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The evolution of humans in Australasia from an environmental perspective

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Abstract

Attempts to understand the evolution within the genus *Homo* in Australasia have relied on two main theories. The Multiregional scenario suggests that cranial morphology reveals a long-standing continuity between fossil and recent hominids in the region. Out of Africa theorist have favoured the idea that *Homo sapiens* evolved in Africa, migrated outward, and replaced archaic hominids, such as *Homo erectus* in Australasia. Neither Multiregionalists nor Out of Africans have seriously factored in the unique geographic and ecological context in which variation in Australasian members of the genus *Homo* evolved. Nonetheless, the mammalian faunas of this region have been strongly shaped by the existence of zoogeographic barriers and different ecological zones. Taking an environmental perspective on the evolutionary history of the human lineage in this region leads to scenario in which both local evolution and replacement play a role. Wallacea, as a water-barrier, has been a tremendously important geographic barrier influencing the distribution and evolutionary course of many mammals, including that of the genus *Homo*. Regional continuity may be assumed for *Homo erectus* in Southeast Asia, from earlier Javanese forms like Trinil and Sangiran to later forms like Ngandong. There is no evidence that *Homo erectus* crossed Wallacea and reached the Sahul. As between 126 and 81 ka the tropical rainforest spread as far as East Java, a number of archaic species, including *Homo erectus*, were replaced by modern species better adapted to survive in a more humid environment. In contrast to *Homo erectus*, *Homo sapiens* was capable of crossing Wallacea. Once *Homo sapiens* reached the Sahul, Wallacea was an important factor for its further evolutionary course. Interestingly, regional continuity may be assumed for *Homo sapiens* on both sides of Wallacea. Looking at the cranial morphology of recent humans, it is obvious that there are two clearly distinguishable cranial patterns, an East Asian (Sunda) and an Australian (Sahul) one.

Keywords: Australasia; *Homo erectus*; *Homo sapiens*; Cranial variation; Biostratigraphy Java

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1. Introduction

Two main theories have been put forth to explain modern human origins. The Noah's Ark or Out of Africa theory emphasises replacement as the dominant mechanism responsible for the disappearance of archaic hominid populations and the spread of modern humans (Bräuer, 1984, 1989, 1992; Stringer and Andrews, 1988; Stringer, 1992a; Rouhani, 1989; Cann, 1992; Stringer and McKie, 1996). Proponents of this theory suggest that a single biological and spatial population of modern humans, probably evolving in Africa, replaced archaic hominid populations (Neanderthals in Europe, *Homo erectus* in Indonesia) throughout the Old World.

The opposing theory, known as the multiregional evolution model, proposes that modern humans evolved from several archaic human populations in various regions of the Old World over a long period of time (Wolpoff et al., 1984; Frayer, 1992; Smith,

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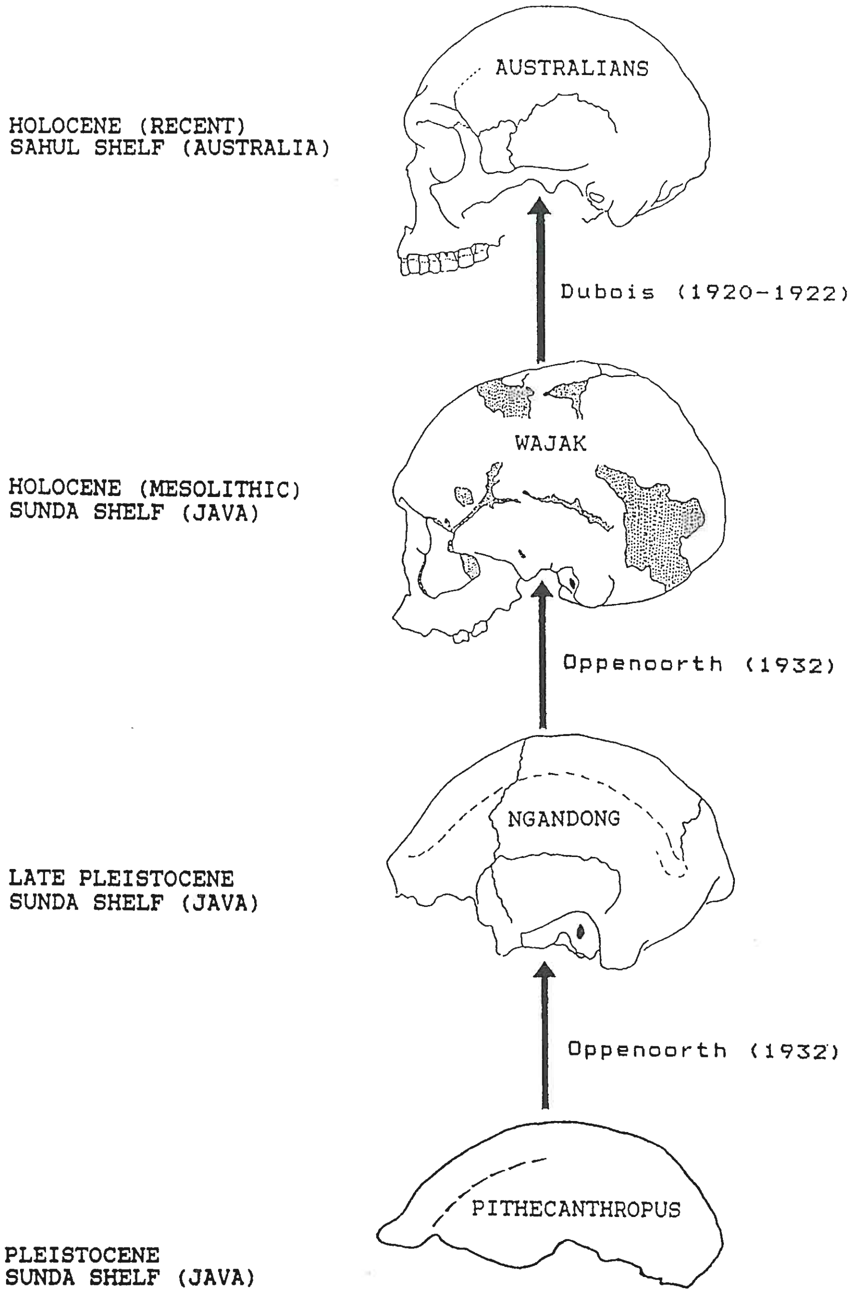

Fig. 1. The historically well known Javanese/Australian evolutionary sequence. The link between prehistoric Java (Wajak) and Australia was first suggested by Dubois in 1920a,b (Dutch)/1922 (English). Oppenoorth (1932) suggested links between *Pithecanthropus*-I, Ngandong (Solo) and Wajak. Keith (1936) was the first to suggest this evolutionary sequence, which became well known after its inclusion in Weidenreich's (1945) diagram of multiregional evolution of humans. Recent research has made clear that, apart from the link between '*Pithecanthropus*' and Ngandong (Solo), this idea is probably wrong, and an alternative scenario is suggested (Fig. 6).

1992; Thorne and Wolpoff, 1992; Wolpoff, 1989, 1992; Wolpoff and Caspari, 1997). The result is the evolution of a single, widespread species, *Homo sapiens*, that preserves specific regional traits. The basic idea of long-lasting regional continuity in Australasia is an old one (Fig. 1; Keith, 1936; Weidenreich, 1945; Coon, 1962), and is still strongly supported (Wolpoff et al., 1984; Wolpoff, 1989;

Kramer, 1991; Thorne and Wolpoff, 1992; Wolpoff and Caspari, 1997). A lineage is often traced from Javanese Pleistocene hominids, like Trinil, Sangiran, and Ngandong, via prehistoric skulls like Wajak (Java) and Kow Swamp (Australia), to recent Australian Aborigines. Recent elaborations incorporate concepts from population biology and genetics to suggest that 'long-lasting morphological clines' are the result of 'a balance of gene flow and opposing selection and drift' (Wolpoff et al., 1984 p.455; see also Thorne and Wolpoff, 1981 p.347).

Both theories can be evaluated and possibly improved by incorporating information on the geographic and palaeoecological circumstances of Australasia. Because geographic and ecological barriers have been an important factor in shaping the distribution and characteristics of Australasian mammalian faunas, I suggest that these same barriers may be at least partly responsible for the distribution and evolutionary history of humans in this part of the world.

In this paper, I review and evaluate current information on the palaeoecology of Java (Sondaar, 1984; Leinders et al., 1985; Theunissen et al., 1990; De Vos et al., 1994; Van der Kaars and Dam, 1995) and cranial morphology in prehistoric and recent Australasian populations (Storm, 1995) in the context of the geographical situation of Australasia. Based on the synthesis of these data, I suggest a scenario for human evolution in this region.

2. The importance of Wallacea

The evolutionary history of any mammalian group in Australasia, including that of the genus *Homo*, is best understood in terms of the geographical characteristics of this region (see also Coon, 1962). Australasia can be divided into three major regions; the Sunda shelf; a transitional region called Wallacea; and the Sahul shelf (Fig. 2). The drawing of zoogeographic lines of these regions has been disputed (Simpson, 1977; Whitmore, 1981; George, 1981; Bellwood, 1987; Harris, 1994). Wallacea encompasses the islands of Timor, Flores and Sulawesi. The relevance is that in times of low sea levels, islands of the Sunda shelf were continuous with the continental landmass of Southeast Asia. To the east and south, low sea levels joined Australia, New Guinea and Tasmania into a single landmass, Sahul. Significantly, during the past two million years, sea levels have never dropped low enough to connect the Wallacean islands to either land masses (Bellwood, 1985).

Wallacea as a zoogeographic barrier is visible in the difference between the mammalian faunas of Sunda and Sahul. The placental character of the Sunda fauna contrasts sharply with the predominantly marsupial character of the Sahul fauna. The intervening Wallacean fauna contains an admixture of both Sunda and Sahul elements, but is mainly Asian (Sunda) in character (Bellwood, 1987). Another important feature is the (former) presence of endemic species in Wallacea, like pygmy proboscideans and giant tortoises (Van den Bergh et al., 1994; Sondaar et al., 1994). Apparently, only mammals that can fly, swim or float on objects (such as floating mats of vegetation or trees) are able to travel from island to island, crossing from one continental landmass through Wallacea to the other. In the distant past, only two placental (Sunda) categories reached Sahul: flying (bats) and floating (rodents) mammals.

3. The biostratigraphy of Java

The task of reconstructing Javan biostratigraphy is a difficult one. No single Javan locality preserves all of the faunas in a single sequence so the chronological relationship of the faunas to each other must be deduced (Fig. 3). Further, most of the faunal units have not been reliably dated.

An early reconstruction of the biostratigraphy of Java by Von Koenigswald (1934, 1935) has been criticised by De Vos et al. (1982 p.208):

> Von Koenigswald (1934, 1935) used locality names for his faunal succession, but his faunal assemblages from the Pleistocene units differ in composition from the fauna actually collected at those 'type' localities,

and

> Besides lumping faunas together, Von Koenigswald also changed the fauna lists

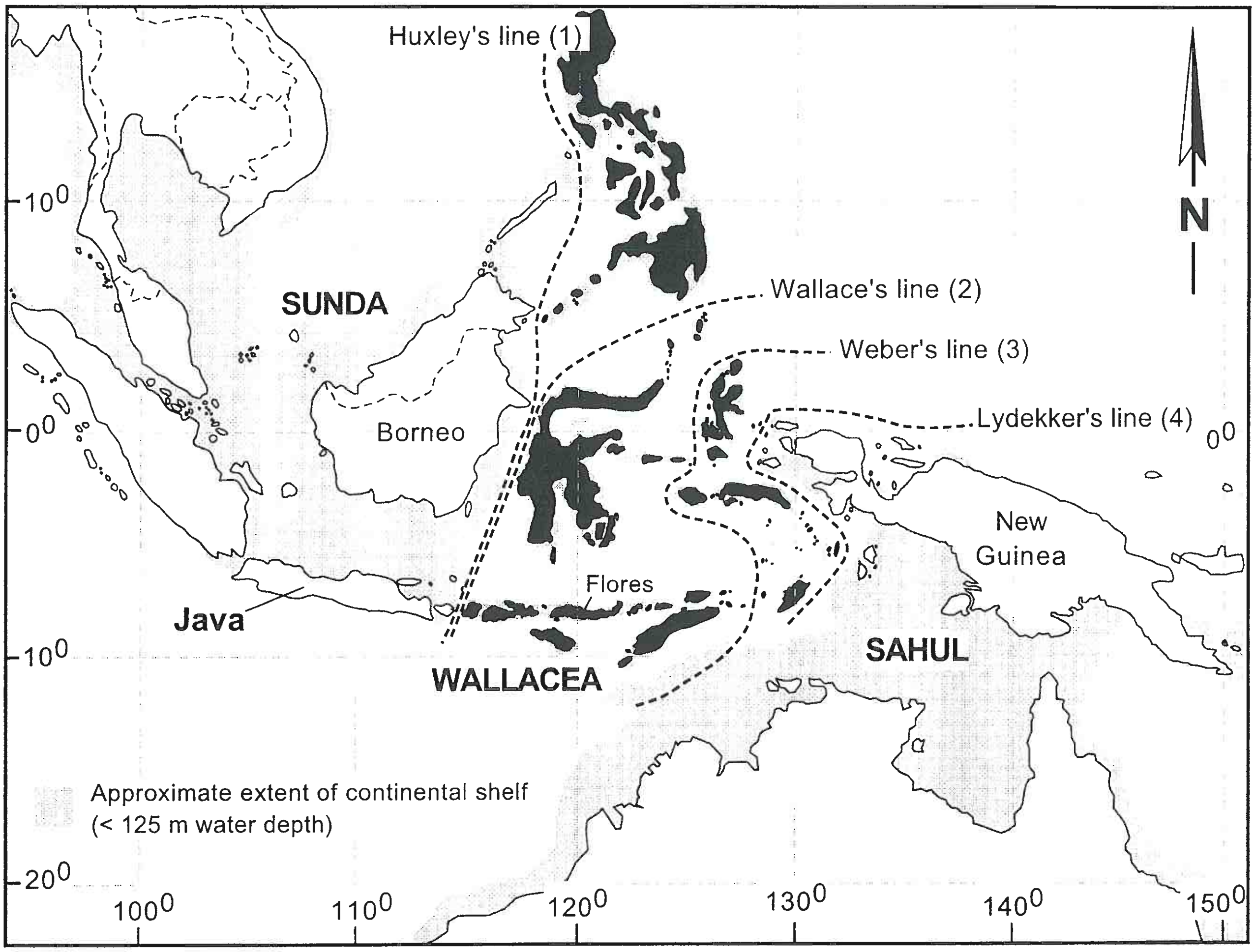

Fig. 2. Australasia can be divided in three major zoogeographic regions: Sunda, Wallacea and Sahul. The zoogeographic lines are based on: Simpson (1977), De Boer and Van Wissen (1978) and George (1981). (1) Huxley's Line (1868): runs between Bali and Lombok, between Borneo and Sulawesi, and west of the Philippines. (2) Wallace's Line (1863–1880): runs between Bali and Lombok, between Borneo and Sulawesi, and south of the Philippines. (3) Weber's Line (1904): runs between Timor and Australia, and west of the Mollucas. (4) Lydekker's Line (1896): runs between Timor and Australia, and east of the Mollucas.

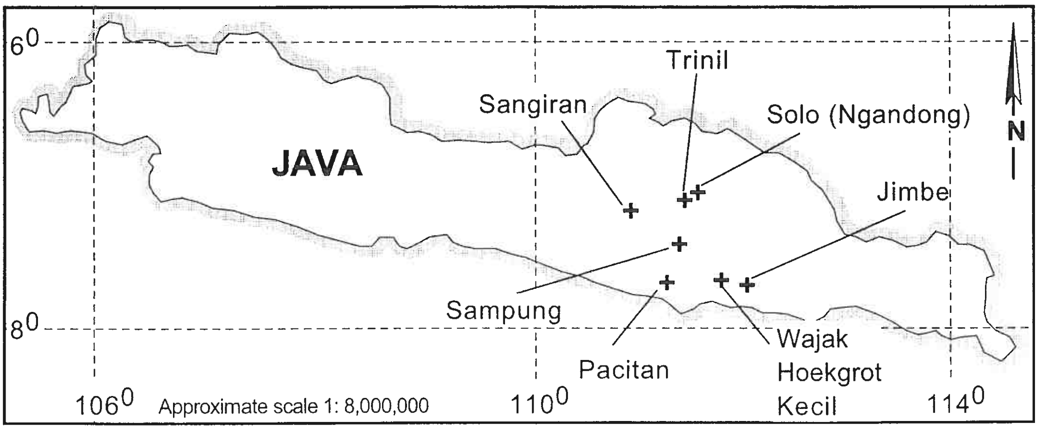

Fig. 3. Prehistoric Javanese sites.

compiled by previous authors without producing clear reasons for doing so.

Because of these shortcomings, De Vos and others tried to create a new biostratigraphic framework for Java in the 1980s (De Vos et al., 1982; De Vos, 1983; Sondaar, 1984; Leinders et al., 1985). These authors considered the composition of the faunas (island versus mainland elements and archaic versus modern elements), and integrated information from dated faunal layers elsewhere in Java, Sangiran (Matsu'ura, 1982), to help with establishing relative and absolute chronology. They also included only fossils of known provenance and only faunas, which originated from a single stratigraphic level at one locality.

The result is the following sequence of faunal units, from oldest to youngest: Satir, Ci Saat, Trinil H.K., Kedung Brubus, Ngandong, Punung and Wajak (Leinders et al., 1985; Theunissen et al., 1990; Van den Bergh et al., 1996a). Most of the dates assigned to these faunal units are derived from the dated and stratigraphically controlled Sangiran area, at which the authors were able to recognise the Satir, Ci Saat, Trinil H.K. and Kedung Brubus faunas (Leinders et al., 1985). The age of the Ngandong fauna is problematic. It is believed by some to be younger than the Kedung Brubus fauna and older than the Punung fauna, dating from the late Middle Pleistocene (Van den Bergh et al., 1996a), while others (Swisher et al., 1996) claim that Ngandong is younger. The Wajak fauna has been directly dated by a C-14 date from the Wajak locality (Storm, 1995). The characteristics of five prehistoric faunal assemblages from Javanese sites in which hominid remains have been found are summarised briefly below (Table 1).

Claims have been made for the presence of hominids in Java as early as 1.81 ± 0.04 and 1.66 ± 0.04 Ma based on ^{40}Ar/^{39}Ar laser incremental heating of hornblende from pumice of the well known hominid sites Mojokerto and Sangiran (Swisher III et al., 1994). On this basis, Swisher and colleagues suggest that *Homo erectus* may have evolved outside Africa. De Vos and Sondaar (1994) accept the technical accuracy of these dates but cast doubts on their association with the hominid fossils.

The Trinil Haupt-Knochen Schicht (Trinil H.K.) fauna can possibly be dated to around 0.9 Ma based on the similarity with the grenzbank fauna at Sangiran (Van den Bergh et al., 1996a). The Trinil H.K. fauna is characterized by typical archaic species like: *Homo erectus*, *Stegodon trigonocephalus*, *Axis lydekkeri*, *Duboisia santeng*, *Bubalus palaeokerabau*, *Bos palaeosondaicus* and *Sus brachygnatus*. Interestingly, it also contains several living forms.

The next oldest faunal unit in the succession, the Kedung Brubus fauna, is similar to the Sangiran fauna dated to around 0.8–0.7 Ma (Van den Bergh et al., 1996a). The Kedung Brubus fauna retains some species from the Trinil H.K. fauna combined with additional archaic forms. These new species are interpreted as immigrants from the Asian mainland. The Kedung Brubus fauna is also richer in species than that of Trinil H.K.

According to the biostratigraphic framework erected by De Vos and colleagues, the next youngest fauna is Ngandong. The Ngandong fauna is striking in that it is composed of archaic species (including *Homo erectus*) that were already present in the Trinil H.K. and Kedung Brubus faunas, without any new immigrant species. This fact suggests a constancy of habitat over a long period of time, possibly beginning in Trinil faunal times. The Ngandong fauna is poorer than that of either Trinil or Kedung Brubus.

The still younger Punung fauna is noticeably different. The Punung fauna is comprised of animals adapted to humid forest and dates probably to the Late Pleistocene. Unlike the preceding faunas, Punung contains no extinct mammals. Punung is a modern fauna with new arrivals like *Pongo pygmaeus*, *Hylobates syndactylus*, *Helartos malayanus*, *Elephas maximus*, *Capricornis sumatraensis*, *Sus barbatus* and *Sus scrofa*. Unfortunately, the human material from Punung is very poor. According to Badoux (1959 p.124): 'two upper incisors, an upper canine and a lower canine', and possibly an upper molar, which he ascribed to the genus *Homo* (cf. '*Pithecanthropus*'). De Vos (1985) identifies the human remains from Punung as *Homo sapiens*.

The final Wajak fauna is dated at 10,560 ± 75 yr B.P. (^{14}C date AA7846), the human remains from the Wajak site are younger, dated at 6560 ± 140 yr B.P. (^{14}C date AA7718). The Wajak fauna closely resembles the Punung fauna, but lacks the species most strongly adapted to the humid forest (e.g. *Pongo pygmaeus*, *Hylobates syndactylus* and *Helarctos malayanus*). The Wajak fauna appears to

Table 1
Mammal Species from Javanese Hominid Sites (Trinil H.K., Kedung Brubus and Ngandong are based on De Vos et al. (1994), Punung on De Vos (1983), and Wajak on Storm, 1995. +: recorded; –: not recorded; ?: uncertain)

	Trinil H.K.	Kedung Brubus	Ngandong	Punung	Wajak
Homo sapiens	–	–	–	+ ?	+
Pongo pygmaeus	–	–	–	+	–
Hylobates syndactylus	–	–	–	+	–
Hylobates moloch	–	–	–	+ ?	–
Macaca nemestrina	–	–	–	+ ?	–
Helarctos malayanus	–	–	–	+	–
Elephas maximus	–	–	–	+	–
Cervus timorensis	–	–	–	+ ?	+
Capricornis sumatraensis	–	–	–	+	–
Bos sondaicus (javanicus)	–	–	–	+ ?	+ ?
Bubalus bubalis	–	–	–	+ ?	+ ?
Sus barbatus	–	–	–	+	–?
Sus scrofa (vittatus)	–	–	–	+	+
Sus verrucosus	–	–	–	+ ?	–?
Lutrogale palaeoleptonyx	–	+	–	–	–
Hyaena brevirostris	–	+	–	–	–
Elephas hysudrindicus	–	+	+	–	–
Rhinoceros unicornis	–	+	–	–	–
Tapirus indicus	–	+	+	+	+
Epileptobos groeneveldtii	–	+	–	–?	–
Hexaprotodon sivalensis	–	+	+	–	–
Sus macrognathus	–	+	+	–	–
Manis palaeojavanica	–	+	–	–	–
Homo erectus	+	+	+	–?	–
Presbytis spec.	+	–	–	–	+
Macaca fascicularis	+	–	+	+ ?	–?
Hystrix javanica	+	–	–	+	+
Panthera tigris	+	+	+	+	+
Prionailurus bengalensis	+	–	–	–	–
Mececyon trinilensis	+	–	–	–	–
Stegodon trigonocephalus	+	+	+	–	–
Rhinoceros sondaicus	+	+	–	+	+
Muntiacus muntjak	+	+	–	+	+
Axis lydekkeri	+	+	+	–	–
Duboisia santeng	+	+	–	–	–
Bubalus palaeokerabau	+	+	+	–?	–
Bos palaeosondaicus	+	+	+	–?	–
Sus brachygnathus	+	–	+ ?	–	–

be a Punung fauna that has been impoverished by the loss of rainforest inhabitants, due to drier climatic conditions.

4. The Palaeoenvironment of *Homo erectus* in Java

The information of the large number of fossils from Java can be used to make some inferences about the palaeoecology of *Homo erectus* in Java. The faunal units Trinil H.K., Kedung Brubus and Ngandong contain what is clearly *Homo erectus*; these faunas suggest an open woodland habitat (De Vos, 1983, 1995). Typical species indicative of a tropical rainforest environment like *Pongo pygmaeus*, *Hylobates* and *Helarctos malayanus* are lacking in these faunas. The dominant element in the Trinil H.K. fauna is the abundant number of large bovids, whose presence suggests a drier biotope (Sondaar, 1984) than a tropical rainforest. Moreover, Trinil H.K., Kedung Brubus and Ngandong all include the large bovid *Bubalus palaeokerabau*. This animal had horns with an enormous spread of about 2.5 m from tip to tip. It is difficult to envision this species as inhabiting a densely wooded environment and it can be taken as indicative of more open habitats.

The idea that *Homo erectus* occurred in open woodland habitats and not in tropical rainforests is not undisputed (Pope, 1985, 1995). Pope (1995 p.494-495) remarks:

> The reconstruction of the Sunda Shelf as an open savanna is not supported by the data. The absence of any demonstrably open-dwelling forms precludes the recognition of any part of Pleistocene Southeast Asia as anything but a tropical forest environment. Equids (*Hipparion*, *Equus*) camelids (*Paracamelus*, *Camelus*), and giraffoids (*Sivatherium*) present elsewhere in Eurasia are entirely absent in Southeast Asia. Conversely, demonstrably tropical forest-dwelling taxa such as orangutans, gibbons, macaques, tapirs, and many other forest forms are present in Far Eastern fossil faunas.

The disagreement is in part based on differences of identification of key specimens. Assertion that Asian apes were present in Pleistocene Java may be in part based on Von Koenigswald equation (1939, 1940), of the Punung fauna (including *Pongo* and *Hylobates*) with the Trinil fauna (De Vos, 1983). In addition, Von Koenigswald (1936, 1938, 1939, 1940), Weidenreich (1937) and Hooijer (1948) identified that the Trinil upper molars, originally described as '*Pithecanthropus*' (Dubois, 1894), as those of an (extinct) orang-utan. If their identification is correct, the Trinil and Punung faunas are rendered more similar. However, this identification of the molars as orang-utan is not convincing (Janssen Groesbeek, 1996). Another element cited by Pope as indicating forested habitat, macaques, is today found in a range of habitats (Fooden, 1982). In contrast to *Macaca nemestrina*, a forest form, *Macaca fascicularis* is not typically found in primary broadleaf evergreen forests. Without more detailed analysis of the adaptations of the particular species in question, the presence of macaques cannot be taken as strongly indicative of a tropical rainforest. The strongly rainforest-adapted species cited by Pope, orang-utans and gibbons, are not present in the Trinil H.K., Kedung Brubus and Ngandong faunas.

Pope observes correctly that groups classically considered indicative of an open environment (camelids, equids and giraffoids) are absent from the Pleistocene Javan faunas. The absence of any particular group, especially in an area with formidable zoogeographic barriers, is a difficult piece of evidence to interpret. Since the faunas of Trinil H.K. and Kedung Brubus (Table 2) are dominated by large bovids and the absence of species indicative of a tropical rainforest, there is no convincing evidence against the reconstruction of Pleistocene Java as an open woodland habitat.

In Java, *Homo erectus* occurred in more open environments, just like its relatives in Africa. This conclusion is supported by the floral evidence as well (Polhaupessy, 1997). At present, the most probable palaeoenvironment for Trinil H.K., Kedung Brubus and Ngandong times seems to be a more open woodland habitat (indicated by large bovids) with water (indicated by *Hexaprotodon sivalensis* and crocodiles) and some forests (indicated by cercopithecidae) in the immediate vicinity; possibly gallery forests along river banks. In contrast, the later Punung fauna is strongly indicative of a more humid, more densely forested environment.

5. Two species of the genus *Homo* in Australasia

The first question is whether one or two species within the genus *Homo* are found in Australasia. To answer this question, I examined a sample of recent (Table 3) and prehistoric skulls (Table 4), scoring each for the presence or absence of a number of characters (Storm, 1995), that have been used to describe or define *Homo erectus* (Andrews, 1984; Stringer, 1984; Rightmire, 1990). Some erectus traits were present but rare in individuals in recent *Homo sapiens*; other *erectus* traits were not expressed at all in this sample (Table 3). In no recent human skull in the sample was the combination of all *Homo erectus* characters observed. These data do not support the idea that *Homo erectus* is an invalid taxon that is part of 'the evolutionary species *Homo sapiens*' (Wolpoff

Table 2
Number of faunal elements in Trinil H.K. and Kedung Brubus (Based on the computer list of February 23, 1990 of Naturalis (National Museum of Natural History), Leiden, The Netherlands. These numbers must not be seen as an exact counting. Nevertheless, it gives a good rough impression of the fossil ratio found)

	Trinil H.K.		Kedung Brubus	
	N	%	*N*	%
Hystricidae		0.06		0.00
Hystrix javanica	2		0	
Cercopithecidae		0.30		0.00
Macaca fascicularis	9		0	
Presbytis spec.	1		0	
Hominidae		0.30		0.14
Homo erectus	10		1	
Small carnivores		0.03	0.14	
P. bengalensis	1		0	
L. palaeoleptonyx	0		1	
Large carnivores		0.36		2.74
Panthera tigris	9		15	
Panthera spec.	3		4	
Hyena brevirostris	0		1	
Tapiridae		0.00		0.41
Tapirus indicus	0		3	
Rhinocerotidae		1.63		6.84
Rhinoceros sondaicus	48		27	
Indet.	6		23	
Elephantidae		12.72		31.74
S. trigonocephalus	392		112	
Elephas hysudrindicus	0		22	
Indet.	29		98	
Suidae		1.12		4.79
Sus brachygnathus	28		0	
Sus macrognathus	0		17	
Indet.	9		18	
Hippopotamidae		0.00		4.92
Hexaprotodon sivalensis	0		36	
Cervidae		24.05		5.75
Axis lydekkeri	765		36	
Cervus kendengensis	31		6	
Bovidae small		7.76		3.28
Duboisia santeng	257		24	
Bovidae large		49.27		37.21
Bubalus palaeokerabau	143		27	
Bos palaeosondaicus	64		27	
E. groeneveldtii	0		9	
Indet.	1424		209	
Crocodilia		2.39		2.05
Crocodilus ossifragus	60		15	
Garialis bengawanicus	19		0	
Total	3310		731	

Table 3
Some *Homo erectus* characters (%) in recent crania from East Asia and Australasia (From Storm (1995); *N* is given between brackets, after percentage. 63 Chinese ('Koelies'), 89 Javanese, and 3 Australian skulls, were stored in the Laboratory for Anatomy and Embryology, University of Leiden, The Netherlands. 16 Javanese, 64 Papuans, and 1 Australian skull were stored in the National Museum of Natural History, Leiden, The Netherlands. 35 Australian skulls were stored in the Natural History Museum, London, UK, and 3 replicas of Australian skulls were stored in 'Universiteitsmuseum', University of Utrecht, The Netherlands). Indices (1) very low neurocranium: (length/height index <65.0); (2) very strong postorbital constriction: (index <75.0). Non-metrical characters (3) supraorbital torus: clearly present as a thick/robust and more or less straight structure. The glabella, superciliary arches and zygomatic trigones all form part of this structure; (4) parietal bones converge: more or less immediately above the supramastoid crest; (5) parietal margin os temporale: the parietal margin of the temporal squama has a low flat/straight superior border; (6) angled os occipitale: viewed from norma lateralis there is a clear, more or less sharp angle between the nuchal and the occipital planes, divided by a distinct occipital torus; (7) strongly developed occipital torus: clearly present as a strongly developed structure which divides the occipital bone into a nuchal and an occipital plane (opistocranion = inion). Tightly speaking, opistocranion was not always at exactly the same point as inion in the Solo skulls (but always close; hence the score ' ± ') (see Hublin, 1978)

	China	Java	New Guinea	Australia
1	0.0% (63)	0.0% (103)	0.0% (56)	0.0% (37)
2	0.0% (62)	0.0% (104)	0.0% (61)	5.3% (38)
3	0.0% (63)	0.0% (105)	0.0% (64)	0.0% (42)
4	0.0% (63)	0.0% (105)	0.0% (64)	2.4% (42)
5	0.0% (62)	0.0% (104)	0.0% (64)	0.0% (42)
6	0.0% (63)	0.0% (105)	0.0% (63)	0.0% (41)
7	0.0% (63)	0.0% (105)	0.0% (62)	0.0% (41)

et al., 1994 p.342). *Homo erectus* is a valid taxon (Rightmire, 1994), in the sense of being a morphospecies with a distinctive and recognisable combination of traits.

The Ngandong skulls are believed to be younger than the hominid specimens from Trinil and Sangiran, dating to the Late Pleistocene or late Middle Pleistocene, and therefore might be expected to be more like *Homo sapiens*. However, this is not the case. In contrast with the sample of recent human skulls, the defining combination of *Homo erectus* traits is consistently found in the Javanese Solo (Ngandong) skulls (Table 4). Although damage to the fossil material prevented a number of measurements from being taken on some specimens, the distinguishing features like a low skull and strong postorbital constriction

Table 4
Some *Homo erectus* characters in Prehistoric crania from Australasia (from Storm (1995). For indices (numbers 1–2) and characters (numbers 3–7) see Table 3. –: absent; ±: ambiguous; +: present; replicas of Solo-I, -III, -IV, -V, -VI were stored in the National Museum of Natural History, Leiden, The Netherlands; replicas of Solo-IX, -X, -XI were stored in 'Universiteitsmuseum,' University of Utrecht, The Netherlands. Original prehistoric skulls from Malaysia, Java and Flores were stored in the National Museum of Natural History, Leiden, The Netherlands. Replicas of prehistoric skulls from Australia were stored in the Natural History Museum, London, UK (Kanalda is original))

	Characters						
	1	2	3	4	5	6	7
Java Pleistocene							
Solo-I			+	+		±	+
Solo-III				+			
Solo-IV			+				
Solo-V			+	+	+	+	±
Solo-VI	+		+	+	+	+	+
Solo-IX			+	+		+	±
Solo-X			+	+		+	±
Solo-XI	+	+	+	+	+	+	+
Malaysia Holocene							
Gua Kepah B347			–	–		–	–
Gua Kepah C77			–				
Java Holocene							
Wajak-1	–	–	–	–	–	–	–
Wajak-2			–			–	–
Hoekgrot			–	–		–	–
Sampung-H			–			–	–
Flores Holocene							
Liang Toge			–	–		–	–
Liang Momer-E	–		–	–	–	–	–
Aimere						–	–
Australia							
Kanalda	–	–	–	–	–	–	–
Keilor			–	–	–	–	–
Kow Swamp-1			±		–		
Kow Swamp-5			±	–	–	–	–
Kow Swamp-15			±				
Mungo-1			–	–		–	–
Mungo-3			–			±	±

were present in skulls that could not be measured. This study (Storm, 1995) showed the morphology of the Solo skulls to be close to that of the East Asian (Chinese) and Indonesian (Javanese) fossils ascribed to *Homo erectus*, in agreement with several authors and studies (Weidenreich, 1951; Jacob, 1967, 1978; Santa Luca, 1980; Rightmire, 1990, 1992, 1994; Stringer and McKie, 1996).

The second question is whether there are transitional forms recognizable in Australasia between *Homo erectus* and *Homo sapiens*. Inspection of the data in Table 4 reveal no individuals that could be interpreted as representing a transitional form between the latest *Homo erectus* and modern humans. Possibly the lack of transitional forms is an artifact caused by the small number of human fossils in Australasia from the time period in question. With presently known specimens, the continuity in cranial morphology between Pleistocene Javan forms (*Homo erectus*) and later, recent Australian forms (*Homo sapiens*) — suggested to exist by Keith (1936), Weidenreich (1945), Coon (1962), Wolpoff et al. (1984), and Thorne and Wolpoff (1992) — cannot be demonstrated in this sample. The findings indicate a morphological distinction between *Homo erectus* and *Homo sapiens* in Australasia (Fig. 4).

6. Did *erectus* and *sapiens* meet?

A late Middle Pleistocene age has been proposed for Ngandong (older than 60–80 ka, Van den Bergh et al., 1996a) and of 900 ka for Sambungmacan (Jacob, 1984). These dates contrast sharply with the results of Swisher et al. (1996). Swisher and colleagues obtained very young dates (27 ± 2–53.3 ± 4 ka) on fossil bovid teeth coming from Ngandong and Sambungmacan. If the dates of Swisher et al. are correct, then this could imply that the Ngandong fauna is younger, not older, than the Punung fauna, which may contain *Homo sapiens*. Further, the young dates for Ngandong raise the question whether the two species within the genus *Homo* co-existed in Southeast Asia for a prolonged period of time.

It is likely that the archaic Ngandong fauna, which is interpreted as an open woodland fauna, is older than the modern Punung fauna, which is interpreted as a modern humid forest fauna (De Vos, 1983). When the modern tropical rainforest expanded southeastward to Java, archaic open woodland species would be expected to become extinct. Because Java occupies the southeastward point of Sunda, open woodland-adapted mammals could not escape by moving farther south or east in front of the expanding tropical rainforest. The barrier Wallacea prevented this. Consequently, after the modern tropical rainforest

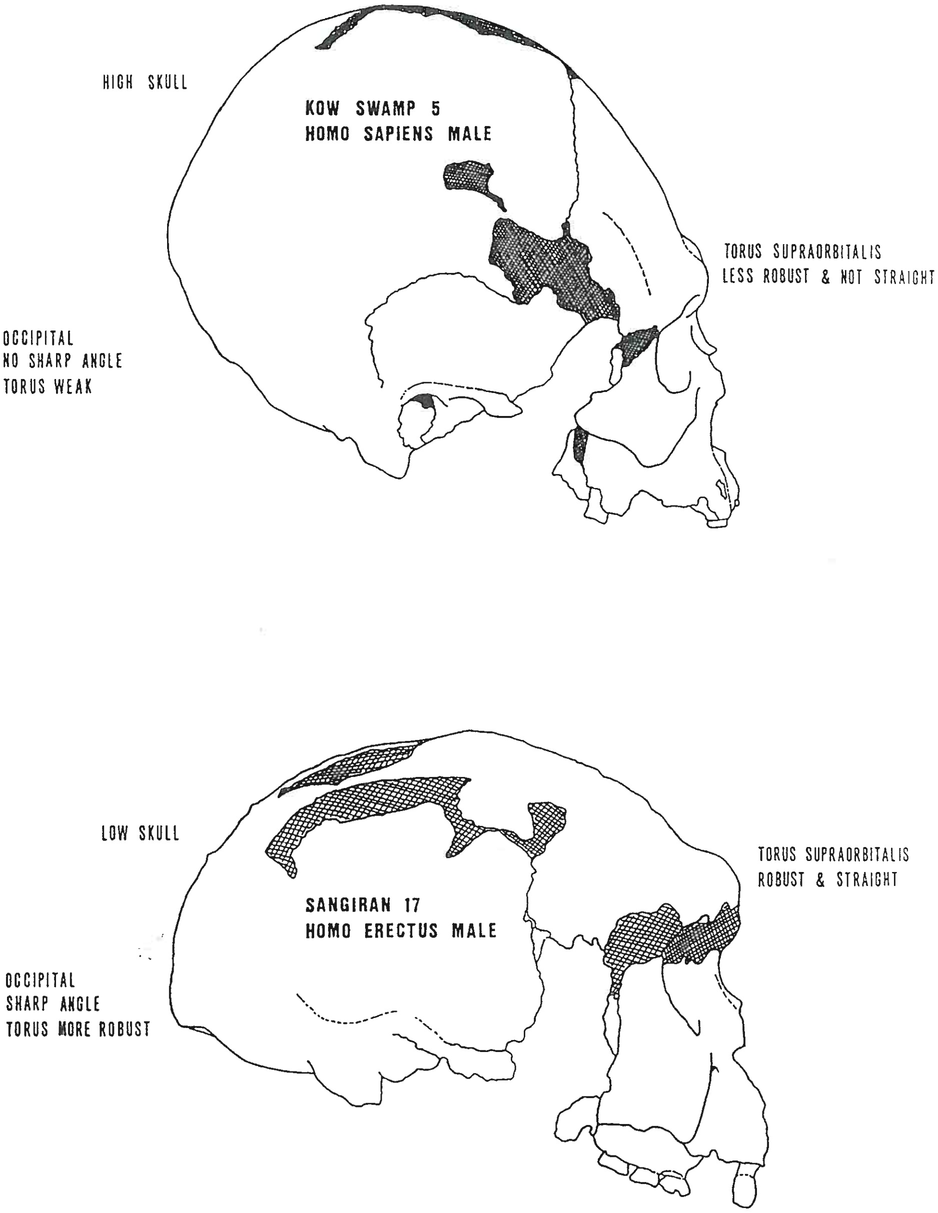

Fig. 4. Two species of the genus *Homo* in Australasia. Kow Swamp-5 is a Late Pleistocene/Early Holocene Australian skull, that can be characterized as a typical general (robust) adult male *Homo sapiens* skull. There are characters in Kow Swamp-5 that are possibly correlated with artificial deformation (Brown, 1981). *Pithecanthropus*-VIII (= Sangiran-17) is the most complete *Homo erectus* skull from Java, probably male and can possibly be dated in the Middle Pleistocene.

invaded Indonesia as far as eastern Java, the open woodland fauna of Ngandong probably went extinct. There does not seem to be any sizeable open region to which the fauna, including *Homo erectus*, could have retreated and from which it could have re-expanded again later when conditions became more favourable. The improbability of a sizeable woodland refuge east or south of Java suggests that Ngandong cannot have been a post-Punung return of open woodland habitat complete with its archaic fauna.

Another issue is the timing of the invasion of Java by tropical rainforest. The interpretation that an archaic open woodland fauna (Ngandong) was followed by a modern tropical rainforest fauna (Punung), which was in turn followed by the modern sub-recent open woodland fauna (Wajak), concurs

Table 5
A possible scenario for the transitional period of *Homo erectus* to *Homo sapiens* in Java. Based on interpretations of the palaeoclimate of Bandung (Dam, 1994; Van der Kaars and Dam, 1995) and the biostratigraphy of Java (Table 1)

Date (ka)	Palaeoclimate Bandung	Palaeontology/ Palaeoecology	*Homo*
0			
10		Wajak	*sapiens*
20		Modern open woodland	
30			
40			
50			
60	Dry/Cooler		
70			
80			
90		Punung	
100	Humid/Warm	Modern humid forest	*sapiens*?
110			
120		Faunal turnover	
130			
140	Dry/Hot		
150			
160		Ngandong	*erectus*
170		Archaic open woodland	
180			
190			
200			

with palaeoclimatic reconstructions based on sedimentological and palynological analyses of sediment cores from the Bandung basin in West Java (Dam, 1994; Van der Kaars and Dam, 1995 (Table 5). According to these studies, around 135 ka, the climate was considerably drier and hot. Between 126 and 81 ka, the climate was primarily humid and warm (interglacial conditions). After 81 ka the climate became drier and cooler. Using the sea level fluctuations from Prentice and Denton (1988), a scenario can be constructed in which the tropical rainforest and its inhabitants reached Java during the humid and warm phase between 126 and 81 ka. If the archaic Ngandong fauna preceded the modern Punung fauna, then Ngandong must be older than 126 ka, contrary to the much more recent dates obtained by Swisher et al. (1996).

In summary, it is difficult to reconcile the reconstructed ecological history of Java with the young dates suggested for Ngandong. It is also difficult to defend with any certainty the possibility that *Homo erectus* and *Homo sapiens* were contemporaries for a significant period of time in this region.

7. Recent human cranial variability

In Australasia there seems to be an interesting pattern in human cranial variability. A morphological distinction can be made between 'Asians' (or 'Mongoloids') and 'Australo-Melanesians' (Bellwood, 1985; Lahr, 1995). Considering the cranial morphology of recent male *Homo sapiens*, I found these two main groups to be clearly recognisable in both indices and non-metrical characters (Storm, 1995; Table 6; Fig. 5).

In comparison with Chinese and Javanese skulls, Papuans and Australian Aborigines show more frequently: (1) a less rounded neurocranium (the neurocranium is often narrow), (2) a (slightly) prognathous face and low cheek height, (3) a stronger presence of superstructures (massive glabella and very marked superciliary arches) and muscle impressions (marked nuchal area), and (4) less retaining of juvenile characters (indistinct frontal and parietal tubera). These two groups correspond to the geographic origin of the specimens, with one being from the East Asian or Sunda side (Chinese and Javanese) and the other occupying the Australian or Sahul side (Papuans and Australian Aborigines). I suggest that the difference in recent cranial morphology within the species *Homo sapiens* can be attributed to the existence of an effective zoogeographic barrier (Wallacea).

Recent and prehistoric Australian Aborigines skulls may show morphologically primitive retentions (Klaatsch, 1908; Larnach and Macintosh, 1966, 1970; Macintosh and Larnach, 1976; Habgood, 1989; Lahr, 1992; Stringer, 1992b; Groves and Lahr, 1994; Storm, 1995). Macintosh and Larnach (1976 p.124) to explain the morphology that can be observed in Australian Aborigines have used the term 'generalised:'

> we could postulate the Aboriginal Australians as the earliest examples of evolving generalised modern *H. sapiens sapiens* to arrive in their ultimate area of migration. This hypothesis would also explain why Aboriginal Australians

Table 6
Cranial characters in recent *Homo sapiens* male skulls. Based on Storm (1995). N is given between brackets after percentage; *: can probably/possibly be seen as a generalised male *Homo sapiens* cranial character. Origin samples: see Table 3. Indices: (definition of the measurements according to Larnach and Macintosh, 1966, 1970; Howells, 1973; Bass, 1987) (1) narrow neurocranium: index(XCB × 100/GOL) < 75.0; (2) low neurocranium: index(BBH × 100/GOL) < 70.0; (3) strong post-orbital constriction: index(MPD × 100/MSB) < 80.0; (4) broad upper face: index(NPH × 100/ZYB) < 50.0; (5) (Slightly) prognathous face: index(BPL × 100/BNL) > 99.9; (6) broad nasal aperture: index(NLB × 100/NLH) > 52.9; (7) narrow palate: index(MAB × 100/MAL) < 110.0. Characters: (definitions of the non-metrical characters according to Larnach and Macintosh, 1966; the Workshop of European Anthropologists, 1980) (8) strong frontal inclination: three classes: vertical, ambiguous (little inclined), and strongly inclined; (9) presence of keeling of the vault: viewed from norma frontalis, two classes: present (trace + distinct), and absent; (10) distinct presence of the median frontal ridge: three classes: absent, trace, and distinct; (11) massive glabella: five classes: smooth, slightly, delimited, marked, and massive; (12) very marked superciliary arches: five classes: smooth, slightly, delimited, marked, and very marked; (13) medium and large zygomatic trigones: three classes: absent(triangular depressed field) + slight, medium, and large(prominent bulbous projection); (14) Missing and indistinct frontal tubera: three classes: missing + indistinct, moderate, and medium + marked; (15) missing and indistinct parietal tubera: three classes: missing + indistinct, moderate, and medium + marked; (16) marked nuchal area: judged are the nuchal lines and external occipital crest, five classes: smooth, slightly, evident, marked, and marked with a rough surface; (17) flattened lower orbital border: three classes: absent (sharp + slightly rounded), trace, and distinct (flattened with three distinct surfaces); (18) Distinct phaenozygy: phaenozygy denotes that the zygomatic arches are easily seen from norma verticalis, three classes: absent (not visible or very small part visible), ambiguous, and distinct (clearly visible); (19) Low cheek height (<22.1 mm.): definition cheek height (WMH) 'the minimum distance, in any direction, from the lower border of the orbit to the lower margin of the maxilla, mesial to the masseter attachment', on the right side, Howells (1973 p.180) uses the left side; (20) distinct palatal torus: the palatal torus is a clear 'mound' of bone, following the course of sutura palatina mediana, three classes: absent, trace/weak, and distinct; (21) small and rounded mentum: for the judgement of the development of the chin five classes: small + rounded, small, medium, prominent, and very prominent

	East Asian (Sunda) side		Australian (Sahul) side	
	China	Java	New Guinea	Australia
1*	15.9% (63)	5.1% (79)	81.4% (27)	90.0% (30)
2	0.0% (63)	0.0% (78)	20.8% (24)	20.7% (29)
3*	0.0% (62)	2.6% (78)	32.1% (28)	50.0% (30)
4	28.8% (59)	28.0% (75)	36.9% (19)	75.0% (16)
5*	16.7% (60)	45.3% (75)	90.4% (21)	56.3% (16)
6*	17.5% (63)	29.5% (78)	37.0% (27)	82.7% (29)
7	7.8% (51)	1.4% (70)	60.0% (15)	28.6% (14)
8*	17.5% (63)	13.9% (79)	30.0% (30)	82.4% (34)
9	6.3% (63)	1.3% (79)	55.2% (29)	50.0% (34)
10	0.0% (63)	0.0% (79)	0.0% (28)	27.3% (33)
11*	1.6% (63)	2.5% (79)	46.7% (30)	76.5% (34)
12*	1.6% (63)	3.8% (79)	55.2% (29)	67.6% (34)
13*	-	0.0% (41)	-	27.2% (33)
14*	27.0% (63)	25.3% (79)	69.0% (29)	97.1% (34)
15*	22.2% (63)	10.1% (79)	26.7% (30)	41.2% (34)
16*	34.9% (63)	19.0% (79)	69.2% (13)	69.7% (33)
17*	4.8% (63)	1.3% (79)	13.3% (30)	44.1% (34)
18*	34.9% (63)	13.9% (79)	92.9% (28)	91.2% (34)
19	11.1% (63)	17.7% (79)	90.0% (30)	77.4% (31)
20	6.5% (62)	2.5% (79)	4.8% (21)	24.2% (33)
21*	0.0% (63)	6.7% (75)	-	52.6% (19)

have retained a moderate to higher frequency of *Homo erectus* traits than other modern *sapiens* groups.

In the context of this paper, I use the term 'generalised' to refer to 'not specialised'; it points to (robust) cranial characteristics that can be found in Late Pleistocene male *Homo sapiens* skulls in general (in Table 6 these characteristics are marked with an asterisk). In comparison with people from the Sunda side, Papuans and Australian Aborigines show a higher frequency of generalised cranial characteristics. There is no evidence that these generalised features are strictly regional traits.

8. A scenario for hominid evolution in Australasia

8.1. The fate of Homo erectus in Australasia

Exactly when *Homo erectus* arrived in Java is not clear; the species may have arrived with the Ci Saat fauna some 1.2 Ma (De Vos, 1995); the species is clearly present around 0.9 Ma (Trinil H.K.). *Homo erectus* persisted from the time of its arrival in Java until the Ngandong fauna (Fig. 6). Interestingly, *Homo erectus*, a species associated with and apparently adapted to more open environments in Africa (Harris and Leakey, 1993; Potts,

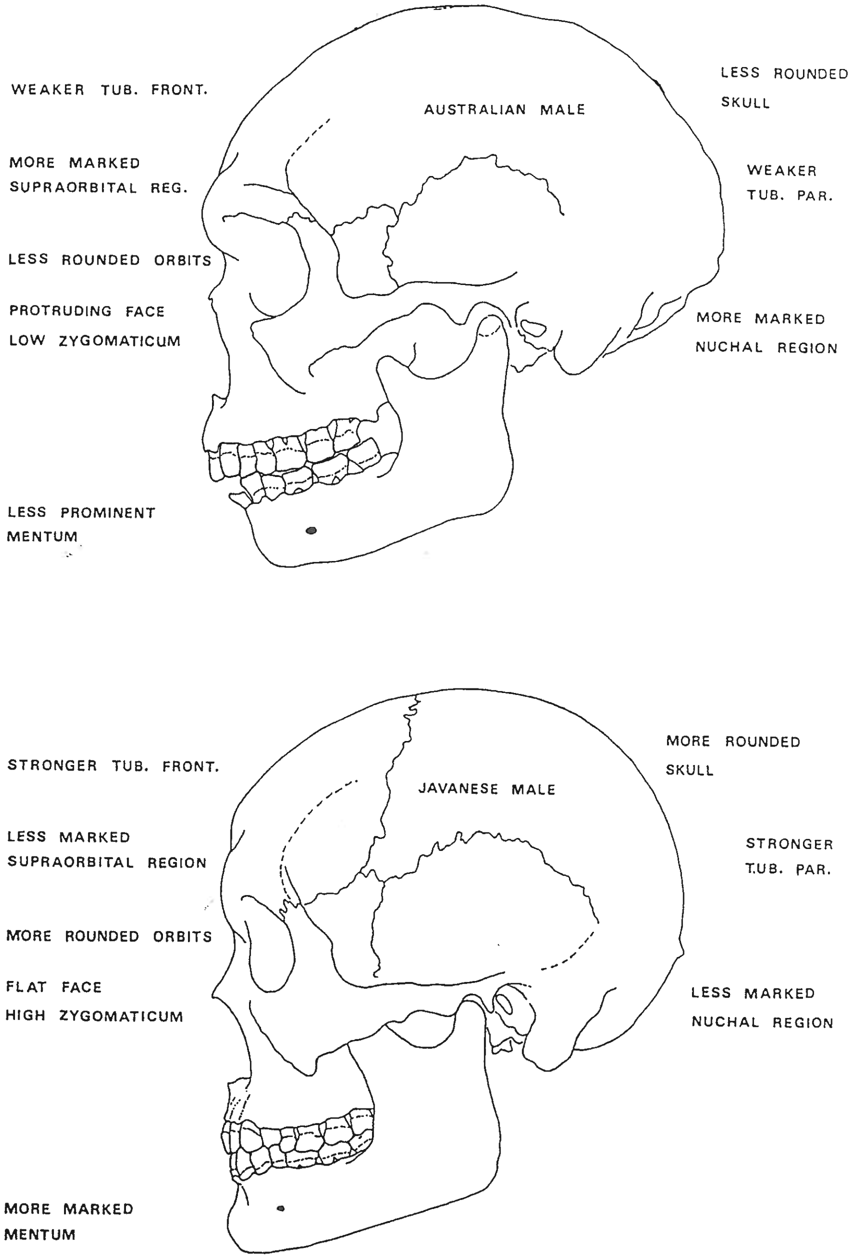

Fig. 5. Two cranial patterns of the species *Homo sapiens*, one from the Sahul side (Australian), the other from the Sunda side (Javanese). Both recent skulls used to make the drawing come from the Laboratory for Anatomy en Embryology, University of Leiden, the Netherlands.

1996), occurs in Java as part of open woodland faunas (Trinil H.K., Kedung Brubus and Ngandong respectively). This species persisted in Java for a long time during the Pleistocene without major alterations of its cranial morphology. The long-lasting presence of this archaic hominid species is consistent with the pattern of morphological stability shown in other large mammal species (*Macaca fascicularis*, *Panthera tigris*, *Rhinoceros sondaicus* and *Muntiacus muntjak*) in Java during this time. It seems likely that the species *Homo erectus* was present in open woodland habitats in Southeast Asia over a period of 1 Ma.

One of the arresting questions concerning *Homo erectus* is whether it was the first large placental mammal to cross Wallacea and reach the Sahul. It

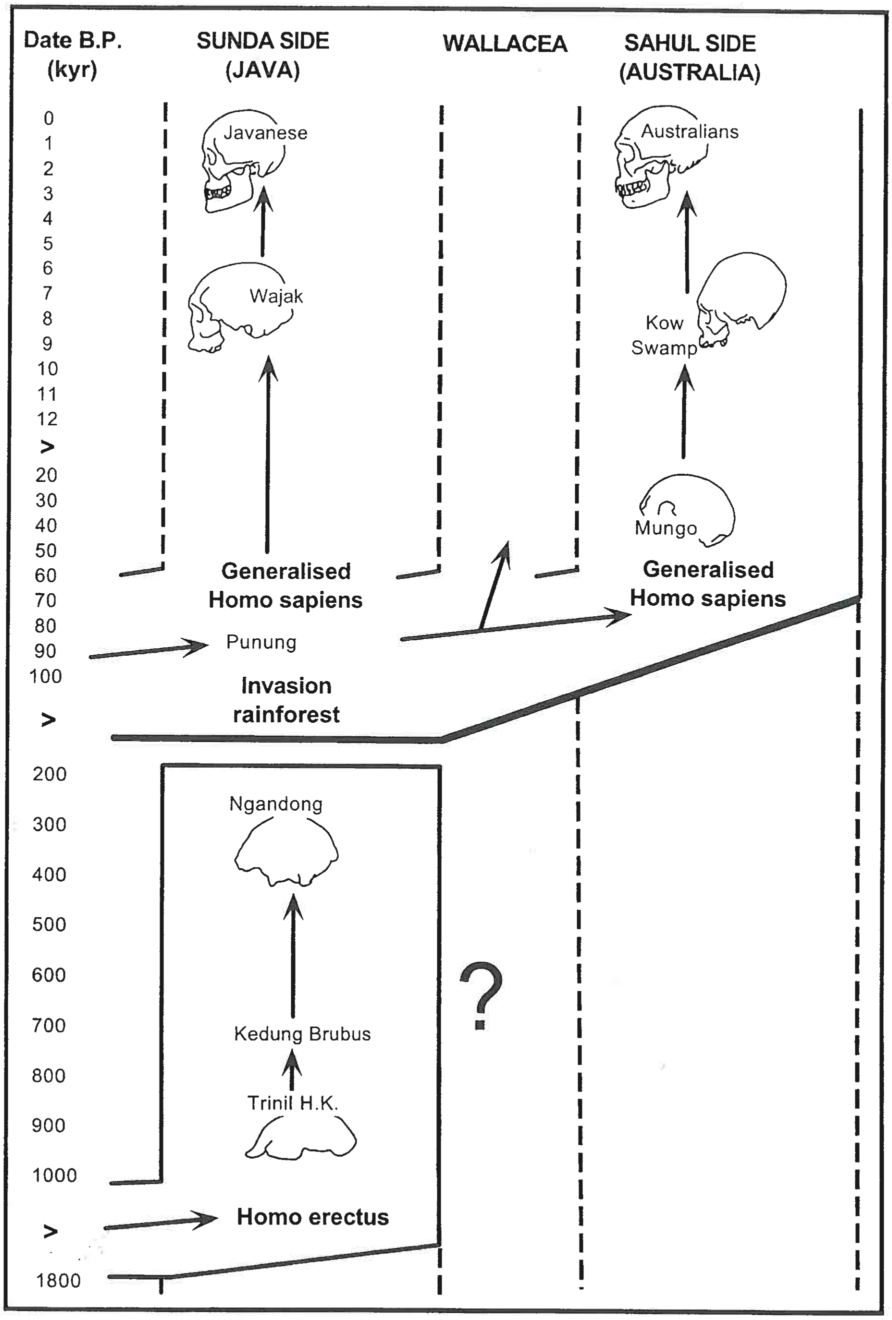

Fig. 6. Schematic representation of the 'Australasian *sapiens* cross-split' scenario. In Java, late *Homo erectus* (Ngandong/Solo) became extinct, just like other archaic mammalian open woodland species, with the 'invasion' of the modern tropical rainforest fauna (Punung) within it modern humans (*Homo sapiens*). Not *Homo erectus*, but *Homo sapiens* was the first large placental mammal that crossed the immense water barrier, Wallacea, to reach the Sahul. After this event Wallacea remained a serious obstruction for the exchange of genes and *Homo sapiens* was split into two morphological cranial patterns during its further evolutionary course.

has been claimed that stone artefacts have been found in Wallacea (near Mata Menge, in West Central Flores) at possibly a little less than 730 ka (Sondaar et al., 1994; Van den Bergh et al., 1996b; Morwood et al., 1997). This could be an indication that *Homo erectus* was able to cross water barriers. However, there is as yet no evidence that *Homo erectus* crossed through Wallacea and reached the Sahul.

A palaeoecological perspective on the evolution of the genus *Homo* in Java is revealing. *Homo erectus* is found in association with extinct genera like *Stegodon*, *Duboisia*, *Hexaprotodon* and with extinct species (in the Trinil H.K., Kedung Brubus and Ngandong faunas), while *Homo sapiens* is associated with extant species (in the Wajak, Sampung, Kecil, Hoekgrot and Jimbe faunas; Storm, 1995). The evolutionary history of the genus *Homo* is analogous with that of the genera *Bubalus*, *Sus*, and *Elephas*. These genera continue to exist through the time period in question; only the species change. Thus, *Homo erectus* is found together with *Bubalus palaeokerabau*, *Sus brachygnatus*, *Sus macrognatus* and *Elephas hysudrindicus*; and *Homo sapiens* with *Bubalus bubalis*, *Sus scrofa*, *Sus verrucosus* and *Elephas maximus*.

Because of the obvious differences of the species composition between the archaic open woodland fauna of Ngandong and the modern humid forest fauna of Punung, the latter is suggested to embody a wave of migration from the Asian mainland that accompanied a southward extension of the Southeast Asian tropical rainforest. As this ecological change proceeded, a number of the archaic species of the Ngandong fauna (including *Homo erectus*) were replaced by modern species. Although *Homo erectus* was capable of dealing with various habitats, this species was presumably not able to survive in a tropical rainforest; this biome was penetrated much later (Campbell, 1983; Foley, 1987; Gamble, 1993). The tropical rainforest can be a hard environment to live in as much of the energy is stored as (inedible) wood and animals that are difficult to catch because they are arboreal or nocturnal (Campbell, 1983; Gamble, 1993). *Homo erectus* was a typical terrestrial (fully) bipedal hominid (Walker and Leakey, 1993), poorly equipped to survive in an environment where a large part of the energy is located high in the trees. Unlike the Asian apes and the Malayan sun bear, *Homo erectus* had no means of exploiting the forest canopy and its rich resources. Modern humans survive in tropical rainforests by using sophisticated hunting techniques to reach high into the trees (like bows and blow-pipes), and/or by maintaining a stable supply of food by cultivating plants (Campbell, 1983; Gamble, 1993). There is no evidence that *Homo erectus* used these hunting and cultivating strategies. Thus, although some species survived between Ngandong and Punung, there was clearly a faunal turnover in which genera and species that were better adapted to the rainforest replaced the archaic, open woodland animals. The genus *Homo* was probably no exception to this general pattern.

8.2. The split of Homo sapiens in Australasia

Knowledge about Late Pleistocene *Homo sapiens* in Indonesia is extremely limited. Javanese *Homo sapiens* remains, once claimed as Pleistocene, come from Wajak (Dubois, 1922; Soejono, 1984). Cultural remains and carbon-14 dates suggest that the human Wajak remains could be younger than previously supposed (Storm, 1992, 1995). Another specimen, the well-known Niah 'Deep Skull', is said to be about 40,000 yr ago (Harrison, 1965). Since the in situ position and stratigraphical profile of the Niah excavations is not really clear (Shutler, 1979), it is no surprise that the antiquity claimed for the Niah Deep Skull has been questioned (Tattersall et al., 1988). Nevertheless, the presence of possibly Late Pleistocene human remains in Niah (Brothwell, 1960; Harrison, 1965), in the Javanese Punung fauna (Badoux, 1959), in the Sumatran fauna of Lida Ajer (De Vos, 1983), and archaeological and human remains in Australia that may be as old as around 60 ka (Roberts et al., 1990; Jones, 1992; Thorne et al., 1999) could suggest that modern humans inhabited Indonesia during the second half of the Upper Pleistocene.

Wallacea has been a tremendously important geographic barrier influencing the distribution and evolutionary course of the genus *Homo*. In contrast to *Homo erectus*, *Homo sapiens* was capable of crossing Wallacea (Fig. 6). Once *Homo sapiens* reached the Sahul, the water-barrier Wallacea influenced the evolutionary course of the species. Looking at the cranial morphology of recent humans, it is obvious that there are two clearly distinguishable cranial patterns, an East Asian (Sunda) and an Australian (Sahul) one (Table 6; Fig. 5). The morphological differences within this single species indicate that Wallacea must have been a significant hindrance for the exchange of genes between the human populations of Sunda and Sahul. These morphological distinctions are upheld by the results of studies of nuclear DNA, which cluster New Guineans and Australians (Sahul populations) together, while various populations from Southeast Asia (Sunda) cluster as another group (Cavalli-Sforza et al., 1994).

Low sea levels about 60–50 ka (Chappell, 1976; Chappell and Shackleton, 1986), would have made it possible for the first migrants to reach Australia at about that time. One of the major questions is whether multiple (Birdsell, 1967, 1993; Thorne, 1971, 1972, 1977; Wolpoff et al., 1984) or single (Macintosh and Larnach, 1976; Habgood, 1985, 1986; Brown, 1987) waves of migration occurred. The genetic and morphological information available (see for instance Cavalli-Sforza et al., 1994; Habgood, 1985, 1986; Brown, 1987, 1992b; Storm, 1995) can best be interpreted as the result of an initial wave of immigrants into the Sahul that proved dominant. Later immigrants had only a limited effect on the already-established genepool.

Once present in the Sahul region, the prehistoric populations evolved gradually into the recent populations of New Guinea and Australia. As can be seen in Table 6, recent skulls from New Guinea and Australia show a relatively high frequency of generalised cranial characters compared with recent skulls from the East Asian (Sunda) populations. This does not mean that the ancient generalised cranial pattern is unaltered in present day Australian Aborigines. Reduced robustness (of parts) of the skull during the Late Pleistocene or Holocene has been observed among Australian skulls (Thorne and Wilson, 1977; Brown, 1987, 1989, 1992a).

Wajak-1 from Java shows a mix of generalised and recent Asian cranial characteristics. This skull shows typical robust generalised male features like its large size, strong frontal inclination, massive glabella, missing/indistinct frontal tubera and distinct phaenozygy, besides typical recent Asian male features like a flat face with prominent zygomatic bones and no marked nuchal region (Storm, 1995). Considering the Pleistocene presence of the generalised cranial pattern in Sahul, the cranial morphology of the prehistoric Wajak skulls and recent Javanese skulls, a microevolutionary cranial change that has probably taken place in Southeast Asia can be visualized (Storm, 1995). During the Holocene (possibly starting in the late Late Pleistocene) the generalised *Homo sapiens* neurocranium became more rounded, the face flatter with higher zygomatic bones, less marked superstructures and muscle impressions in the supraorbital and nuchal regions. Juvenile characters, like the frontal and parietal tubera, became more strongly retained into adulthood.

Differences between Holocene skulls in Southeast Asia (Indonesia) have been explained in terms of migration. Robust Australo-Melanesian populations, as represented by the Wajak skulls, were replaced or absorbed by later (Neolithic) populations with a more gracile, 'Mongoloid' appearance. According to Bellwood (1985 p.89) this idea "has a respectable pedigree, and is still supported by most recent authors". Clearly Von Koenigswald (1952 p.96) endorsed this view:

> It was not before the late Neolithic — the period of the quadrangular axe — that the first Indonesians arrived at their present habitat in southeast Asia, where they replaced a mainly macrodont population of Australomelanesoid affinities, which is well established by skeletal remains (not the teeth alone). The older population then became extinct, viz., was pushed to the east. Dealing with two racially different populations no conclusions can be drawn about 'microevolution in situ with diminution in size' being responsible for the smaller teeth of the present inhabitants of this region, as suggested by Hooijer.

An explanation in terms of local evolution featuring a trend toward gracilisation/reduction, as has been observed in other parts of the world: Europe (Frayer, 1977; Spoor and Sondaar, 1986, 1988), Africa (Carlson and Van Gerven, 1979; Rightmire, 1984; Armelagos et al., 1984; Calcagno, 1986) and Australia (Thorne and Wilson, 1977; Brown, 1987, 1989, 1992a), may be just as satisfactory (Hooijer, 1950, 1952; Bulbeck, 1981, 1982; Brace and Vitzthum, 1984; Turner, 1987). For instance, a gracilising lineage could be envisioned from Wajak, via Sampung and Neolithic Hoekgrot, to the present day Javanese (Storm, 1995).

9. Concluding remarks

Examination of variations in cranial morphology within the genus *Homo* in Australasia confirms that *Homo erectus* and *Homo sapiens* are good morphospecies, readily distinguished. Cranial variations within recent *Homo sapiens* populations of

Australasia reflect the effectiveness of Wallacea as a zoogeographic barrier. Two cranial patterns can be recognised: a Sunda and a Sahul pattern.

Australasia as a zoogeographic region is strongly influenced by the rise and fall of sea levels and the resultant ease of migration through the Sunda and Sahul region. Wallacea has been a long-standing and effective barrier to the migration of mammals, including the genus *Homo*, and to the free exchange of genes within species. Review of the palaeoecological indicators within the ancient and more recent prehistoric faunas of Java suggests a long initial period of drier open woodland habitats (Trinil H.K., Kedung Brubus and Ngandong), during which *Homo erectus* was part of these archaic faunas. The Punung faunal unit, which succeeds the Ngandong faunal unit, marks an abrupt change to a humid tropical rainforest environment. The Punung fauna probably represents an invasion from mainland Southeast Asia. It is possible that *Homo sapiens* first appeared in Java as part of this new, modern fauna, which can perhaps be dated between 126 and 81 ka.

Regional continuity in Australasia may be assumed for *Homo erectus* in Southeast Asia, from earlier forms like Trinil and Sangiran to later forms like Ngandong. Again, regional continuity may be assumed for *Homo sapiens* on both sides of Wallacea. However, it is not demonstrated that regional continuity has crossed the species boundary, i.e. from Middle Pleistocene *Homo erectus* to modern humans of Australia.

From the viewpoint of environment exploitation (geographic expansion, habitat tolerance and the number of ecological niches) *Homo sapiens* was more efficient than *Homo erectus*. There is no evidence that the latter species reached the Sahul and the expansion of the tropical rainforest as far as East Java meant probably the extinction of *Homo erectus* in this part of the world.

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