatran cave faunas comprise the Lida Ayer and Sibrambang caves. The recently discovered Cipunduy fauna from West Java, which has been radiocarbon dated at around 30,000 years, awaits detailed study but seems to contain only species present in both the Punung and the Holocene composite faunas, notably Elephas maximus.

sea level fluctuations, namely seismostratigraphy (Vail *et al.* 1977; Haq 1991). However, this method is not able to detect short-term fluctuations. During the Pleistocene

period only one major low sea level stand can be recognized world-wide using this method. This period started at 0.8 myr BP, when low sea levels apparently lasted for sufficiently prolonged periods and were of significantly large magnitude to mark their presence in a large number of seismic profiles. The beginning of this period of a generally lowered sea level at 0.8 myr perfectly matches the drastic change in mode of short-term sea level fluctuations as deduced from the $\delta^{18}O$ derived sea level charts. The date of 0.8 myr is therefore considered as of major importance.

For the Late Pleistocene-Holocene interval there is a third sea level fluctuation curve based on dated raised coral terraces from the Huon Peninsula in Papua New Guinea (Chappell and Shackleton 1986). This curve is shown in Figure 3 together with the curve of Prentice and Denton (1988) for this younger interval. Comparison of the two curves reveals some discrepancies in the intermediate glacial stages but they are in good agreement concerning minimum and maximum sea levels during glacial and interglacial periods respectively. This shows again that the sea levels as depicted in these curves should not be taken as absolute values but as relative indications of sea level fluctuations.

For Java it is fairly safe to consider actual bathymetry in combination with sea level fluctuation charts in order to interpret the existence of land connections with Southeast Asia during the Late Pleistocene. Java is not subject to such strong tectonic forces as have been shown to occur in the eastern part of the Indonesian region. In Timor the introduction of continental lithosphere into the subduction complex has caused a strong uplift of 1500 m in some parts of the island during the last 200 kyr (Fortuin and de Smet 1991). Also, in other parts of East Indonesia the presence of uplifted coral terraces indicates strong uplift. However, highly elevated coral or coastal terraces of Late Pleistocene age are not found in Java, suggesting relative stability there. In the modern bathymetric setting a sea level lowering of 50 meters would be enough to connect Java, Sumatra and Borneo with the Asian mainland, as shown in Figure 4. However, Java would still remain quite isolated as a large elongated bay would have separated Java from Borneo to the north.

DISCUSSION

A description and interpretation of the various Javanese faunas is given by de Vos *et al.* (1982) and Sondaar (1984). Full faunal lists for the fossil faunas are given in Table 1, based on these papers and on Cranbook (1987) for the recent fauna of Java. Small mammals have been excluded to lessen bias caused by different sampling
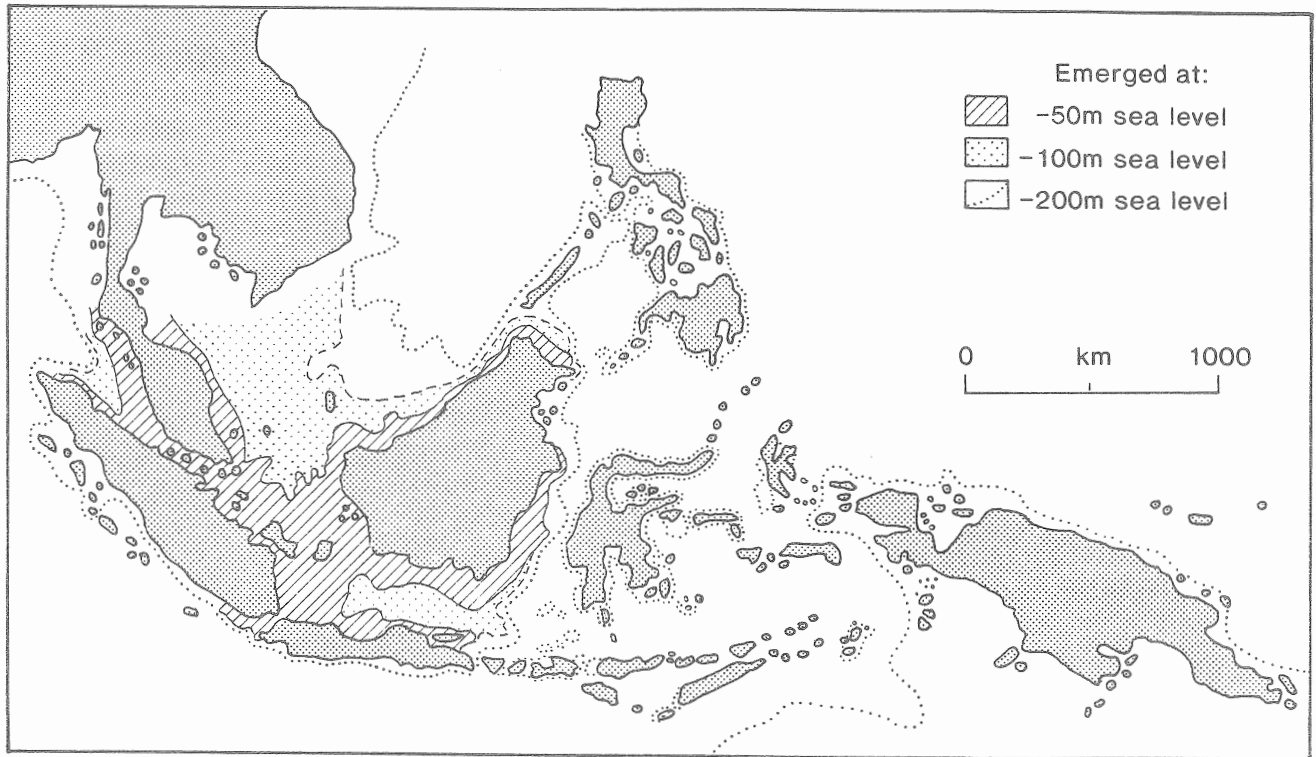
Figure 4: Bathymetric map of the Indonesian region showing the 50, 100 and 200 meter isobaths. In the relatively stable and shallow Sunda Platform, global sea level fluctuations have had a major impact on the faunal migrations. The bathymetry of the East Indonesian Banda Arc system is likely to have been altered greatly during the Pleistocene due to tectonic movements, notably the introduction of Australian continental crust into the Banda Arc subduction system.

techniques and taphonomic differences for each fossil type locality. For example, a number of rodents and bats are recorded from Holocene cave deposits while from fluviatile localities (Satir, Ci Saat, Trinil H.K. and Kedung Brubus) no, or very few, rodents are known due to the fact that these deposits were not sieved, or only sieved to a limited extent. In Table 1 the following groups are excluded: Rodentia (apart from the medium sized Hystricidae), Chiroptera, Lagomorpha and Insectivora. The fauna list of the Holocene cave deposits is a composite list from four different localities: Wajak, Sampung, Goa Jimbe and Hoekgrot, based on de Vos *et al.*, in press). This composite list might blur details concerning the Holocene faunal succession, but for our purpose it is justified because the time-span covered by these localities amounts at most several thousands of years, which is negligible compared to the timespan of the Lower and Middle Pleistocene faunas considered here.

The recent fauna has the largest number of species (33). This must be due to the incompleteness of the older fossil record. The recent fauna contains even more species than those fossil faunas considered as fully balanced (like the Kedung Brubus fauna). The recent fauna contains 13 first recordings, most of which are relatively small sized carnivores rarely encountered as fossils (lower right of Table 1). It is likely that most of these apparent new recordings in the recent fauna were already present in Holocene or earlier times. The incompleteness of the fossil faunal lists is also reflected by the fact that for 11 fossil mammal species from Java no stratigraphic control exists (lower left of Table 1). They all represent rare species. Some of these fossil species come from the Sangiran area, others from the Bumiayu area, but exact localities and stratigraphic levels are not known for any. One of these species is likely equivalent to one of the two oldest faunas, either Satir or Ci Saat. This is *"Elephas" indonesicus*, of which a single upper molar exists from

Table 1: Faunal lists for the localities discussed.

Java fauna list

	SATIR	BUKURAN SITE BELOW TUFF 9	CI SAAT	TRINIL	KEDUNG BRUBUS	NGANDONG	PUNUNG	HOLOCENE CAVES COMPOSITE	RECENT
Manis palaeojavanica					•				
Manis javanica								•	•
Ursus malayanus								•	•
Paradoxurus hermaphroditus								•	•
Arctogalidia sp.								•	•
Panthera sp.			•?						
Panthera tigris subsp.				•	•	•		•	•
Prionailurus (=Felis) bengalensis				•	•	•	•	•	•
Aonix (=Amblonyx) cinerea				•					•
Lutrogale palaeoleptonyx				•					
Martes flavigula								•	
Hyaena brevirostris					•				
Mececyon trinilensis				•					
Cuon? javanicus					•				
Cuon javanicus (=alpinus)									•
Tetralophodon bumiajuensis	•								
Stegodon cf. elephantoides		•							
Stegodon trigonocephalus			•	•	•				
Stegodon? hypsilophus						•?			
Elephas hysudrindicus				•	•				
Elephas maximus							•	•	•
Rhinoceros sondaicus				•	•	•		•	•
Rhinoceros unicornis kendengindicus					•				
Tapirus indicus					•			•	•
Hexaprotodon simplex	•								
Hexaprotodon sivalensis		•	•	•	•				
Muntiacus muntjak		•	•	•	•	•		•	•
Cervids	•	•							
Tragulus javanicus								•	•
Axis lydekkeri				•	•	•			
Axis kuhli								•	•
Rusa sp.					•				
Rusa (=Cervus) timorensis						•	•	•	•
Duboisia santeng				•	•				
Capricornis sumatraensis								•	•
Epileptobos groeneveldtii					•				
Bubalus palaeokerabau				•	•				
Bubalus bubalus (=arnee)								•	•
Bibos palaesondaicus				•	•				
Bibos sp.						•			
Bos javanicus (=Bibos sondaicus)							•	•	•
Bovids	•								
Sus brachygnathus				•	•	•	•?		
Sus macrognathus					•	•			
Sus scrofa vittatus								•	•
Sus sp.							•		
Sus verrucosus								•	•
Nycticebus coucang								•	•
Presbytis (=Trachypithecus) cristatus				•	•	•	•	•	•
Presbytis comata									•
Macaca fascicularis								•	•
Macaca nemestrina								•	•
Hylobates syndactylus								•	•
Hylobates moloch								•	•
Pongo pygmaeus							•	•	•
Homo erectus				•?	•	•			
Homo sapiens							•	•	•
Hystrix (=Acanthion) brachyurus				•	•	•	•	•	•
Hystrix javanica									•
Panthera pardus									•
Felis viverrina									•
Herpestes javanicus									•
Viverricula indica									•
Mustela lutreolina									•
Melogale personata									•
Mydaus javanensis									•
Lutra lutra									•
Lutra sumatrana									•
Arctitis binturong									•
Prionodon linsang									•

Fossil species lacking stratigraphical information:

Hystrix gigantea
Hemimachairodus zwierzyckii
Megantereon sp.
Homotherium ultimum
Panthera pardus
Lutrogale robusta
Megacyon sp.
Nestoritherium cf. sivalense
Merycopotamus dissimilis
Leptobos? problematicus
"Elephas" indonesicus

the Bumiayu area of west central Java. This upper molar comes from the Ci Panglosoran river and it has been described on different occasions as either an M1 of a largesized elephant (*Elephas planifrons*; van der Maarel 1932) or as an M2 of a dwarf elephant (*Elephas celebensis*; Maglio 1973; Hooijer 1974). Kretzoi (1950) made it the type for a new species, *Stegoloxodon indonesicus*. Although closely related to *"Elephas" celebensis* (the latter only recorded from Late Pliocene to Early Pleistocene deposits in South Sulawesi and showing several plesiomorphic characters, such as the occasional presence of lower tusks and the retention of premolars; see van den Bergh *et al.* 1992), we hold the opinion that *"E." indonesicus* represents a distinct pygmy elephant that evolved on Java in isolation. Both pygmy species possibly descended from the same ancestral mainland stock, perhaps from *Elephas planifrons* or from a more primitive elephant like *Primelephas*. The distinction between the Sulawesi and Java species is based on the slightly distinct molar morphology and on the fact that other Late Pliocene faunal elements known from southwest Sulawesi, such as *Celebochoerus heekereni*, are not recorded from Java, and likewise, faunal elements from the earliest faunas on Java, such as *Tetralophodon bumiajuensis* and *Hexaprotodon simplex* are not recorded from South Sulawesi.

Leptobos problematicus was originally described as *Cervus problematicus* by von Koenigswald (1933), based on a hornless female skull fragment without dentition, also from an unknown stratigraphical level in the Bumiayu area. Comparison of this skull fragment with the type material of several bovid species from the Siwaliks stored in the collections of the British Museum of Natural History revealed that it does not represent a cervid at all, but instead corresponds closely with *Leptobos*.

Two other archaic taxa probably pertaining to the older faunal units of Java but of unknown stratigraphical level are *Nestoritherium* cf. *sivalense* and *Merycopotamus dissimilis*. The latter was considered as a guide fossil for the so-called Ci Julang fauna (von Koenigswald's 1935), which has been abandoned in the new biostratigraphical scheme for Java (Sondaar 1984).

Some taxa are not known from a certain fauna but are present in both older and younger faunal stages. For example, *Hexaprotodon sivalensis* is not known from the Trinil H.K. fauna but occurs in both the Ci Saat and Kedung Brubus faunas. Its absence in the Trinil H.K. fauna might be due to local environmental circumstances at the Trinil site during deposition of the "Hauptknochenschicht", which could have been unsuitable for the presence of *H. sivalensis*. For convenience,

taxa for which there is no proof of occurrence in a certain faunal unit, but which are present in both an older and younger faunal unit, are included in the countings for that unit in the following discussion. In Table 1 they are indicated with a dashed line in such a case.

Finally, it should be noted that in only a few cases is a taxon considered equivalent to a certain fauna when the species itself has not been recovered from the type locality of that fauna. Because this practice has caused much confusion in the past, for instance when von Koenigswald established his biostratigraphy of Java in the 1930s, these taxa are indicated with a question mark in Table 1, indicating that they are derived from another locality than the type locality, but of supposed similar age. This is the case with *Homo erectus* in the Ci Saat fauna; this species is certainly present in the younger Trinil H.K. fauna but not in the older Satir type fauna. *Homo erectus* fossils derived from the upper part of the black clays above tuff 9 in the Sangiran area suggest a presence in at least the later part of the Ci Saat faunal stage. Also *Stegodon*? *hypsilophus*, a relatively high-crowned pygmy proboscidean of Stegodontine affinity, is provisionally included here in the Kedung Brubus fauna. Hooijer (1955) attributes a small distal portion of a humerus from Kedung Brubus to *Stegodon hypsilophus*, but de Vos and Sondaar (1982) are of the opinion that the presence of one humerus fragment is not conclusive evidence for including this taxon in the Kedung Brubus fauna. However, based on the origin of the type specimens from north of Jetis and Perning, this taxon is thought to be equivalent with the Kedung Brubus fauna (Sondaar 1984; van den Bergh *et al* 1992).

From Table I it follows that the faunal succession of Java shows a gradual enrichment of species, reaching a maximum number of 25 taxa in the 0.8-0.7 myr Kedung Brubus fauna. In the younger faunas the number of species remains similar to the Kedung Brubus fauna, at between 18 and 25 medium to large sized taxa (excluding the recent fauna with 33 taxa, of which a large number are relatively small sized carnivores rarely encountered as fossils). The successive faunal stages are insufficiently dated to permit calculations of numbers of appearances and extinctions per fixed amount of time.

The groups to which the three taxa of the Satir fauna belong are all supposed to be good swimmers (proboscideans, cervids and hippos). Such animals frequently occur in impoverished island faunas (Sondaar 1977). Carnivores are absent in the Satir fauna, while the presence of the giant tortoise *Geochelone atlas* (though not recorded in the Satir type fauna proper) also indicates island circumstances. Sweepstake dispersal (Simpson

1965) has been the presumed migration mechanism for Java during the Satir faunal stage (Sondaar 1984), implying that a sea barrier had to be crossed. This could be accomplished only by certain animals that could survive for some time in the water.

The first marked glaciation, presumably leading to a global lowering of sea level, occurred at 2.4 myr. However, there is no proof so far for such an early mammalian colonization of Java and the oldest well defined fauna, the Satir island fauna, might have invaded the island at only around 2 myr. The clear island character of this fauna would imply that parts of Java had emerged above sea level due to vertical tectonic movements and volcanic processes around that time, but that no connections with the Southeast Asian mainland yet existed. Java was fairly inaccessible at that time. Recent work in Flores suggests that early hominids, presumably *Homo erectus*, had colonized the paleo-island of Flores at the beginning of the Middle Pleistocene (van den Bergh *et al.* this volume). Hominids were apparently able to cross water barriers, willingly or accidentally, at around 700 kyr BP. However, based on the information presented above we reject a supposedly Late Pliocene hominid invasion of Java as proposed by Swisher *et al.* (1994) because it contradicts so many other geological, faunistic and dating results.

The relative poorness of the Ci Saat and Trinil H.K. faunas was interpreted by Sondaar (1984) to indicate relatively isolated circumstances for Java at that time. He proposed a filter-route dispersal for these faunas. There might have been only a type of limited and periodic land connection between Java and the mainland during this time interval. If one accepts the presence of *Homo erectus* in the Ci Saat faunal stage, based on the occurrence of fossils from the uppermost part of the Sangiran Formation and the correlation of this stratigraphic zone in the Sangiran area with the Ci Saat type localities near Bumiayu, it can be concluded that *Homo erectus* was already able to cope well with such environmental barriers and could reach Java at a time when such barriers prevented many of the mainland faunal elements from reaching Java. It is not necessary, however, to assume overseas dispersal at this stage because Java must have had limited land connections of relatively brief existence. The presence of felids in the Trinil fauna and perhaps also in the Ci Saat fauna would imply at least a limited (intermittent) land connection between Java and the Asian mainland.

It seems that with the presently available information, during the period before 0.8 myr, prior to the Kedung Brubus faunal stage, the immigration to Java of large

vertebrates was rather limited and slow. While this period covers a considerable timespan from perhaps 2 myr to 0.8 myr, there are around 25 new recordings of taxa during this entire timespan of 1.2 million years. These 25 new recordings include the four taxa considered as archaic listed under fossil species lacking stratigraphic control in Table 1. They also include *Geochelone atlas*. This corresponds with a new recording rate of 2.1 taxa per 100,000 years, or, at most, 2.7 taxa per 100,000 years if all taxa without stratigraphic control are included in one of the faunal units older than Kedung Brubus. We speak of "new recording rate" and not of "immigration rate" because some taxa might have evolved locally on Java from taxa present in earlier faunal units. For example, *Panthera* sp. from the Ci Saat fauna might represent the same lineage as the successive *Panthera* tigris subspecies from the younger faunal units.

Most drastic was the faunal turnover occurring between the impoverished Satir faunal stage and the Ci Saat faunal stage. Both *Tetralophodon bumiajuensis* and *Hexaprotodon simplex* were replaced by new immigrants (*Stegodon* and *Hexaprotodon sivalensis* respectively) supposedly competing with the island taxa. Cervids, also occurring in the Satir fauna, are presently being restudied by de Vos, and it remains to be seen how many species are represented and if they continued in the younger Ci Saat and Trinil faunas. *Geochelone* disappeared, presumably due to the hunting activities of *Homo erectus*. At present it remains impossible to say over which timespan the transition from the Satir to the Ci Saat faunal stage took place. According to the recent information presented above *Geochelone* now appears to have continued until around 1.16±0.24 myr. Also, a new species (for Java) of *Stegodon* cf. *elephantoides* was collected from the upper part of the Sangiran Formation from layers of around 1.2 myr (stratigraphically several metres below the *Geochelone* level). It thus follows that *Geochelone* still continued until after the first immigration of *Stegodon* to Java. This suggests that there was perhaps a gradual transition from the Satir to the Ci Saat faunal stage. So far the model of Sondaar (1984), in which several taxa from the Satir island fauna were replaced by competing new immigrants in the Ci Saat and Trinil faunas, still stands. However, the timespan during which these replacements took place might have been considerable longer than was thought previously.

The Kedung Brubus fauna has for the first time a balanced mainland character and a maximum number of 25 species are represented. Of these 25 species, 10 represent new recordings, 5 of which in turn probably represent immigrations from the Southeast Asian mainland

(*Rhinoceros unicornis kendengindicus, Hyaena breviros- tris, Tapirus indicus, Manis palaeojavanica* and *Lutrogale palaeoleptonyx*). The time span between the Trinil and Kedung Brubus faunas only represents be- tween 100,000 to 200,000 years, which would give a new recording rate of 5 to 10 species per 100,000 years. This new recording rate is 2 to 5 times greater than that for the entire period preceding the Kedung Brubus faunal stage. This, and the maximum number of taxa recorded in the Kedung Brubus fauna, suggests that for the first time a broad land connection between Java and the Southeast Asian mainland existed for a prolonged period of time. Most taxa from the Trinil fauna continue to be present in the Kedung Brubus fauna and extinctions seem to have been very limited. This could indicate that no drastic climatic changes accompanied the transition from the Trinil to the Kedung Brubus faunal stage. The overall environmental conditions must have remained quite open, because large bovid remains dominate both faunas (de Vos *et al.* 1982). This seems in accordance with pa- lynological results from the Sangiran area (A.-M. Sémah 1984), where the upper part of the "black clays" (=Sangiran Formation) just below the Grenzbank (South Cemoro section) and the lower part of the "Kabuh For- mation" (=Bapang Formation) just above the Grenzbank (Jengglong section) are poor in tree pollen and spores and dominated by pollen of herbaceous plants, indicating an open vegetation. There is some discrepancy with another one meter thick section situated one meter above the Grenzbank (Bapang section), where there is a rapid in- crease in spores and *Podocarpus* trees, suggesting increasing humidity. This discrepancy might be due to local circumstances or horizontal facies changes (A.-M. Sémah 1984), or to long distance transport of *Podocarpus* pollen.

When we compare these results with the sea level curve of Figure 2 there can hardly be any doubt that the drastic change in sea level fluctuation mode that occurred around 0.8 myr (with a lowering in both mean and abso- lute sea levels) resulted in an increased accessibility of Java and the establishment of a fully developed mainland fauna as represented by the Kedung Brubus fauna. The increased number of megaherbivores in the Kedung Brubus fauna (8, versus the 4 in the Trinil fauna) and the supposedly increased aridity generated by the exposure of the entire Sunda Shelf, might have resulted in the most open woodland vegetation condition since the first mammalian colonizations of Java in the Late Pliocene.

With the Ngandong fauna not much drastic change in faunal composition can be demonstrated, except perhaps for a slight impoverishment, although the Ngandong

fossil material should be thoroughly re-examined. Most changes seem to represent local evolution on a subspe- cies level (de Vos *et al.*, in press). Based on this meagre evidence it is thought that, since the Kedung Brubus fau- nal stage, the environmental conditions in Java remained quite stable until the Ngandong stage.

Turning to the next faunal stage, the Punung fauna, we can observe that 17 taxa present in the Kedung Brubus fauna are now absent (Table 1). On the other hand, there are 10 new recordings in the Punung fauna. As we have no adequate information on the absolute age of the intermediate Ngandong fauna we cannot say over which timespan this faunal turnover took place, but it is clear that it marked a major environmental change. The Punung fauna contains large numbers of primates such as *Pongo* and *Hylobates*, for the first time indicating a hu- mid forest environment (de Vos 1983). This is in sharp contrast to the older faunas, which represent open wood- land habitats.

It is likely that most replacements recorded in the Punung fauna took place during a time interval when the sea level was around 40-65 m below PDL before 70 kyr, but after the glacial maximum at around 135 kyr (Figure 3), when presumably dry climatic conditions prevailed in the exposed Sunda shelf region. At least for west Java there is now strong evidence for such drier conditions during the penultimate glaciation. In a drilling core over hundred meters thick from the Bandung Basin (Dam 1994), the occurrence of pedogenic carbonate concretions (kankar nodules) at a depth of 50-58 m points to a sub- stantial evaporation surplus and a considerably longer dry season than occurs at present. This kankar interval has been dated with the U/Th disequilibrium method to ap- proximately 135 kyr (equivalent with oxygen isotopic stage 6, Martinson *et al.* 1987). Because the migration to Java of the orang utan, first recorded in the Punung fauna, certainly required a continuous forest canopy, it is unlikely that this migration took place during the penul- timate glacial maximum.

It can even be argued that the immigration must have taken place after the high sea level stand at 125 kyr, when climatic conditions were supposedly warm and humid as evidenced by palynological data from the same Bandung Basin core mentioned above (van der Kaars and Dam 1994). Though these climatic conditions were po- tentially suitable for a rainforest fauna to enter the island, Java was probably isolated from the mainland by a sea barrier at that time, which would have been insurmount- able for the orang utan. More likely, the immigration of the forest elements of the Punung fauna took place during the later part of oxygen isotopic stage 5, roughly between

110 kyr and 70 kyr. Palynological evidence (van der Kaars and Dam 1994) indicates that the climate remained warm and humid until around 81 kyr, while sea level during this stage was fluctuating around 50 m below PDL. With a sea level of around 50 m below PDL, Java would have been largely surrounded by sea (Figure 4), providing relative humid conditions. At the same time a land corridor in the west would have permitted overland migration to Java. This lowstand, in combination with relatively humid conditions, probably permitted the rain-forest elements such as *Pongo* and *Hylobates* to enter Java. These taxa had supposedly been driven south by the preceding glacial maximum at 135 kyr via the so-called Sino-Malayan route (de Vos *et al.*, in press). They probably survived during the penultimate glacial maxi-mum in isolated mountainous and humid environments on the Sunda Shelf, to spread further south into Java be-tween 110 kyr and 70 kyr.

As stated before, the supposed age of the Punung fauna is only 80 to 60 kyr, although this is rather specu-lative and not based on direct age determinations. However, the presence of *Homo sapiens* in the Punung fauna would suggest an age younger than 110 – 80 kyr. *Pongo* is not recorded from the Holocene composite cave fauna and probably disappeared from Java during the last glacial, when drier conditions and increased seasonality again disrupted the rain forests in that region (Morley and Flenley 1985). These climatic changes are evidenced by an increase in grass pollen and a decrease in fern spores at this time in deep sea cores from the region (van der Kaars 1991). Small mountainous areas with rainforest could have served as refuges for some of the typical for-est dwellers during this stage, but apparently *Pongo* was not able to cope with these changes and disappeared from Java.

Interestingly, the Punung fauna records the oldest oc-currence of *Homo sapiens* in Java (de Vos 1985). The Punung material contains two upper incisors, an upper canine, a lower canine and an upper molar, all too small to be attributed to the dentition of *Pongo*. Von Koenig-swald (1940) identified these specimens as belonging to *Pithecanthropus*, probably because he considered the Punung fauna equivalent to the Trinil fauna. Later, von Koenigswald (1975), when he considered the Punung fauna to be of post-Trinil age, stated that a few isolated teeth indicated the presence of man. According to de Vos (1985) these teeth can be attributed to *Homo sapiens*. Also, the Sumatran cave faunas of similar age to the Punung fauna contain a semi-shovel-shaped right upper central incisor and a left upper molar, identified as *Homo sapiens* by Hooijer (1948).

After the Holocene transgression sea level rose rap-idly and rainforests expanded again. *Pongo pygmaeus* became trapped in Sumatra and Borneo (see also Vu The Long *et al.*, this volume). Though *Homo sapiens* was possibly responsible for a number of disappearances ob-served at the transition between the last two faunal stages, the Holocene and recent, climatic changes cer-tainly played a role. Excluding the small carnivorous species, there are only 2 new recordings for the recent fauna, namely *Hylobates moloch* and *Presbytis comata*. These are only present on Java and perhaps represent endemics that became trapped on Java after the Holocene transgression.

CONCLUSIONS

For the Late Pliocene to Early Pleistocene period not enough information is at present available to correlate major faunal changes with sea level fluctuations and cor-responding climatic changes. At present there are no data that support the view that Java was already populated by mammals during the first drastic sea level lowering at 2.4 myr. This suggests that Java at that time might have been largely submerged and was first colonized by terrestrial vertebrates after it emerged due to local tectonic and vol-canic processes. After its emergence during the Plio-Pleistocene transition Java was first inhabited by an un-balanced island fauna for a rather long period (Satir faunal stage). The presumed mode of dispersal was a sweepstake route across a sea barrier. During the late Early Pleistocene (Ci Saat and Trinil faunal stages) Java presumably became intermittently connected to Asia, but not for extensive periods. It seems that major environ-mental barriers still separated Java from the SE Asian mainland (filter route). *Homo erectus* colonized Java during this period.

The second period of drastic sea level lowering at 0.8 myr is very well matched by the high number of new faunal appearances recorded in the interval between 0.9 and 0.7 myr. The first appearance of *Homo sapiens* oc-curred with the invasion of a basically distinct faunal type (Punung faunal stage), indicating a tropical rain-forest environment. This invasion presumably took place during the later part of oxygen isotopic stage 5 between 70 kyr and 110 kyr, when the sea level was about 50 meters below present and warm and humid climatic conditions still prevailed.

NOTE

1 The "black clays" from Sangiran, classically known as the Pucangan Formation, have recently been named the Sangiran Formation (IJJST, 1992), to stress the lithological and time differences with the Pucangan Formation as developed in the type section, which is several hundred kilometers to the east of Sangiran. Similarly, we prefer to designate the so-called "Kabuh Formation" at Sangiran with the new name Bapang Formation as proposed by IJJST (1992).

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