



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Journal of Human Evolution 49 (2005) 536–545



News and Views

## Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java

Paul Storm<sup>a,\*</sup>, Fachroel Aziz<sup>b</sup>, John de Vos<sup>a</sup>, Dikdik Kosasih<sup>b</sup>,  
Sinung Baskoro<sup>b</sup>, Ngaliman<sup>b</sup>, Lars W. van den Hoek Ostende<sup>a</sup>

<sup>a</sup> National Museum of Natural History, Postbus 9517, 2300 RA Leiden, The Netherlands

<sup>b</sup> The Geological Museum, Jl. Diponegoro 57, Bandung 40122, Indonesia

Received 17 February 2005; accepted 1 June 2005

**Keywords:** *Homo sapiens*; *Pongo pygmaeus*; Tropical rainforest; East Java

### Introduction

Information on late Pleistocene *Homo sapiens* in Indonesia is very limited and the age of the latest occurrence of *Homo erectus* is fiercely debated (Swisher et al., 1996; Grün and Thorne, 1997; Storm, 2001). The presence of hominins in the Javanese Punung assemblage has been noted previously (von Koenigswald, 1939; Badoux, 1959), but no description or specific identification of the hominin specimens was made and the exact provenance of the material was unclear, as the site information was lost. In this paper, we describe a hominin fossil associated with a tropical rainforest assemblage from Java. Not only have we relocated the original sites mentioned in earlier reports (von Koenigswald, 1939; Badoux, 1959) as yielding faunal and hominin remains, we have also discovered a third site yielding in situ fossils

strongly indicative of a rainforest fauna. These discoveries provide important information bearing directly on these debates and uncertainties.

### East Javanese sites with a tropical rainforest fauna

The first reports of fossil rainforest faunas on Java came in the early 1930s when von Koenigswald and Tweedie, surveying the region of Pacitan and Punung, East Java, found two sites with mammal fossils in karstified hills, but failed to record the exact location of the sites. In 1935–1936, von Koenigswald excavated one of these sites west of Mendolo Kidul, which is now known as Punung I (Badoux, 1959; Bosscha Erdbrink, personal communication<sup>1</sup>). Later, in 1938,

\* Corresponding author.

E-mail address: [oermens@hetnet.nl](mailto:oermens@hetnet.nl) (P. Storm).

<sup>1</sup> Personal communications took the form of 1) a letter from D.P. Bosscha Erdbrink to P. Storm, dated November 27, 1997, and 2) copies of photographs taken by D.P. Bosscha Erdbrink (in June 1936 and April 1938) with text, given to P. Storm on December 6, 1998.



Fig. 1. Excavation of Song Agung by von Koenigswald (center, wearing light shirt). Bosscha Erdbrink took this picture in June 1936. Bosscha Erdbrink marked the area of Punung I (in the background) with an arrow.

von Koenigswald collected fossils from a second site, about 5 km northwest of Punung I, near Tabuhan (Badoux, 1959; Bosscha Erdbrink, personal communication), which is now known as Punung II. After collection, fossils from the two sites were mixed, as noted by Badoux (1959) when he described them, and they could not be sorted by provenance. In 1976, Hooijer gave an additional list of the Punung fauna, but, unfortunately, the locality of the site was not given.

In September 2003, a joint Indonesian–Dutch team successfully relocated the two original sites with the help of photographs graciously provided by the late Bosscha Erdbrink, who was present during the excavations in the 1930s. Punung I (coordinates: S. 08° 08.511, E. 111° 01.975) is close to another site, Song Agung (coordinates: S. 08° 08.543, E. 111° 01.837).

Because photographs taken by Bosscha Erdbrink in 1936 of details of the rock at the site of Song Agung could be directly compared with the current situation in the field, we could locate this site beyond doubt. From there, it was easy to find the area of

Punung I, as it is indicated on one of the photographs made by Bosscha Erdbrink (of the site Song Agung) by an arrow (Fig. 1). It lies opposite Song Agung, at the slope of a hill. Here we found a “yellow” breccia (without fossils) and a white breccia with one fossil fragment of the tooth of a deer. Punung II is close to the right side of the entrance of the cave Gua Tabuhan (co-ordinates: S. 08° 07.388, E. 110° 58.642). For Punung II, it was not possible to translate the situation of Bosscha Erdbrink’s photograph (1938) to the present situation because of drastic alterations to the landscape (i.e., building of a road, stairs to the cave, and the presence of a large tree). However, according to Bosscha Erdbrink, Punung II is close to the right side of the entrance of Gua Tabuhan. There we found fossilized teeth of extant mammals (muntjak, deer, bovid, and pig). Porcupines had gnawed the teeth, which is very characteristic for the Punung fauna. This area must be a remnant of von Koenigswald’s original locality (according to Bosscha Erdbrink, von Koenigswald did not excavate in this area but collected surface finds).

In addition, the team found and documented in situ fossils stemming from a modern tropical rainforest at a new site, Gunung Dawung (co-ordinates: S. 08° 07.562, E. 110° 59.252). Fossils at this site, named after the indigenous name of the limestone rocky wall, were found both in situ and washed out into the field directly next to the source (Table 1; Fig. 2), a “yellow” breccia. In situ fossils were prepared directly out of this breccia. In the field, they were found by surveying the surface, and by using a sieve of 0.5 mm. Besides teeth, we also found small bone fragments.

The fossils found in Gunung Dawung clearly stem from a tropical rainforest environment. In this site, at least 28 orangutan (*Pongo pygmaeus*) teeth (Fig. 3) have been found. This animal can be linked with a tropical rainforest environment (Galdikas, 1982; Schwartz, 1988; Rijksen and Meijaard, 1999). The remains of other mammals, such as the siamang (*Hylobates syndactylus*) and the sun bear (*Helarctos malayanus*), indicate a similar environment. Gunung Dawung represents the same fauna as those from the so-called Punung sites (Table 1). Remains of the mammals

Table 1  
Fossil mammals from the Punung area

Taxon	Common name	Punung A	Punung B	Gunung Dawung
<b>Insectivora</b>				
<i>Echinosorex</i> sp.	Moon rat	+	–	–
<b>Rodentia</b>				
<i>Hystrix brachyura</i>	S.E. Asain porcupine	+	+	+
<i>Hystrix lagrelli</i>	Small porcupine	–	–	+
<i>Leopoldamys sabanus</i>	Long-tailed giant rat	–	–	+
“ <i>Rattus</i> ” sp.	Rat	–	–	+
<b>Anthropoidea</b>				
<i>Homo sapiens</i>	Modern human	+	–	–
<i>Pongo pygmaeus</i>	Orangutan	+	+	+
<i>Hylobates syndactylus</i>	Siamang	+	–	+
<i>Hylobates</i> cf. <i>leuciscus</i>	Gibbon	+	–	–
<i>Macaca</i> sp.	Macaque	+	–	–
<i>Trachypithecus</i> sp.	Leaf monkey	–	+	+
<b>Carnivora</b>				
<i>Panthera tigris</i>	Tiger	+	–	–
<i>Helarctos malayanus</i>	Sun bear	+	+	+
<i>Neofelis nebulosa</i>	Clouded leopard	–	+	–
<b>Artiodactyla</b>				
<b>Bovidae</b>				
	Bovids	+	+	+
<i>Capricornus sumatrensis</i>	Mountain goat	+	–	–
<i>Muntiacus muntjac</i>	Muntjak deer	+	–	+
<i>Cervus</i> sp.	Deer	+	–	+?
<i>Sus</i> sp.	Pig	+	+	+
<b>Perissodactyla</b>				
<i>Rhinocerus sondaicus</i>	Javan rhinoceros	+	+	+
<i>Tapirus indicus</i>	Tapir	+	+	+
<b>Proboscidea</b>				
<i>Elephas</i> sp. ( <i>maximus</i> )	Elephant	+	+	–

Punung A is a mixture of Punung I and II, excavated by von Koenigswald, and based on a re-interpretation of Badoux (1959) by de Vos (1983, 1985). Punung B is based on Hooijer (1976). Hooijer mentioned that the material was collected from the “Punung fissure,” but it is not clear from which of the two “fissures.” There is a possibility that the material was collected at a third site because von Koenigswald and Badoux did not give the exact locations of the two original sites of Punung I and II. Gunung Dawung is the only localized unmixed site in East Java that contains mammals that indicate the presence of a tropical rainforest. – = absent, + = present, ? = uncertain.

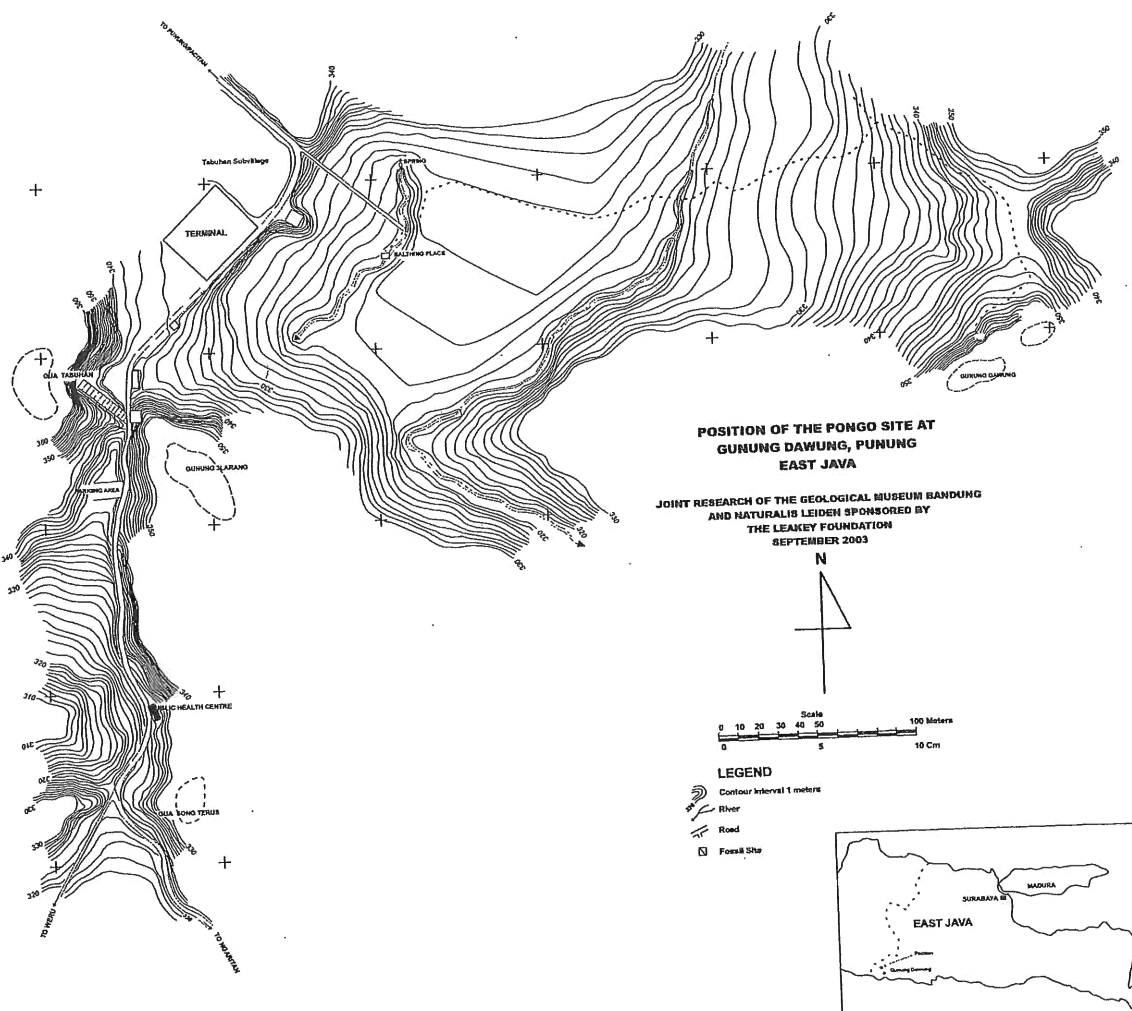


Fig. 2. Location map of the site Gunung Dawung.

mentioned above are also known from Vietnam, Borneo, and Sumatra (de Vos, 1995; Vu The Long et al., 1996), demonstrating a connection with mainland Southeast Asia for Sumatra, Borneo, and Java, as orangutans, siamangs, and sun bears are not known to cross water barriers.

Currently, there is no broad natural distribution of evergreen rainforest in East Java; very little is left of this habitat. The natural distribution of the vegetation types in East Java is a mixture of rainforest, deciduous forest, and montane forest (Whitten et al., 1996), and there are no large rainforest mammals, such as orangutans and gibbons. Closed rainforest habitat must have

disappeared prior to 10 ka because, after 81 ka, the climate became drier and cooler in Java (van der Kaars and Dam, 1995), and the Wajak fauna, dated at  $10,560 \pm 75$  yrs BP, which includes extant species, lacks those species that are associated with closed rainforest environments (Storm, 1995; Shutler et al., 2004).

Porcupines were a major agent in the preservation of the Punung fossils. It is well known that porcupines collect bones and bring them to their lairs (Brain, 1981), where they gnaw on them, often removing the roots of teeth (almost) completely and leaving unmistakable grooves on the small remnants of bones and roots. The intense gnawing by

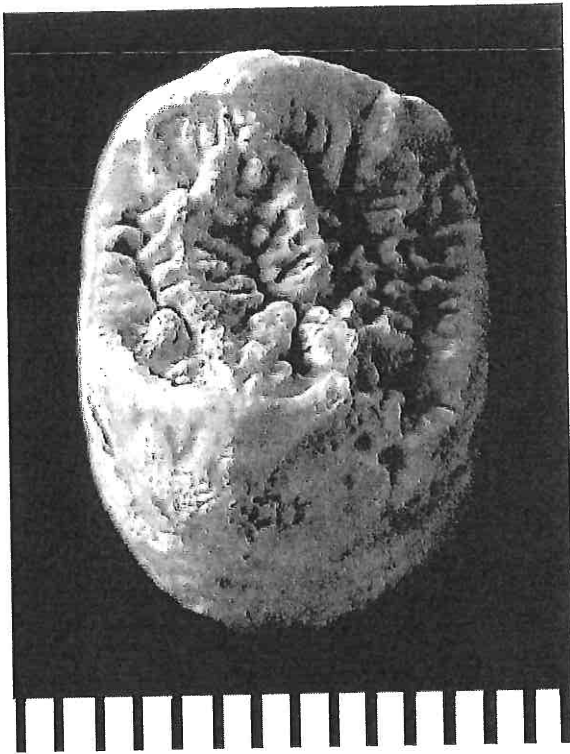


Fig. 3. Occlusal view of the left P<sup>4</sup> (GD-94) of an orangutan (*Pongo pygmaeus*) from the site Gunung Dawung. Scale in millimeters. Notice the strong occlusal crenulation, very typical for this species.

porcupines in rainforests is probably related to the relative rarity of skeletal remains in this environment. In the karstified region of Punung, this means that the bones are brought out of a situation that is hostile to fossilization, into an environment more conducive to preservation.

The Punung fauna is unique for Java in two respects. First, it represents a tropical rainforest environment. So far, all other faunas, old and young, represent drier environmental circumstances (de Vos, 1983). The Punung sites are the only localities that have yielded mammals indicative of the presence of a tropical rainforest, such as orangutans and gibbons. Second, Punung stems from a breccia. Older faunal remains from Java, such as those from Trinil, Kedung Brubus, and Ngandong, associated with the remains of *Homo erectus* all come from river or lake deposits. Javanese faunal remains younger than those from Punung, such as those from Wajak, Hoekgrot,

Kecil, and Jimbe, are clearly associated with *Homo sapiens* and are probably the result of human burial practices (Storm, 1995).

Despite its obvious scientific importance, little attention has been paid to the Punung faunal assemblage. This lack of interest may be due to four factors: 1) the exact locations where the Punung fossils had been collected were unknown, and could therefore not be considered as good in situ evidence of the occurrence of a tropical rainforest in East Java; 2) von Koenigswald (1939, 1940) considered Punung as a “normal Trinil (middle Pleistocene) assemblage,” and Hooijer (1952) confused the issue further by including rainforest inhabitants such as *Pongo pygmaeus* and *Hylobates* in a putative Trinil fauna—these works obscured the existence of the Punung fauna; 3) Badoux’s (1959) dissertation referred to five human teeth in the Punung fauna, but did not describe them, and his work was published in a relatively obscure manner—therefore, his view that Punung was younger than Trinil remained unnoticed, even though von Koenigswald (1975, 1982) adopted his ideas; 4) the human remains of Punung were never fully described or published, only mentioned (von Koenigswald, 1939; Badoux, 1959; de Vos, 1985).

#### The human premolar from Punung

Now that we have established the presence of a Pleistocene rainforest on Java, the identification of the human remains in that fauna becomes even more important. Unfortunately, in January 2001, the five teeth mentioned in previous work (Badoux, 1959) could not be found in the Punung collection of von Koenigswald (Senckenberg Naturmuseum in Frankfurt am Main, Germany). However, we did find a tooth with a note saying “*Homo* sp.” in the Punung collection.

This tooth (PU-198; Fig. 4) is a human left P<sup>3</sup>; it is not one of the teeth (two I<sup>2</sup>s, an upper and lower C, and possibly an upper M) mentioned by Badoux (1959). As is the case for other Punung fossils, porcupines have gnawed the roots of this P<sup>3</sup>. The crown is completely preserved and shows some wear. It is identified as an upper premolar because it shows an oval occlusal outline, a lingual

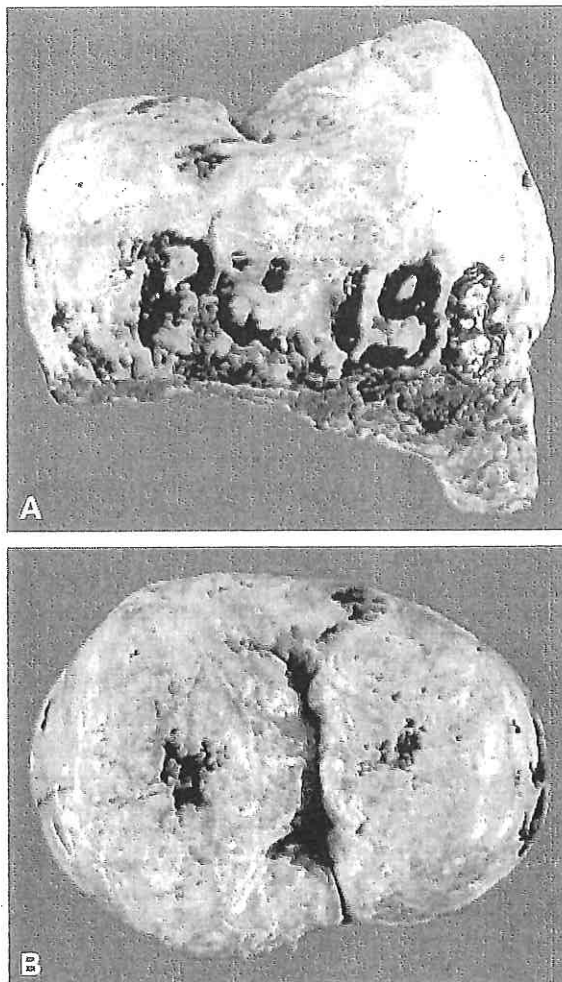


Fig. 4. A) Lateral view of the left human P<sup>3</sup> (PU-198) from the Punung fauna; B) occlusal view of the left human P<sup>3</sup> (PU-198) from the Punung fauna.

cusps not much smaller than the buccal one, and the presence of a well-developed median groove. Its identification as a P<sup>3</sup> is clear because the outline is clearly not symmetrical. The buccal cusp is somewhat larger than the lingual one, the mesial surface has a concave contour, the median groove extends to the mesial surface, and the remaining part of the root around the cervix is kidney-shaped, which means that there must have been two unfused or fused radices.

The intriguing question, of course, is whether this premolar can be identified as representing *H. erectus* or *H. sapiens*. Weidenreich (1937) mentioned

a number of differences between Chinese *H. erectus* and *H. sapiens*; regarding the P<sup>3</sup>, this tooth is larger in *H. erectus* than in *Homo sapiens*, and it has a cingulum and a projecting tuberculum molare. As far as the cingulum is concerned, in mesial and distal views, there is a raised area near the region of the cervix in the robust *H. erectus* specimen “*Sinanthropus*” 19. However, this feature is not diagnostic of *H. erectus* because, in the premolars of smaller *H. erectus*, e.g., from specimens such as KNM-ER 3733 and KNM-ER 1808, this raised area is noticeably smaller or absent. A similar raised area can also be found in recent *H. sapiens*. According to Weidenreich (1937), a tuberculum molare is present in *H. sapiens*, but is smaller than in *Homo erectus*. The robust specimen “*Sinanthropus*” 19 has a marked ridge on the mesial side of the buccal surface. However, in a smaller *H. erectus* specimen, KNM-WT 15000, only a raised area can be found, as is the case in recent *H. sapiens*. Therefore, we conclude that the use of the two non-metric characters mentioned above to separate *H. erectus* from *H. sapiens* is problematic, as both features may be related to size. Size itself is, in this case, probably a better way to distinguish the two species (Fig. 5), with *H. erectus* being larger. The dimensions of

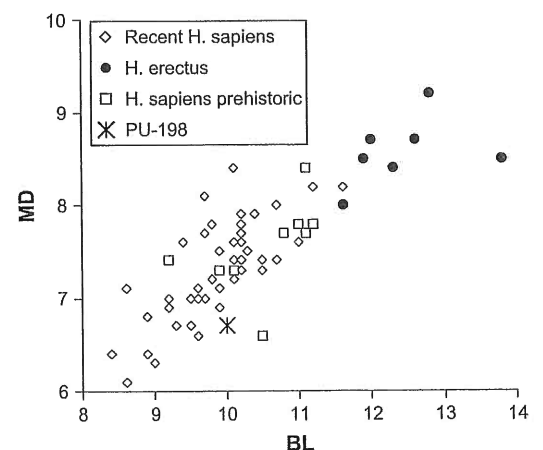


Fig. 5. Bivariate plot of the mesiodistal (MD) and buccolingual (BL) dimensions (in millimeters) of the P<sup>3</sup>s of *H. erectus*, *H. sapiens*, and PU-198. The comparative sample includes recent and prehistoric *H. sapiens* specimens from Australasia ( $n = 46$  and  $n = 9$ , respectively) and *H. erectus* specimens from Java, China, and Africa ( $n = 7$ ). See Table 2 for raw data.

Table 2  
Mesiodistal (MD) and buccolingual (BL) dimensions (in millimeters) of the P<sup>3</sup>s of *Homo erectus* and *Homo sapiens* from Australasia

Specimen	Museum <sup>1</sup>	Literature source <sup>2</sup>	MD	BL	Right/Left
PU-198	SN		6.7	10.0	L
<i>Homo erectus</i>					
<i>Pithecanthropus</i> IV		TK	8.4	12.3	
<i>Sinanthropus</i> -19		W	9.2	12.8	R
<i>Sinanthropus</i> -77		W	8.7	12.6	L
<i>Sinanthropus</i> -142		W	8.0	11.6	
KNM-WT 15000		BW	8.5	11.9	L
KNM-ER 3733		BW	8.7	12.0	R
KNM-ER 1808		BW	8.5	13.8	L
Prehistoric <i>H. sapiens</i>					
Wajak-2 (Java)	NMNH		7.7	11.1	Mean R/L
Wajak-3 (Java)	NMNH		7.4	9.2	L
Hoekgrot W16 (Java)	NMNH		8.4	11.1	L
Jimbe-1 (Java)	NMNH		7.8	11.0	Mean R/L
Jimbe-2 (Java)	NMNH		7.7	10.8	R
Liang Toge (Flores)	NMNH		7.3	9.9	Mean R/L
Liang Momer (Flores)	NMNH		7.3	10.1	Mean R/L
Kanalda (Australia?)	NHM		7.8	11.2	Mean R/L
Kow Swamp 15 (Australia, cast)	NHM		6.6	10.5	Mean R/L
Recent <i>H. sapiens</i>					
Java (B1A)	NMNH		8.1	9.7	L
Java (B1B)	NMNH		7.4	10.1	R
Java (B1D)	NMNH		7.9	10.2	R
Java (B1E)	NMNH		8.4	10.1	R
Java (B1F)	NMNH		7.8	9.8	L
Java (B2A)	NMNH		6.7	9.5	L
Java (B2B)	NMNH		8.0	10.7	L
Java (B2C)	NMNH		7.7	10.2	L
Java (B3A)	NMNH		7.6	9.4	L
Java (B3B)	NMNH		7.6	10.2	R
Java (B3D)	NMNH		7.7	9.7	L
Java (B3E)	NMNH		7.6	10.2	L
Java (B3F)	NMNH		6.4	8.4	L
Java (B4A)	NMNH		7.0	9.5	L
Java (B4B)	NMNH		7.1	8.6	R
Java (B4C)	NMNH		7.6	10.1	L
Papua New Guinea (B14A)	NMNH		6.7	9.3	L
Papua New Guinea (B14F)	NMNH		6.1	8.6	L
Papua New Guinea (B15D)	NMNH		6.6	9.6	R
Papua New Guinea (B18C)	NMNH		6.3	9.0	R
Papua New Guinea (B20C)	NMNH		7.1	9.9	R
Papua New Guinea (B20F)	NMNH		6.9	9.9	L
Papua New Guinea (B21A)	NMNH		7.4	10.5	R
Papua New Guinea (B21B)	NMNH		7.4	10.2	L
Papua New Guinea (B22A)	NMNH		7.2	9.8	L
Papua New Guinea (B22D)	NMNH		7.6	10.2	R
Papua New Guinea (B22E)	NMNH		6.8	8.9	R
Papua New Guinea (B23B)	NMNH		7.0	9.2	L
Papua New Guinea (B26B)	NMNH		7.0	9.7	L
Papua New Guinea (B26E)	NMNH		6.4	8.9	R
Papua New Guinea (B26F)	NMNH		7.5	10.3	L



Table 2 (continued)

Specimen	Museum <sup>1</sup>	Literature source <sup>2</sup>	MD	BL	Right/Left
Papua New Guinea (B28A)	NMNH		7.1	9.6	L
Australia (PA PHR 310)	NHM		6.9	9.2	R
Australia (PA PHR 316)	NHM		8.2	11.6	Mean R/L
Australia (PA PHR 317)	NHM		8.2	11.2	Mean R/L
Australia (PA PHR 327)	NHM		7.6	11.0	R
Australia (PA PHR 413)	NHM		7.4	10.7	Mean R/L
Australia (PA PHR 415)	NHM		7.2	10.1	Mean R/L
Australia (PA PHR 417)	NHM		7.9	10.4	R
Australia (PA PHR 422)	NHM		7.5	9.9	L
Australia (PA PHR 425)	NHM		7.0	9.6	Mean R/L
Australia (PA PHR 428)	NHM		7.3	10.2	Mean R/L
Australia (PA PHR 430)	NHM		7.8	10.2	R
Australia (PA PHR 434)	NHM		7.6	10.1	Mean R/L
Australia (PA PHR 435)	NHM		7.3	9.9	Mean R/L
Australia (PA PHR 436)	NHM		7.3	10.5	L

<sup>1</sup> Museum abbreviations: SN = Senckenberg Naturmuseum, Frankfurt am Main, Germany; NMNH = National Museum of Natural History, Leiden, The Netherlands; NHM = Natural History Museum, London, U.K.

<sup>2</sup> Literature source abbreviations: TK = Tobias and von Koenigswald, 1964; W = Weidenreich, 1937; BW = Brown and Walker, 1993.

PU-198 place this premolar in the range of *H. sapiens* (Table 2; Fig. 5).

## Discussion

From a theoretical point of view, it is more likely to find *H. sapiens* in a tropical rainforest environment than *H. erectus*. For a hominin, the tropical rainforest is a hard environment to live in, as much of the energy is stored as inedible wood or in the form of animals that are difficult to catch because they are arboreal or nocturnal (Gamble, 1993). Although *H. erectus* was probably capable of dealing with various habitats, this species is not known to have been able to survive in a tropical rainforest; this biome was penetrated only much later (Foley, 1987; Gamble, 1993). Modern humans survive in tropical rainforests by using sophisticated hunting techniques, like bows and blowpipes, to reach high into the trees and/or by maintaining a stable supply of food by cultivating plants (Gamble, 1993). There is no evidence that *H. erectus* used these hunting and cultivating strategies.

This theoretical stance can be evaluated using the large number of Javanese fossils to make some inferences about the paleoecology of *H. erectus* in Java. The faunal units Trinil H.K., Kedung

Brubus, and Ngandong contain what is clearly *H. erectus*; these faunas suggest an open woodland habitat (de Vos, 1995; Storm, 2001). Thus, from a theoretical point of view it is unlikely that *H. erectus* could have survived in a tropical rainforest, and the paleontological and archaeological records offer no evidence to the contrary.

The young dates obtained by Swisher et al. (1996)—i.e.,  $27 \pm 2$  ka to  $53.3 \pm 4$  ka—for fossil bovid teeth coming from Ngandong and Sambungmacan raised the possibility of the prolonged co-existence of *H. erectus* and *H. sapiens* in Java. However, the technical accuracy of these dates has been questioned (Grün and Thorne, 1997). Moreover, it is difficult to reconcile the young dates suggested for Ngandong with the ecostratigraphy of Java (Storm, 2001). Ngandong represents an archaic fauna with a number of extinct species, whereas only extant species are found in the Punung fauna. Therefore, it is obvious that Punung is younger than Ngandong.

Our interpretation that a tropical rainforest fauna (Punung) followed an open woodland fauna (Ngandong) is supported by independent paleoclimatic reconstructions based on sedimentological and palynological analyses of sediment cores from the Bandung Basin in West Java (van der Kaars and Dam, 1995). According to these



studies, around 135 ka, the climate was considerably drier and hot. Between 126 ka and 81 ka, the climate was primarily humid and warm. After 81 ka, the climate became drier and cooler. Interestingly, in the humid and warm phase of Java, sea levels were 40–60 meters below present levels between 120 ka and 90 ka, during the stadials MIS-5b and MIS-5d (Lambeck et al., 2002). This means that a scenario can be constructed in which the tropical rainforest and its inhabitants reached Java during this period. If we are correct in thinking that the archaic Ngandong fauna preceded the modern Punung fauna, Ngandong must be older than 126 ka, contrary to the much more recent dates obtained by Swisher et al. (1996).

### Acknowledgements

We thank the L.S.B. Leakey Foundation for funding this project. Without the help of D.P. Bosscha Erdbrink, we would not have been able to relocate the lost Punung sites. Christine Hertler (Goethe University, Germany) helped us find our way in the collection of von Koenigswald (Senckenberg Naturmuseum, Frankfurt am Main, Germany) and Robert Kruszynski helped find the way in the collection of Australian Aborigines at the Natural History Museum, London, UK. Alan Walker (Penn State University, USA) kindly provided casts of upper third premolars of *Homo erectus* specimens. Tom van der Colk financed a part of this project and we thank him for his view on the human P<sup>3</sup> of Punung. Dees J. van Weers (University of Amsterdam, the Netherlands) identified the teeth of porcupines. We thank Pat Shipman (Penn State University, USA), Chris Stringer (Natural History Museum, London, UK), and Gert van den Bergh (Royal Netherlands Institute for Sea Research, The Netherlands) for reading the manuscript and their remarks. Axel Stolp (JWG University, Zoological Institute, Germany) made the photographs of the human P<sup>3</sup> from the Punung fauna. We thank the following persons for their help in the field: Iwan Kurniawan (Geological Museum, Bandung, Indonesia), Hans Brinkerink, Edi Susilo, Suwarno, Joko Haryono, and Suntoro.

### References

- Badoux, D.M., 1959. Fossil mammals from two fissure deposits at Punung (Java). Ph.D. Dissertation, University of Utrecht.
- Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.
- Brown, B., Walker, A., 1993. The dentition. In: Walker, A., Leakey, R. (Eds.), *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge, pp. 161–192.
- de Vos, J., 1983. The *Pongo* faunas from Java and Sumatra and their significance for biostratigraphical and paleoecological interpretations. *Proc. K. Ned. Akad. Wet.* 86, 417–425.
- de Vos, J., 1985. Faunal stratigraphy and correlation of the Indonesian hominid sites. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York, pp. 215–220.
- de Vos, J., 1995. The migration of *Homo erectus* and *Homo sapiens* in south-east Asia and the Indonesian archipelago. In: Bower, J.R.F., Sartono, S. (Eds.), *Human Evolution in Its Ecological Context*. DSWO Press, Leiden University, Leiden, pp. 239–260.
- Foley, R., 1987. Another Unique Species: Patterns in Human Evolutionary Ecology. Longman, Harlow.
- Galdikas, B.M.F., 1982. Orang utans as seed dispersers at Tanjung Puting, Central Kalimantan: implications for conservation. In: De Boer, L.E.M. (Ed.), *The Orang Utan: Its Biology and Conservation*. Dr. W. Junk Publishers, The Hague, pp. 285–298.
- Gamble, C., 1993. *Timewalkers: The Prehistory of Global Colonization*. Penguin Books, London.
- Grün, R., Thorne, A., 1997. Dating the Ngandong humans. *Science* 276, 1575–1576.
- Hooijer, D.A., 1952. Fossil mammals and the Plio-Pleistocene boundary in Java. *Proc. K. Ned. Akad. Wet. B* 55, 436–443.
- Hooijer, D.A., 1976. Preliminary note on the fissure fauna of Punung. In: Bartstra, G.J. (Ed.), *Contributions to the Study of the Palaeolithic Patjitan Culture Java, Indonesia. Part I*. E.J. Brill, Leiden, p. 108.
- Lambeck, K., Esat, T.M., Potter, E.-K., 2002. Links between climate and sea levels for the past three million years. *Nature* 419, 199–205.
- Rijksen, H.D., Meijaard, E., 1999. *Our Vanishing Relative: The Status of Wild Orang-utans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Dordrecht.
- Schwartz, J.H. (Ed.), 1988. *Orang-utan Biology*. Oxford University Press, Oxford.
- Shutler Jr., R., Head, J.M., Donahue, D.J., Jull, A.J.T., Barbetti, M.F., Mats'ura, S., de Vos, J., Storm, P., 2004. AMS radiocarbon dates on bone from cave sites in southeast Java, Indonesia, including Wajak. *Mod. Quaternary Res. SE Asia* 18, 89–93.
- Storm, P., 1995. The evolutionary significance of the Wajak skulls. *Scripta Geologica* 110, 1–247.

- Storm, P., 2001. The evolution of humans in Australasia from an environmental perspective. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 171, 363–383.
- Swisher III, C.C., Rink, W.J., Antón, S.C., Schwarcz, H.P., Curtis, G.H., Suprijo, A., Widiasmoro, 1996. Latest *Homo erectus* of Java: potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science* 274, 1870–1874.
- Tobias, P.V., von Koenigswald, G.H.R., 1964. A comparison between the Olduvai hominines and those of Java and some implications for hominid phylogeny. *Nature* 7, 515–518.
- van der Kaars, W.A., Dam, M.A.C., 1995. A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 117, 55–72.
- von Koenigswald, G.H.R., 1939. Das Pleistocän Javas. *Quartär* 2, 28–53.
- von Koenigswald, G.H.R., 1940. Neue Pithecanthropus-Funde 1936–1938. Ein Beitrag zur Kenntnis der Praehominiden. *Wet. Med.* 28, 1–232.
- von Koenigswald, G.H.R., 1975. Early man in Java: catalogue and problems. In: Tuttle, R.H. (Ed.), *Paleoanthropology, Morphology and Paleocology*. Mouton Publishers, Den Haag, pp. 303–309.
- von Koenigswald, G.H.R., 1982. Distribution and evolution of the orang utan, *Pongo pygmaeus* (Hoppius). In: De Boer, L.E.M. (Ed.), *The Orang Utan: Its Biology and Conservation*. Dr. W. Junk Publishers, The Hague, pp. 1–15.
- Vu The Long, de Vos, J., Ciochon, R.L., 1996. The fossil mammal fauna of the Lang Trang Caves, Vietnam, compared with Southeast Asian fossil and recent mammal faunas: the geographical implications. *Indo-Pacific Prehist. Assoc. Bull.* 14, 101–109.
- Weidenreich, F., 1937. The Dentition of *Sinanthropus pekinensis*: A Comparative Odontography of the Hominids. *Palaeontol. Sin. D* 1, 1–180.
- Whitten, T., Soeriaatmadja, R.E., Afiff, S.A., 1996. *The Ecology of Java and Bali*, Vol. II. Periplus Editions, Singapore.