



The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago

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Abstract

The Quaternary faunal evolution for the Indonesian Archipelago reflects the unique relationship of each island with SE Asian mainland. The recent sub faunas of Sundaland (Kalimantan, Sumatra, Java, and Bali) preserved broad connections with the SE Asian mainland during the latest glacial. They are all balanced and show many mainland components. Alternatively, Wallacea (Sulawesi and the Lesser Sunda Islands) has always been geographically isolated from the mainland. Wallacea faunas thus remain unbalanced (they lack large carnivores) and endemic. A significant turnover arrives throughout the region with pronounced global sea level recessions around 0.8 Ma, during the transition from Early Pleistocene (EP) to the Middle Pleistocene (MP). By way of comparison, the palaeontological records of Japan and Taiwan also preserve this turnover, with EP–MP recessions bringing East Asian mainland immigrants.

On Java, the earliest, Late Pliocene to early Pleistocene Satir fauna indicates island conditions. Java became connected to the SE Asian mainland towards the end of the early Pleistocene. Global cooling brought open woodlands on Java, an environment evidently preferred by *Homo erectus* in the Ci Saat fauna and Trinil H.K. fauna. As EP–MP sea level recessions created a wide corridor across the Sunda Shelf, Siwaliks and the SE Asian mainland terrestrial mammals invaded, as is seen in the Kedung Brubus fauna. The succeeding Ngandong fauna maintains an open woodland character but shows some endemism (*Homo erectus* and *Stegodon trigonocephalus*, among others, can be distinguished on a subspecies level). The Late Pleistocene marks the earliest known tropical rainforest, and the corresponding Punung fauna is of Chinese affinity (with *Pongo*, *Hylobates*, and *Elephas maximus*). *Homo sapiens* probably arrives at this point as well. The youngest fossil faunas known from Java are the still poorly known Cipeundeuy Fauna (ca. 30 ka) and the Holocene faunas from Wajak and Sampung.

While Sulawesi and Flores remained isolated throughout the Quaternary, only a limited number of terrestrial vertebrates arrived by crossing sea barriers. Endemic island faunas with pygmy elephantoids and giant tortoises were present during the Early Pleistocene. EP–MP sea level recessions allowed large to medium sized elephantoids to replace the dwarf species. Around the same time, *Homo erectus* appears on the island of Flores. Modern faunas eventually replaced the Middle Pleistocene island faunas, but the time frame has yet to be pinpointed. Sulawesi presents a unique case. Its current fauna holds no Walanae representatives. Apart from the phalangers, which must have come from the east. The ancestors of all other large Sulawesi land vertebrates, fossil and extant, reached the island by crossing the Sunda Sea. As the South Sulawesi fauna was stable until the Middle Pleistocene, this area must have constituted a separate palaeo-island. Some localized developments can be observed (e.g. shortening of the metapodials in *Celebochoerus*, increasing hypsodonty in *Stegodon*). © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Quaternary; Indonesia; Zoogeography; Land vertebrates; Islands; Sea level change; Hominids

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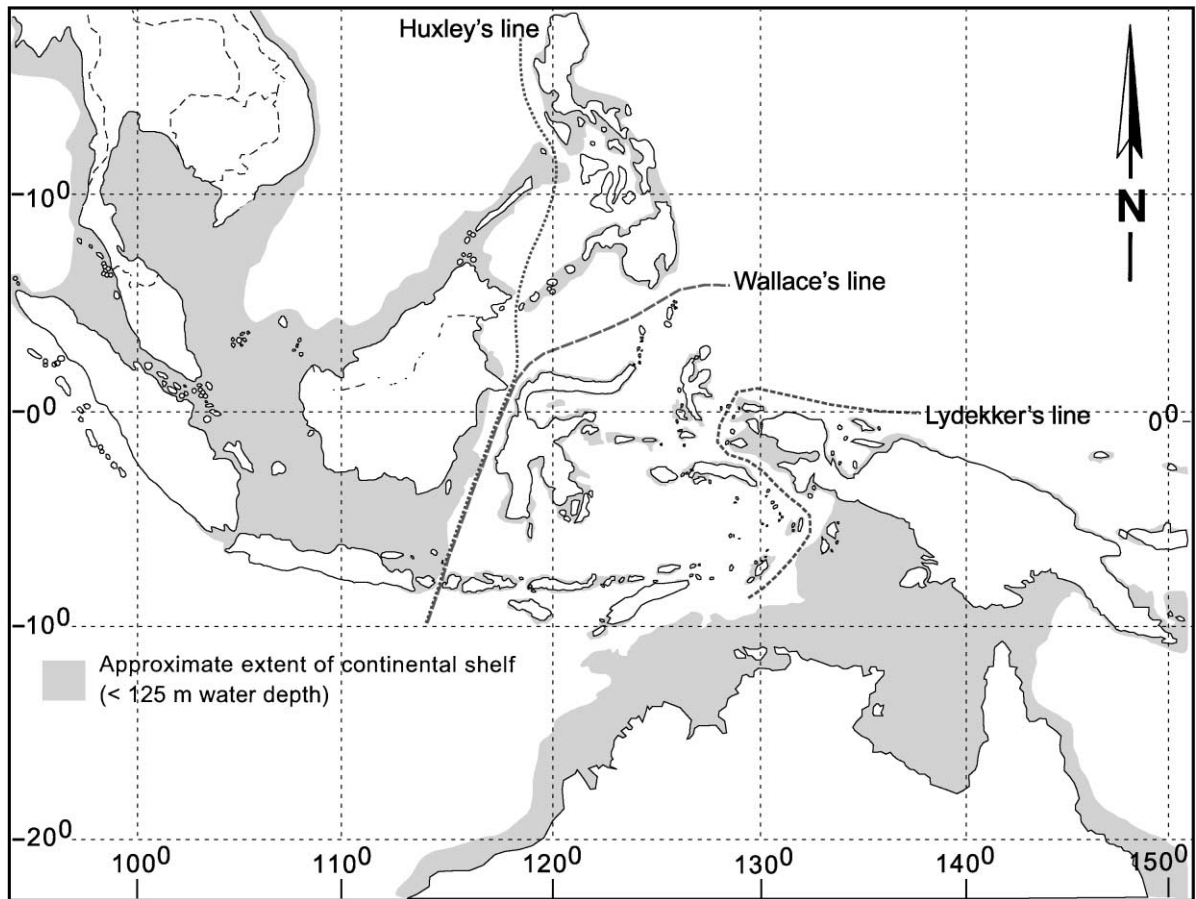


Fig. 1. Map of the Indonesian region, showing the 125 m isobath, and the most significant zoogeographic boundaries, Huxley's Line (also known as Wallace's Line) and Lydekker's Line.

1. Introduction

Modern and fossil land vertebrate faunas of the Indonesian Archipelago can be divided into balanced mainland faunas and unbalanced endemic island faunas. Unbalanced island faunas consist of a limited number of genera of mammalian herbivores, while large carnivores are lacking. The fossil record from Java is fairly complete and the faunal evolutionary history is relatively well known. It can thus serve as a basis for comparison with the faunal records of Flores and Sulawesi, which are also fairly complete. This paper will both provide an overview of the current state of knowledge concerning the fossil faunas of terrestrial vertebrates from Indonesia and contextualize the appearance

of hominids within a wider framework of faunal evolution.

2. Area description

The zoogeographic boundary separating Sundaland (comprising the larger islands Borneo, Sumatra, Java and Bali) in the west from Celebes and Lombok in the east, was first mapped by Wallace (1869) (Fig. 1). Soon thereafter, Huxley (1869) extended Wallace's Line northward between Borneo and the Sulu Archipelago, across the Sulu Sea and further through the Mindoro Strait west of the Philippines. However, because Wallace considered the Philippine realm to be Asiatic, he disputed Huxley's northward extension

of his line. Although Huxley referred to it as Wallace's Line, it should properly be referred to as Huxley's Line (Fig. 1), since it corresponds with the edge of the southeast Asiatic continental shelf as far as Mindoro Strait (Simpson, 1977).

Many more lines were drawn based on the distribution of different animal groups (Simpson, 1977). Today, the most significant of these is perhaps Lydekker's Line (Fig. 1), which delineated the boundary between the Australian Region and the Austro–Malayan Region. The latter was considered a transitional zoogeographic zone between the Oriental and Australian Regions with its western boundary Wallace's Line thus east of the Philippines and Lydekker's Line running along the western edge of the Sahul Continental shelf, thus forms the eastern counterpart of Huxley's Line. In 1928, Dickerson named the island region between Sunda and Sahul, which includes the Philippines, Wallacea. As Simpson (1977) argues, too many zoogeographic boundaries have been drawn, because most researchers have based their assessments not on the fauna as a whole but on specific faunal groups, such as birds, landsnails, mammals, and bats. The ability to disperse across water barriers is not the same for every group of organisms, and may even differ among members of a single (genera or species) group. By delineating absolute boundaries between the Oriental and Australian regions it seemed impossible to please all zoogeographers at the same time. Simpson, therefore proposed, to keep the Oriental Faunal Region bounded by the Sunda Shelf (Huxley's Line) and the Australian Region bounded by the Sahul Shelf (Lydekker's Line), while calling for an end to assigning the intervening islands to a particular sub-region or intermediate zone. There is no real objection to designate the entire island region between the Sunda and Sahul Shelves as a transitional zone, with influences from both neighboring faunal regions and with local radiations and dispersal. However, the fauna on each island, with its particular composition, affinity, history, and ecology should be studied on its own.

3. Faunal successions

3.1. Java

During the 1980s, a new biostratigraphic scheme was proposed for the Quaternary terrestrial deposits

of Java (de Vos et al., 1982; Sondaar, 1984; de Vos, 1983; de Vos, 1985), which replaced von Koenigswald's (1933, 1934, 1935a,c,d) widely used classical biozonation for Java, which was based on composite faunal assemblages and contained various inconsistencies (de Vos et al., 1982; Braches and Shutler, 1984a; Theunissen et al., 1990). The new biostratigraphic scheme for the Pleistocene of Java proposed by de Vos et al. (1982) and Sondaar (1984) is based on the faunal contents from single localities or composite faunas from localities closely superposed in thick stratigraphic sequences. This new mammalian biostratigraphy of Java runs from young to old (Sondaar, 1984; Leinders et al. 1985; de Vos, 1996; Van den Bergh, 1999):

Wajak Fauna:	6–10 Ka
Punung Fauna:	ca. 60–125 Ka
Ngandong Fauna:	Late Pleistocene
Kedung Brubus Fauna:	ca. 0.7–0.8 Ma
Trinil H.K. Fauna:	ca. 0.9 Ma
Ci Saat Fauna:	ca. 1.0–1.2 Ma
Satir Fauna:	ca. 1.5–2.0 Ma

Not everything is known about this faunal succession. Major gaps have to be filled in between the Kedung Brubus and the Ngandong faunal stages, while the Ci Saat faunal stage is still hardly known. The fossil record still poorly covers the time range from 2 Ma until 1 Ma (Satir and Ci Saat faunal stages).

To date, there is no evidence of mammals on Java at 2.4 Ma, when the first marked glacio-eustatic sea level lowerings are thought to have occurred (Sémah, 1986; Van den Bergh et al., 1996b). Java gradually started to emerge above sea level due to tectonic and volcanic processes during the Late Pliocene (Van Bemmelen, 1949). The Satir fauna (Table 1) is the oldest recognizable faunal unit on Java, of which the chronostratigraphic position is known. It has an age of between 2 and 1.5 Ma and is characteristic for island conditions. *Sinomastodon bumiajuensis* is the only elephantoid known to occur in this fauna. From the Upper Pliocene and Lower Pleistocene deposits from Java scattered findings of dwarfed elephantoids are known, of which the stratigraphic position and age can only be roughly estimated. These are the archaic and small-sized '*Elephas*' *indonesicus* from Ci

Table 1 (continued)

Fauna unit	Satir	Ci Saat	Trinil H.K.	Kedung Brubus	Ngandong	Punung	Holocene caves composite	Recent
Age	2.0–1.5 Ma	1.2–1.0 Ma	0.9 Ma	0.8–0.7 Ma	Late Pleistocene	125–60 ka	10–6 ka	Recent
Interpretation	Island; Partly mangrove	?	Open woodland	Open woodland	Open woodland	Humid forest	Open woodland	Open woodland
<i>Axis lydekkeri</i>		+	+	+				
<i>Axis kuhli</i>							+	
<i>Rusa</i> sp.				+	+			
<i>Rusa</i> (= <i>cervus</i>) <i>timorensis</i>							+	+
<i>Duboisia senteng</i>			+	+				
<i>Capricornis sumatraensis</i>						+		
<i>Epileptobos groeneveldtii</i>				+				
<i>Babulus palaeokerabau</i>			+	+	+			
<i>Babulus bubalus</i> (= <i>arnee</i>)						+	+	
<i>Bibos palaesondaicus</i>			+	+	+			
<i>Bibos</i> sp.						+		
<i>Bos javanicus</i> (= <i>Bibos sondaicus</i>)							+	+
<i>Bovidae</i>		+						
<i>Sus brachgnathus</i>			+		+			
<i>Sus macrognathus</i>				+	+			
<i>Sus scrofa vittatus</i>						+	+	+
<i>Sus</i> sp.						+		
<i>Sus verrucosus</i>							+	+
<i>Nycticebus coucang</i>							+	+
<i>Presbytis</i> (= <i>Trachypithecus</i>) <i>cristatus</i>			+				+	+
<i>Presbytis comato</i>								+
<i>Macaca fascicularis</i>			+		+		+	+
<i>Macaca nemestrina</i>						+		
<i>Hylobates syndactylus</i>						+		
<i>Hylobates moloch</i>								+
<i>Pongo pygmaeus</i>						+		
<i>Homo erectus</i>		+	+	+	+			
<i>Homo sapiens</i>						+	+	+
<i>Hystrix</i> (= <i>Acanthion</i>) <i>brachyurus</i>			+			+	+	
<i>Hystrix javanica</i>							+	+
<i>Panthera pardus</i>								+
<i>Felis viverrina</i>								+
<i>Herpestes javanicus</i>								+

Table 1 (continued)

Fauna unit	Satir	Ci Saat	Trinil H.K.	Kedung Brubus	Ngandong	Puning	Holocene caves composite	Recent
Age	2.0–1.5 Ma	1.2–1.0 Ma	0.9 Ma	0.8–0.7 Ma	Late Pleistocene	125–60 ka	10–6 ka	Recent
Interpretation	Island; Partly mangrove	?	Open woodland	Open woodland	Open woodland	Humid forest	Open woodland	Open woodland
<i>Viverricula indica</i>								+
<i>Mustela lutreolina</i>								+
<i>Melogale personata</i>								+
<i>Mydaus javanensis</i>								+
<i>Lutra lutra</i>								+
<i>Arcitais binturong</i>								+
<i>Lutra sumatrana</i>								+
<i>Prionodon linsang</i>								+

Pangglosoran near Bumiaju (Van den Bergh et al., 1992), and the pygmy stegodonts from Sambungmacan (Aziz and Van den Bergh, 1995) and Cirebon (Van den Bergh, 1999). A giant tortoise is also present in the Satir Fauna (not shown in Table 1). As well as some herbivores frequently encountered on islands (hippos and deer). This association suggests isolated island conditions for Java at the beginning of the Quaternary. Hominids are not present during this stage.

The fairly isolated conditions of Java seem to have continued until ca. 0.8 Ma, as is suggested by the still unbalanced character of the ca. 0.9 Ma old Trinil Fauna (Table 1), with endemics such as *Stegodon trigonocephalus* and *Duboisia santeng*. The Trinil Fauna (*sensu* de Vos and Sondaar, 1982) bears the first solid proof for the presence of *Homo erectus*, although some scattered hominid remains may be slightly older. Nevertheless, the very high ages for two hominid sites on Java (1.81 ± 0.04 Ma and 1.66 ± 0.04 Ma), published by Swisher et al. (1994) are not based on solid evidence and seem far too old (de Vos and Sondaar, 1994; Van den Bergh, 1999).

During the early period of mammalian colonization of Java, between 2.4 and 0.8 Ma, the eustatic sea level as deduced from ice volume estimations based on isotopic ratios in foraminifera tests, is thought to have shown moderate fluctuations, with a mean of around 70 m below present day level (PDL) and lowest sea levels at around 100 m below PDL (Vrba et al., 1989). This fluctuation mode appears to have remained constant until around 0.8 Ma (Fig. 2). A major faunal immigration event to Java, leading to a maximum number of mammalian species (mostly medium to large-sized mammals as little is yet known of the rodents), is recorded in the 0.7–0.8 Ma Kedung Brubus Fauna (Table 1). This event coincides with the onset of a distinct mode of eustatic sea level fluctuations as compared to the foregoing period (Van den Bergh et al., 1996b). It is during the Kedung Brubus Faunal stage that *Elephas* (*E. hysudrindicus*) first entered Java.

The composition of the younger Ngandong Fauna appears largely similar to the Kedung Brubus Fauna. However, various species, including *Homo erectus* and *Stegodon trigonocephalus* can be distinguished on a subspecies level (de Vos et al., 1994; Van den Bergh, 1999; Coppens, 1999: 73). Open woodland

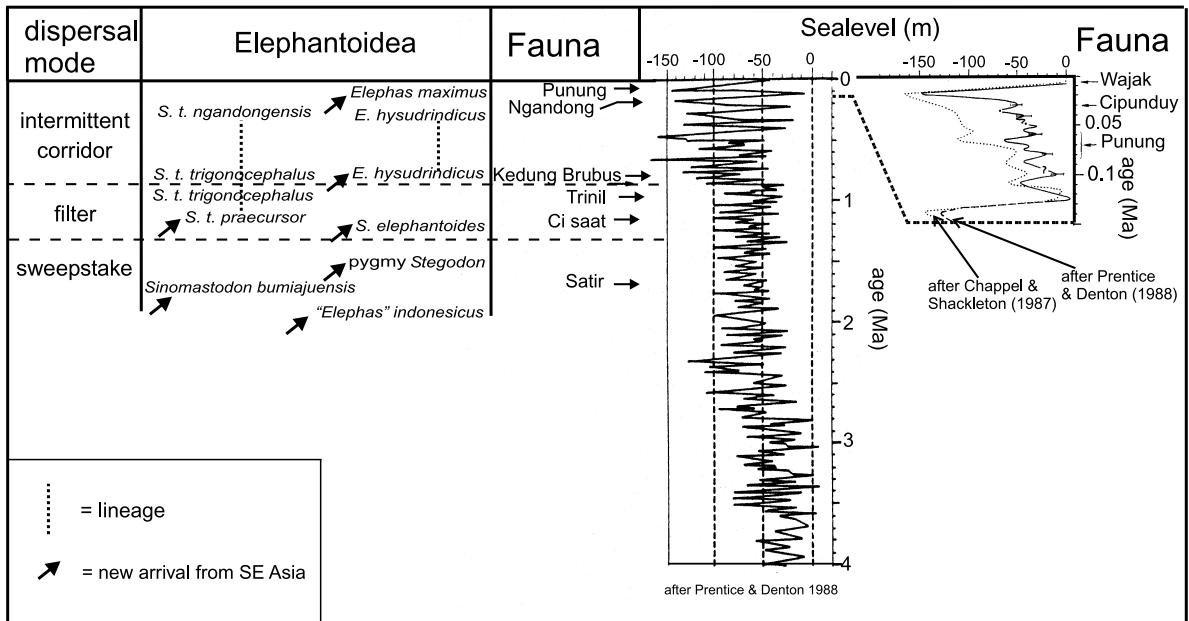


Fig. 2. Correlations between the faunal stages from Java and glacio-eustatic sea level fluctuations. Also shown are the ranges of the elephantoids. Major events occur between the Trinil and Kedung Brubus faunal stage and between the Ngandong and Punung faunal stage.

conditions were still established on Java at this time. Very young ages of 53.3 ± 4 to 27 ± 2 ka have been published recently for the Ngandong fossils (Swisher et al., 1996), but the age remains strongly contested (Van den Bergh, 1999). Therefore we maintain more conservative estimates of around 135 ky (penultimate glacial maximum).

A major change in environmental conditions on Java must have taken place toward the end of the Pleistocene. On the one hand, when comparing the Kedung Brubus and Ngandong faunas with the Punung Fauna (Table 1), it follows that 17 taxa still present in the Kedung Brubus fauna are lacking in the Punung Fauna. On the other hand, there are 10 new recordings in the Punung fauna. The Punung fauna contains large numbers of primates such as *Pongo* and *Hylobates*, for the first time indicating humid forest conditions on Java (de Vos, 1983). This is in sharp contrast with the previous faunas, which represent an open woodland environment (Trinil, Kedung Brubus and Ngandong Faunas). Most replacements recorded in the Punung fauna likely took place during a time interval when the sea level was some 40–65 m below PDL prior to 70 ka, but after the glacial maximum at 135 ka (Fig. 2). During the glacial maximum

at 135 ka dry climatic conditions presumably 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 core from the Bandung Basin (Dam, 1994), the occurrence of pedogenic carbonate concretions (kankar nodules) at a depth of 50–58 m points to a substantial evaporation surplus and a considerably longer dry season than occurs at present. This kankar interval has been dated with the U/Th disequilibrium method at approximately 135 ka (equivalent with oxygen isotopic stage 6). The entrance on Java of *Pongo pygmaeus*, first recorded in the Punung fauna, certainly required a continuous forest canopy. It is therefore unlikely that it coincided with the dry period during the glacial maximum. The Punung Fauna probably also includes *Homo sapiens* (de Vos, 1996). The major faunal event leading to the establishment of the Punung Fauna on Java probably took place after the period of high sea level at 125 ka, when climatic conditions started to become more humid, as evidenced by palynological data from a core from the Bandung Basin (Van der Kaars and Dam, 1994). Though these humid climatic conditions were potentially suitable for a rainforest fauna to enter the island,

Java was most likely isolated from the mainland by a sea barrier at that time (Fig. 2). A sea-barrier would have been an insurmountable obstacle for the orang utan. More likely, the immigration of the typical forest elements of the Punung fauna occurred during the later part of oxygen isotopic stage 5, roughly between 110 and 70 ka. Palynological evidence (Van der Kaars and Dam, 1994) indicates that the climate remained warm and humid until ca. 81 ka, while sea level during this stage fluctuated around 50 m below PDL (Chappell and Shackleton, 1987). With a sea level of 50 m below PDL, Java would have been largely surrounded by sea, providing relatively humid conditions. At the same time, a land corridor in the west would have permitted overland migration to Java. Thus a sea level lowstand of around 50 m below PDL, in combination with relatively humid conditions, probably permitted the typical rainforest elements such as *Pongo* and *Hylobates* to enter Java. These rainforest taxa had supposedly been driven south by the preceding glacial maximum at 135 ka via the so-called 'Sino-Malayan route' (de Vos, 1996). They could have survived during the penultimate glacial maximum in isolated mountainous and humid environments on the Sunda Shelf only, to spread further south into Java between 110 and 70 ka.

The presumed age of the Punung fauna is 80–60 ka, however, this is rather speculative since it is not based on direct age determinations, but on faunal similarities between the Punung assemblage and the Sumatran cave faunas (Drawhorn, 1994). Nevertheless, an age of 80–60 ka would be in accordance with the arguments concerning sea level fluctuations outlined above, it is taken as a reasonable estimate.

Elephas maximus remains from Cipeundeuy originate from a sand quarry near Bandung, West Java (Van den Bergh, 1999). They represent the oldest unambiguous remains of *E. maximus* in Java, as the material from the Punung fissures attributed to this species is rather fragmentary. Their Late Pleistocene age has been well established through radiocarbon dating of two samples from just below and above the fossil-bearing fluvial layer at Cipeundeuy, with ages of 35,500 ± 4600/–2900 B.P. and 29,600 ± 450/–420 B.P., respectively (Dam, 1994). Examination of the accompanying fossil assemblage from the same fluvial layer, comprising around 140 fossils of

mostly postcranial elements, revealed the presence of the following taxa: *Elephas maximus* (sin. M₂ fragm., sin. M₂, anterior M₃ fragm., dex. M¹ fragm., dex. M¹ or M² fragm.), *Rhinoceros sondaicus* (M², I₁), *Muntiacus* sp. (mandible with P₂–M₃, M², distal tibia fragm.), medium-sized cervid (*Axis* sp.; mandible with P₄–M₃, 3 proximal metatarsus fragments, 2 distal humerus fragments), large cervid (various antler fragments), *Bubalus* sp. (horncore fragm.), bovid (metatars prox., M², horncore fragm. with rounded keel), *Hystrix* sp. (gnaw marks on fossil bone). The Cipeundeuy Fauna is younger than the West Sumatran Cave Faunas, which include *E. maximus* and which are characterized by the dominance of *Pongo* teeth. Hooijer (1955) assumed a Holocene age for this fauna, but aspartic acid racemization datings on fossils from Jambu and Lida Ajer Caves, place them between 60 and 80 ka (Drawhorn, 1994). Based on faunal similarity the age of the Punung Fauna from Java was assumed to be similar to that of the Sumatran Cave Faunas (de Vos, 1983). As far as can be determined, the poorly known Cipeundeuy Fauna only contains recent elements, and is younger than the Punung Fauna. It is older than the Holocene Cave Faunas from Java (Wadjak, Sampung). Despite evidence that the Punung Fauna may record the oldest known remains of *E. maximus* on Java and that the fauna from Sampung record the latest occurrence of the Asian elephant, the remains from these two sites are too fragmentary to allow for any certainty at species level. The Cipeundeuy remains, therefore, constitute the only unambiguous evidence for the presence of *E. maximus* on Java.

During or following the latest glaciation, impoverishment of the Javanese fauna occurred. *Pongo* is not recorded from the Holocene composite cave fauna (including faunal elements from the caves Wajak, Sampung, Hoekgrot, and Goa Jimbe) of Table 1. It probably disappeared from Java during the last glacial maximum, when drier conditions and increased seasonality again disrupted the region's rain forests (Morley and Flenley, 1987). These climatic changes are also evidenced by an increase in grass pollen and a decrease in fern spores in deep-sea cores from the region (Van der Kaars, 1991). Small mountainous areas with rainforest environments could have served as refuge for some of the typical forest dwellers during this stage. However, *Pongo* was apparently

unable to cope with these changes and disappeared from Java. Comparisons between the Late Pleistocene Punung Fauna and the Holocene composite Fauna (Table 1), indicate that along with *Pongo* a large number of other species also disappeared from Java and that replacement by new immigrations during the last glacial maximum were limited. *E. maximus*, still recorded from the Sampung Cave, eventually disappeared on Java as well. This was probably due to a decrease in land area following the Holocene sea level rise combined with an increase in human population pressure.

3.2. Sulawesi

Based on extensive fossil collecting along with the reconstruction of a litho- and chronostratigraphic framework, at least three successive terrestrial vertebrate faunas can be distinguished in South Sulawesi, all of which are characteristic for isolated island conditions (Van den Bergh, 1999). These three successive faunas are, from young to old:

Sub-Recent to Recent Fauna	Late Pleistocene–Holocene
Tanrung Fauna	Middle or Late Pleistocene
Walanae Fauna	2.5 Ma–Early (Middle?) Pleistocene

The Walanae Fauna comprises all fossil land vertebrates derived from the Beru Member of the Walanae Formation (Fig. 3), exposed along the Walanae River valley in South Sulawesi. This assemblage of fossil species has also been recovered from single layers from two excavations at fossil-rich localities (Van den Bergh, 1999). The oldest exposed layers within this faunal assemblage have an age of around 2.5 Ma. Based on a combination of micropalaeontological, palaeomagnetic, and electron spin resonance (ESR) age determinations (Van den Bergh, 1999), this age is reasonable accurate. However, it cannot be excluded that some or all of its faunal elements were present on emerged parts of South Sulawesi prior to deposition of the Beru Member. The upper time constraints of the Walanae Fauna are less certain. Deposition of the upper part of the Beru member (Subunit B of the Beru Member *sensu* Van den Bergh, 1999), seems to have been influenced by E–W compressional tectonic activity during the

Early Pleistocene. This lithostratigraphic unit may even extend into the Middle Pleistocene, as is suggested by ESR dating of mammalian teeth (Van den Bergh, 1999). The Walanae fauna comprises the taxa *Celebochoerus heekereni*, *Geochelone atlas*, *Trionychidae* sp., *Crocodylus* sp. and ‘*Elephas*’ *celebensis*, which have all been encountered in the basal layers (Subunit A) of the Beru Member near the locality Sompe (or Sompoh) in the westward dipping flank of the Sengkang Anticline. The genera to which all of the above-mentioned species belong are still present in the younger layers pertaining to Subunit B of the Beru Member. The occurrence of the dwarfed *Stegodon sompoensis* in the oldest layers of Subunit A of the Beru Member has not yet been proven, although it is clearly present in the upper part of Subunit A and in Subunit B of the Beru member. The location of the species of Sompe has been recorded in the Van Heekeren collection (Hooijer, 1964), but this collection has probably become mixed with specimens from younger deposits (Van den Bergh, 1999).

C. heekereni is the most frequently occurring species in the Walanae Fauna. This suid appears to have evolved towards a short-legged variety or even a distinct species during the timespan covered by the Beru Member (Van den Bergh, 1999). Shortening of metapodials is a common trend in island artiodactyla (Sondaar, 1977). While a large-sized *Stegodon* may originate from Subunit B deposits, it should be noted that neither the short-legged *Celebochoerus* variety nor the large-sized *Stegodon* species are represented by in situ findings. Nevertheless, large-sized *Stegodon* remains have been found only where the youngest layers of the Beru Member — those of Subunit B — come to the surface.

It is also important to note that the Walanae Fauna as defined here does not include *Anoa*, *Babirusa* or *Sus*, and differs in this respect from the concept of the *Archidiskodon–Celebochoerus* Fauna of Hooijer (1954). As mentioned before, a large-sized *Stegodon* may have been present during deposition of the youngest interval of the Beru Member (Subunit B), but this remains to be confirmed by in situ findings. The occurrence of two pygmy Elephantoidea, ‘*E.*’ *celebensis* and *S. sompoensis* in the Walanae fauna is unequivocal.

Vertebrate fossils that represent a fauna clearly distinct from the Walanae Fauna and of presumed

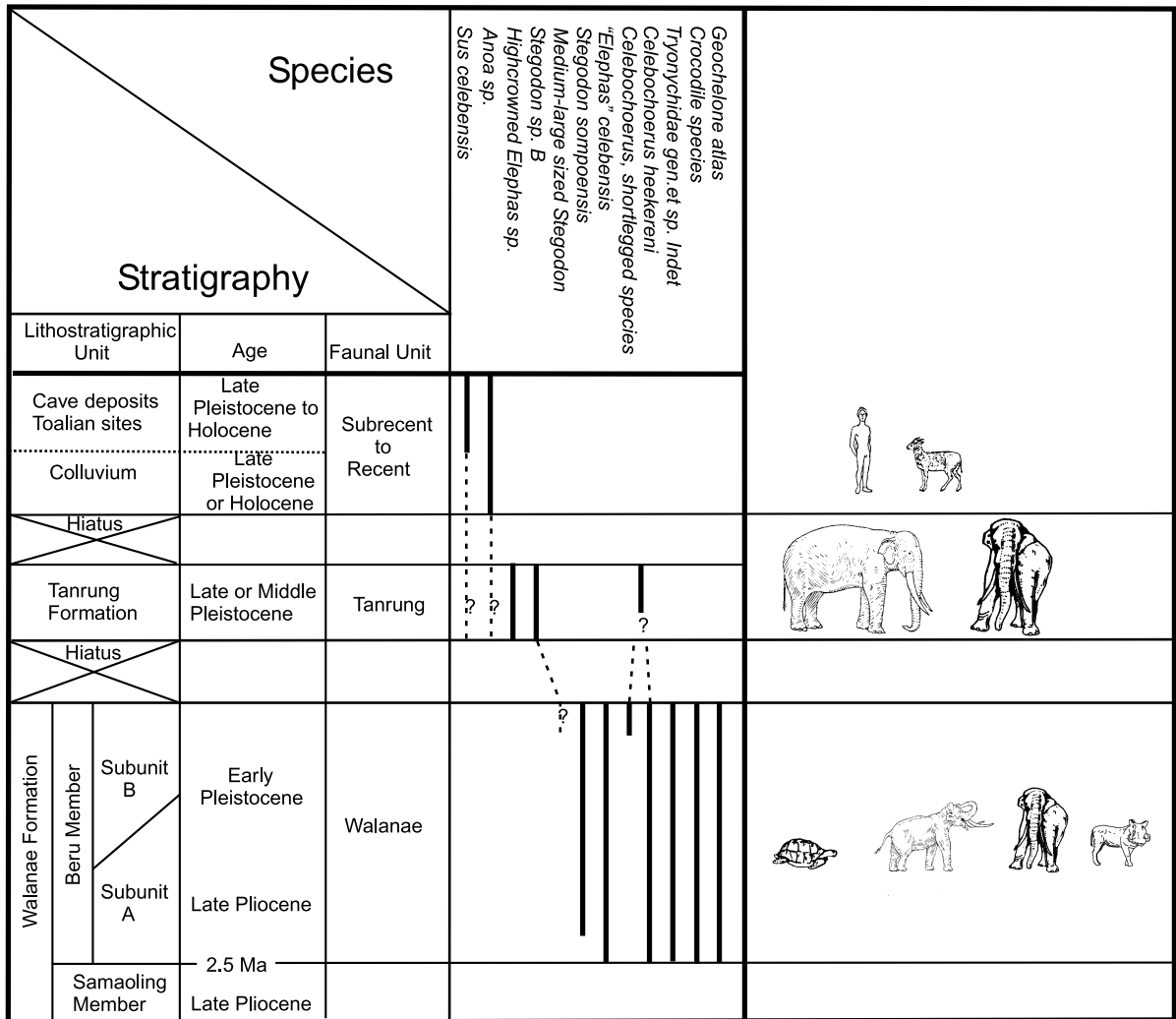


Fig. 3. Stratigraphic scheme, showing the land vertebrate faunal succession of South Sulawesi. Characteristic elements of the successive faunal units are shown to the right. The subrecent (Toalian) to recent fauna is largely omitted, for its composition is referred to Hooijer (1950), Clason (1976) and Musser (1987), respectively.

Middle or Late Pleistocene age, originate from the Tanrung Formation. This formation was deposited after the major Plio-Pleistocene deformation phase that occurred in South Sulawesi, and unconformably overlies gently folded sediments of the Walanae Formation. The fauna from this formation has been designated as Tanrung Fauna (Van den Bergh, 1999). It lacks pygmy elephantoids and *Geochelone atlas*, but contains the intermediate to large-sized *Stegodon* sp. B (Van den Bergh, 1999).

A molar fragment found in the Tanrung River

which, based on attached matrix, was most likely derived from the Tanrung Formation, has been attributed to an advanced, high-crowned *Elephas* sp. (Van den Bergh et al., 1994). This molar fragment has an hypsodonty index of 2. As elsewhere in Eurasia, such high-crowned elephants, like *Elephas hysudrindicus* from the Kedung Brubus and Ngandong Faunas of Java and *Elephas [Palaeoloxodon] namadicus*, appear for the first time during the Middle Pleistocene (Maglio, 1973). Therefore, this specimen puts a time constraint on the maximum age of the Tanrung Fauna

as that of Middle Pleistocene. *Celebochoerus* occurs in the Tanrung Fauna, based on in situ but rolled fragments. These remains are characterized by a relatively small size when compared to *Celebochoerus* remains from the Walanae Formation. *Anoa* molars are represented by surface findings that are likely derived from the unconsolidated alluvial deposits overlying the Tanrung Formation. Colluvial and alluvial deposits locally overlying the Walanae and Tanrung formations yielded remains of *Anoa* sp. *Anoa* has also been reported from various Late Pleistocene to Holocene cave deposits (Hooijer, 1950; Clason, 1976). These caves are located around 25 km NE of Ujung Pandang. At one of these sites, Leang Burung, radiocarbon dating on shell remains yielded ages of up to 31,000 year (Glover, 1981). *Anoa* molars have also been found in the bedding of the Tanrung and Paciro Rivers. Their distinct fossilization suggests that they were washed out from the Younger Alluvial deposits unconformably overlying the Tanrung Formation. Of further interest is the fossilized skull fragment attributed to *Sus celebensis* by Hooijer (1969), which was reportedly recovered from the Paciro River. Hooijer included this species in his *Archidiskodon–Celebochoerus* fauna, but based on our findings there is no justification for doing so. Our excavations at various localities have shown that *S. celebensis* does not co-occur with *C. heekereni* in the Walanae Formation, neither does *Anoa depressicornis*. The *S. celebensis* skull, which appeared heavily rolled, might have originated from the Tanrung Formation, since the Tanrung River flows into the Paciro River. However, it may also have originated from the younger alluvium unconformably overlying the Tanrung Formation and now cropping out along the Tanrung and Paciro Rivers. Both species are still extant in Sulawesi. Their oldest proven in situ occurrence is at the Toalian cave sites described by Hooijer (1950) and in the colluvium locally developed in the Sengkang Anticline area.

The (sub) Recent Sulawesi fauna is highly distinct from the Walanae and Tanrung faunas, in lacking elephantoids and *C. heekereni*. The modern fauna was probably established on South Sulawesi sometime during the Late Pleistocene. Some species, of which fossils have been found in the Toalian Cave deposits, are no longer present in South Sulawesi

but do live elsewhere in Sulawesi. Most of the recent vertebrate species have been omitted in Fig. 3.

Seen in the context of regional geology, it is probable that the ancestors of the various taxa recognized in the fossil and (sub) Recent Faunas reached Sulawesi by crossing at least one sea barrier (Van den Bergh, 1999). During periods of low sea level, these sea barriers must have been less extensive than those of present-day Sulawesi. The distance between west Sulawesi and the east coast of Borneo may have been reduced to a minimum of ca. 50 km during periods of low sea level. This distance is within the swimming capacity of modern elephants (Johnson, 1978). At the same time, several shallow carbonate platforms south of the Makassar Basin may have also served as stepping stone islands.

Recent evidence suggests that arrival of the first humans on Sulawesi may have occurred much earlier than the end of the Late Pleistocene as had previously been. The gravel deposits associated with group 1 artifacts of Keates and Bartstra (1994), are possibly much older than Late Pleistocene, as Van den Bergh (1999) has argued. These exposed gravels, in the surroundings of Beru, are not related to a Walanae River terrace system, as posited by Van Heekeren (1958), but instead belong to Subunit B of the Beru Member, which is the youngest exposed interval of the Walanae Formation in this area. Other coarse gravels associated with artifacts near the locality Jampu belong to an old alluvial fan system, which could develop in relation to the Early–Middle Pleistocene compressive phase, resulting in the uplift of distinct fault-bounded blocks. Based on compositional differences, these Alluvial Fan Gravels are supposedly younger than Subunit B of the Beru Member, and may be Middle or Late Pleistocene in age. No fossil vertebrates are associated with these Alluvial Fan Gravels.

3.3. Flores

Vertebrate remains have been found at several sites throughout the Soa Basin (Ngada District, West Central Flores), such as Mata Menge, Ola Bula and Boa Leza, excavated by Theodor Verhoeven between 1957 and 1974, and other localities discovered more recently (Sondaar et al., 1994; Van den Bergh et al., 1996a; Morwood et al., 1998). Except for the

Flores

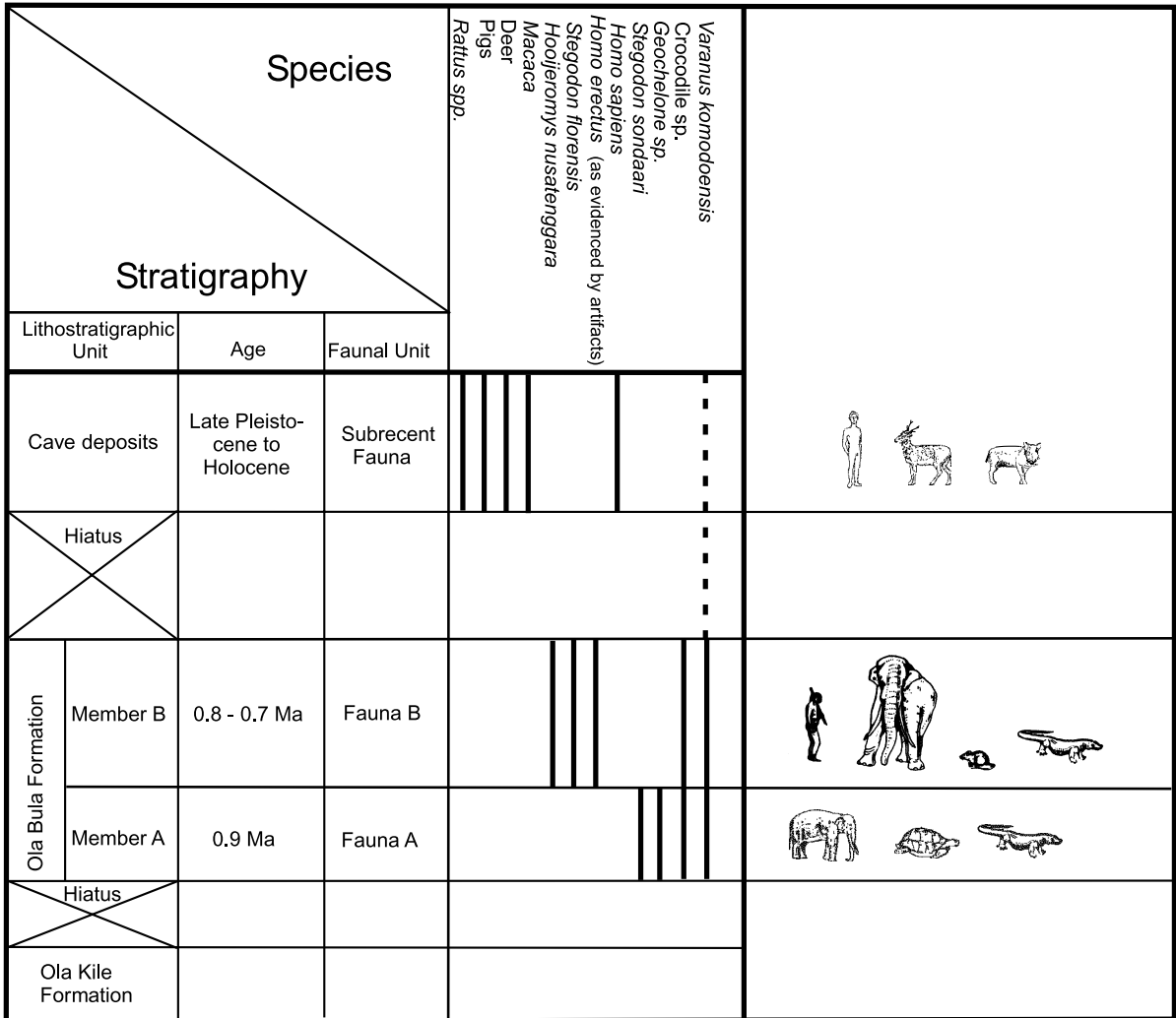


Fig. 4. Stratigraphic scheme, showing the land vertebrate faunal succession of Flores. For details concerning the Subrecent fauna is referred to Hooijer (1967), Brongersma (1958), and Van den Bergh (1999).

locality Tangi Talo (or Bhisu Sau), discovered by Sondaar in 1982, all of these fossil localities are situated in fluvio-lacustrine layers pertaining to Member B of the Ola Bula Formation (Van den Bergh, 1999). Tangi Talo is the only locality pertaining to the older tuffaceous Member A of the Ola Bula Formation. The assemblage from Tangi talo includes a giant tortoise, a dwarfed stegodont — *Stegodon sondaari* — *Varanus komodoensis* and a small crocodile species (Fig. 4). The Member B localities by contrast all contain

remains of the medium to large sized *Stegodon florensis*, while they all lack remains of the pygmy *S. sondaari* and of giant tortoises. Furthermore, while remains of a giant rat, *Hooijeromys nusatenggara*, can also be found in Member B localities, these were not encountered at Tangi Talo. At Mata Menge, a few teeth from a small crocodile were also recovered, while at Dhozo Dhalu a single tooth of *V. komodoensis* has been found in association with the younger fauna. This still extant species seems to have been the only

element from Fauna A that continued into the younger Fauna B and even in the extant fauna of Flores. Based on superposition, it can be deduced that a younger island fauna characterized by *S. florensis* (Fauna B) succeeds an older island fauna with giant tortoises and *S. sondaari* (Fauna A).

No artifacts have been found in the fossiliferous layer at Tangi Talo or in the surrounding sediments of Member A. However, at Mata Menge stone artifacts occur in association with the *S. florensis* remains (Maringer and Verhoeven, 1970; Sondaar, 1984; Morwood et al., 1997). The artifact bearing deposits at Mata Menge have been dated by means of palaeomagnetism (Sondaar et al., 1994), and fission track dating (Morwood et al., 1998), indicating an age of around 0.8–0.7 Ma. This contrasts with the Tangi Talo fauna, which is slightly older, 0.9 Ma. This in turn suggests that *Homo erectus* was the maker of the artifacts. The colonization of the island Flores by humans therefore coincides with a faunal turnover on the island.

Fauna B was replaced by a Sub-recent to Recent Fauna (Fig. 4) during the later stage of the Quaternary, but due to a lack of fossil evidence, the duration and age of this transition has yet to be reconstructed. The composite list of species from the Holocene cave deposits (Fig. 4) is based on material excavated by Verhoeven from the abri site Liang Toge (West Flores, near Warukia), as well as various other cave and abri sites, including Liang Michael, Liang Melima, Liang Momer, Liang Nintal, Liang Panas, Liang Rundung, Liang Toge, Liang Wakar, Liang X and Nderuk. The material from these sites was classified by Hooijer (in: Verhoeven, unpublished report, 1950, 1957, 1967), Brongersma (1958: varanids) and Musser (1981: murids). Apart from the genus *Rattus*, all murids appeared to represent endemic species of Flores. Jacob (1967) gives a date of 3550 ± 525 B.P. for Liang Toge. While material from different caves might vary considerably in age, it is expected that most if not all is of Late Pleistocene or Holocene age. We refer to Musser (1981) for a list of recent mammal species from Flores. Chiroptera have been omitted from both the Subrecent fauna list. Most, if not all, large mammals in the Sub-recent fauna list, such as pigs, deer, *Macaca*, and various *Rattus* species, were introduced by humans. The endemic murids must have evolved locally. Stegodonts,

tortoises and *Hooijeromys nusatenggara* are entirely absent from the Sub-recent cave deposits.

4. Discussion

4.1. Migration routes to Java

Originally, the fossil mammalian faunas of Java were interpreted as descendents of an ancient Indian stock (Martin, 1884; Dubois, 1908). The dispersal to Java was attributed primarily to the former existence of landbridges. The islands west of Sumatra as well as the Nicobar Islands and Andamans were seen as a continuous (nowadays mostly submarine) ridge, which could have been exposed during the Pliocene-Pleistocene, thus serving as a migration route from Burma to Sumatra and Java (Moolengraaff, 1922; Rensch, 1936). However, to date, none of these 'ridge' islands have produced fossils of an ancient continental fauna.

Von Koenigswald (1935a,b) distinguished 7 biostratigraphical units on Java. According to his report the dispersal of mammalian faunas to Java took place in three steps: First, during the Pliocene the exposed Sunda Shelf allowed migration to Java of the so-called Siva-Malayan Fauna. The land-connection was considered to be of such a short duration that the mammal dispersal was not very extensive. Second, during the Pleistocene, a more long-lasting connection via the Philippines and Borneo was suggested, which allowed dispersal of the so-called Sino-Malayan Fauna to Java. Assuming that certain elements from the Javanese Pleistocene were of Chinese origin, this hypothesis was based on the presence of a Pleistocene fauna in Taiwan and the Philippines and the lack of fossil evidence from the Sunda shelf area. At the time, fossil mammals from Sulawesi had yet to be discovered. Third, the modern fauna was thought to have entered Java during the latest Pleistocene when Java, Borneo, Sumatra and the Malay Peninsula were united for a brief period of time.

De Terra (1943) and Colbert (1943) suggested that the Javanese Siva-Malayan and Sino-Malayan Faunal elements could have originated from a secondary ancestral stock, such as that found in Burma, rather than from Indian and Chinese sources. They favored migration to Java from SE Asia (Burma) via the

exposed Sunda Shelf. However, de Terra (1943) also stated that the route to Sulawesi via Taiwan and the Philippines could have been an alternative, rather than an exclusive Pleistocene route. On de Terra's map, the route via the Philippines does not even reach Java, leading Colbert (1943) to reject the idea that a mammalian fauna could have reached Java via the Philippines.

The discovery of fossil vertebrates on Sulawesi and Flores, and later on Timor and Sumba, proved that various large mammalian taxa, notably elephantoids, had been able to cross Wallace's line. Adhering to the hypothesis that dwarfing occurred repeatedly on different islands at different times, the dwarf stegodonts from Flores, Timor and Sulawesi were initially thought to be the result of parallel evolution (Hooijer, 1972). Hooijer believed that the Philippines might have played a role in the dispersal to Sulawesi. According to an alternative hypothesis, put forward subsequently by Audley-Charles and Hooijer (1973) and Hooijer (1975, 1982), the dwarf stegodonts of the various islands would have formed part of a single interbreeding population. The various islands were supposed to have been connected by landbridges in the past, and the entire interconnected area was called 'Stegoland'. This idea was met with skepticism (Simpson, 1977; Sondaar, 1981; Musser, 1987; Aziz, 1990). The pygmy stegodonts on the various islands are clearly different from one another (Van den Bergh et al., 1992; Van den Bergh, 1999). Yet other fossil faunal elements, such as the giant tortoises of Flores and Sulawesi, can be distinguished from each other at least on size. Sondaar (1981) argued that different islands had different tortoise species, analogous to the various species inhabiting the Galapagos Islands. The postcranial *Geochelone* material recently excavated at Tangi Talo, Flores, is on average approximately two times smaller in linear dimensions is on average than the *Geochelone* postcranials from South Sulawesi and Timor. This suggests isolation of the tortoise populations on these islands (Van den Bergh, 1999). If former land connections existed between the three islands, as has been suggested by Audley-Charles and Hooijer (1973), Hooijer (1982) and Azzaroli (1996), it could be argued that other endemic fossil species, such as *Celebochoerus heekereni*, '*Elephas*' *celebensis* and *Varanus komodoensis*, should be common elements in the fossil faunas from these

three islands. However, this is not the case. Moreover, the Recent mammalian faunas from Flores, Timor and Sulawesi have little in common other than some widely distributed flying mammalian species and terrestrial mammals that were undoubtedly introduced by humans (Groves, 1976; Cranbrook, 1981; Musser, 1987). Based on an analysis of extant and fossil faunal elements, Groves (1976, 1985) concluded that the faunal elements from Sulawesi bear the closest relationship to those from the Middle Siwaliks. He thought it most likely that this fauna had entered Sulawesi via the Makassar Strait, some of the smaller elements even reaching Sangihe and Talaud. Mainly based on the Recent faunas, the author discarded faunal links between the Philippines and Sulawesi, but suggested instead a migration route to Sulawesi across the present Strait of Makassar, narrowed or closed by a land connection during the Pleistocene. Hooijer (1975), on the contrary, considered the Philippine islands Luzon and Mindanao as an important link in the dispersal route of ancient Asiatic faunal elements to Sulawesi.

Based on the total absence of species of freshwater fish in Sulawesi other than those likely to have been introduced by humans, Cranbrook (1981) concluded that there has been no direct, unbroken connection between Sulawesi and the principal landmass of the Sunda shelf. He considered the mammalian fossil evidence as too fragmented to draw firm conclusions concerning migration routes between Sulawesi, the Philippines, Java, and the islands of the Banda Arc. In his view, the distribution of stegodonts and bats throughout the SE Asian Archipelago demonstrated the availability of dispersal routes only open to large herbivorous and flying mammals. He further noted that direct, ephemeral land connections might have existed between South Sulawesi and the Lesser Sunda Islands, as suggested by floral evidence. Braches and Shutler (1984b) doubted that the Philippine route played a major role in the dispersal of the so-called Sino-Malayan Fauna to Java, and found it questionable that a landbridge ever existed between the Philippines and Taiwan or the Chinese mainland. They deemed it possible that elements of a land fauna, capable of crossing salt-water barriers and originating from Sundaland and/or China, became isolated on Luzon throughout the Pleistocene, allowing a typical endemic Philippine fauna to evolve. Also

Heaney (1985) saw no evidence for the former existence of any substantial landbridges to the main body of the Philippines during the Middle or Late Pleistocene, but he postulated a Middle Pleistocene connection from the Palawan chain to Borneo at a time when Borneo was part of the Asian land mass.

Musser (1987) noted that overseas migration of mammals to Sulawesi might have begun already during the Late Miocene or Early Pliocene. With the exception of the phalangers, the origin of the native Sulawesi faunal elements was thought to be mainland Asia. He also speculated that the fossil fauna from the Walanae Formation might have lived on a separate palaeo-island, and was unrelated to the extant Sulawesi fauna. Recent excavations and stratigraphic work (see Van den Bergh, 1999) provided substantial evidence in favor of this hypothesis. It can be concluded that Walanae Fauna only contained extinct vertebrates, viz. *S. sompoensis*, '*E.*' *celebensis*, *Geochelone atlas* and *Celebochoerus heekereni*, and that species that are still living on Sulawesi recently, such as *Anoa depressicornis* and *Sus celebensis*, should not be included in the Walanae Fauna.

Adhering to the new faunal succession for Java, which is based on faunas originating from single localities, it follows that the faunal elements considered by von Koenigswald (1935a,b) to be typical of Chinese origin, such as *Pongo* and *Hylobates*, are not represented in the Early and Middle Pleistocene faunas of Java. Von Koenigswald's (1935a,b) concept of the Early and Middle Pleistocene Djetis and Trinil Faunas was shown to be erroneously based on the mixing of the Late Pleistocene Punung fissure assemblage (which does contain purely Chinese elements) with older faunal assemblages (de Vos et al., 1982; Sondaar, 1984). The older Javanese faunas are dominated by either species only recorded from the Siwaliks and SE Asia, or by species having a much wider distribution, including China. The exception seems to be *Tetralophodon bumiajuensis*. Saegusa (1996) demonstrated that fossil remains from the Bumiaju area in west Central Java and from the Sangiran area, which were originally attributed to *Tetralophodon bumiajuensis* by Van der Maarel (1932), should be assigned to *Sinomastodon* instead. *Sinomastodon* is known from Late Miocene to Early Pleistocene deposits from China and Japan (Tobien et al., 1986; Saegusa 1996), but has not yet been

recorded from the Indian Subcontinent. *Sinomastodon* may have been driven south during one of the earlier cold episodes during the Late Pliocene.

Dispersal towards Java initially took place by means of sweepstake dispersal during the Late Pliocene and Early Pleistocene, mainly via the Siva-Malayan route (Satir Fauna sensu Sondaar, 1984). During the late Early Pleistocene, a limited land connection came into existence between Java and the Asian continent, allowing more species to enter Java via the same Siva-Malayan route, this time constituting a filter route (Trinil H.K. Fauna sensu de Vos et al., 1982). This dispersal wave included *Homo erectus*. Towards the end of the Early Pleistocene and periodically during the Middle Pleistocene, more extensive land connections came into existence, allowing fully balanced mainland faunas to enter Java via the Siva-Malayan route (corridor route). Van den Bergh et al. (1996b) correlated the formation of this corridor route with the marked and long lasting glacio-eustatic sea level lowerings that started at ca. 0.8 Ma. Faunal composition of the 0.8–0.7 Ma Kedung Brubus Fauna and the younger Ngandong Fauna suggests that palaeo-environments on Java were mainly marked by open woodlands (de Vos and Sondaar, 1982; Sondaar, 1984). Relatively dry conditions associated with this type of environment would be in accordance with fully emerged Sunda Shelf.

A fauna of clearly Chinese origin did not enter Java until the Late Pleistocene (de Vos, 1996; Long 1996). The Punung Fauna is a tropical rainforest fauna which shows close resemblance to Late Pleistocene faunas recorded from Sumatra (Lida Ayer, Djambu and Sibrambang caves), Borneo (Niah), Vietnam (Lang Trang) and the South Chinese fissure faunas of Kwangsi and Yunnan (de Vos, 1983, 1996; de Vos et al., 1994; Long, 1996). This dispersal probably took place during and subsequent to the penultimate low sea level stand of the Saale Glaciation, when the Sunda Shelf was fully emerged and allowed dispersal from southern China and Vietnam via the Sino-Malayan corridor route (Van den Bergh et al., 1996b). The South Chinese fauna was supposedly driven south during the Saale Glaciation. At this stage *Homo sapiens* is thought to have first reached Java along with a tropical rainforest fauna. During the Holocene break-up of the Sunda Shelf, the faunas on

the various greater Sunda islands became impoverished in response to reduced land areas and changing climatic conditions.

4.2. Evidence from other regions

Otsuka (1984) mentions the following taxa from the Pleistocene T'ouk'oushan Group in the Chochen district of Taiwan: stegodonts, *Mammuthus*, *Rhinoceros*, *Bubalus*, *Sus*, various cervids, *Macaca*, and *Panthera*. The author attributes these elements to the Chochen Fauna, which he considers to be of late Early Pleistocene to early Middle Pleistocene age. However, within the Chochen Fauna three time-successive zones were distinguished, from old to young: (1) the *Parastegodon akashiensis*–*Stegodon sinensis* Zone; (2) the *Elaphurus formosanus*–*Rhinoceros sinensis hayasakai* Zone; and (3) the *Mammuthus*–*Armeniacus taiwanicus* Zone. The oldest zone is characterized by the occurrence of 2 stegodonts, *Parastegodon akashiensis* and *S. sinensis*, and 3–5 cervids, including *Elaphurus formosanus*. Saegusa (1996) argued that *P. akashiensis* from Japan is synonymous with *S. aurorae*, a subhypsodont stegodont from Japan with diminutive size, which evolved from the Chinese *S. zdanskyi*. He further noted that sub-hypsodont *Stegodon* molars are known from Taiwan, and are very similar to those of *S. aurorae* from Japan. He, Otsuka also contends that it is not clear whether their similarity is due to descent from a common ancestor or to convergence. Subhypsodonty is only encountered in dwarfed island stegodonts (Van den Bergh, 1999). Deer are also common elements in island faunas (Sondaar, 1977), and it appears likely that the fauna from the oldest mammal-bearing strata of the T'ouk'oushan Group represents an island fauna. Considering *S. sinensis*, Saegusa (1996) reports that this species is based on a fragment of a dP³, while further noting that several permanent molars which had been subsequently assigned to this species, can now more accurately be allocated to *S. orientalis*. The latter species is present in Southern China from the late Early Pleistocene until the Late Pleistocene, and invaded Japan around 0.5 Ma ago, replacing *S. aurorae* (Kamiya, 1995; Saegusa, 1996). The Taiwanese specimens attributed to *S. sinensis* may also turn out to be synonymus with *S. orientalis*. The latter species

is, in fact, also recorded by other authors from different localities on Taiwan (Otsuka, 1984).

The next Zone distinguished by Otsuka (1984), the *E. formosanus*–*R. sinensis* Zone, is characterized by a wider range of taxa, including *Panthera* sp., *Sus* sp., *Bubalus* sp., *Rhinoceros sinensis*, and various cervids, whereas stegodonts are not recorded from this interval. *Macaca* sp. is only represented by fossils picked up from a river and has not been included in the zonation scheme of the author. The youngest, *M. armeniacus taiwanicus* Zone is fairly similar to the foregoing zone, but differs insofar as it includes *Mammuthus*, and excludes *Rhinoceros*. In comparison to the Chinese mainland, the younger Taiwanese fauna is somewhat impoverished, but the occurrence of *Panthera* gives it a continental character. Filter route dispersal has been the likely mode of dispersal towards Taiwan. It is tempting to speculate that the increased accessibility of Taiwan as recorded from the transition between the *P. akashiensis*–*Stegodon sinensis* Zone and the *E. formosanus*–*R. sinensis* Zone, could be correlated with the marked Pleistocene sea level lowering that proceeded from about 0.8 Ma onward (Fig. 2). The faunal succession of Taiwan shows much similarity with that observed in the Pleistocene of Japan, presumably because both were derived from the same Chinese mainland faunas. In Japan, pre-Middle Pleistocene faunas contain only stegodonts (*S. shinshuensis*, which later evolved into the dwarfed *S. aurorae*), cervids (including *Elaphurus*), and between ca. 1 and 0.7 Ma, *Mammuthus shigensis*. From the Early/Middle Pleistocene transition, an increasingly wide variety of mammalian species is recorded from Japan, including *Rhinoceros sinensis*, *S. orientalis*, *Panthera* sp., *Mammuthus armeniacus*, *Sus* sp., *Bubalus* sp. and several other mammalian species (Kamei, 1981; Kamei et al., 1988). Furthermore an island fauna here seems to have been replaced by a more continental fauna around the Early/Middle Pleistocene transition, as in Java and possibly, Taiwan as well.

The faunal succession from the Philippines is less well known, but appears to be more impoverished and endemic than the Taiwanese fauna. Von Koenigswald (1956) described various mammalian remains from the Philippines. From Luzon he mentioned some bovine and cervid teeth, a fragmentary jaw of a rhinoceros (considered an endemic species, *Rhinoceros*

philippinensis von Koenigswald, 1956), remains of a giant tortoise, and various molar and tusk fragments of *Stegodon*. Amongst the *Stegodon* material is a sinistral mandibular ramus from Fort McKinley. The mandible contains an M₃ fragment with 7 ridges preserved plus a posterior rootmass showing that at least 2 more ridges were present posteriorly, judging from the plate accompanying the description (von Koenigswald, 1956: pl. IV). The molar is only 5 cm wide, indicating a dwarfed form, which was named *Stegodon luzonensis* von Koenigswald, 1956. Two small molar fragments both consisting of two ridges were attributed to *Stegodon* cf. *trigonocephalus*. However, the fact that the width of the preserved ridges is less than 64 mm, does not exclude the possibility that they belong to a pygmy stegodont. Von Koenigswald (1956) also identified a fragmentary lower molar as belonging to a pygmy elephant, which he named *Elephas beyeri*. The specimen was labeled as being from the Anda area of Cabarruyan Island. Its plateformula is $-10 \times$ as far as preserved. Unworn ridges are twice as high as wide (67 and 32 mm, respectively), suggesting that it is a highly advanced form, perhaps closely related to *Elephas namadicus*. The lamellar frequency is reported as 5–6 in 5 cm, which would give a LF of 10–12 in 10 cm. According to Maglio (1973) the M₁ of *Elephas namadicus* has 9–11 lamellae, an average W of 46 mm, and a LF ranging from 6.5 to 8.1. Thus von Koenigswald's (1956) conclusion that the specimen represents a pygmy elephant seems valid.

Angel Bautista kindly sent a cast of a suid molar originating from Cagayan Valley, Luzon, to John de Vos at the NNM. The molar resembles those of *Celebochoerus* as well as those of *Babyrousa*, while both display a simple molar structure. From Mindanao von Koenigswald (1956) mentioned the occurrence of a pygmy *Stegodon*. The fossil, a posterior fragment of a lower molar consisting of $-4 \times$ ridges, was named *Stegodon mindanensis* Naumann, 1890. Judging from the plates originally presented by Naumann and reproduced by von Koenigswald (1956, pl. VI), the fragment most likely represents a dP₄, although von Koenigswald (1956) considered it to be a 'permanent molar'. With a W of 37.3 mm; this milk-molar would fall beyond the range of variation of the W of the dP₄ of *Stegodon trigonocephalus* (W of dP₄ = 42.5–54 mm), and von Koenigswald was right to have

assigned it to a pygmy *Stegodon*. Interestingly, the unworn crown was said to be 33 mm high, which gives a *h/w* index of 88, comparable to that of the pygmy stegodont molars from Flores and Timor.

The Philippine fossil fauna appears clearly endemic and impoverished, lacking carnivores and containing various pygmy elephantoids, and thus indicating island conditions. The ages of the Philippine faunal elements have not yet been ascertained. Possible faunal links between the Walanae Fauna from South Sulawesi and the Philippine fossil faunas could be *Celebochoerus*, a giant tortoise, *Stegodon*, and *Elephas*. Until more data become available on the Philippine fossil fauna(s), no conclusive statement can be made concerning such relationships. However, it can be said that the fossil faunal elements from Sulawesi which may bear the closest relationship with elements from the fossil faunas of the Philippines, are not recorded from the youngest faunal unit in South Sulawesi, namely the sub-Recent to Recent Fauna. There have been at least two *Stegodon* colonizations of South Sulawesi widely separated in time (Van den Bergh, 1999). The Late Pliocene *S. sompoensis* present in the Walanae Fauna can be linked to the *S. ganesa/trigonocephalus* group (sensu Saegusa, 1996), but not to Chinese, Japanese or Taiwanese stegodonts, making a descendance from a Philippine invader highly unlikely. *Stegodon* sp. B occurs in Middle Pleistocene deposits on South Sulawesi and has also been found in Pleistocene deposits on Sangihe. Scanty *Stegodon* sp. remains have also been found in Central Sulawesi (Van den Bergh et al., 1994). Due to a lack of skull material, phylogenetic relationships are difficult to assess. The advanced molar ridge formula of *Stegodon* sp. B suggest that it may have close links with the Middle Pleistocene *S. florensis* from Flores or with the Late Pleistocene *S. trigonocephalus ngandongensis* from Java. Possible links with Philippine stegodonts remain even more uncertain.

The modern faunas of Sulawesi and Luzon/Mindanao, show marked differences indicating that no faunal exchange took place in the more recent past. The Recent mammalian fauna of the island of Sangihe located between Sulawesi and Mindanao includes, among some more widespread mammals, *Phalanger celebensis*, *Callosciurus leucomus*, and *Tarsius spectrum*, all endemic species, which also

occur on Sulawesi (Groves, 1976). In contrast, Sangihe does not share any non-flying mammals in common with the Philippines, suggesting that its modern fauna originated entirely from Sulawesi. Combining a sea level lowering of 200 m and the present-day bathymetry, it follows that a distance of 175 km of sea would have to be crossed to reach Sangihe from the southern-most tip of Mindanao. From northern Sulawesi, a total distance of 170 km would also have to be crossed, but five small islands in between could have been used as stepping stones so that the largest overseas distance would be no more than ca. 35 km.

Some terrestrial mammalian genera with two or more species endemic to Sulawesi appear to have undergone a radiation during a supposedly long-standing isolation. These genera include *Anoa*, *Macaca*, *Crocidura* and various rodent genera (Fooden, 1969; Groves, 1976; Musser, 1987). Both radiative adaptations and multiple colonization events have been inferred. The modern mammalian fauna of Sulawesi has little in common with the Philippines, apart from some widespread mammals and flying mammals. The extant Philippine dwarf buffalo, *Bubalus mindorensis*, is a derivative of the extant Indo-Burmese waterbuffalo, *B. arnee*, whereas the two species of Sulawesi dwarf buffalo, *Anoa depressicornis* and *Anoa qarlesi* have probably their closest progenitors in the genus *Hemibos* (Groves, 1976). *Hemibos* has been recorded from Late Pliocene Siwalik deposits older than 2.5 Ma (Hussain et al., 1992). The four to seven species of stump-tail macaques living in Sulawesi nowadays are thought to have been derived from a single invader and are not closely related to the two subspecies of *Macaca fascicularis* living in the Philippines (Fooden, 1991). The Sulawesi macaques belong to the relatively primitive but widely dispersed *silenus-sylvanus* group. This group is probably spread out early, followed by extensive local extinction that led to wide gaps in the distributionary pattern of this group. The Philippine macaques, by contrast, belong to the *fascicularis* group. One of the Philippine subspecies, *M. f. philippinensis*, is restricted to the northern Philippine islands around the periphery of the species range, and is thought to have been isolated in the Philippines since the end of the penultimate glacial maximum (ca. 160 ka). The other subspecies,

M. f. fascicularis, occurs on the south central islands of the Philippines and also inhabits Borneo and other areas in SE Asia. It probably dispersed from Borneo to the Philippines during the last glacial maximum (Fooden, 1991).

A similar pattern can be observed amongst the suids from the area. *Sus celebensis*, a member of the *verrucosus* group and endemic to Sulawesi, probably has close affinity to the ancestral group of the *Sus* lineage. This is according to Groves (1981) who compared the various extant species and subspecies of the genus *Sus* in detail. *Sus celebensis* presumably reached Central Sulawesi (not South Sulawesi as it is not recorded from the Walanae Fauna) as early as the Late Pliocene or Early Pleistocene. As a possible ancestor, Groves mentioned the poorly known *Sus stremmi* von Koenigswald from the Kali Glagah Formation in the Bumiaju area. Hardjasmita (1987), who studied the skulls and dentition of fossil and recent *Sus* from Indonesia, considered the ancestor of *S. celebensis* to be either *Sus macrognathus* Dubois (present in the Kedung Brubus Fauna and in the Ngandong Fauna) or *Sus verrucosus* Müller and Schlegel, the extant Javanese warty pig descended from *S. macrognathus*. The Philippine suids, on the other hand, are considered by Groves (1981) as subspecies of *Sus barbatus*, and definitely do not represent *S. celebensis*, as had been previously postulated by various authors. *S. barbatus* has a more widespread distribution than *S. verrucosus*, occurring in peninsular Malaysia, Sumatra, Borneo and the Philippines, but not Java. The same author further mentioned that the subspecies occurring on Palawan Island, *S. b. ahoenobarbus*, is quite intermediate between the Bornean *S. b. barbatus* and the subspecies distributed around the periphery of the species range, *S. b. philippensis* from the islands Luzon, Mindanao and Mindoro. This pattern suggests that *Sus barbatus* entered the Philippines relatively recently from Borneo via the Palawan ridge.

4.3. Mammalian dispersals to Sulawesi

Both the fossil and extant faunas of Sulawesi exhibit a high degree of endemism. Based on the considerations mentioned above, we follow Cranbrook (1981) and Musser (1987) in concluding that there have been no uninterrupted subaerial connections between

Sulawesi, the Philippines and Sundaland during the entire Neogene and Quaternary. The hypothesis proposed by Musser's hypothesis also seems logical, in that it implies the southwestern Sulawesi peninsula once constituted a separate palaeoisland, separated from the northern part where the ancestors of the Recent Fauna are thought to have evolved into the modern fauna. Alternatively, it would be hard to explain why not even a single fossil attributable to a species closely related to one of the extant Sulawesi mammals, was encountered among the thousands of fossils excavated from layers in the Walanae Formation. Two major dispersal waves to South Sulawesi can thus be envisaged:

First Wave — All Walanae Fauna elements (*Celebochoerus*, *Geochelone*, *Stegodon sompoensis* and '*Elephas*' *celebensis*) appear to have close affinity with relatives from the Siwaliks (Groves, 1976; Cranbrook, 1981; Musser, 1987; Van den Bergh, 1999). It seems highly unlikely that the ancestors of the Walanae Fauna elements reached Sulawesi via the China–Taiwan–Philippine route. Rather, it is probable that they reached South Sulawesi (then constituting a separate palaeoisland) from the Sunda Shelf during the Pliocene, perhaps via one or more stepping stone islands (later on transformed into a shallow marine carbonate platform, the Recent Doang Doang Platform south of the South Makassar Basin). '*Elephas*' *indonesicus*, *Geochelone* and the pygmy *Stegodon* from Sambungmacan, all from the older, Late Pliocene to Early Pleistocene fossil-bearing strata on Java, could represent descendants from the same ancestral stocks that continued their way toward South Sulawesi. The ancestors of *Anoa* and *Sus celebensis* may also have reached Sulawesi relatively early, but current data suggests that these taxa crossed the Makassar Strait toward what is now Central Sulawesi. These taxa do not seem to have reached the South Sulawesi palaeo-island until that part was connected with the rest of Sulawesi during the course of the Pleistocene. *Babyrousa* may be the only large mammalian taxon of which the progenitors reached Central Sulawesi at a very early date already, i.e. during the Palaeogene. It is possible that during the mid-Oligocene, when the last subaerial connection with the Sunda Shelf may have existed (Van den Bergh, 1999), the ancestral population reached Sulawesi over land. From here it can be postulated

that multiple colonization events were likely responsible for the earlier mammalian population of Sulawesi, rather than a single dispersal wave. Considering the Walanae Fauna from the palaeo-island of South Sulawesi alone, the present data suggest a longstanding faunal equilibrium from ca. 2.5 Ma until the end of the Early Pleistocene, without new arrivals.

Second Wave — A second wave of immigrants to South Sulawesi, represented by two elephantoids, *Stegodon* sp. B and an advanced *Elephas* sp. as recorded from the Middle Pleistocene Tanrung Formation, may have come from either the Philippines or from Sundaland, by means of sweepstake dispersal. The close affinities of these two elephantoids cannot yet be ascertained due to the scantiness of fossil material. Apart from *Celebochoerus*, it also seems possible that the Walanae Fauna became extinct during the Middle Pleistocene. The faunal turnover recorded in Sulawesi presumably occurred after 0.8 Ma. Following that time, new dispersals toward Sulawesi may have been facilitated by periodically lower sea levels than those during the previous period. As stated earlier, Java, Japan and perhaps Taiwan as well also experienced major faunal immigration events from the Asian mainland beginning in the early Middle Pleistocene. The fact that dispersal to Sulawesi was limited in comparison with the other islands mentioned, may simply be attributed to Sulawesi having not become connected to the Asian mainland (sweepstake dispersal), whereas the other islands were clearly connected to some extent with the continent during the Middle Pleistocene (filter or corridor route).

4.4. Colonization of the Lesser Sunda Islands

For the Early Pleistocene stegodont of Flores, *S. sondaari*, close links with any of the other SE Asian stegodonts cannot be determined at present. *S. sondaari* has some primitive molar traits and, therefore cannot have evolved from the more advanced *S. sompoensis* or *Stegodon* sp. B. from Sulawesi. Van den Bergh (1999) suggests that it may have derived from *Stegodon elephantoides*, known from Burma and a single locality on Java dated at ca. 1.2 Ma B.P. The ancestral form of *S. sondaari* should have reached Flores from the Sunda Shelf by crossing some water barrier.

On the other hand, the Middle Pleistocene *Stegodon florensis* may have reached Flores via Sulawesi, which contradicts the commonly held belief that all stegodonts on the Lesser Sundas entered these islands from the west (e.g. Hooijer, 1975). Similar traits found in molars of *Stegodon* sp. B from the Tanrung Fauna on Sulawesi and *S. florensis* point in this direction. Both species are not yet fully dwarfed, but have relatively narrow molars and overlapping hypsodonty indices. However, skull material would be required to substantiate possible relationships between the Middle Pleistocene stegodonts of Sulawesi and Flores. Alternatively, *S. florensis* may have descended from a Javanese ancestor (*S. trigonocephalus*). If dispersal from Sulawesi to Flores has taken place, it must have been by means of overseas dispersal, given that the two islands have no other extinct or extant faunal elements in common (apart from those extant species likely to have been carried around by humans). When entering the Lesser Sunda Islands from the north by overseas dispersal, stegodonts would not have to cross the straits between Bali and Lombok, and between Sumbawa and Flores, where very strong surface currents presumably constituted major barriers for sea-crossing stegodonts. It is known, for example, that strong currents surely prevented large herbivores from reaching the Balearic Islands (Spain) during the entire Plio-Pleistocene time-span (Sondaar et al., 1995), whereas other Mediterranean islands were colonized time and again by elephants, cervids, hippos and a few small mammals (Sondaar, 1977).

4.5. *The earliest human water crossings in the context of global change*

Based on the dated palaeolithic artifacts from Mata Menge (Sondaar et al., 1995; Van den Bergh et al., 1996a; Van den Bergh, 1999; Morwood et al. 1998), the arrival of the first humans on the island Flores around 0.8 Ma, coincides with a marked faunal turnover, not only regionally but also worldwide. In the Mediterranean region, for instance, this transitional period is characterized by widespread migrations, first appearances and extinctions of land mammal taxa (Alberdi et al., 1997). In the *Homo erectus* bearing faunas of Java this event can be recognized by a clear faunal turnover with new arrivals and

extinctions in the 0.8–0.7 myr old Kedung Brubus Fauna (Van den Bergh et al., 1996b). Concomitant with this transition was the onset of dramatic global climatological oscillations and periodically lower sea levels than in the previous period (Haq, 1991). According to the oxygen isotope record, this transitional period marks the onset of global climatic changes (Chappell and Shackleton, 1987). Early Pleistocene isotope records show low amplitude, 40–50 ka quasi-periodic cycles (orbital obliquity), whereas Middle Pleistocene records are of a high amplitude, low frequency nature (100 ka cycles, orbital eccentricity). The eustatic sea level declined at lower levels over a more prolonged time-period leaving its mark in the seismostratigraphic record (Haq, 1991). Land faunas changed drastically in response to these environmental changes. In the Mediterranean a drastic faunal restructuration and the first appearance of many modern mammal lineages took place between 0.8 and 0.9 Ma (Alberdi et al., 1997).

The first colonization of Flores by humans during the same period may have been triggered by a combination of increased environmental stress and lower sea levels, the latter enhancing accessibility after 0.8 Ma. However, full land connections are unlikely to have formed due to the strongly unbalanced and endemic character of the land faunas from these islands throughout the Pleistocene. Thus, these early humans to reach Flores should have crossed some water barrier. Three possible migration routes have been proposed for early human dispersal eastward out of SE Asia into Wallacea and further towards greater Australia (Birdsell, 1977; Sondaar, 1989; Irwin, 1992). Birdsell (1977) suggested two possible routes based on the assumption that those with the shortest possible crossings would be the most favored ones and that such voyages would have been easier during episodes of lower sea level. One route is from Java via the Lesser Sunda Islands to Timor and on to northern Australia. The other is from Sulawesi Halmahera, and on to West Irian. However, assuming the ability that the shortest overseas distances were crossed is not necessarily valid, as it does not take into account prevailing surface water currents and wind directions which may have been even more significant factors for ‘passive’ or ‘floating’ seafarers. Besides, as noted by Irwin (1992), a boat that is seaworthy enough to cross 10 miles can also cross

100 or more miles, provided it does not become water-logged and the weather remains relatively stable.

Sondaar (1989) added another route, which runs from China across Taiwan to the Philippines, Sulawesi and the Lesser Sundas, and from there to Australia. He called this the giant rat route, because from all these islands fossil and/or extant species of giant rats are known. Giant rats are still on the menu of modern humans living on those islands (Verhoeven, 1950; Musser, 1981), and could have served as an important protein source for palaeolithic humans that had become stranded on one of the islands along this route. Sondaar further reasoned that Pleistocene human dispersal along this route would have been interrupted by long periods of residence on the intermediate islands before crossing to the next island, so that local evolutionary and behavioral patterns may have developed.

At this point, there is no convincing evidence that *Homo erectus* already inhabited Sulawesi and the Philippines in the Middle Pleistocene. Palaeolithic industries are known, however, from South Sulawesi, Luzon and Mindanao (Shutler and Mathisen, 1979; Glover, 1981; Bautista, 1991; Keates and Bartstra, 1994). Better age assessments of the early human occupation of these islands are needed. As for South Sulawesi Van den Bergh (1999) argues that the conglomerates associated with the group 1 artifact assemblage of Bartstra et al. (1991); Keates and Bartstra (1994) may be much older than the Late Pleistocene age posited by these authors. Further indications for a much earlier human occupation of Sulawesi could be sought in the similar faunal turnover patterns observed on Flores and South Sulawesi. The elephantoids from the younger Middle Pleistocene faunas on both islands show only a slight tendency to become smaller, but not as small as the elephantoids from the Early Pleistocene faunas, which they replaced. The absence of dwarfing in *Stegodon florensis* has been ascribed to the presence of a predator in the associated fauna: Palaeolithic hunters (Sondaar, 1989).

5. Conclusions

The transition from Early to Middle Pleistocene is clearly marked in the fossil faunal succession of the islands of Java, Sulawesi and Flores. A major factor

contributing to these faunal turnovers must have been the pronounced lower sea levels that prevailed from ca. 8.0 Ma onward. On Java this led to full land connections and invasions from the Siwaliks and the SE Asian mainland. The islands of Japan and Taiwan also experienced major faunal immigrations during the Middle Pleistocene, while the older faunas on these islands indicate island conditions. On Sulawesi and Flores, which remained islands throughout their Quaternary history, these sea level lowerings seem to have increased the accessibility for taxa with a relatively high potential to cross water barriers. Faunal turnovers are recorded for these islands around the Early to Middle Pleistocene transition. On Flores *Homo erectus* was among the new colonizers.

Apart from the phalangers which must have come from the east, the ancestors of all other large Sulawesi land vertebrates, fossil and extant, seem to have arrived by crossing the sea between the Sunda Shelf and Sulawesi. Overseas dispersal from the Philippines is improbable. Faunal stability on South Sulawesi prevailed until the Middle Pleistocene, and only local evolution occurred (e.g., shortening of the metapodials in *Celebochoerus heekereni*, increasing hypsodonty in *Stegodon*). Because the Walanae Fauna does not contain any ancestors of the extant Sulawesi fauna, and must have also been isolated for quite some time, South Sulawesi must have constituted a separate palaeo-island until at least the Middle Pleistocene. Only after the early Mid-Pleistocene sea level lowering did new immigrants invade South Sulawesi and most elements from the Walanae Fauna become extinct.

On Java a second major faunal turnover event occurred during the Late Pleistocene. A fauna of Chinese affinity entered Java for the first time as documented by the Punung Fauna. The faunal turnover at this stage marks a transition from open woodland to tropical rainforest environments, and at this point *Homo sapiens* entered Java. More data are needed on Sulawesi and Flores during this time interval, but it is probable that the modern faunas on these islands became established around the same time.

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