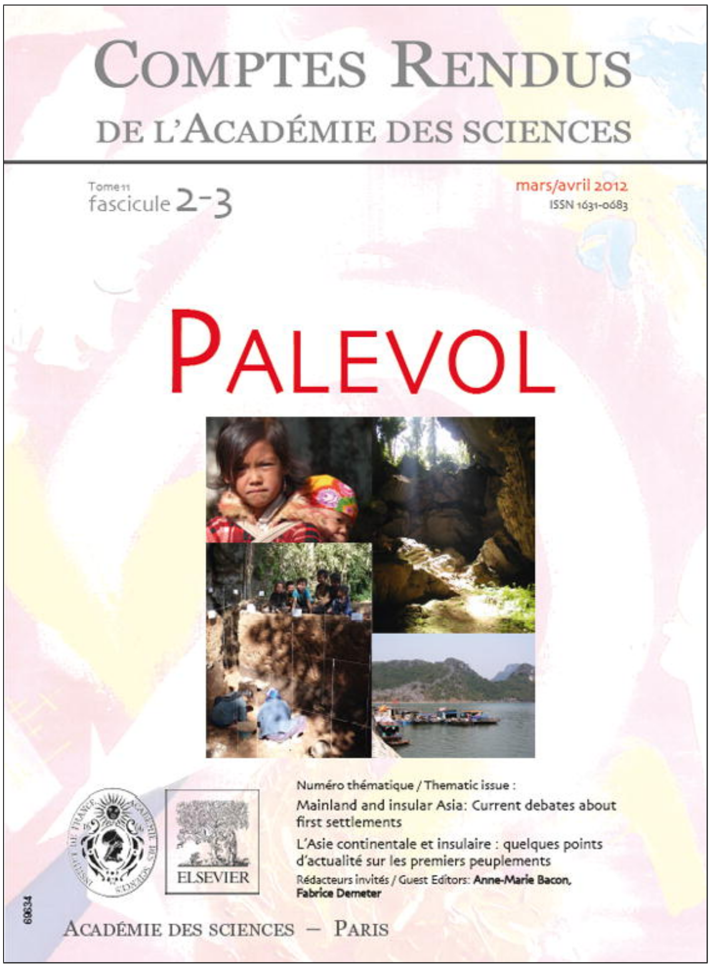
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A carnivorous niche for Java Man? A preliminary consideration of the abundance of fossils in Middle Pleistocene Java

Une niche carnivore pour l'Homme de Java ? Étude préliminaire sur l'abondance des fossiles dans le Pléistocène Moyen de Java

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ABSTRACT

Considering anatomical and archaeological aspects of *Homo erectus*, it is likely that meat of vertebrates was an important part in its diet. Unfortunately, no or hardly any information is available for Java Man (*Homo erectus*). Therefore, in this paper, the Number of Identified Specimens (NISP) of five Middle Pleistocene Javanese sites are examined, and the Minimum Number of Individuals (MNI) from two of them are calculated, to acquire information about the possible ecological role of Javanese *Homo erectus*. Although one has to be extremely careful with the interpretation of fossil bone assemblages in order to try to gain some insight about the abundance of species in palaeocommunities, it is argued that both the NISP and the MNI indicate that the bone accumulations reflect at least two trophic levels in the ecological pyramid, that of primary and secondary consumers. The occurrences of the remains of *Homo erectus* are comparable with the quantity of secondary consumers, i.e., large carnivores. This could suggest that this species had, as an omnivore, a carnivorous niche, in Java.

RÉSUMÉ

Les aspects anatomiques et archéologiques d'*Homo erectus* suggèrent que la viande provenant des faunes de vertébrés a pu constituer une part importante de leur alimentation. Malheureusement, il y a peu de données disponibles pour l'Homme de Java (*Homo erectus*). C'est pourquoi, dans cet article, afin de recueillir des informations sur le possible rôle écologique de l'*Homo erectus* de Java, nous avons calculé le nombre de specimens identifiés (NSPI) dans les assemblages de cinq sites du Pléistocène moyen de Java, et le nombre minimum d'individus (NMI) pour deux d'entre eux. Bien qu'il soit nécessaire d'être extrêmement prudent sur l'interprétation des assemblages d'os fossiles, en vue d'interpréter l'abondance des espèces dans les paléocommunautés, il ressort de cette étude que les paramètres NSPI et NMI indiquent que les accumulations des ossements reflètent au moins deux niveaux trophiques dans la pyramide écologique, ceux des consommateurs primaires et secondaires. La quantité des restes d'*Homo erectus* est comparable à celle des consommateurs secondaires, i.e. les grands carnivores. Ce résultat suggèrerait que cette espèce a eu, bien qu'étant également omnivore à Java, une niche carnivore.

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1. Introduction

In trying to understand the evolutionary history of a taxon, ecology is of critical importance. The distribution and adaptations of species are closely linked with biotic and abiotic factors. Organisms, including hominins, evolve within the context of their surrounding. The ecological parameters within which Java Man (*Homo erectus*) existed appeared to be unclear, but fortunately progress has been made (Bettis et al., 2009; de Vos, 1983; Joordens et al., 2009; Sémah and Sémah, 2001). Scientists do not agree on the palaeoenvironmental conditions in which this species lived (Storm, 2001a) and its ecological role within the community is unknown. There are no direct anatomical or archaeological indications for a meat-eating role for Java Man, and no probable living floors or campsites have been identified that would yield such evidence. Therefore, in this article, I examine the Number of Identified Specimens (NISP) of fossils of five Javanese sites and calculate the Minimum Number of Individuals (MNI) from two of them, in order to try to gain some more insight into the suggested carnivorous role of *Homo erectus* (Shipman and Walker, 1989). Although attempting to reconstruct a part of a palaeocommunity in this way is a hazardous undertaking (Klein and Cruz-Uribe, 1984; Ringrose, 1993), from the appearance of *Homo erectus* fossils in Java, I will explain that it is nevertheless likely that this hominin was, just like (large) carnivores, relatively rare.

2. Theoretical background

The temporal and spatial biogeographic distribution of *Homo erectus* depends on which fossils are included within this species. Therefore, it is necessary to consider briefly the taxonomy of this species before its distribution and abundance are considered. Only looking at parts of a once-living organism, the problem of defining *Homo erectus* may never be solved, because even in neospecies, the border between species and subspecies is often not clear, and can be artificial, an observation that has a relatively long history (Darwin, 1859). Probably, suggested species like *Homo ergaster* and *Homo soloensis* (Holloway et al., 2004) have to be included as local variants, subspecies of *Homo erectus*. Because we are dealing with a rough palaeoecological question, it is postulated that the exact taxonomic status is no problem. For the purpose of this paper, *Homo soloensis* will be discussed as *Homo erectus* (Antón, 2001; Baab, 2008; Caparros, 2001; Kaifu et al., 2008; Storm, 2001a).

Several definitions of the ecological niche concept can be given (Chase and Leibold, 2003), for instance: “the role of an organism within a community” (Krebs, 1978: p. 227), or: “the sum of a species’ use of the biotic and abiotic resources in its environment” (Campbell et al., 2008: p. 1199). The two above-mentioned quotes are suitable and broad, but it is important to have an explicit link with the intake of food. Thus, the definition given in Merriam-Webster’s Collegiate Dictionary fits nicely: “the ecological role of an organism in a community esp. in regard to food consumption” (Chase and Leibold, 2003: p. 5). For this paper, it is in important to distinguish habitat and niche. The habitat is “the range of environments in which a species occurs” (Krebs, 1978: p. 227). The habitat of an organism can be regarded as its “address”, the niche as its “profession” (Campbell et al., 2008). Thus, in contrast with the paper of Bettis et al. (2009), in this paper, it is the niche of *Homo erectus* that is considered, not its habitat.

According to the trophic levels in the ecological pyramid, it is obvious that in living communities the number of herbivores is much larger than that of carnivores and omnivores that partially include meat in their diet (Shipman and Walker, 1989). This often means that the chances that the remains of herbivores will end up in a bone collection are larger than those of carnivores and omnivores. This is what paleontologists often experience, but is of course not a rule (Shipman, 1981). From a taphonomic point of view, one may question seriously if it is possible to reconstruct a once living community from a collection of fossil remains (Klein and Cruz-Uribe, 1984). Ringrose (1993) remarks (page 123): “It is this palaeocommunity which we would like to reconstruct, although in practice we fall far short of this goal, as has been pointed out by, amongst others, Grayson (1981) and Lyman (1982). The operations of various processes mean that almost all information relating to absolute abundances is lost, and that to relative abundances is severely distorted”. Because reconstructing a palaeocommunity is such a risky undertaking, not only Kedung Brubus and Trinil, but also three other of the largest Pleistocene sites excavated by Dubois, and both the NISP and MNI of Kedung Brubus and Trinil are considered, and I will only deal with a rough palaeoecological question: was Javanese *Homo erectus* rare or not?

In view of the occurrence of *Homo erectus* in Java, as far as can be deduced from the NISP and MNI, it is important that there are indications that the fossil assemblages roughly reflect the original mammal communities, in this case, at least two trophic levels. Herbivores are clearly the most abundant in the fossil collections studied here, contrary to what we experience for instance in the Pleistocene Rancho La Brea tar seeps, where there is a predominance of carnivores (Spencer et al., 2003).

Shipman and Walker (1989) predicted a number of changes that are likely to have occurred when hominins became significantly predatory; one of them is the occurrence of lower population densities. According to these two authors (page 382): “In terms of dietary transitions from herbivory to carnivory, this density rule predicts that almost any species that moves from the primary consumer or herbivore trophic level to that of secondary consumer or carnivore will face a density dilemma. To wit: since carnivores must be much scarcer than herbivores, a species transformed from herbivory to carnivory is likely to be much too densely distributed.” And (page 387): “Two possible evolutionary solutions to the density dilemma could be expected to be visible in the fossil record. These are: (1) a decrease in body size; (2) an increase in geographic range.” They discussed these two aspects, but not density itself. The research presented in this paper, about the population density of *Homo erectus* in Java, can be seen as a test of their prediction.

A number of indications suggest meat-eating for *Homo erectus*. In this paper, Stanford and Bunn (2001: p.

5–6) are followed for the definition of meat-eating: the consumption of vertebrate fauna, which includes all body tissues. If there was an increase in meat consumption in hominins, a number of changes may be expected (Foley, 2001; Shipman and Walker, 1989). Shipman and Walker (1989: p. 375) give three general categories in which changes can be expected during a shift from herbivory to carnivory: food-procurement, food-processing and position in the food web. The following aspects can possibly be associated with meat-eating:

Food-procurement:

1. Striding gait for endurance running;
2. Strong social behavior.

Food-processing:

3. Relatively small cheek teeth;
4. Gouging and battering of the teeth;
5. Relatively smaller gut;
6. Hypervitaminosis A;
7. Appearance of handaxes;

Ecology:

8. Wide geographic distribution;
9. Low density in the ecosystem;

The above-mentioned first eight aspects can be seen as indirect and direct indications for the consumption of meat. Admittedly, not all are strong, and could (partly) also have interpretations other than carnivory. In this article, I will deal with the last mentioned aspect, the low density in the ecosystem, which is directly related to the ecological niche.

3. Middle Pleistocene Javanese sites

The fossils considered in this paper are well mineralized. Based on the state of fossilization and faunal composition, it is thought that all five sites stem from the period in which *Homo erectus* was present in Java, during the Middle Pleistocene, roughly between 900,000–130,000 years ago. In Java, the end of the Middle Pleistocene is marked by a faunal turnover, with the extinction of an archaic open woodland fauna, and the introduction of a modern tropical rainforest fauna, the so called Punung fauna (Storm, 2001a, 2001b; Storm and de Vos, 2006; Storm et al., 2005). As far as we know at this moment, *Homo erectus* was part of the last archaic Middle Pleistocene Ngandong fauna, while *Homo sapiens* was possibly part of the first modern Upper Pleistocene Punung fauna.

The Trinil fauna can possibly be dated to around 0.9 ka, based on the similarity with the grenzbank fauna at Sangiran; the Kedung Brubus fauna is similar to the Sangiran fauna, dated to around 0.8–0.7 ka (Van den Bergh et al., 1996). The age of Ngandong is still a puzzle. Swisher et al. (1996) and Yokoyama et al. (2008) obtained young, Upper Pleistocene dates for Ngandong and Sambungmacan. But it is difficult to reconcile the reconstructed ecological history of Java with the young dates. It is logical to reason that the archaic Ngandong fauna is older than the modern Punung fauna (de Vos, 1983). Based on sedimentological and palynological analyses of sediment cores from the Bandung basin in West Java (Dam, 1994; Van der Kaars and Dam, 1995), the last mentioned fauna has a likely age between 126 and 81 ka (Storm, 2001a; Storm and de Vos, 2006), which is confirmed by the dates of Westaway et al. (2007). They remark (page 709): “The Punung Fauna contained in the dated breccia is of early Last Interglacial age (between 128 ± 15 and 118 ± 3 ka)”. Consequently, Ngandong must be older than 126 ka. Moreover, the U-series near Matar and Tapan (Bartstra et al., 1988) give a possible time range for Ngandong between 190 and 165 ka, and Indriati et al. (2010) give a significantly older age (mean 546 ± 12 ka) for pumice collected in fossiliferous deposits of Ngandong and Jigar. In other words: we have older and younger dates for Ngandong, but in the light of the paleoecology of Java and the new dates for the Punung fauna, a Middle Pleistocene age for Ngandong, older than 126 ka, is more likely than a younger one.

4. Material and methods

In this article, I will focus on the vertebrate faunal composition and structure of two well-known hominin sites: Kedung Brubus and Trinil, and three of the other richest sites also excavated by Dubois in the late 19th century: Bangle, Sumber Kepuh and Teguan. The fossils from the above-mentioned sites are included in the electronic database of the National Museum of Natural History in Leiden, the Netherlands. For this study, the record of 2002 was used. The hominin remains and many bovid teeth found in Trinil are not included in the electronic database. Hooijer (1946, 1950, 1955, 1958, 1962) described a large number of Pleistocene Javanese fossils. In most cases, the presence of a taxon and the nomenclature recorded in the database is closely followed in this study. In a situation of suspicion of misidentification, the database was not followed.

The NISP is at species and genus level (for instance *Python* sp.), and in a large number of cases only the order or family could be identified (for instance Proboscidea or Bovidae). Considering only the raw numbers of fossils at each site is not entirely satisfactory because a single skeleton may yield different numbers of bones. For instance, Cervidae produce extra skeletal remains – that are often large – in the form of antlers. The total number of Cervidae found in Trinil is 1075, the total number of antler (fragments) is 101, that is 9.4% (no distinction is made between antlers carried and those shed). Furthermore, it produces larger values for animals that reach a site as whole bodies (Ringrose, 1993). In order to try to eliminate this problem, I have also calculated the MNI for various taxa.

Unfortunately, the numbers of fossils are for a number of sites, Bangle, Sumber Kepuh and Teguan, too low to give a reliable impression of the MNI. Because of the richness of the numbers of fossils found in the Kedung Brubus and Trinil, the MNI of only these two sites will be considered. Table 1 gives an overview of the fossil hominins of Kedung Brubus and Trinil.

I calculated the MNI from the skeletal element and side (right or left) that occurred in the greatest number as they were registered in the electronic database of the National

Table 1
Number of Identified Specimens (NISP) (*Homo erectus*) in Kedung Brubus and Trinil. This table is based on Oakley et al. (1975). Because in Kedung Brubus only one hominin fossil has been found, the Minimum Number of Individuals (MNI) is 1. In Trinil, three (parts of a) left hominin femurs have been found, therefore the MNI is 3.

Tableau 1
Nombre de Spécimens Identifiés (NSPI) (*Homo erectus*) à Kedung Brubus et Trinil. Ce tableau est basé sur les données de Oakley et al. (1975). A Kedung Brubus, un seul fossile d'homininé a été trouvé, le Nombre Minimum d'Individus (NMI) est donc de 1. A Trinil, trois (parties de) fémurs gauches ont été trouvés, le NMI est donc de 3.

Fossil	Description
Kedung Brubus 1	right corpus mandibulae
Trinil 1	upper right M3
Trinil 2 (Skull I)	calotte, holotype of *Pithecanthropus (Homo) erectus*
Trinil 3 (Femur I)	left femur (well preserved femur with exostosis)
Trinil 4	upper left M2
Trinil 5	lower left P3
Trinil 6 (Femur II)	proximal part right femur
Trinil 7 (Femur III)	left femur
Trinil 8 (Femur IV)	right femur
Trinil 9 (Femur V)	left femur

Museum of Natural History. No small fragmented postcranial elements were counted but complete and larger parts, like for instance: atlas, right femur, right proximal part of femur or right distal part of femur. In this theoretical example, the MNI would be 2, because there are two right proximal parts of a femur and two right distal parts of a femur. No cranial fragments were used to indicate that there was more than one individual present. Thus, I tried to avoid to counting two or more individuals as their bones could represent one individual. I did not separate cervids by the condition of the antlers (loose or attached to the skull) nor did I separate individuals of any taxon into age classes or sex.

5. Results

Table 2 gives an overview of the NISP that have been found in the five largest sites. The Trinil fauna includes taxa not found in other sites, such as chondrichthyes, osteichthyes and squamata as well as a small number of avian remains. Possibly the quantity and quality of the excavations in Trinil are responsible for the collection of unusual or rare faunal remains. Not only the above-mentioned vertebrates occur in relatively low numbers but so do mammals like rodents and small carnivores, as can clearly be seen in Figs. 1 to 5, which are based on the numbers in Table 3. The smaller bone fragments are rare. It is very likely that taphonomic reasons and the circumstances in which the fossils have been found are the main causes for this observation. For this reason, to obtain a rough impression of the relative abundance of animals in Middle Pleistocene Java, one has to concentrate on the larger faunal components, like large Testudinata, Crocodilia, hominins, large carnivores, Cervidae, Bovidae, Hippopotamidae, Suidae, Rhinocerotidae, Tapiridae and Proboscidea. The above-mentioned taxa include herbivores, omnivores and carnivores.

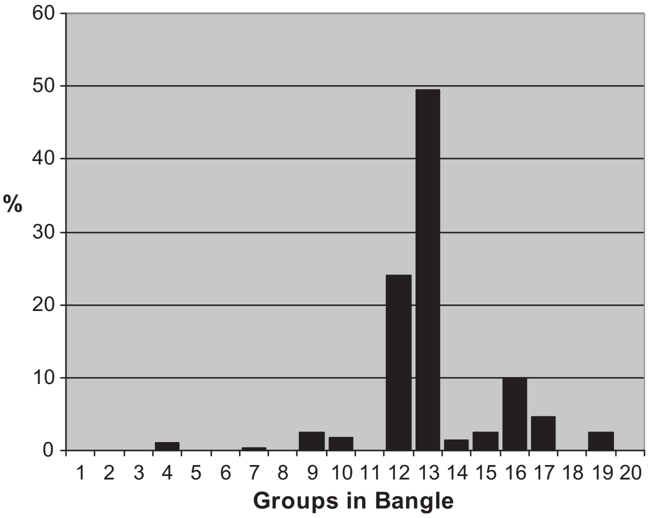

Fig. 1. Number of Identified Specimens (NISP) (%) in Bangle (NISP = 283, the figure is based on Table 3). 1 = Chondrichthyes, 2 = Osteichthyes, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Birds, 7 = Rodentia, 8 = Hominins (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora large, 11 = Carnivora small, 12 = Cervidae, 13 = Bovidae large, 14 = Bovidae small, 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

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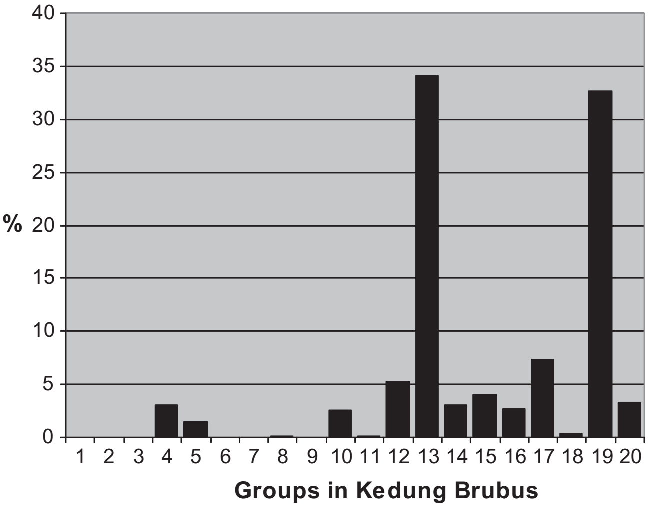

Fig. 2. Number of Identified Specimens (NISP) (%) in Kedung Brubus (NISP = 865, figure is based on Table 3). 1 = Chondrichthyes, 2 = Osteichthyes, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Birds, 7 = Rodentia, 8 = Hominins (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora large, 11 = Carnivora small, 12 = Cervidae, 13 = Bovidae large, 14 = Bovidae small, 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

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Table 2
Number of Identified Specimens (NISP) Pleistocene Javanese sites.
Tableau 2
NSPI calculés pour les sites pléistocènes de Java.

		Bangle	Kedung Brubus	Sumber Kepuh	Teguan	Trinil
1	**Chondrichthyes**					
	Eulamia gangetica	0	0	0	0	1
	Odontaspis cuspidata	0	0	0	0	1
2	**Osteichthyes**					
	Anabas testudineus	0	0	0	0	1
	Clarias batrachus	0	0	0	0	5
	Clarias leiacanthus	0	0	0	0	1
	cf. *Macrones nemurus*	0	0	0	0	2
	Ophicephales palaeostriatus	0	0	0	0	17
	Ophicephales sp.	0	0	0	0	5
	Siluroidae	0	0	0	0	17
3	**Squamata**					
	Python sp.	0	0	0	0	1
	Varanus sp.	0	0	0	0	4
4	**Testudinata**					
	Batagur sp.	3	11	0	0	121
	Chitra sp.	0	15	0	0	64
5	**Crocodilia**					
	Crocodilus ossifragus	0	12	2	3	60
	Garialis bengawanicus	0	1	0	3	20
	Crocodilia	0	0	0	0	15
6	**Birds**					
	Branta cf. *ruficollis*	0	0	0	0	1
	Ephippiorhynchus cf. *asiaticus*	0	0	0	0	1
	Leptoptilos cf. *dubius*	0	0	0	0	2
	Pavo muticus	0	0	1	0	0
	Tadorna tadornoides	0	0	0	0	1
7	**Rodentia**					
	Hystrix sp.	1	0	3	0	0
	Hystrix lagrelli	0	0	0	0	2
	Rattus trinilensis	0	0	0	0	2
	Muridea	0	0	0	0	1
8	**Hominidae**					
	Homo erectus	0	1	0	0	9
9	**Cercopithecidae**					
	Macaca fascicularis	5	0	0	0	11
	Presbytes aygula	0	0	1	0	0
	Trachipithecus cristatus	2	0	3	1	1
	Colobinae	0	0	0	0	1
10	**Carnivora large**					
	Crocuta bathygnatha	0	1	0	2	0
	Helarctos malayanus	1	0	0	0	0
	Panthera pardus	0	0	0	0	0
	Panthera tigris	4	15	0	1	10
	Panthera sp.	0	6	0	1	3
11	**Carnivora small**					
	Lutrogale palaeojavanica	0	1	0	0	0
	Prionailurus bengalensis	0	0	0	0	1
12	**Cervidae**					
	Axis lydekkeri	28	39	0	6	1075
	Rusa sp.	37	5	0	8	0
	Muntiacus muntjak	3	2	1	2	0
13	**Bovidae large**					
	Epileptobos groeneveldtii	3	9	0	8	0
	Bibos palaeosondaicus	4	28	3	5	51
	Bubalus palaeokerabau	5	25	1	9	94
	Bovidae	128	233	209	114	1406
14	**Bovidae small**					
	Duboisia santeng	4	26	0	3	231

Table 2 (*Continued*)

		Bangle	Kedung Brubus	Sumber Kepuh	Teguan	Trinil
15	**Hippopotamidae**					
	Hexaprotodon sivalensis	7	35	0	5	0
16	**Suidae**					
	Sus brachygnathus	0	4	0	1	78
	Sus macrognathus	6	6	0	10	0
	Sus sp.	22	13	1	8	0
17	**Rhinocerotidae**					
	Rhinoceros unicornis (kend.)	0	14	0	2	0
	Rhinoceros sondaicus	9	26	0	4	44
	Rhinoceros sp.	4	23	0	6	6
18	**Tapiridae**					
	Tapirus indicus	0	3	0	0	0
19	**Proboscidea**					
	Elephas hysudrindicus	1	23	0	15	0
	Stegodon trigonocephalus	6	129	0	37	499
	Proboscidea	0	130	0	33	1
20	**Pholidota**					
	Manis palaeojavanica	0	29	0	0	0
	Total	**283**	**865**	**225**	**287**	**3866**

In each of the 5 sites, the assemblage is dominated by bones of one or more of the larger mammal herbivores, i.e. Cervidae, Bovidae or Proboscidea (Table 3 and in Figs. 1 to 5: Bangle, 24% Cervidae and 49% large Bovidae; Kedung Brubus, 34% large Bovidae and 33% Proboscidea; Sumber Kepuh, 95% large Bovidae; Teguan, 47% large Bovidae and 30% Proboscidea; Trinil: 28% Cervidae, 40% large Bovidae and 13% Proboscidea). In general, bones of Bovidae are the most abundant. An observation that has also been made in East African sites (Bobe et al., 2007). Remains of Hippopotamidae, Rhinocerotidae, Tapiridae, Suidae, hominins, Crocodilia and Carnivora do not come in large numbers.

Comparing the relative MNI of Kedung Brubus and Trinil (Table 4; Fig. 6), one of the most striking differences is the small number of different large mammal species in Trinil compared with that at Kedung Brubus. There are twice as many different species of large mammals in Kedung Brubus compared to species at Trinil, even though the total number of fossils found in Trinil (total $N = 3866$) is much greater than the total number of fossils found in Kedung Brubus (total $N = 865$). Trinil was excavated with great energy over several years because of its promising rewards in the form of the *Pithecanthropus* (*Homo*) *erectus* fossils. This fact probably accounts for the number of fossils of smaller animals

Table 3
Number of Identified Specimens (NISP) (%) Pleistocene Javanese sites. Ba = Bangle, KB = Kedung Brubus, SK = Sumber Kepuh, Te = Teguan, Tr = Trinil.
Tableau 3
NSPI (%) calculés pour les sites pléistocènes de Java. Ba = Bangle, KB = Kedung Brubus, SK = Sumber Kepuh, Te = Teguan, Tr = Trinil.

	NISP					Percentages				
Groups	Ba	KB	SK	Te	Tr	Ba	KB	SK	Te	Tr
1. Chondrichthyes	0	0	0	0	2	*0.00*	*0.00*	*0.00*	*0.00*	*0.05*
2. Osteichthyes	0	0	0	0	48	*0.00*	*0.00*	*0.00*	*0.00*	*1.24*
3. Squamata	0	0	0	0	5	*0.00*	*0.00*	*0.00*	*0.00*	*0.13*
4. Testudinata	3	26	0	0	185	*1.06*	*3.01*	*0.00*	*0.00*	*4.79*
5. Crocodilia	0	13	2	6	95	*0.00*	*1.50*	*0.89*	*2.09*	*2.46*
6. Birds	0	0	1	0	5	*0.00*	*0.00*	*0.44*	*0.00*	*0.13*
7. Rodentia	1	0	3	0	5	*0.35*	*0.00*	*1.33*	*0.00*	*0.13*
8. Hominidae	0	1	0	0	9	*0.00*	*0.12*	*0.00*	*0.00*	*0.23*
9. Cercopithecidae	7	0	4	1	13	*2.47*	*0.00*	*1.78*	*0.35*	*0.34*
10. Carnivora large	5	22	0	4	13	*1.77*	*2.54*	*0.00*	*1.39*	*0.34*
11. Carnivora small	0	1	0	0	1	*0.00*	*0.12*	*0.00*	*0.00*	*0.03*
12. Cervidae	68	46	1	16	1075	*24.03*	*5.32*	*0.44*	*5.57*	*27.81*
13. Bovidae large	140	295	213	136	1551	*49.47*	*34.10*	*94.67*	*47.39*	*40.12*
14. Bovidae small	4	26	0	3	231	*1.41*	*3.01*	*0.00*	*1.05*	*5.98*
15. Hippopotamidae	7	35	0	5	0	*2.47*	*4.05*	*0.00*	*1.74*	*0.00*
16. Suidae	28	23	1	19	78	*9.89*	*2.66*	*0.44*	*6.62*	*2.02*
17. Rhinocerotidae	13	63	0	12	50	*4.59*	*7.28*	*0.00*	*4.18*	*1.29*
18. Tapiridae	0	3	0	0	0	*0.00*	*0.35*	*0.00*	*0.00*	*0.00*
19. Proboscidea	7	282	0	85	500	*2.47*	*32.60*	*0.00*	*29.62*	*12.93*
20. Pholidota	0	29	0	0	0	*0.00*	*3.35*	*0.00*	*0.00*	*0.00*
Total	**283**	**865**	**225**	**287**	**3866**	***100.00***	***100.00***	***100.00***	***100.00***	***100.00***

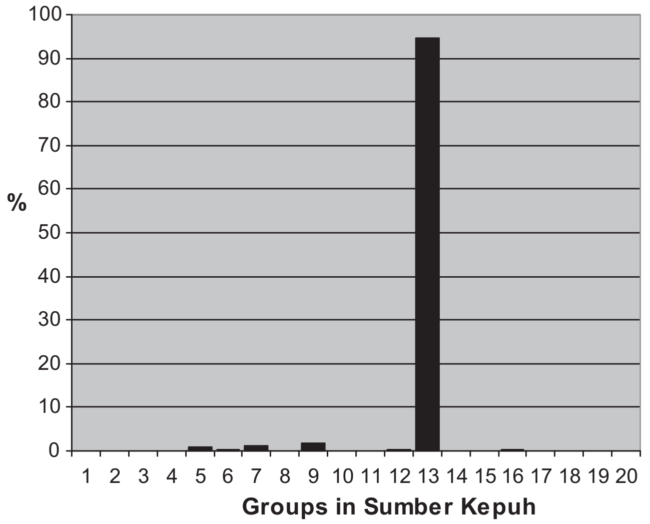

Fig. 3. Number of Identified Specimens (NISP) (%) in Sumber Kepuh (NISP = 225, figure is based on Table 3). 1 = Chondrichthyes, 2 = Osteichthyes, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Birds, 7 = Rodentia, 8 = Hominins (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora large, 11 = Carnivora small, 12 = Cervidae, 13 = Bovidae large, 14 = Bovidae small, 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

Fig. 3. Nombre de Spécimens Identifiés (NSPI) (%) à Sumber Kepuh (NSPI = 225, la figure est basée sur les données du Tableau 3). 1 = Chondrichtya, 2 = Osteichtya, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Aves, 7 = Rodentia, 8 = Homininae (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora (grande taille), 11 = Carnivora (petite taille), 12 = Cervidae, 13 = Bovidae (grande taille), 14 = Bovidae (petite taille), 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

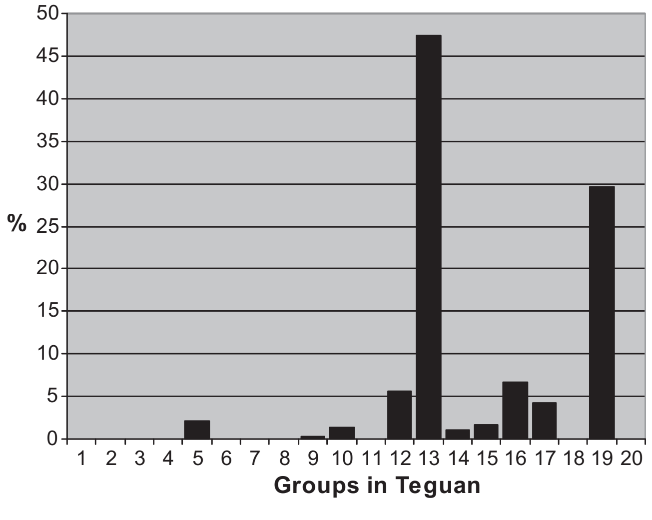

Fig. 4. Number of Identified Specimens (NISP) (%) in Teguan (NISP = 287, the figure is based on Table 3). 1 = Chondrichthyes, 2 = Osteichthyes, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Birds, 7 = Rodentia, 8 = Hominins (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora large, 11 = Carnivora small, 12 = Cervidae, 13 = Bovidae large, 14 = Bovidae small, 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

Fig. 4. Nombre de Spécimens Identifiés (NSPI) (%) à Teguan (NSPI = 287, la figure est basée sur les données du Tableau 3). 1 = Chondrichtya, 2 = Osteichtya, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Aves, 7 = Rodentia, 8 = Homininae (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora (grande taille), 11 = Carnivora (petite taille), 12 = Cervidae, 13 = Bovidae (grande taille), 14 = Bovidae (petite taille), 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

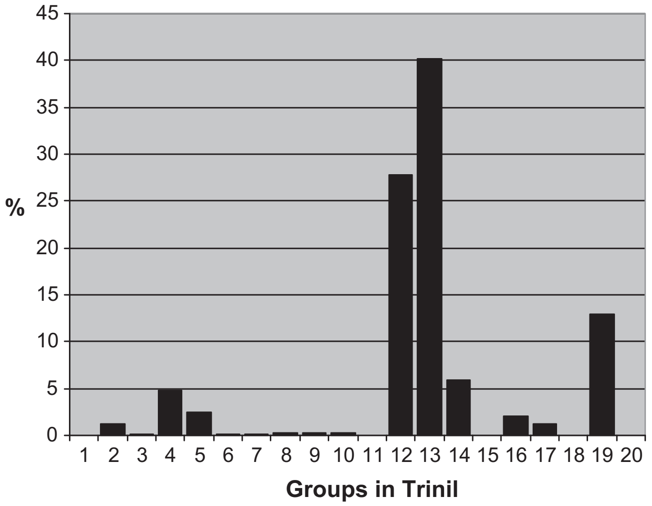

Fig. 5. Number of Identified Specimens (NISP) (%) in Trinil (NISP = 3866, the figure is based on Table 3). 1 = Chondrichthyes, 2 = Osteichthyes, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Birds, 7 = Rodentia, 8 = Hominins (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora large, 11 = Carnivora small, 12 = Cervidae, 13 = Bovidae large, 14 = Bovidae small, 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

Fig. 5. Nombre de Spécimens Identifiés (NSPI) (%) à Trinil (NSPI = 3866, la figure est basée sur les données du Tableau 3). 1 = Chondrichtya, 2 = Osteichtya, 3 = Squamata, 4 = Testudinata, 5 = Crocodilia, 6 = Aves, 7 = Rodentia, 8 = Homininae (*Homo erectus*), 9 = Cercopithecidae, 10 = Carnivora (grande taille), 11 = Carnivora (petite taille), 12 = Cervidae, 13 = Bovidae (grande taille), 14 = Bovidae (petite taille), 15 = Hippopotamidae, 16 = Suidae, 17 = Rhinocerotidae, 18 = Tapiridae, 19 = Proboscidea, 20 = Pholidota.

found at Trinil. Thus, it is unlikely that the more restricted diversity of large mammal species at Trinil is an artefact caused by excavation techniques. The Trinil fauna also does not exhibit evidence of the loss of certain size classes of fossils, so this difference is unlikely to be strictly taphonomic. A reasonable explanation for the taxonomically restricted fauna is that it reflects the once-living animal community, which was perhaps relatively isolated during Trinil times (de Vos, 1982).

By MNI, the best-represented bones of species at Trinil are herbivores (Table 4; Fig. 6): *Axis lydekkeri* (36%), *Bibos palaeosondaicus* (17%), *Bubalus palaeokerabau* (14%), *Duboisia santeng* (10%) and *Stegodon trigonocephalus* (9%) in descending order of abundance. Remains of small mammals are present but occur only in small percentages, probably due to taphonomic reasons. The percentages of Kedung Brubus must be interpreted more carefully than those of Trinil because of the smaller total assemblage size at Kedung Brubus. Nevertheless, the most abundant fossils of species at Kedung Brubus match those at Trinil: *A. lydekkeri* (8%), *B. palaeosondaicus* (14%), *B. palaeokerabau* (8%), *D. santeng* (10%) and *S. trigonocephalus* (18%).

6. Discussion

In ideal circumstances, one evaluates the taphonomic context and collection methods used in the field in detail, before one analyses the relative abundances within the fossil record (Bobe et al., 2007). In this case, this is hampered by the history of the collections studied, and beyond the

Table 4
Number of Identified Specimens (NISP) (at species level) and Minimum Number of Individuals (MNI) of mammals in Kedung Brubus and Trinil.
Tableau 4
Nombre de Spécimens Identifiés (NSPI) et Nombre Minimum d'Individus (NMI) (au niveau de l'espèce) calculés pour les mammifères présents à Kedung Brubus et Trinil.

	Kedung Brubus				Trinil			
Species	N	*% N*	MNI	*% MNI*	N	*% N*	MNI	*% MNI*
1. Hystrix lagrelli	0	*0.00*	0	*0.0*	2	*0.09*	2	*1.1*
2. Rattus trinilensis	0	*0.00*	0	*0.0*	2	*0.09*	1	*0.6*
3. Homo erectus	1	*0.24*	1	*2.0*	9	*0.43*	3	*1.7*
4. Macaca fascicularis	0	*0.00*	0	*0.0*	11	*0.52*	1	*0.6*
5. Trachypithecus cristatus	0	*0.00*	0	*0.0*	1	*0.05*	1	*0.6*
6. Crocuta bathygnatha	1	*0.24*	1	*2.0*	0	*0.00*	0	*0.0*
7. Panthera tigris	15	*3.56*	1	*2.0*	10	*0.47*	1	*0.6*
8. Lutrogale palaeojavanica	1	*0.24*	1	*2.0*	0	*0.00*	0	*0.0*
9. Prionailurus bengalensis	0	*0.00*	0	*0.0*	1	*0.05*	1	*0.6*
10. Axis lydekkeri	39	*9.26*	4	*7.8*	1075	*51.00*	63	*36.2*
11. Rusa sp.	5	*1.19*	1	*2.0*	0	*0.00*	0	*0.0*
12. Muntiacus muntjak	2	*0.48*	1	*2.0*	0	*0.00*	0	*0.0*
13. Epileptobos groeneveldtii	9	*2.14*	1	*2.0*	0	*0.00*	0	*0.0*
14. Bibos palaeosondaicus	28	*6.65*	7	*13.7*	51	*2.42*	30	*17.2*
15. Bubalus palaeokerabau	25	*5.94*	4	*7.8*	94	*4.46*	24	*13.8*
16. Duboisia santeng	26	*6.18*	5	*9.8*	231	*10.96*	18	*10.3*
17. Hexaprotodon sivalensis	35	*8.31*	1	*2.0*	0	*0.00*	0	*0.0*
18. Sus brachygnathus	4	*0.95*	1	*2.0*	78	*3.70*	9	*5.2*
19. Sus macrognathus	6	*1.43*	2	*3.9*	0	*0.00*	0	*0.0*
20. Rhinoceros unicornis (ken.)	14	*3.33*	3	*5.9*	0	*0.00*	0	*0.0*
21. Rhinoceros sondaicus	26	*6.18*	3	*5.9*	44	*2.09*	4	*2.3*
22. Tapirus indicus	3	*0.71*	2	*3.9*	0	*0.00*	0	*0.0*
23. Elephas hysudrindicus	23	*5.46*	2	*3.9*	0	*0.00*	0	*0.0*
24. Stegodon trigonocephalus	129	*30.64*	9	*17.6*	499	*23.67*	16	*9.2*
25. Manis palaeojavanica	29	*6.89*	1	*2.0*	0	*0.00*	0	*0.0*
Total	**421**	***100.00***	**51**	***100.0***	**2108**	***100.00***	**174**	***100.0***

scope of this article. Therefore, the results of this research should be regarded as preliminary considerations that need further testing.

Both the use of the NISP and MNI have advantages and disadvantages, and one may have a preference to use one of them, depending on the situation and questions one likes to be answered (Grayson, 1984; Klein and Cruz-Uribe, 1984; Ringrose, 1993; Shipman, 1981). Because so little is known of the taphonomic history and excavating techniques used by Dubois, the choice was to use both. Nevertheless, it is good to realize that the two sites, Kedung Brubus and Trinil, are seriously excavated and the impression is that Dubois intention was to collect all fossils. De Vos and Aziz (1989: p. 416) remark about Trinil: "Summarizing, we may deduce from the data mentioned above that the total surface of the trenches was about 2433 m^2. About 2317 m^2 on the left bank and about 106 m^2 on the right bank. Furthermore, we can deduce that Dubois excavated at Trinil for about 49 months. From the letters of Kriele and De Winter, the monthly- and quaternary reports, we can deduce that the numbers of labourers varied between 25 and 50 and that all fossils came from the main fossil layer (the so-called Hauptknochenschicht)." This last remark is important, as far as can be reasoned from the, in general, beautiful sharp state of preservation of the fossils, there has been no long distance transport of many of the fossils. Because of this, and the fact that they are found in one layer, the "Hauptknochenschicht", the bones must have been deposited quietly in a short period of time. In other words, they must represent the remains of a once living community. Sondaar (1984: pp. 225–226) remarks about Kedung Brubus: "The fauna from Kedung Brubus and its biostratigraphic position has also been recently revised by De Vos & al., (1982), Sondaar & al., (1983) concluded that the fossils labelled "Kedung Brubus" in the Dubois collection originate from one stratigraphical level near the village Kedung Brubus." Also for Kedung Brubus, there are no indications of long distance transport of many of the fossils. In other words, in both Trinil and Kedung Brubus there are no signs of large-scale mixing or selection of bones by animals, including hominins; they can be regarded as representing palaeocommunities and are treated as faunal units, stemming from an open woodland (de Vos et al., 1982; Leinders et al., 1985; Storm, 2001a, 2001b; Theunissen et al., 1990; Van den Bergh et al., 1996).

Although one has to be very careful in trying to reconstruct palaeocommunities from collections of bones (Ringrose, 1993), arguments can be given that in this case a rough estimate can be made of at least two trophic levels in the ecological pyramid of Middle Pleistocene East Java, i.e. primary consumers (the second trophic level consisting of herbivores) and secondary consumers (the third trophic level consisting of carnivores). Higher levels can be recognized when carnivores feed on carnivores, i.e., tertiary and quaternary consumers. In reality predators fulfill often both roles. Considering the NISP (of the larger faunal components, like large Testudinata, Crocodilia, hominins, large carnivores, Cervidae, Bovidae, Hippopotamidae, Suidae, Rhinocerotidae, Tapiridae and Proboscidea) of the largest five sites excavated by Dubois, it is always the bones of

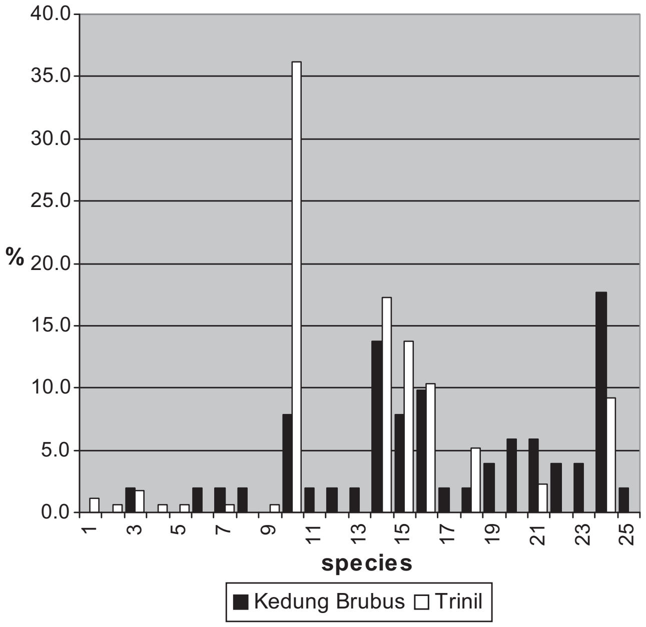

Fig. 6. Minimum Number of Individuals (MNI) (%) mammals Kedung Brubus (total MNI = 51) and Trinil (total MNI = 174) (the figure is based on Table 4). 1 = *Hystrix lagrelli*, 2 = *Rattus trinilensis*, 3 = *Homo erectus*, 4 = *Macaca fascicularis*, 5 = *Trachypithecus cristatus*, 6 = *Crocuta bathygnatha*, 7 = *Panthera tigris*, 8 = *Lutrogale palaeojavanica*, 9 = *Prionailurus bengalensis*, 10 = *Axis lydekkeri*, 11 = *Rusa* sp., 12 = *Muntiacus muntjak*, 13 = *Epileptobos groeneveldtii*, 14 = *Bibos palaeosondaicus*, 15 = *Bubalus palaeokerabau*, 16 = *Duboisia santeng*, 17 = *Hexaprotodon sivalensis*, 18 = *Sus brachygnathus*, 19 = *Sus macrognathus*, 20 = *Rhinoceros unicornis* (*kendengindicus*), 21 = *Rhinoceros sondaicus*, 22 = *Tapirus indicus*, 23 = *Elephas hysudrindicus*, 24 = *Stegodon trigonocephalus*, 25 = *Manis palaeojavanica*.

Fig. 6. Nombre Minimum d'Individus (NMI) (%) pour les mammifères de Kedung brubus (total NMI = 51) et Trinil (total NMI = 174) (la figure est basée sur les données du Tableau 4). 1 = *Hystrix lagrelli*, 2 = *Rattus trinilensis*, 3 = *Homo erectus*, 4 = *Macaca fascicularis*, 5 = *Trachypithecus cristatus*, 6 = *Crocuta bathygnatha*, 7 = *Panthera tigris*, 8 = *Lutrogale palaeojavanica*, 9 = *Prionailurus bengalensis*, 10 = *Axis lydekkeri*, 11 = *Rusa* sp., 12 = *Muntiacus muntjak*, 13 = *Epileptobos groeneveldtii*, 14 = *Bibos palaeosondaicus*, 15 = *Bubalus palaeokerabau*, 16 = *Duboisia santeng*, 17 = *Hexaprotodon sivalensis*, 18 = *Sus brachygnathus*, 19 = *Sus macrognathus*, 20 = *Rhinoceros unicornis* (*kendengindicus*), 21 = *Rhinoceros sondaicus*, 22 = *Tapirus indicus*, 23 = *Elephas hysudrindicus*, 24 = *Stegodon trigonocephalus*, 25 = *Manis palaeojavanica*.

herbivores that are the most abundant, while those of (large) carnivores are rare. This is far from a subtle difference (Figs. 1 to 5). Taking into account the MNI of the two largest sites excavated by Dubois, the above-mentioned differences are less spectacular but this is due to methodology, compared with the NISP, outcomes of calculations of the MNI are leveled. The result of the MNI clearly confirms the picture based on the NISP; bones of herbivores are the most abundant, while those of (large) carnivores are rare (Fig. 6). Thus, by using two different methods the outcome remains the same. There are no indications that the above-mentioned bone collections are the main result of selection by hominins (cutmarks on bones or presence of artifacts), as is possibly the case with Javanese sites like Wajak, Hoekgrot and Sampung (Storm, 1995) or other animals, like porcupines (marks of gnawing), in the sites of Punung and Gunung Dawung (Storm and de Vos, 2006; Storm et al., 2005).

The MNI of fossil vertebrate remains from Trinil and Kedung Brubus both indicate that cervids, bovids and Proboscideans clearly dominate the paleontological record whilst large carnivores and omnivores (hominins and Suidae) are represented in much lower numbers. However, fossils of hippos, rhinos and tapirs, are relatively rare, and individual herbivore species like *Epileptobos groeneveldtii* and *Elephas hysudrindicus* occur only in Kedung Brubus but not in large numbers (Fig. 6). In addition, judging the NISP in all five sites (Table 2), large herbivores species like *E. groeneveldtii*, *Hexaprotodon sivalensis*, *Rhinoceros unicornis*, *Rhinoceros sondaicus*, *Tapirus indicus* and *E. hysudrindicus*, confirm the idea that bones of large herbivores do not always automatically come in large numbers. This is also true for South African sites (Brain, 1981: Table 5), where remains of Perissodactyla and Proboscidea do not show a high frequency.

Poor survival of small bones cannot account for the relatively low abundance of very large mammals like *Rhinoceros sondaicus* in Javanese sites. Since home range size covaries with body size, it is to be expected that very large herbivores (megafauna) will be less abundant than medium- and large-sized herbivores such as deer or bovids. Another explanation could be that (Ringrose, 1993: p. 124): "a far higher proportion of fast-breeding, short lived, animals will be available for deposition than actually exist in the population at any one time, and conversely for longer-lived animals." These two reasons could explain the less abundant occurrence of *H. sivalensis*, *R. unicornis*, *R. sondaicus*, and *E. hysudrindicus*. *T. indicus* is a solitary living animal, which could explain that bones of this animal too, are relatively rare in fossil assemblages. Thus possibly, only *E. groeneveldtii* does occur in unexpectedly small numbers.

In the same way, one could suggest that hominins are rare as fossils because they were longer-lived slow breeders. However, this would not explain the differences between the abundance of the genera *Australopithecus* and *Paranthropus* on the one hand, and that of *Homo* on the other (Table 5; see later in the discussion).

Ngandong is well known for its large number of fossil hominins, which may give the impression that remains of *Homo erectus* are not rare in this bone assemblage. However, this is not the case because Ngandong has yielded more vertebrate fossils than any other Pleistocene site in Java. There are 23,553 registered fossils from Ngandong, of which 13 (0.06%) are fossil hominins, i.e. *Homo erectus*, (Ter Haar, 1934). For Kedung Brubus and Trinil these numbers are respectively: 0.12 and 0.23% (Table 3). Unfortunately, most of the Ngandong faunal specimens were lost during World War 2 (personal communication de Vos, 2007), so these data come from written catalogues, not specimens. Interestingly, Von Koenigswald (p. 219) remarked about the Ngandong fauna in the introduction of Weidenreich's (1951) description of the Solo skulls that: "More than two thirds of the finds consist of the remains of deer and cattle."

Thus, in the three Javanese *Homo erectus* sites, Trinil, Kedung Brubus and Ngandong, that have yielded large numbers of specimens, larger herbivores are numerous (Table 3, add Cervidae, Bovidae, Hippopotamidae, Rhinocerotidae, Tapiridae and Proboscidea: Kedung Brubus

Table 5
Minimum number of individuals (MNI) mammals South African sites/members (data taken from Brain, 1981). Only the richer members have been considered. ST = Sterkfontijn, SK = Swartkrans.
Tableau 5
Nombre minimum d'individus (NMI) calculé pour les mammifères des sites/membres d'Afrique du Sud (données extraites de Brain, 1981). Seuls les membres de sites les plus riches ont été considérés. ST = Sterkfontein, SK = Swartkrans.

	Numbers			Percentages		
Groups	ST-4	SK-1	SK-2	ST-4	SK-1	SK-2
A. africanus	45	0	0	*13.6*	*0.0*	*0.0*
P. robustus	0	85	0	*0.0*	*27.2*	*0.0*
Homo sp.	0	3	1	*0.0*	*1.0*	*0.4*
Cercopithecidae	198	89	8	*59.8*	*28.5*	*3.2*
Carnivora	17	37	17	*5.1*	*11.9*	*6.7*
Carnivora small	0	2	4	*0.0*	*0.6*	*1.6*
Artiodactyla	43	55	160	*13.0*	*17.6*	*63.2*
Suidae	2	7	4	*0.6*	*2.2*	*1.6*
Perissodactyla	7	7	13	*2.1*	*2.2*	*5.1*
Proboscidea	1	0	0	*0.3*	*0.0*	*0.0*
Hyracoidea	13	24	37	*3.9*	*7.7*	*14.6*
Rodentia	5	3	5	*1.5*	*1.0*	*2.0*
Lagomorpha	0	0	4	*0.0*	*0.0*	*1.6*
Total	331	312	253	*100.0*	*100.0*	*100.0*

87% and Trinil 88%) while the fossils of hominins are rare, comprising less than 1%. Carnivores are also rare (larger carnivores: Kedung Brubus 2.5% and Trinil 0.3%). Since the numbers of herbivores and carnivores in these fossil faunas occur in the relative proportions predicted by the trophic levels in the ecological pyramid, the rarity of *Homo erectus* opens the possibility that this species, too, filled a carnivorous niche.

Considering the abundance of larger mammals within palaeontological sites, without strong selecting criteria for certain species of the palaeocommunity, the simple expectation is that the remains of secondary consumers will be scarce and those of primary consumers will be plentiful. This seems irrespective of mixing of remains, as for instance is the case with bones fished out of the North Sea. Although "a fossil fauna passes through several stages before it reaches the analyst" (Klein and Cruz-Uribe, 1984: p. 3) – five stages can be recognized: the life, death, deposited, fossil and sample assemblage – this often does not remove the fact that primary consumers leave many more bones than secondary consumers. This can be seen, for instance, in a large site like Elandsfontijn, South Africa, in which both the NISP and MNI of large mammals are considered (Klein et al., 2007). Admittedly, the relative representation of larger carnivores (13.1%) is not very small, it is still unmistakably smaller than that of the larger herbivores. Probably, the remains of *Homo erectus* are just like the bones of tigers, hyenas and *Homotherium*, hard to find and repeatedly lacking or sporadic in palaeontological excavations because larger omnivores and carnivores were rare in palaeocommunities.

In South Africa the occurrence of the genus *Homo* deviated from earlier and contemporary hominins in an interesting way. For instance Lewin and Foley (2004: p. 275) remark in their textbook about the occurrence of baboons and australopithecines: "Judging from the fossil record, australopithecines were as common on the landscape as other large, open-country primates (specifically, baboons). Thus, foraging strategies of hominins and baboons would not have differed dramatically. If australopithecines had been significant carnivores, for example, their population density would have been much lower than that of the principally vegetarian baboons". Although one has to be very careful with comparing sites with different taphonomic histories (Klein and Cruz-Uribe, 1984), considering the MNI of mammals of larger fossil assemblages of South African sites (Brain, 1981) one observes interesting patterns (Table 5). Just as the Javanese sites, remains of herbivores dominate, like Cercopithecidae (baboons) and Artiodactyla (there is one exception SK-2 were Cercopithecidae do not come in large numbers). Carnivores come in smaller numbers, although this picture is less clear in SK-1. Both *Australopithecus africanus* and *Paranthropus robustus* show a frequency comparable with that of herbivores (ST-4 and SK-1), while *Homo* sp. is rare (SK-1 and SK-2). This could suggest an herbivorous niche for *Australopithecus* and *Paranthropus*, and at the same time a more carnivorous niche for *Homo*.

Unfortunately, it is not possible to monitor the transition from mainly herbivory to omnivory in Java itself. Another possibility to test the idea of "lower densities could indicate carnivory" is maybe to use a non-hominin predominantly herbivorous primate like *Trachypithecus cristatus*. The latter mentioned species does not only occur in Trinil but also in Bangle, Sumber Kepuh and Teguan (Table 2). The occurrence of *Trachypithecus cristatus* does not confirm the above-mentioned hypothesis because remains of this species are relatively rare in all four sites. However, I would be skeptical about accepting this refutation because the body mass of *Trachypithecus cristatus* must have been considerably smaller than that of *Homo erectus*. From a taphonomic point of view, it is clear that in the discussed Javanese sites the remains of small animals are underrepresented. Moreover, as the Middle Pleistocene of Java is interpreted as an open woodland (de Vos, 1983; Leinders et al., 1985; Storm, 2001a, 2001b), a species like *Trachypithecus cristatus* was possibly not abundantly present because of the lack of suitable habitat. From this point of view, the best place to test this idea further is Africa. Here we do not only find Middle Pleistocene remains of species of *Homo* but also of *Australopithecus* and *Paranthropus*, species that must have had a body mass and shape closer to each other.

Historically seen the remains of *Homo erectus* in the analyzed Javanese bone assemblages have been given more attention than those of other fossils. If these hominin remains would have been treated in the same way as the rest of the fauna, there is a possibility that the NISP and MNI would have been lower. Another problem is that not all bovid teeth found have been considered in the analysis. Many teeth of Bovidae that have been found in Trinil are not included in the electronic database of the National Museum of Natural History (Leiden, The Netherlands). If these fossils had been included, this should have raised the NISP, and likely the MNI, of bovids. Both problems do not influence the interpretation that *Homo erectus* was probably rare in palaeocommunities. If the two above-mentioned problems would have been tackled, this should have resulted in less abundance of *Homo erectus*, in other words, it should have strengthen the possibility to see *Homo erectus* (partly) as a carnivorous primate.

7. Concluding remarks

Considering large animals, in the discussed Middle Pleistocene Javanese sites, the bones of herbivores clearly come in larger numbers than those of carnivores and omnivores. This conclusion is based on the analysis of five sites, two of them rich in fossil remains. Two different methods (NISP and MNI) applied to these two rich sites, Kedung Brubus and Trinil, lead to the above-mentioned result. Therefore, it is reasonable to assume that, despite all kinds of taphonomic question marks that can be made, these fossil assemblages roughly represent at least two trophic levels in the ecological pyramid of once living communities, that of primary and secondary consumers. The rare occurrence of *Homo erectus*, based on the numbers of fossils and MNI of the three richest sites of Java (Trinil and Kedung Brubus, and in Ngandong only the number of fossils), is comparable with those of larger carnivores and omnivores. This could suggest a higher position in the ecological pyramid of palaeocommunities.

I do not say that the NISP and MNI prove that in Java *Homo erectus* fulfilled a carnivorous niche. What I do say is that this preliminary study of the abundance of fossils in Java does not contradict the idea that *Homo erectus* was (partly) carnivorous. Of course, a number of reasons can be brought forward for trying to explain the rarity of *Homo erectus* remains in Java, but the “carnivorous niche” offers possibly the most logic and parsimonious one. If true, it is without doubt an intriguing observation that a primate that expands its range so wide to include Africa, large parts of Asia and possibly Europe, is so rare in palaeocommunities. This could be an indication that one is dealing with a serious shift to a carnivorous niche. Because this could be an exceptional situation for a larger mammal, knowledge about the niche is a key factor for understanding hominin evolution (Joordens et al., 2009), and admittedly, reconstructing palaeocommunities is far from easy, further testing of this idea is needed.

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