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Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia)

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ABSTRACT

Knowledge about dietary niche is key to understanding hominin evolution, since diet influences body proportions, brain size, cognition, and habitat preference. In this study we provide ecological context for the current debate on modernity (or not) of aquatic resource exploitation by hominins. We use the *Homo erectus* site of Trinil as a case study to investigate how research questions on possible dietary relevance of aquatic environments can be addressed. Faunal and geochemical analysis of aquatic fossils from Trinil Hauptknochenschicht (HK) fauna demonstrate that Trinil at ~1.5 Ma contained near-coastal rivers, lakes, swamp forests, lagoons, and marshes with minor marine influence, laterally grading into grasslands. Trinil HK environments yielded at least eleven edible mollusc species and four edible fish species that could be procured with no or minimal technology. We demonstrate that, from an ecological point of view, the default assumption should be that omnivorous hominins in coastal habitats with catchable aquatic fauna could have consumed aquatic resources. The hypothesis of aquatic exploitation can be tested with taphonomic analysis of aquatic fossils associated with hominin fossils. We show that midden-like characteristics of large bivalve shell assemblages containing *Pseudodon* and *Elongaria* from Trinil HK indicate deliberate collection by a selective agent, possibly hominin.

Introduction

Paleoenvironmental reconstructions of hominin sites provide ecological context for studies of hominin evolution. Habitat characteristics, the nature of predators and competitors, and especially the availability of food resources all determine the realized hominin niche. Diet (and dietary change) is widely considered to be an important factor in hominin evolution (Roebroeks, 2007; Ungar, 2007). So far, emphasis has been mainly on reconstruction of terrestrial, non-aquatic palaeoenvironments (savannah, woodland, riparian woodland) and on availability of terrestrial food resources (e.g., Reed, 1997; Wood and Strait, 2004; Peters and Vogel, 2005; Copeland, 2007; Clark and Plug, 2008). Terrestrial paleoenvironments often include lakes, rivers, deltas, and marshes (e.g., Harris et al., 1987; Feibel et al., 1991; Huffman, 2001; Huffman and Zaim, 2003; Wrangham, 2005; Bettis et al., 2008), which provide drinking water and potential sources of plant and animal foods for hominins.

Little is known about the use of aquatic resources by early hominins (see Erlandson, 2001 for a review). Hominin fossils are often found in association with aquatic fauna. This can be attributed to the fact that coastal margins of aquatic systems such as lakes, rivers, and deltas are taphonomically favorable for fossilization. Mere association of fossil hominins and aquatic fauna is in general not regarded as an indication for consumption of these resources by hominins. Aquatic exploitation is only considered as a relevant factor in hominin evolution when consumption of aquatic food sources can be proven, as has been done for modern humans: *Homo sapiens* from coastal South Africa consumed marine foods at least as early as ~164 ± 12 ka (Marean et al., 2007). Stewart (1994) has studied patterns of possible fish exploitation in early Pleistocene sites at Olduvai Gorge where *H. habilis* and *H. erectus* fossils were found, making “a strong, although not absolute, case for early hominid fish procurement” (Stewart, 1994: 229). The lack, so far, of proof of aquatic exploitation by early hominins has in practice been interpreted as evidence for the opposite (e.g., Marean et al., 2007). This interpretation has strengthened the prevailing assumption that systematic exploitation of aquatic resources is a modern human behavior that is not present in other hominin species. The recently published evidence of Neanderthals in Gibraltar exploiting

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marine resources such as dolphins, seals, molluscs, and fish (Stringer et al., 2008) has challenged this assumption of modernity. Shipman (2008) concluded that the coastal Gibraltar sites have yielded excellent evidence of Neanderthal behaviors that are usually cited as hallmarks of modern human behavior: the exploitation of marine resources and seasonality or scheduling in the use of resources. If Neanderthals living in a coastal habitat were so capable, it favors the question: could other hominins living in a coastal habitat, such as *Homo erectus* on Java, also have accessed aquatic foods?

Homo erectus is one of the earliest hominin species that must have had a considerable amount of animal protein in its diet, as is evident from the fact that its human-like, barrel-shaped thorax could not have provided enough room for the typical long, plant eater's gut (Aiello and Wheeler, 1995). Whether this animal protein was completely derived from terrestrial ecosystems or also came from aquatic fauna—and if so, in what proportion—is unknown. *H. erectus* was an ecological generalist (Wood and Strait, 2004), an opportunistic omnivore likely to have exploited a broad range of dietary elements ranging from plants (fruits, leaves, tubers, seeds) to invertebrates (insects, molluscs), as well as small and large vertebrates. In this respect, *H. erectus* can be compared to omnivorous cercopithecids such as baboons and macaques (Elton, 2006). Both baboons and macaques are known to include aquatic foods in their diet. For instance, the Chacma baboon, *Papio ursinus,* preys on intertidal crabs, limpets, periwinkles, mussels, shrimp, sea lice, and shark embryos (Carlton and Hodder, 2003; Peschak, 2004; Clymer, 2006). The Long-tailed (or Crab-eating) macaque, *Macaca fascicularis,* feeds on crabs, shrimp, aquatic molluscs, frogs, octopi, and fish (Son, 2003; Malaivijitnond et al., 2007; Stewart et al., 2008). In a similar way, aquatic organisms may have been a potential food source for *H. erectus*, and thus aquatic environments may have been important parts of the hominin habitat.

The aim of this study is to provide ecological context for the current debate on modernity (or not) of aquatic resource exploitation by hominins. A suitable area to study possible dietary relevance of aquatic environments for hominins is the Solo Basin on Java, Indonesia (Fig. 1), where *Homo erectus* occurred in a coastal environment encompassing lagoonal, riverine, and sea coast habitats (Huffman, 1999; Huffman et al., 2006). The site of Trinil, where the first *H. erectus* calvaria and femur were found by Eugène Dubois (1894), is particularly convenient for an investigation of aquatic environments. A paleogeographical model of East Java during the Pleistocene (Huffman, 2001; Huffman and Zaim, 2003) indicates that Trinil was situated in a riverine environment at ~65 km distance from lagoonal lakes of Sangiran, close (~15 km) to the sea coast of Randublatung Embayment, and at ~100 km from the Mojokerto Delta (Fig. 2). About 400,000 fossils of terrestrial vertebrates, aquatic vertebrates, and aquatic invertebrates have been excavated from Trinil during expeditions by Dubois from 1891–1900 (Dubois, 1907, 1908), by Selenka from 1906–1908 (Selenka and Blanckenhorn, 1911), and by other parties (see Van Benthem Jutting, 1937). We use these historical collections to reconstruct aquatic paleoenvironments at Trinil in the early Pleistocene and to establish potential availability of aquatic food resources for Javanese *H. erectus*. Further, we provide an ecological comparison with subsistence patterns of other (non-hominin) terrestrial mammals living in coastal habitats. This allows us to discuss the probability of aquatic resource exploitation by hominins, and specifically by *Homo erectus* on Java.

Stratigraphy and chronology of the Pleistocene Solo Basin

The oldest Javanese *Homo erectus* fossils (e.g., Sangiran 27, 4, 31; Indriati and Antón, 2008) were found in the coastal deltaic and lacustrine-marshy deposits of the upper Sangiran (or Pucangan) Formation (Fig. 3a), as part of the endemic, unbalanced island-type Ci Saat fauna (De Vos et al., 1994; Huffman et al., 2006). This fauna contains predominantly species capable of water crossings, such as cervids, *Hexaprotodon*, *Stegodon,* and the felid *Panthera*. The latter is a relatively strong swimmer that can cover distances of 6 to 29 km (Sunquist and Sunquist, 2002).

The increasingly abundant presence of *Homo erectus* continues in the overlying Bapang (or Kabuh) Formation. The sediments of this formation indicate an environmental change from a lacustrine to an aggrading fluvial system (Larick et al., 2001). The Trinil Hauptknochenschicht (HK) fauna in the lower part of the Kabuh Formation contains more species than the Ci Saat fauna, including poor swimmers. This increased species diversity suggests the establishment of a terrestrial connection between the emerging island of Java and the SouthEast Asian mainland (De Vos et al., 1994). Trinil HK is considered to be contemporaneous with the Grenzbank level in the lower part of the Bapang Formation in the nearby Sangiran Dome (Soeradi et al., 1985), dated at ca. 1.5 Ma (early Pleistocene; Swisher et al., 1994; Larick et al., 2001; Bettis et al., 2008; Fig. 3a). However, there is disagreement about the age of Trinil HK: several other researchers prefer a younger age of ~0.9 Ma for Trinil HK (e.g., Van den Bergh et al., 2001; Antón and Swisher, 2001; Antón, 2003; Bouteaux et al., 2007). In the upper part of the Kabuh Formation, fossils of the Kedung Brubus fauna indicate a more mainland character than the Trinil HK Fauna and maximal faunal interchange with the SE Asian mainland (De Vos et al., 1994). The youngest *H. erectus* fossils were found in fossiliferous Solo River terrace deposits at Ngandong (Oppenoorth, 1936; Antón, 2003).

Methods

For reconstruction of aquatic paleoenvironments we focus on the Trinil HK fauna in the lower part of the Kabuh Formation (Fig. 3a,b,c), which also comprises the *Homo erectus* calvaria and femur found by Eugène Dubois (1894). We review fossil fish, mollusc, mammal, bird, and reptile faunas using fossil material and published accounts from historical collections curated at Naturalis National Museum of Natural History (Leiden, The Netherlands). In addition, we perform geochemical (strontium isotope) analyses of fish and mollusc fossils in order to study source waters and salinities of the aquatic habitats. Finally, we assess availability of potential aquatic food sources, based on aquatic faunal inventories. Working with historical collections has a drawback. Although all material derives from Trinil HK layers, as presented in Figure 3b and 3c (Dubois, 1907, 1908; Selenka and Blanckenhorn, 1911; Van Benthem Jutting, 1937), exact stratigraphical provenance within this sequence is not always provided by the excavators. As a consequence, paleoenvironmental reconstructions are relatively general in character and not as detailed as could be achieved when fossils were collected from excavations with a specific reconstruction purpose. The fossils collected by Dubois most likely represent all the fauna encountered in the excavations, since he was known to collect "everything" from large mammals to fish bones and mollusc fragments. The Trinil site presently cannot be excavated because of permanent high water levels of the Solo River. Thus, the rich historical collections from Trinil are the best source of paleoenvironmental information we can access.

Faunal analysis

Fish fossils have been collected from Trinil during excavations by Dubois and by Selenka (Dubois, 1907, 1908; Selenka and Blanckenhorn, 1911). The composition of the fossil fish assemblage at Trinil is based on our study of the fish fossils in the Dubois

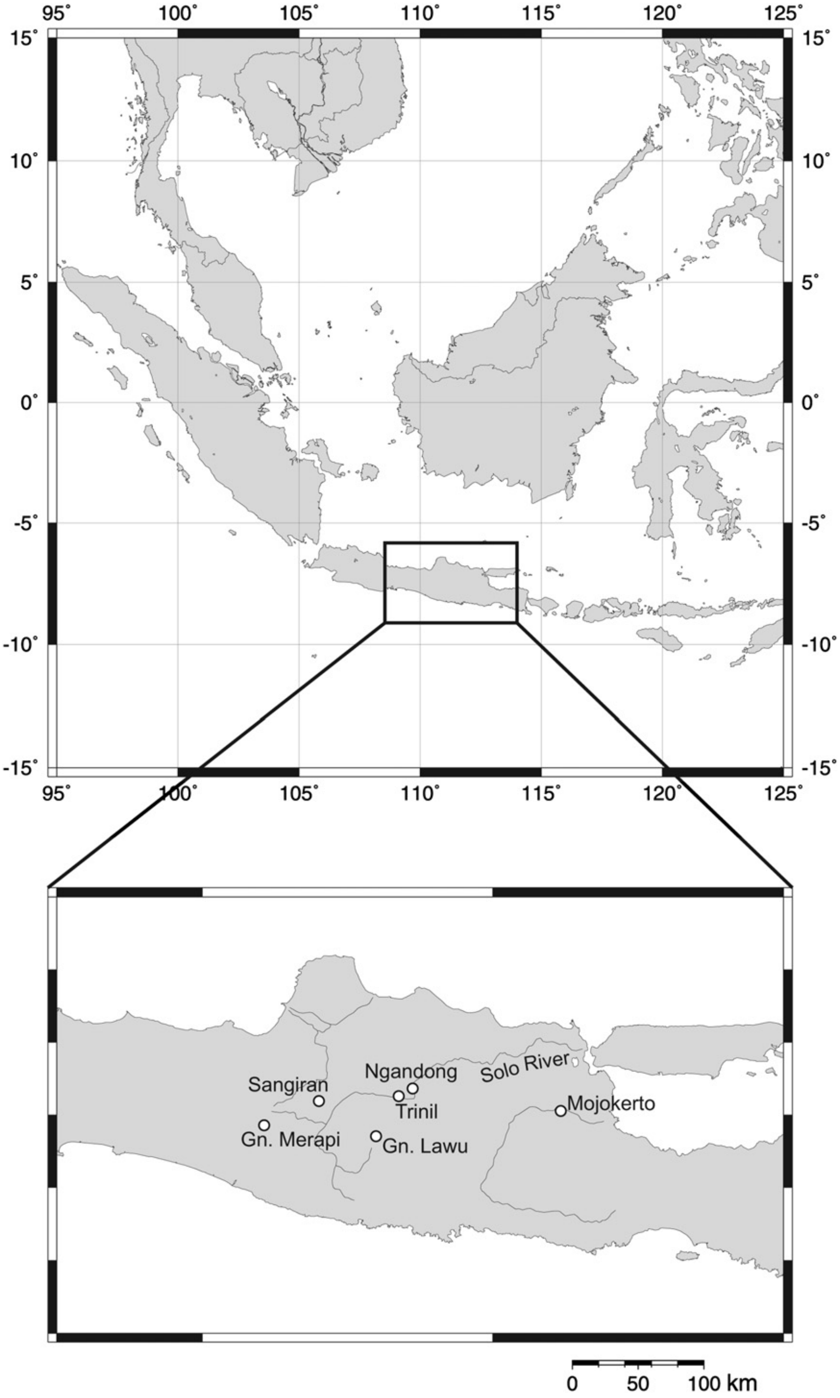

Fig. 1. Map of the Indonesian region with islands Sumatra, Borneo, and Java. Inset rectangle: Central Java showing present-day river systems, hominin sites, and volcanoes. Gn. = Gunung (volcano).

collection and on published accounts of fish fossils from the Dubois and Selenka collections (Boeseman, 1949; Dubois, 1907, 1908; Hennig, 1911; Koumans, 1949). Ecological and size data of fish species were obtained from Fishbase (www.fishbase.org).

Both Dubois and Selenka also assembled extensive collections of fossil shells (Dubois, 1907, 1908; Dozy, 1911; Martin, 1911; Martin-Icke, 1911). Furthermore, fossil shells were excavated at Trinil by the Geological Survey of the Netherlands Indies, Bandung, in the 1930's. The non-marine shells from these collections were studied in detail by Van Benthem Jutting (1937). She mentioned that marine shells were found at Trinil, but they were not considered in her publication. To obtain a more complete picture of paleoenvironmental conditions in Trinil, we identified both non-marine and marine molluscs in molluscan bulk samples (fossiliferous sediment samples) collected by Dubois from the sandstone and andesititic tuff layers at Trinil (Fig. 3b,c). These samples had not been studied before by malacologists and provide new data on the mollusc fauna. They are curated as part of the Dubois Collection at Naturalis, Leiden (collection numbers 1543, 1546, 6900, 8138, 9608, 9609, 9665, 9687, 9691, 9694, 9697, 9779, 9820). Three bulk samples (Trinil 9691, 1546, 9697) were analysed in detail by identifying and counting every recognizable shell larger than 2 mm from 1.5 kg of fossiliferous sediment. Data on

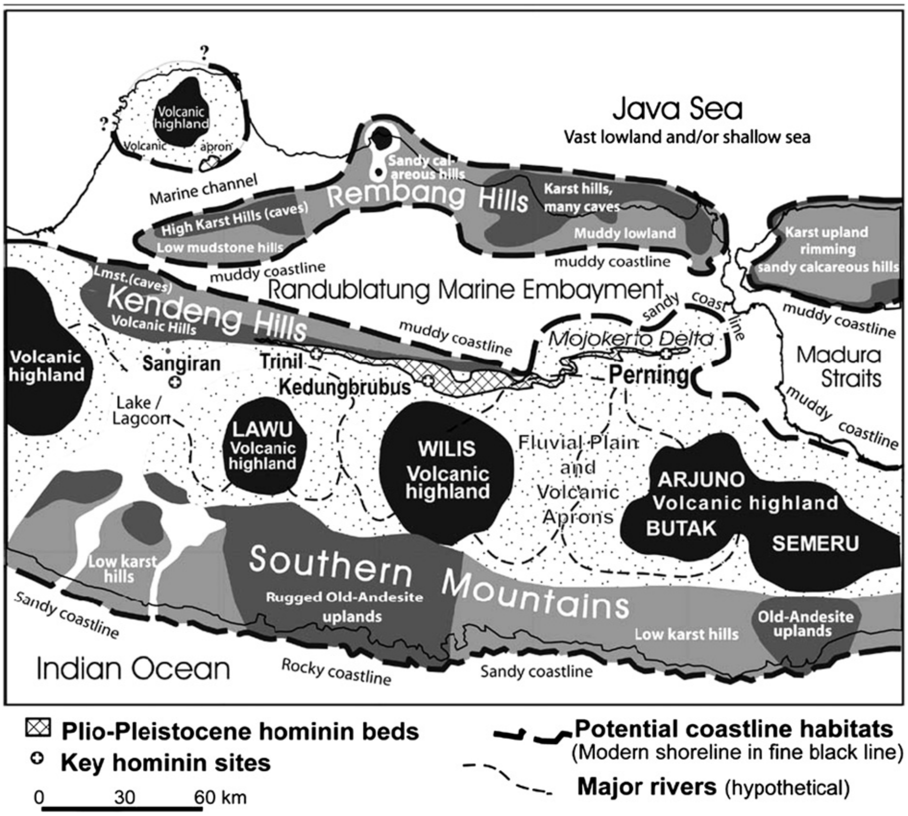

Fig. 2. Paleogeographic model of Pleistocene Central Java (from Huffman and Zaim, 2003; adapted from Huffman et al., 2000). The geological reasoning behind this model is addressed in Huffman (2001). The model illustrates the close proximity of diverse long-standing paleogeographic features of the eastern Javan landscape during the period of *Homo erectus* habitation. It is diagrammatic, not intended to show paleogeography at any specific moment in time.

the mammalian, reptilian, and avian faunal composition from Trinil were obtained from published accounts (e.g., De Vos and Sondaar, 1982; Weesie, 1982; Delfino and De Vos, 2006).

Geochemical analysis

Strontium isotope analyses were applied in order to determine water provenance and water salinities of the aquatic paleoenvironments at Trinil. In well-preserved shells, fish bones, stingray stings, and other aquatic fossils, Sr isotope ratios of the fossils are unaffected by biological or climatological fractionation processes and reflect the Sr isotope ratio of the host water in which they were growing (Faure, 1986). In the early Pleistocene there were two main sources of freshwater that determined the strontium isotope ratio ($^{87}Sr/^{86}Sr$) of waters in the Solo Basin: 1) run-off from the volcano Gunung Merapi on Central Java draining volcanics with Sr isotope values of ~0.705–0.706 (Gertisser and Keller, 2003) and 2) run-off from Gunung Lawu on East Java draining volcanics with Sr isotope values of ~0.7046–0.705 (Whitford, 1975; Carn and Pyle, 2001). In addition, episodic marginal marine influence of seawater with a Sr isotope ratio of ca. 0.7091 was also a possible contribution (McArthur et al., 2001). Due to the relatively high Sr concentration in seawater (100–1000 times higher than freshwater; Palmer and Edmond, 1989; Vonhof et al., 1998, 2003), even a minor seawater component in the aquatic system will strongly influence the $^{87}Sr/^{86}Sr$ of aquatic fossils.

Strontium isotope ($^{87}Sr/^{86}Sr$) analyses were carried out on a modern freshwater shell from the Solo river collected by Dubois near Trinil and on well-preserved fossil material (seven shells, three fish bones) from Trinil and the Sangiran Dome following the approach and methods outlined in Vonhof et al. (1998, 2003). We analyzed species that we expected to represent a variety of habitats in the Solo Basin. SEM inspection of the fossil shells revealed that the original lamellar aragonite structure was still present (Fig. 4a,b) with occasional evidence for minor aragonite dissolution (Fig. 4c). Diagenetic overgrowth was absent. The absence of diagenetic aragonite leads us to believe that diagenetic alteration of the original Sr-isotope signal has not occurred.

For isotopic analysis of Sr in shell fossils, about 0.001 g of cleaned HCl-leached shell was dissolved in 1 ml 5 N HAc. After centrifuging the samples within 30 minutes from the start of the reaction, the supernatant was pipetted off and Sr was separated by use of an ion exchange resin. For Sr isotope analysis of fish bone and spine fossils, a small piece of cleaned bone was added to 1 ml 5 N HAc for 30 minutes to dissolve any carbonate present. After centrifuging, the supernatant was pipetted off and discarded, and about 0.001 g of the remaining leached bone was dissolved in 3 N HNO_3 for subsequent Sr separation with 'Elchrom Sr spec' ion exchange resin. $^{87}Sr/^{86}Sr$ ratios were determined by standard mass spectrometric methods (Thermofinnigan MAT 261 and 262), and normalized to $^{86}Sr/^{88}Sr = 0.1194$. The average $^{87}Sr/^{86}Sr$ ratio of the NBS 987 standard ($n = 14$) was 0.710245 ± 0.000009. Sr in the blanks was $< 0.05\%$ of the Sr measured. To obtain an approximate value of the Sr concentration of Central-East Javan freshwater, a water sample was taken from the modern Solo river at Waduk Ngablak (7°51′32″ S, 110°25′26″E) where living bivalve shells were present in the river. The sample remained unfiltered and unacidified prior to analysis. The Sr concentration of the sample was measured using ICP-MS (Thermo electron X-series II) and linear regression against a single element Sr standard (CPI).

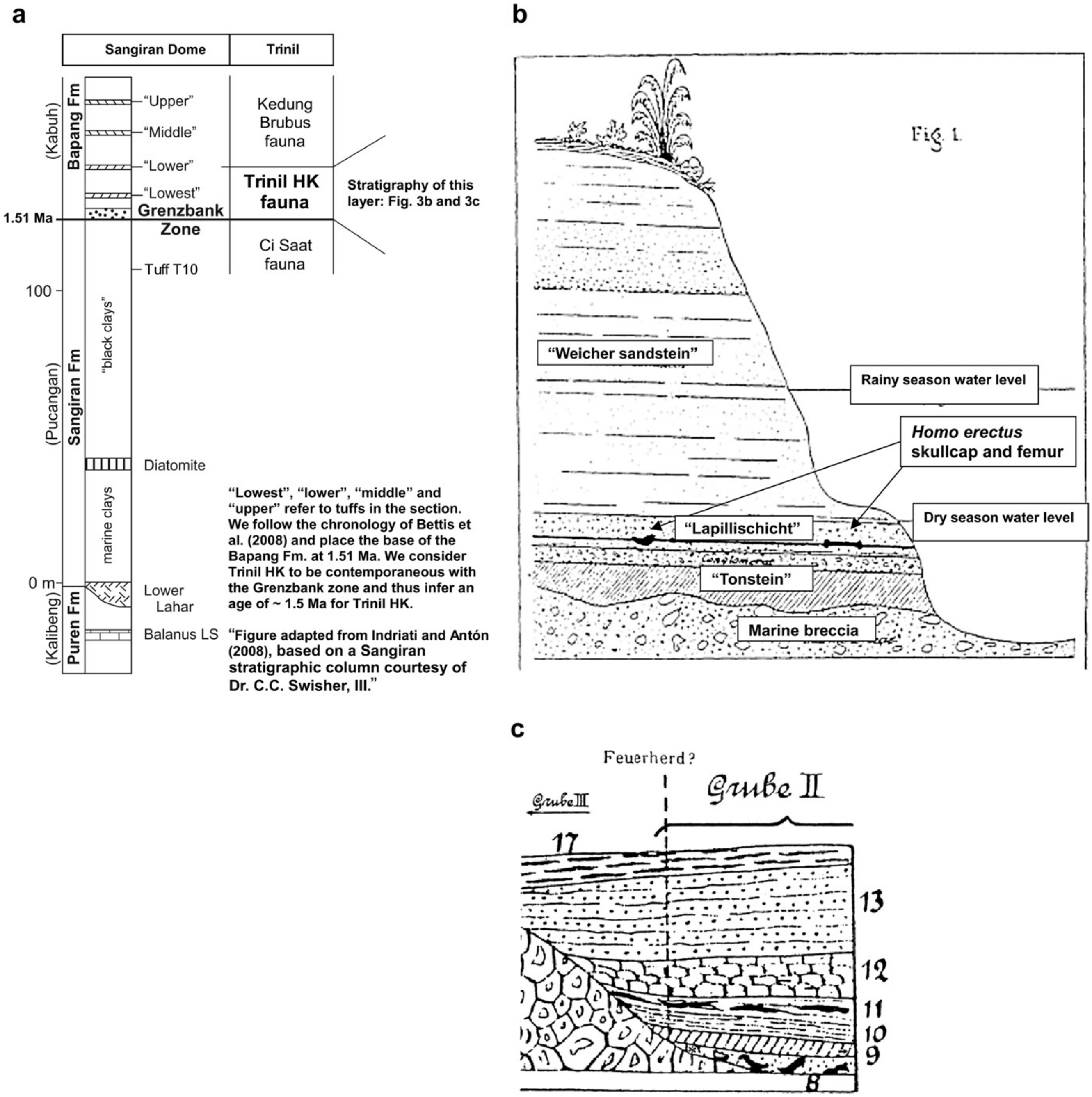

Fig. 3. (a) Stratigraphy of the Plio-Pleistocene Solo Basin. The age of the Grenzbank deposits (≈Trinil HK) was determined by Larick et al. (2001) to be ~1.51 Ma, while others assumed a younger age of ~0.9 Ma (e.g., Bouteaux et al., 2007). The Sangiran Formation is also known as the Pucangan Formation, and the Bapang Formation also as the Kabuh Formation (Duyfjes, 1936). (b) Stratigraphy of Trinil HK, the type locality of *Homo erectus*, according to Dubois (1896). Sequence from top down: modern soil layer, soft sandstone layer, lapillibed or main bone bed (with position of *H. erectus* skullcap and femur), conglomerate, mudstone, marine breccia. Two river water levels are indicated, the lower one is the level during the dry season and the higher one the level during the wet season. The thickness of the lapillibed is about 1 m, that of the conglomerate about 0.5 m. (c) Stratigraphy of the "Pithecanthropusschichten" (Trinil HK) according to Carthaus (1911) in Selenka and Blanckenhorn (1911). This excavation in Grube II (Trench II) by the Selenka expedition was situated at the same place as Dubois' excavations but more landward (De Vos and Aziz, 1989). 8 = Bone bed, 9 = Plant leave bed, 10 = Sandstone-like tuff (white-striped), 11 = Tuff with loam patches, 12 = Volcanic mud tuff, sandstone, 13 = Sand-stone like tuff (light-coloured), 17 = Soil. The wedge in the lower left of the drawing is a conglomerate underlying the bone bed.

Results

Faunal analysis: fish

In total, we have encountered nine fish species in the fossil fauna from Trinil (Table 1). The collections are numerically dominated by catfish remains: *Clarias batrachus*, *Clarias leicanthus*, *Hemibagrus nemurus*, and unidentified silurids (Table 2).

Two spine fragments (1639c) from the Dubois collection, identified by Koumans (1949) as "Siluroidae fin spines," were found to be tail spines (stings) of stingrays (Fig. 5). The spine characteristics (estimated total spine length, lack of dorsal groove) match with those of *Pastinachus sephen* and *Himantura chaophraya* (Schwartz, 2007; Cuny and Piyapong, 2007). The conspicuous robustness of the spine is similar to the robustness documented from an (incomplete) spine specimen of the Giant Freshwater Stingray *Himantura*

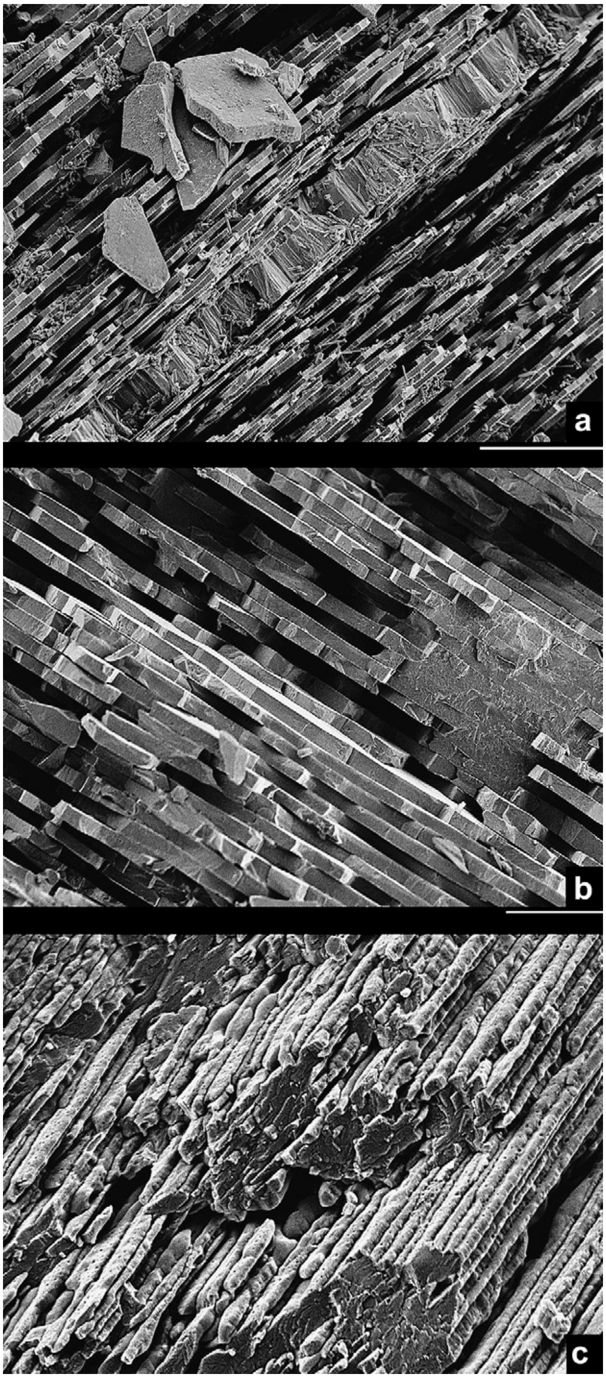

Fig. 4. a: Well-preserved lamellar aragonite of the bivalve *Pseudodon vondembuschianus trinilensis* (DUB 5234). b: Well-preserved lamellar aragonite of the bivalve *Elongaria orientalis* (DUB 11364). c: Lamellar aragonite of the gastropod *Tarebia* cf. *granifera* (DUB 9963) with minor aragonite dissolution.

chaophraya (Cuny and Piyapong, 2007). Gilles Cuny (pers. comm.) concluded that the fossil stingray can be tentatively assigned to the latter species. A definite identification can be made only if complete spines of the fossil stingray and of *H. chaophraya* are found.

Faunal analysis: molluscs

Among the mollusc fossils from Trinil (Tables 3 and 4), well-preserved, fragile species are common, as are paired bivalves. Only a few abraded specimens were found; the preservation state was very similar for all shells. The most abundant species in the Dubois and Bandung collections is the large-bodied (ca. 100 mm length) pearly freshwater mussel *Pseudodon vondembuschianus trinilensis* (Fig. 6a). The Selenka collection contains only four *Pseudodon* valves, although Martin (1911) remarked upon the abundance (“zahlreich”) of these bivalves in Trinil HK deposits. The collections also contain many fragments of *Pseudodon* shells. The second and third-most abundant species are the small gastropod *Tarebia granifera* and the bivalve *Elongaria orientalis*. Of the other mollusc species, only a few (∼ 1–20) specimens are present.

Van Benthem Jutting (1937) noted conspicuous characteristics of the shell assemblages. *Pseudodon* is by far the most numerous species, with about 10 to 200 times as many shells as the other species. The *Pseudodon* shells are characterized by uniformity in large size (90 to 120 mm length) and absence of smaller and juvenile specimens. There are only two specimens of 80 mm length or less in the collections from Trinil, namely samples 9744 (69 mm) and 9747 (80 mm) in the Dubois collection. The collected fragments do not show the occurrence of any young *Pseudodon*. Many valves are paired. Two forms of *Pseudodon* shells can be distinguished in the collections, one broad and one stretched; the latter has a rostrum-like tailend that curves downwards. The two different forms are, according to Van Benthem Jutting (1937), “reaktionsformen” (eco-phenotypes). The two different forms are frequently associated in lots carrying the same field label, indicating that they were found together as fossils. Another characteristic is that the *Pseudodon* shells were only found in a very limited area: a total of 369 valves are present in collections from Trinil itself; four valves were collected from Kedung Brubus plus two fragmented valves from Tritik, but none from elsewhere on Java.

Elongaria orientalis shells are also relatively numerous in the collections (Table 4), although less so than the *Pseudodon* shells. Many of the shells are defective: in most cases the posterior part is missing. The *Elongaria* shells have a length of 40–60 mm (middle to adult size), and no remains of young individuals (< 25 mm length) are present in the collections. Two shell forms occur side by side in the samples: one shell form has a stretched and slightly uplifted posterior end in which the ventral side is horizontal or a little convex, and one shell form has a curved and descending tailend and a conspicuously concave base-line.

The bulk samples collected by Dubois are dominated by the gastropods *Melanoides* aff. *tuberculata, Tarebia granifera* (Fig. 6f,g), and *Thiara scabra. Pseudodon vondembuschianus trinilensis* has not been encountered in the samples (except one partial *Pseudodon* valve in sample 1543), and only a few, subadult specimens of *Elongaria orientalis* were found in some of the bulk samples. Marine molluscs are present in low numbers. The marine chemosymbiont bivalve *Eamesiella* aff. *corrugata* (Fig. 6b–e) was found in eight samples (6900, 9608, 9609, 9665, 9687, 9691, 9694, 9779). The three bulk samples that were analyzed in detail (1546, 9691, and 9697) contain 28 mollusc species (Table 5). The fauna is dominated by freshwater to oligohaline cerithoidean species but also contains 17 brackish-marine species previously unknown from Trinil. Furthermore, low numbers of obligate fresh water taxa were found. The shells are well preserved: for example, several of the *Eamesiella* valves could be matched.

The species composition of the Dubois, Selenka, and Bandung collections (Table 4) differs from that of the Dubois bulk samples (Table 5). The bulk samples contain relatively low numbers of (marginal) marine species while the other collections do not, but this is because marine shells were already separated from these collections in the 1930’s (Van Benthem Jutting, 1937). The large bivalves *Pseudodon* and *Elongaria* are the most numerous shells in the Dubois, Selenka, and Bandung collections, while they are lacking and rare, respectively, in the Dubois bulk samples.

Table 1
The fossil fish of Trinil[a]

Current name	Synonyms	Length	Common name	Habitat
_Anabas testudineus_* (Bloch, 1792)	_Anabas microcephalus_	25 cm	Climbing perch	Lakes, rivers, brooks, flooded areas, stagnant water bodies, estuaries; often in areas with dense vegetation. Can walk overland using its auxillary air breathing organ.
_Channa cf. striata_* (Bloch, 1793)	_Ophiocephalus palaeostriata_	100 cm	Snakehead	Muddy lowland rivers, swamps, estuaries. Air-breather, can survive periods outside water.
_Clarias batrachus_* (Linnaeus, 1758)	_Clarias magur_	47 cm	Walking catfish	Lowland streams, swamps, dry river pools, stagnant and muddy water. Can leave the water and walk to migrate to other water bodies using its auxillary air breathing organ. Can tolerate brackish waters.
_Clarias leiacanthus_* (Bleeker, 1851)	_Clarias magur_	33 cm	Forest walking catfish	Forest streams, muddy pools. Airbreathing organ.
_Hemibagrus nemurus_* (Valenciennes, 1840)	_Macrones nemurus_	65 cm	Asian redtail catfish	Muddy rivers, flooded forests.
_Glyphis gangeticus_* (Müller & Henle, 1839)	_Carcharias gangeticus, Eulamia gangetica_	204 cm	Ganges shark	Muddy, turbid rivers, lakes, and estuaries.
Pristis sp.*	_Pristis sp._	600 cm	Sawfish	Rivers, lakes, estuaries, shallow coastal waters
Himantura cf. _chaophraya_* (Monkolprasit and Roberts, 1990)	previously not identified	500 cm	Giant Freshwater Stingray	Sandy bottoms of large rivers and estuaries
_Carcharius taurus_* (Rafinesque, 1810)	_Odontaspis_ cf. _cuspidata_	320 cm	Sand tiger shark	Continental shelf up to 190 m deep, shallow bays, estuaries, sometimes enters river mouths.

[a] Fossil identification, except for *Himantura* cf. *chaophraya*, as in Dubois, 1907, 1908; Hennig, 1911; Koumans, 1949; Boeseman, 1949. Current species/family/common names as well as length and habitat information: www.fishbase.org. *edible species.

Faunal analysis: mammals, reptiles, and birds

A list of the mammalian, reptilian, and avian species found at Trinil is presented in Table 6, with an indication of the typical habitat for each species. The 18 mammal species are terrestrial (i.e., non-aquatic), except for the otter *Lutrogale* sp. The reptiles are all aquatic or semi-aquatic, and four out of the five bird species are (semi-)aquatic. The composition of the fauna indicates a paleoenvironment consisting of lowland tropical forest, grasslands, floodplains, swamps, lakes, and rivers. None of the species can be considered to be typically marine, although at least 11 of the 18 species are known to occur in estuaries and mangrove areas.

Geochemical analysis

Table 7 presents the Sr isotope ratios of several fish and mollusc fossils from Trinil (Dubois Collection) and Sangiran Dome (Von Koenigswald Collection), as well as the Sr isotope ratio of a recent shell collected from the Solo River near Trinil. All molluscan shells and fish bones—including the stingray spines—have Sr isotope ratios lower than the values typical of early Pleistocene seawater (0.709102–0709136; McArthur et al., 2001), confirming that these fish and molluscs were living in a non-marine habitat. The Sr isotope ratio of a *Physunio* shell collected by Dubois from the Solo River near Trinil is 0.705499 ± 0.000011, showing the influence of Gunung Merapi volcanics on the modern river Solo water. In contrast, the lower Sr isotope ratio (0.704946) of a fossil *Tarebia* shell from Trinil (sample no. 11422) indicates a relatively important contribution of Gunung Lawu source water to the Pleistocene Trinil aquatic habitat. It is striking that several aquatic fossils (11364, 9694, F588, 9693; Table 7) have Sr isotope ratios considerably above 0.706, the maximum value expected for Central-East Javan freshwater systems (Whitford, 1975; Carn and Pyle, 2001; Gertisser and Keller, 2003). These values suggest admixture of marine water into the Solo Basin freshwater system.

To test this, we applied a binary mixing model (Vonhof et al., 1998, 2003) with Central-East Java freshwater and early to middle Pleistocene seawater as endmembers (Table 8). The measured Sr concentration of the modern Solo River is 0.413 ppm, which is about 4–5 times higher than expected for freshwater draining volcanic areas, with a Sr isotope ratio of ∼0.705 (Palmer and Edmond, 1989). This high value is likely to be caused by the strong anthropogenic influence (erosion, agriculture, industrial pollution) on modern Javan rivers, thus not being representative for the Sr concentration of Pleistocene East-Central Javan freshwater. Anthropogenic influence on modern rivers is a typical problem in Sr geochemistry (Palmer and Edmond, 1989; Bentley, 2006). Therefore, we also ran the binary mixing model with an inferred typical non-anthropogenic Sr concentration (0.097 ppm) for volcanic catchments, based on the average Sr concentration of five rivers draining such catchments (Palmer and Edmond, 1989). The results of the binary mixing model

Table 2
Fish fossil elements of Trinil[a]

Name	Dubois Collection	Sekenka collection
Anabas testudineus (Bloch, 1792)	3 opercula	
Channa cf.. *striata* (Bloch, 1793)	2 left interopercula 1 right operculum 1 right epi- and ceratohyale 1 basisphenoid fragment	4 frontalia 1 operculum
_Clarias batrachus_* (Linnaeus, 1758)	3 occipitalia superiora 2 left frontalia 6 postclavicula fragments 7 pectoral spines	1 postclavicula
Clarias leiacanthus (Bleeker, 1851)	1 right frontal	
Hemibagrus nemurus (Valenciennes, 1840)	9 pectoral spines	
Siluroidea unidentified	3 pectoral spines 2 pectoral spine fragments 1 dorsal spine	13 pectoral spines
Glyphis gangeticus (Müller & Henle, 1839)	15 teeth from upper jaw 1 tooth from lower jaw	12 teeth 2 vertebrae
Pristis sp.		1 rostral spine
Himantura cf. *chaophraya*? (Monkolprasit and Roberts, 1990)	2 pieces of tail spine	
Carcharius taurus (Rafinesque, 1810)	2 teeth with bases	
Non-identified fish	10 vertebrae	1 tooth 8 vertebrae

[a] Fossil identification, except for *Himantura* cf. *chaophraya*, as in Dubois, 1907, 1908; Hennig, 1911; Koumans, 1949; Boeseman, 1949.

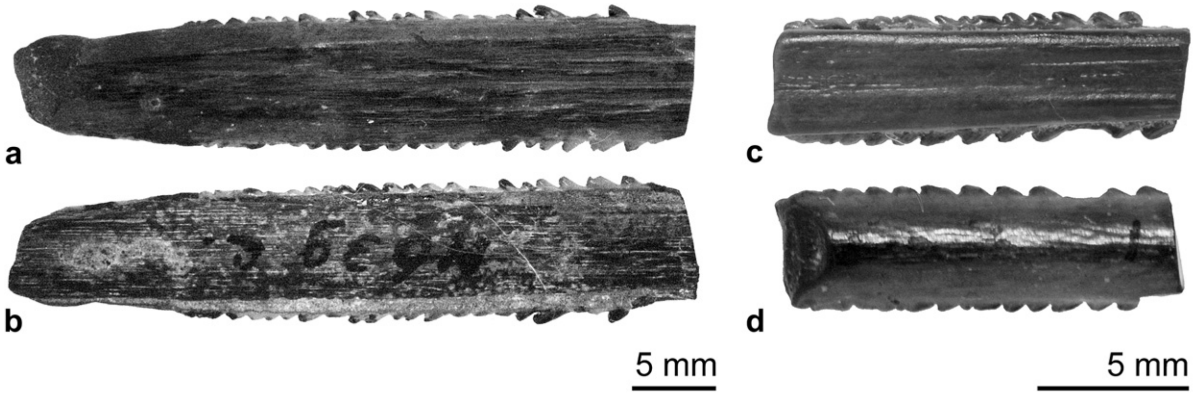

Fig. 5. Stingray spine pieces from Trinil (DUB11639c) tentatively assigned to *Himantura* cf. *chaophraya* (Monkolprasit and Roberts, 1990). a: Ventral side of large specimen. b: Dorsal side of large specimen. c: Ventral side of small specimen (probably juvenile). d: dorsal side of small specimen. The spines have a straight shape and symmetrical rows of barbs. Dorsal surface is smoothly convex, without dorsal groove. The ventral surface has two marginal grooves bordering a flat axial rib. The sides of the rib are squared off, although in a few specimens the marginal grooves slightly undercut the rib. The spines are conspicuously robust with a width of up to 10 mm (range 4–10 mm) and a barb frequency of circa seven barbs per cm (range 5–10 per cm). Based on typical stingray spine proportions, estimated maximum total spine length would have been at least 200 mm.

with the inferred "natural" Sr concentration of 0.097 ppm (Fig. 7a) indicate the occurrence of a salinity range between 0.5–5 ppt causing low salinity brackish (oligohaline) conditions. The results of the binary mixing model with the "anthropogenic" Sr concentration of 0.413 ppm (Fig. 7b) indicate that the relatively high Sr isotope ratios would reflect a salinity range of 5–12 ppt, causing low to moderately brackish (oligohaline to mesohaline) conditions in the Solo Basin at the level of the Trinil HK (Fig. 8).

Table 3
Mollusc species from Trinil[a]

Species name	Family name	Habitat
Pila conica (Gray, 1828)*	Ampullariidae	Vegetation zone of stagnant water, ponds, swamps
Bellamya javanica (Von dem Busch, 1844)	Viviparidae	Bottom- or plant dweller, lives in ponds and swamps
Stenothyra sp. (Robba et al., 2003)	Stenothyridae	Brackish water mudflats
Digoniostoma truncatum (Eydoux and Souleyet, 1852)	Bithyniidae	Bottom- or plant dweller, lives in ponds and swamps
Cerithium sp.	Cerithiidae	Shallow marine
Brotia testudinaria (Von dem Busch, 1842)	Pachychilidae	Eurytopic: in running as well as stagnant freshwater, between sea level and 1500 m altitude
Melanoides aff. *tuberculata* (Müller, 1774)*	Thiaridae	Ponds, rivers, lakes, estuaries; can tolerate brackish water
Melanoides cf. *plicaria* (Born, 1780)*	Thiaridae	Uncertain
Tarebia granifera (Lamarck, 1822)*	Thiaridae	Lakes, rivers, shallow fast-flowing freshwater streams, ponds and swamps, occasionally in slightly brackish water
Thiara zollingeri fennemai (Martin, 1905)	Thiaridae	Freshwater, may have tolerated brackish water
Thiara cf. *tjemoroensis* (Martin, 1905)*	Thiaridae	Uncertain
Thiara scabra (Müller, 1774)*	Thiaridae	From sea level up to 2000 m, in stagnant or running water, also in brackish estuaries
Melongena sp.	Melongenidae	Estuaries, salt marshes, mangroves, shallow marine biotopes
Quirella cf. *lyngei* (Robba et al., 2003)	Pyramidellidae	(marginal) marine, parasite
Cingulina sp.	Pyramidellidae	(marginal) marine, parasite
Didontoglossa cf. *decoratoides* (Habe, 1955)	Retusidae	Sandy mud bottoms, 10–50 m depth
Gyraulus convexiusculus (Hutton, 1849)	Planorbidae	Vegetation zone of stagnant water, ponds, swamps
Lymnaea javanica (Mousson, 1849)	Lymnaeidae	Vegetation zone of stagnant water, ponds, swamps
Ameria duboisi (v. Benthem Jutting, 1937)	Lymnaeidae	Vegetation zone of stagnant water, ponds, swamps
Quirella cf. *lyngei* (Robba et al., 2003)	Pyramidellidae	Marine soft bottom
Jupiteria sp.	Nuculanidae	Marine soft bottom
Anadara cf. *granosa* (Linnaeus, 1758)	Arcidae	Tidal flat and muddy bottoms seaward fringe of mangroves
Mytilidae indet.	Mytilidae	Marine or marginal marine, substrate dependent
Eamesiella aff. *corrugata* (Deshayes, 1843)	Lucinidae	Marine to brackish chemoautotrophe
Cycladicama cumingii (Hanley, 1844)	Ungulinidae	Marine, sand-mud bottom, 10–50 m depth
Tellimya sp. 1 (Robba et al., 2002)	Montacutidae	Marine, parasite
Arcopagia pudica (Hanley, 1844)	Tellinidae	Muddy bottom infralittoral zone and in front of mangroves
Arcopagia yemensis (Melvill, 1898)	Tellinidae	Marine soft bottom
Gari sp.	Psammobiidae	Marine soft bottom
Theora lata (Hinds, 1843)	Semelidae	Marine soft bottom
Elongaria orientalis (Lea, 1840)*	Unionidae	Lakes and rivers
Rectidens sumatrensis (Dunker, 1852)*	Unionidae	Lakes and rivers
*Pseudodon vondembuschianus trinilensis** (Dubois, 1908)	Unionidae	Forest streams and sandy, shallow areas in lakes and rivers
Corbicula pullata (Philippi, 1850)*	Corbiculidae	Streams, quiet fresh to occassionally brackish waters
Corbicula gerthi (Oostingh, 1935)*	Corbiculidae	Streams, quiet fresh water
Geloina sp.	Corbiculidae	Estuaries, mud flats, mangroves
Dentalium sp.	Dentaliidae	Marine

[a] Fossil identification based on Van Benthem Jutting (1937) and our analysis of previously unstudied bulk samples collected by Dubois and curated at Naturalis, Leiden. *species assumed to be edible. Habitat information from Dillon (2000) and Robba et al. (2002, 2003).

Table 4
Number of shell fossils in collections of Dubois, Selenka, and the Geological Survey Bandung[a]

Species name	Dubois	Selenka	Geol. S.B.
Pila conica	2	1	–
Bellamya javanica	2	3	–
Digoniostoma truncatum	–	3	–
Brotia testudinaria	–	15	8
Tarebia granifera	14	16	29
Thiara zollingeri fennemai	5	2	–
Thiara scabra	–	2	–
Gyraulus convexiusculus	–	1	–
Lymnaea javanica	11	6	–
Ameria duboisi	2	1	–
Elongaria orientalis	22/2	8/2	14/2
Rectidens sumatrensis	2/2	–	9/2
Pseudodon vondembuschianus trinilensis	263/2	4/2	102/2
Corbicula pullata	1/2	–	–
Corbicula gerthi	15/2	–	–

[a] Shells from bulk samples are not included. Bivalve species are reported as halves (two valves make a single specimen). The gastropods from the Selenka collection derive from layers just above and just below the Hauptknochenschicht and from the Hauptknochenschicht itself (Martin-Icke, 1911). The provenance of the bivalves from the Selenka collection is not clearly indicated ("Pithecanthropusschichten"; Martin, 1911). The same applies to the shells from Dubois and Bandung collections.

Discussion

Trinil paleoenvironments

The aquatic fossils found in Trinil HK deposits should be regarded as belonging to the same fauna (Dubois, 1908). The Trinil fish fauna includes species living in turbid lowland rivers, lakes, areas with submerged trees and aquatic vegetation, swampy areas with low oxygen content, and estuaries with brackish water. *Himantura chaophraya* is a recently described large stingray occurring on sandy bottoms of estuaries and large rivers of Asia and Oceania (Monkolprasit and Roberts, 1990). The shark *Glyphis gangetica* as well as the sawfish *Pristis* sp. are also typical freshwater-estuarine dwellers. In contrast, the sand tiger shark *Carcharius taurus* is a coastal marine species that only rarely enters river mouths.

The mollusc fauna from Trinil HK is dominated by freshwater species, some of which may tolerate slightly brackish (lagoonal) conditions, and furthermore contains relatively low numbers of strict freshwater, as well as brackish to marine species. The latter group contains several extant species currently living in brackish mudflats, lagoons, and near or in mangroves. The ecological signature of the mollusc fauna is consistent with that of the fish fauna, indicating predominantly near-coastal lowland freshwater settings:

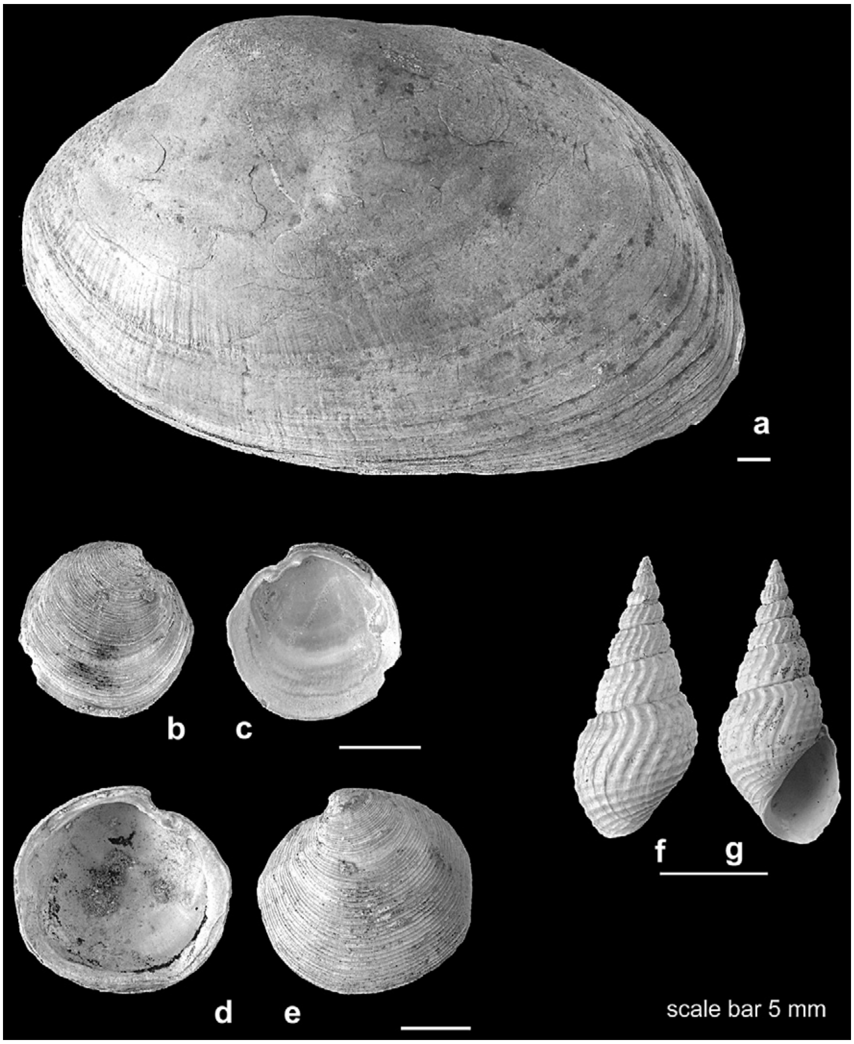

Fig. 6. Selected molluscs from Trinil HK, collected by the Dubois Expedition, 1900. a: *Pseudodon vondembuschianus trinilensis* (Dubois, 1908). b–e: *Eamesiella* aff. *corrugata* (Deshayes, 1843). f–g: *Tarebia granifera* (Lamarck, 1822).

Table 5
Molluscs counted from bulk samples Trinil 9691, 1546, 9697[a]

	9691	1546	9697
Bellamya javanica (Von dem Busch, 1844)	1	4 fr.	10
Stenothyra sp. (Robba et al., 2003)		1	85
Digoniostoma cf. *truncatum* (Eydoux and Souleyet, 1852)			4
Bithinyidae sp. operculum			1
Cerithiidae sp.	2		3
Melanoides aff. *tuberculata* (Müller, 1774)		138	c. 780
Melanoides cf. *plicaria* (Born, 1780)	21	51	31
Tarebia granifera (Lamarck, 1822)	522	72	>1000
Thiara scabra (Müller, 1774)	754	9	c. 600
Thiara cf. *tjemoroensis* (Martin, 1905)	16	4	24
Neogastropoda indet.	1		
Quirella cf. *lyngei* (Robba et al., 2003)	1		12
Cingulina sp.			1
Didontoglossa cf. *decoratoides* (Habe, 1955)			6
Dentalium sp.			2
Jupiteria sp.	1/2		2 + 3/2
Anadara cf. *granosa* (Linnaeus, 1758)			1 fr.
Mytilidae indet.			1/2
Eamesiella aff. *corrugata* (Deshayes, 1843)	99/2	1 fr.	59/2
Cycladicama cumingii (Hanley, 1844)	1/2		8/2
Tellimya sp.1 (Robba et al., 2002)			1/2
Arcopagia yemensis (Melvill, 1898)	10/2		4/2
Arcopagia pudica (Hanley, 1844)	1/2		
Gari sp.	1/2		
Theora lata (Hinds, 1843)	5/2		8/2
Elongaria orientalis (Lea, 1840)	1/2	1/2 + 2 fr.	1/2 + 2 fr.
Corbicula pullata (Philippi, 1850)	13/2	26/2	35/2
Corbicula gerthi (Oostingh, 1935)	6/2	3/2	3/2

[a] Countable shells larger than 2 mm were counted from 1.5 kg. bulk sediment sample. Bivalve species are reported as halves (two valves make a single specimen). Bulk samples derive from the sandstone and andesitic layers (soft sandstone layers, Fig. 3b) above the "Lapillischicht." Dubois uses the words "zandsteen" (sandstone) and "tuf" (tuff) in ways that seem to indicate the same. For instance, in one of his notebooks (p. 245, Dubois Archive, Box 3) he mentions "andesietzandsteen bij Trinil" with the word "tuf" written just above "zandsteen." The labels of the bulk samples are marked "zandsteen" or "andesiet tuf." We assume he refers to the same layer: "weicher sandstein" (soft sandstone) in Figure 3b, which has been presented in a more detailed way by Carthaus (layers 10–13, Fig. 3c).

shallow rivers and lake water with both muddy and well-aerated clean sandy bottoms, lagoons, and swamps with low-oxygen and brackish conditions. The presence of marine shells corroborates the occurrence of marine influence in the freshwater system, as does the presence of the marine sand tiger shark *Carcharius taurus*. Together, the mollusc, fish, bird, reptile, and mammal faunas from Trinil indicate the presence of a coastal plain environment containing lowland tropical forest, as well as open grasslands. In these environments, rivers, lakes, lagoons, swamp forests, and swamps with limited marine influence were present. The Sr isotopic results corroborate the presence of mostly freshwater settings with some marine influence (oligohaline, salinity not exceeding 5 ppt).

A modern analog of the aquatic paleoenvironments at the time of deposition of Trinil HK could be the tropical lowland freshwater swamp forest biotope, which occurs along the lower reaches of tropical rivers and around tropical lakes. An example of this biotope is the Sundarbans freshwater swamp forest, situated inland of the Sundarbans mangroves in India and Bangladesh. Other examples are the Tonle Sap Great Lake in Cambodia and the Chao Phraya freshwater swamp forest in Thailand. We have compared faunal species lists of Trinil HK with species lists of the Sundarban freshwater swamp forest, including the oligohaline eastern part of the Sundarban mangrove system in Bangladesh. Of the nine fish species documented from Trinil HK, eight occur in the Sundarban wetlands (Sanyal, 1999). The stingray *Himantura chaophraya* is absent from the Sundarbans (where other *Himantura* species do occur), but *H. chaophraya* does occur in the Chao Phraya freshwater swamp forest ecoregion in Thailand (Monkolprasit and Roberts, 1990). In Table 9, we compare the mammalian, reptilian, and avian species list from Trinil HK with species occurring in the Sundarban wetlands. In total, 24 of the 28 species from Trinil correspond completely (at species level) or closely (at genus level) to species occurring in the Sundarban wetland. Two other species from Trinil, *Stegodon trigonocephalus* and *Duboisia santeng* are extinct endemics that have no present-day counterpart. We conclude that the nature (in terms of local environmental conditions and faunal composition) of the aquatic environment of Trinil HK is comparable to that of the modern coastal tropical freshwater swamp forest biotope. However, this does not imply that the Trinil HK environment is comparable to the Sundarbans, Tonle Sap, or Chao Phraya freshwater swamp forests in terms of scale, geography, and geology.

De Vos (1982) studied the composition of the mammalian fauna from Trinil HK and inferred the presence of an open grassland and savanna ecosystem in the Trinil area. This may seem contradictory to the presence of a wetland system, but the Tonle Sap freshwater swamp forest biotope includes extensive areas of seasonally inundated grasslands, the so-called hydromorphic savanna (Campbell et al., 2006). We conclude that the aquatic part of the Trinil area during deposition of Trinil HK contained rivers, lakes, swamp forests, lagoons, and marshes with minor marine influence, laterally grading into grasslands possibly subjected to regular inundation. Bettis et al. (2008) reconstructed paleoenvironments in the Sangiran area. They found that during Trinil HK times (~1.5 Ma, Cycle 1 of the Bapang Formation), the Sangiran landscape consisted of low-lying, frequently flooded areas that supported a moist savanna with scattered trees and shrubs. Riparian forest occupied the active river channel belt, where shifting channels left many sandbars and shallow abandoned channels. This reconstruction agrees well with our interpretation of paleoenvironments at Trinil.

The mollusc fauna from Trinil HK requires a more detailed interpretation because of the observed difference in species composition between the Dubois bulk samples and shell collections made by Dubois, Selenka, and the Geological Survey Bandung. The large bivalves *Pseudodon* and *Elongaria* are the most numerous shells in the Dubois, Selenka, and Bandung collections, while they are not or hardly present in the Dubois bulk samples. The absence of these shells in the bulk samples is puzzling, since Dubois (1908: 1249) specifically stated that two species of freshwater mussel, one large (*Pseudodon*; JJ) and one small (*Elongaria*; JJ), are the most numerous ("allerhaüfigsten") mollusc species at Trinil. The stratigraphic provenance of the bulk samples is known: they all derive from the soft sandstone layer (see caption Table 5; Fig. 3b; layers 10–14 in Fig. 3c). We therefore assume that the many large bivalves in the collections derive primarily from the layer below the soft sandstone layer, namely the Hauptknochenschicht ("Lapillischicht" or main bone bed) itself. The abundance of large bivalves in this layer, in contrast to the rarity in the layer above, will be discussed later in this section.

Availability and "catchability" of aquatic food resources

The nine fish species from Trinil HK are edible by humans and could have been possible food resources for *Homo erectus*. Since the earliest known barbed harpoons made of bone date from ~90 ka (Brooks et al., 1995), it is unlikely that *H. erectus* could have used tools such as bone fish hooks or harpoons to capture live fish from deeper water. Lack of these tools most probably eliminates the availability of the large elasmobranch fish *Glyphis gangeticus* (Ganges shark), *Pristis* sp. (Sawfish), and *Carcharius taurus* (Sand tiger shark) as "catchable" food resources. Spearing of stingrays (*Himantura* cf. *chaophraya*) with a pointed (bamboo) stick or spear may have been a possibility. Oppenoorth (1936) mentioned that modern humans from Indonesia use stingray spines as spear tips

Table 6
Mammal, reptile, and bird species from Trinil[a]

Mammalia	Family	Habitat
Panthera tigris (Linnaeus, 1758)	Felidae	Tropical and evergreen forests, woodlands, grasslands, rocky country, savannas, swamps, mangrove forests. Strong swimmer.
Felis (=*Prionailurus*) *bengalensis* (Kerr, 1792)	Felidae	Forests and rainforests in low and mountainous areas, usually not in arid areas. Lives close to watercourses, also in mangroves.
Cuon (=*Mececyon*) *trinilensis* (Janensch, 1911)	Canidae	Large variety of habitats: dry plains, forests, shrublands, grasslands, mangroves.
Rhinoceros sondaicus (Desmarest,1822)	Rhinocerotidae	Lowland rainforest, wet grasslands and large floodplains, mangroves
Stegodon trigonocephalus (Martin, 1887)	Stegodontidae	Unknown. Capable swimmer
Bubalus palaeokerbau (Dubois, 1908)	Bovidae	Probably wet habitats ranging from riverine forests and grasslands, to marshes and swamps
Bibos palaesondaicus (Dubois, 1908)	Bovidae	Probably woodlands, close to water
Duboisia santeng (Dubois, 1891)	Bovidae	Probably forests
Muntiacus muntjak (Zimmerman, 1780)	Cervidae	Forests, grasslands, savannas, tropical deciduous forests, tropical scrub forests. From sea level up to 3000 m. Never far from water.
Axis lydekkeri (Martin, 1892)	Cervidae	Probably forests, grassy floodplains
Cervus sp.	Cervidae	Probably forests, grasslands, marshes
Sus brachygnathus (Dubois, 1908)	Suidae	Probably forests, grasslands
Hystrix (=*Acanthion*) *brachyura* (Linnaeus, 1758)	Histricidae	Variety of habitats: deserts, rocky areas, mountains, savannas, and forests
Lutrogale sp.	Mustelidae	Probably swamp forests, freshwater wetlands, forested rivers, lakes
Rattus trinilensis (Musser, 1982)	Muridae	Unknown
Macaca fascicularis (Raffles, 1758)	Cercopithecidae	Forests, riverine and swamp forests, mangroves. Strong swimmer
Trachypithecus cristatus (Raffles, 1821)	Cercopithecidae	Forests, coastal areas, mangroves, and riverine forests
Homo erectus (Dubois, 1892)	Hominidae	Probably upland areas, savannas, riverine areas, coastal deltas
Reptilia		
Crocodylus siamensis (Schneider, 1801)	Crocodylidae	Freshwater swamps, rivers, lakes, sometimes in estuaries.
Gavialis bengawanicus (Dubois, 1908)	Gavialidae	Probably rivers
Batagur sp.[b]	Geoemydidae	Probably rivers and mangroves
Trionyx sp.[b]	Trionychidae	Probably rivers, lakes
Hardella isoclina[b] (Dubois, 1908)	Bataguridae	Probably rivers, lakes
Varanus sp.	Varanidae	Probably rivers, grasslands, forests, swamps, mangroves
Aves		
Leptoptilos cf. *dubius* (Gmelin, 1789)	Ciconiidae	Tropical lowland wetlands
Ephippiorhynchus cf. *asiaticus* (Latham, 1790)	Ciconiidae	Tropical lowland wetlands and marshes
Branta cf. *ruficollis* (Pallas, 1769)	Anatidae	Grassland, freshwater and coastal wetlands; breeding in the Arctic, wintering in southern areas
Tadorna tadornoides (Jardin and Selby, 1828)	Anatidae	Lakes; breeding in Australia, wintering in northern areas
Pavo muticus (Linnaeus, 1766)	Phasianidae	Forests, grasslands, savannas, scrubland. Capable swimmers, foraging on riverbanks as well as in streams and marshes

[a] Based on published accounts (De Vos and Sondaar, 1982; Weesie, 1982; De Vos et al., 1994; Delfino and De Vos, 2006).
[b] The aquatic turtles have not been identified with certainty and are in need of revision. Habitat information from Francis (2008), Daniel (2002), and Robson (2000).

and suggested that the barbed stingray spine, found at the same level and at a distance of ~10 m from *H. erectus* calvaria VI at Ngandong, served the same purpose. However, the earliest documented use of composite bone tools dates from the Middle Stone Age (MSA) in Africa in association with *H. sapiens* (D'Errico and Hensilwood, 2007), and there is no indication that Javanese *H. erectus* used this type of advanced technology.

Table 7
Bulk Sr isotope ratios of fish and molluscan fossils from the Solo Basin[a]

No.	Genus/species	Location	Sr isotope ratio
DUB1639c	*Himantura* cf. *chaophraya?*	Trinil	0.705897 ± 0.000007
DUB1646	Unidentified fish vertebra	Trinil	0.705839 ± 0.000011
DUB5234	*Pseudodon vondembuschianus trinilensis*	Trinil	0.706146 ± 0.000014
DUB11422	*Tarebia granifera*	Trinil	0.704946 ± 0.000011
DUB11364	*Elongaria orientalis*	Trinil	**0.707568 ± 0.000008**
DUB9694	*Tarebia granifera*	Trinil	**0.708345 ± 0.000008**
DUB9694	*Lucina sp.*	Trinil	**0.708723 ± 0.000009**
F588[b]	*Himantura* cf. *chaophraya?*	Sangiran	**0.707636 ± 0.000009**
DUB9963	*Tarebia granifera*	Cenklik (Sangiran)	**0.708208 ± 0.000009**
DUB9963	*Lucina* sp.	Cenklik (Sangiran)	**0.708587 ± 0.000013**
Recent[c]	*Physunio eximius*	Solo river, Trinil	0.705499 ± 0.000011

[a] DUB: Dubois Collection, Leiden. In bold: Sr isotope ratios higher than expected for Central-East Javan freshwater.
[b] Von Koenigswald Collection, SMF.
[c] recent from Solo River near Trinil, Dubois Collection housed at the ZMA-UvA.

Hemibagrus nemurus (Asian redtail catfish) lives in large muddy rivers where it would be hard to catch without technology. However, catfish enter flooded forests to spawn in summer (Roberts, 1993). Catching the fish (by hand or club) when they were in shallow water among the roots of trees may have been feasible. The fish species *Anabas testudineus* (Climbing perch), *Channa* cf. *striata* (Snakehead), *Clarias batrachus* (Walking catfish), and *Clarias leicanthus* (Forest walking catfish) have auxillary breathing organs permitting occasional (often seasonal) overland excursions to migrate to other bodies of water. Because of their considerable size (25–100 cm), such "crawling" fishes on land or in very shallow water would have been attractive and easy targets for omnivorous terrestrial predators without boats or specialized fishing tools. For instance, hand capture of Snakehead (and other aquatic animals) is practiced by modern humans in the dry season along the Mekong River in Cambodia (Deap et al., 2003). We infer that these four fish species would have been catchable prey for *Homo erectus*. The species are known as popular and nutritious food for modern human populations (Talwar and Jhingran, 1991).

At least eleven of the 32 mollusc species from Trinil HK (Table 3) are edible by humans (Van Damme, 1984; Kress, 2000; IBISWorld, 2003). The species occur in shallow water and can be harvested by

Table 8
Input for binary mixing model

[Sr] "anthropogenic" Javan freshwater	0.413 ppm (measured)
[Sr] "non-anthropogenic" Javan freshwater	0.079 ppm (inferred; Palmer and Edmond, 1989)
[Sr] seawater	7.8867 ppm (Vonhof et al., 1998)
Sr isotope ratio freshwater endmember	0.704946 (measured *Tarebia* 11422)
Sr isotope ratio Early Pleistocene seawater	0.709102 (McArthur et al., 2001)
Sr isotope ratio Middle Pleistocene seawater	0.709136 (McArthur et al., 2001)

hand (e.g., Yang, 1990). Shells of three pearly freshwater mussel species (*Pseudodon, Elongaria,* and *Rectidens*) and of the gastropod *Pila* have been found in an early Holocene kitchen midden in Sampung Cave on Java and are still consumed by modern humans on Java (Van Es, 1930; Van Benthem Jutting, 1932), confirming edibility and dietary value of these species for hominins. We conclude that at least four fish species (Table 1) and eleven mollusc species (Table 3) were potential food sources for *Homo erectus* on Java.

Probability of aquatic exploitation by hominins in coastal habitats

If aquatic resources such as molluscs and fish were available for hominins on Java, what is the probability that they indeed consumed these resources? In coastal areas, terrestrial predators often consume aquatic foods and have a considerable impact on the local aquatic ecosystem (Polis and Hurd, 1996; Roth, 2003). Systematic, often seasonal, predation by non-human terrestrial mammals on freshwater and marine fauna occurs widely. Carlton and Hodder (2003) reviewed occurrence of terrestrial mammals as predators in marine intertidal communities and documented 121 records of intertidal predation among 38 species of terrestrial mammals. For instance, mice, rats, pigs, chacma baboons, brown bears, black bears, striped and spotted hyenas, coyotes, domestic dogs, grey and red wolves, jackals, and foxes in coastal habitats catch and consume crabs, molluscs, fish, and other aquatic fauna (Carlton and Hodder, 2003; Smith and Partridge, 2004).

Climatic and seasonal characteristics may trigger systematic aquatic exploitation. For instance, mammals living in perennially or seasonally impoverished near-coastal systems may turn to the adjacent and potentially more productive aquatic system for food. In the arid deserts adjacent to the Gulf of Mexico, coyotes (*Canis latrans*) feed on a variety of aquatic organisms, including sea turtles, marine mammals, fish, birds, invertebrates, and algae (Rose and Polis, 1998). Chacma baboons (*Papio ursinus*) are known to capture and consume aquatic molluscs and crustaceans, especially when the protein content of their terrestrial plant food is low (Avery and Siegfried, 1980).

In other instances, seasonal abundance of aquatic foods is a positive attractor for aquatic exploitation. Systematic seasonal aquatic exploitation has been documented for brown bears and black bears preying on spawning salmon in late summer and early fall (Hilderbrand et al., 1999; Jacoby et al., 1999). Coastal brown bears in Alaska dig up and consume soft-shelled clams and razor clams on tidal flats in early summer (Smith and Partridge, 2004). A recent study by Darimont et al. (2008) has shown that grey wolves (*Canis lupus*) preferentially feed on salmon in autumn, even when their terrestrial prey (deer) is abundantly present and in good condition. Darimont et al. (2008) concluded that the high nutrient value of the salmon (especially the fatty acid DHA) and the fact that it is a "benign" prey that does not fight back are probably reasons for the wolves' preference of salmon over deer.

The literature cited above shows that systematic aquatic exploitation (either year-round or seasonal) by terrestrial mammals is normal and predictable mammalian behavior when the mammal is 1) omnivorous, 2) living in a coastal marine or freshwater habitat, 3) where nutritious and catchable aquatic prey is available. Considered in the perspective of aquatic exploitation by terrestrial mammals in coastal habitats, the systematic and seasonal aquatic exploitation by *Homo sapiens* (Marean et al., 2007) and *H. neanderthalensis* (Stringer et al., 2008) does not differ from that of other mammals. Also, transport of aquatic prey to a base (such as a cave, in the case of *H. sapiens* and *H. neanderthalensis*) is not "modern" behavior. For example, Navarrete and Castilla (1993) reported that Norway rat burrows in coastal Chile contain remains of ∼40 intertidal prey species such as limpets, bivalve molluscs, crabs, and fish. Erlandson and Moss (2001) provide many more examples of terrestrial omnivorous animals transporting aquatic food (remains) to dens, nests, burrows, and caves on land. A label of "modernity," if applicable at all to aquatic exploitation, should perhaps be reserved for aquatic exploitation with evidence of advanced technology such as fish hooks and boats. The assumption, that early hominins living in a coastal habitat with catchable nutritious aquatic fauna were restricted to eating terrestrial resources, does not agree with published accounts of common mammalian behavior. Therefore, instead of having to provide evidence of aquatic exploitation before it is considered as a realistic option, we propose that the default assumption in hominin evolutionary research should be that omnivorous hominins who lived in coastal habitats with catchable aquatic fauna could have consumed aquatic resources.

Significance of the aquatic fossil assemblage in the Trinil collection

In our study of aquatic paleoenvironments at Trinil we have demonstrated that all three conditions for aquatic exploitation by

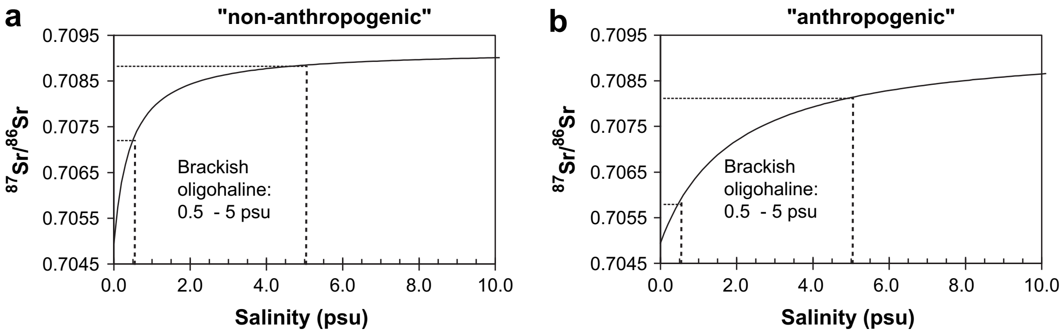

Fig. 7. Mixing hyperbolas of the freshwater versus seawater end members for Pleistocene Trinil. a: mixing curve calculated with inferred "non-anthropogenic" Solo River Sr concentration of 0.097 ppm. b: mixing curve calculated with measured "anthropogenic" Solo River Sr concentration of 0.413 ppm. Salinity expressed as psu (practical salinity units). The outcome of the mixing model is not sensitive to the values for seawater Sr isotope ratios changing over time in the early Pleistocene (0.709102–0.709136; McArthur et al., 2001), so chronology uncertainties do not affect the results.

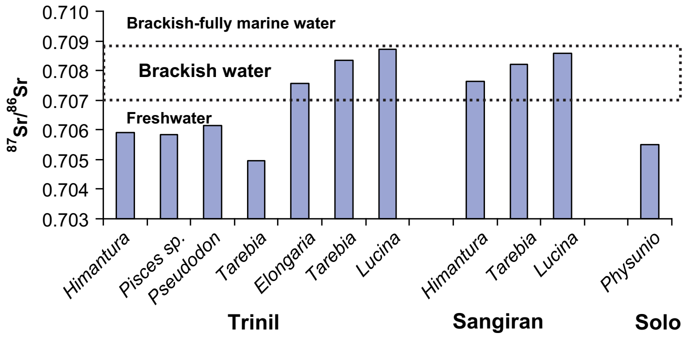

Fig. 8. Sr isotope ratios of aquatic fossils from Trinil and Sangiran, and of a *Physunio* shell from the modern Solo River. The dotted rectangle indicates the Sr isotope ratios corresponding to a brackish salinity range (oligohaline: 0.5–5 psu: practical salinity units), based on results of the mixing model using the "non-anthropogenic" freshwater Sr concentration (Fig. 7).

terrestrial mammals are met in the early Pleistocene on Java. The omnivorous terrestrial mammal *Homo erectus* was living in the wetland habitat of the Solo Basin (Sangiran and Trinil), as well as in the coastal delta habitat of Mojokerto (Huffman et al., 2006). Edible, nutritious aquatic fauna was available and catchable. Thus, it is valid to hypothesize that *H. erectus* on Java consumed aquatic resources.

The next step will be to test the hypothesis. As this concerns the early Pleistocene time period, we expect that it will be relatively difficult to find unequivocal, "smoking gun" evidence of aquatic exploitation, such as hominin tools or bones in a cave with cut-marked or burned aquatic fossils. However, because aquatic food sources contain constituents such as the fatty acid DHA (Kainz et al., 2004) with strong physiological effects on brain gene expression, development, and cognition (Calderon and Kim, 2004; Kitajka et al., 2004; Kawakita et al., 2006), it is important to actively search for subtle clues indicating early use of aquatic foods.

It would theoretically be possible to test the hypothesis of aquatic exploitation by measuring stable isotope ratios of nitrogen and carbon in dental collagen (Lee-Thorp and Sponheimer, 2006; Richards et al., 2006; Richards, 2007) of fossil *Homo erectus* teeth. However, the antiquity of Javan *H. erectus* teeth most likely precludes the extraction of well-preserved collagen and thus the study of N and C isotope ratios. A further drawback is that isotopic analyses involve destructive sampling of precious hominin fossil teeth. A non-destructive approach is to focus on anomalies in species composition and taphonomy of the aquatic fossil assemblages from hominin sites. In hominin sites with possible signs of fish exploitation, the number of fish fossil elements is very high: for instance Stewart (1994) has documented recovery of thousands of fossils of the catfish *Clarias batrachus* from Bed I and Bed II at Olduvai Gorge. The total number of fish fossil elements recovered from Trinil is low, thus providing no indication of exploitation of this possible resource at Trinil.

The number of shells of most of the molluscan species is also low and on the same order of magnitude as the fish fossils, again showing no indication for possible exploitation. However, the presence of a relatively large number of only adult, large-size *Pseudodon* shells excavated from a very limited area (Hauptknochenschicht in Trinil), in both the Dubois and Bandung collections, is a discrepancy in the aquatic assemblage that merits further attention for these shells. Collector's bias (preferring large-size *Pseudodon* shells) could have played a role. But then the Dubois and Bandung collectors (excavating about thirty years apart) would have had exactly the same bias, which seems unlikely. In addition, the fact that *Pseudodon* fragments were collected as well, indicates that the collectors did not pick up only "nice" specimens. It appears that they collected a representative sample, as is also noted by Van Benthem Jutting (1937). It is highly unlikely that the lack of juvenile shells constitutes a preservation bias against smaller and thinner shells as smaller and fragile specimens of various other species are present. The fact that many of the *Pseudodon* valves are still paired and well-preserved would suggest that the molluscs were not dead and transported by water before fossilization but were buried in live position. However, the complete absence of small, juvenile shells as well as the mixed occurrence of two different (but equally large-sized) shell forms argues against interpretation of burial of a live population (Van Benthem Jutting, 1937). Instead, the discrepancies suggest that the *Pseudodon* shells could have been brought together, prior to fossilization, by a size-selective collecting agent who may have used them for consumption of molluscan flesh.

The *Elongaria* shell assemblage collected from Trinil is in these aspects comparable to the *Pseudodon* assemblage: a relatively large number of shells, no young individuals but only adults, two shell forms mixed in single field lots. It is striking that the posterior part of the *Elongaria* shells is often missing. In a Holocene kitchen midden from Sampung Cave on Java, many *Pseudodon* and *Elongaria* shells have been found among mammal, bird, and fish remains, together with human tools (Van Es, 1930). Two forms of *Elongaria* shells were present in the Sampung Cave kitchen midden (Van Benthem Jutting, 1937), just as in the Trinil collections. Van Benthem Jutting (1932:105) writes: "In the Lamellibranchs (bivalves, JJ), as far as they have been shattered, invariably the siphonal region of of the valves is missing to a larger or a smaller extent. Apparently the people duly recognized this posterior end as the most fragile part of the shell." The *Elongaria* assemblage from Trinil, just like *Pseudodon*, appears to indicate collection by a selective agent for the purpose of mollusc consumption. The *Pseudodon* and *Elongaria* assemblages from Trinil have the characteristics of shell middens (e.g., Waselkov, 1987; Rosendahl et al., 2007): large adult shells only, many complete shells, no signs of damage due to water rolling, signs of damage due to being deliberately opened, presence of human (hominin) bones in the same layer. We conclude that they represent a subtle clue of possible aquatic predation by non-hominins or by hominins. A possible non-hominin predator could be the otter *Lutrogale* sp., although the extant Smooth-coated otter *Lutrogale perspicillata* is not known to produce shell middens. This otter preys on fish, crustacea, molluscs, frogs, turtles, and birds, using its molars to crush molluscs (Gurung and Singh, 1996). If *Lutrogale* was the non-hominin mollusc predator at Trinil, we would expect mainly shell fragments and shells with bite marks, instead of the many undamaged *Pseudodon* valves present in the collections.

If *Homo erectus* at Trinil collected *Pseudodon* and *Elongaria* molluscs for consumption, we predict that traces of handling and processing (such as typical breakage patterns or cut marks on the shells) may be present in the shell collections. A study investigating damage patterns and handling traces on *Pseudodon* and *Elongaria* shells from Trinil is currently underway.

Table 9
Comparison of mammal, reptile, and bird species composition of Trinil and recent Sundarban freshwater swamp forest[a]

Trinil	Sundarban freshwater swamp forest
Mammalia	**Mammalia**
Panthera tigris	*Panthera tigris* (Tiger)
	Panthera pardus (Leopard)
Felis (=*Prionailurus*) *bengalensis*	*Felis bengalensis* (Leopard cat)
	Felis chaus (Jungle cat)
	Felis viverrina (Fishing cat)
	Manis crassicaudata (Indian pangolin)
Cuon (=*Mececyon*) *trinilensis*	*Cuon alpinus* (Dhole/Asiatic wild dog)[b]
	Canis aureus (Golden jackal)
	Vulpes vulpes (Red fox)
Rhinoceros sondaicus	*Rhinoceros sondaicus* (Javan rhinoceros)
	Rhinoceros unicornis (One-horned rhinoceros)
Stegodon trigonocephalus	
Bubalus palaeokerbau	*Bubalus bubalus* (Water buffalo)
Bibos palaesondaicus	*Bos* (=*Bibos*) *gaurus* (Indian Bison)
	Bos (=*Bibos*) *frontalis* (Gaur)
Duboisia santen	
Muntiacus muntjak	*Muntiacus muntjak* (Barking deer)
Axis lydekkeri	*Axis porcinus* (Hog deer)
	Axis axis (Chital)
Cervus sp.	*Cervus duvaucelii* (Swamp deer)
	Cervus axis (Spotted deer)
	Cervus unicolor (Sambhar deer)
Sus brachygnathus	*Sus scrofa* (Wild boar)
Hystrix (=*Acanthion*) *brachyura*	*Hystrix brachyura* (Malayan porcupine)
Lutrogale sp.	*Lutrogale perspicillata* (Smooth-coated otter)
	Aonyx cinera (Oriental small-clawed otter)
Rattus trinilensis	*Golunda ellioti* (Indian bushrat)
Macaca sp.	*Macaca mulatta* (Rhesus macaque)
Trachypithecus cristatus (Silvered leaf monkey)	
Homo erectus	*Homo sapiens* (Modern human)
Reptilia	**Reptilia**
Crocodylus siamensis	*Crocodylus palustris* (Marsh crocodile)
	Crocodylus porosus (Estuarine crocodile)
Gavialis bengawanicus	*Gavialis gangeticus* (Gharial)
Batagur sp.[c]	*Batagur baska* (River terrapin)
Trionyx sp.[c]	*Trionyx gangeticus* (Indian softshell turtle)
Hardella isoclina[c]	*Hardella thurii* (Crowned river turtle)
Varanus sp.	*Varanus favescens* (Yellow monitor)
	Varanus bengalensis (Common Indian monitor)
	Varanus salvator (Water monitor)
Aves	**Aves**
Leptoptilos cf. *dubius*	*Leptoptilos dubius* (Greater adjutant)
Ephippiorhynchus cf. *asiaticus*	*Ephippiorhynchus asiaticus* (Black-necked stork)
Branta cf. *ruficollis*	
Tadorna tadornoides	*Tadorna ferruginea* (Ruddy shelduck)
Pavo muticus	

[a] The Trinil faunal list is complete (De Vos and Sondaar, 1982; Weesie, 1982; De Vos et al., 1994; Delfino and De Vos, 2006). The species list from the Sundarban freshwater swamp forest is not complete but contains the larger mammals (27 out of ca. 35 mammal species, i.e. excluding bats, mice etc), and a selection of reptiles and birds (Gopal and Chauhan, 2006; www.worldwildlife.org/wildfinder; Francis, 2008; Daniel, 2002; Robson, 2000).

[b] Historical range of *Cuon alpinus* included the Sundarban wetlands; still present in the Myanmar mangroves (Oo, 2002).

[c] The aquatic turtles have not been identified with certainty and are in need of revision.

Another factor that deserves further investigation is how climate (or climate change) could have influenced dietary preference and prey selection of *Homo erectus* on Java. Bettis et al. (2008) suggest that *Homo erectus* populations inhabiting Sundaland (including Sangiran and Trinil) repeatedly became environmental refugees during the Pleistocene, especially during glacial terminations and interglacials. These periods were characterized by a rise in sea level and increased atmospheric moisture, thus reducing the extent of dry savanna and open forest. Bettis et al. (2008) imply that these conditions were unfavorable for *Homo erectus* inhabitants and may have forced them into highlands during these periods. We have shown that *Homo erectus*, similar to other terrestrial omnivores (Carlton and Hodder, 2003), had an alternative option, namely to make use of aquatic resources provided by lowland wetland areas.

Conclusions

The aim of our study is to provide ecological context for the current debate on modernity (or not) of the use of aquatic resources by hominins. We have used early Pleistocene Trinil as a case study to investigate how questions of the possible dietary relevance of aquatic environments for early hominins can be addressed. At the time of deposition of the Trinil HK sequence, the aquatic part of the Trinil area contained rivers, lakes, swamp forests, lagoons, and marshes with minor marine influence, laterally grading into grasslands that were possibly subjected to regular inundation. It was, in terms of local environmental conditions and faunal composition, comparable to the modern tropical freshwater swamp forest biotope, which occurs along the lower reaches of tropical rivers and around tropical lakes.

The Trinil HK aquatic environment yielded aquatic food resources, including at least eleven edible mollusc species and four edible fish species which could be collected or caught with little or no technology. We have shown that, from an ecological point of view, the default assumption in hominin evolutionary research should be that omnivorous hominins living in coastal habitats with catchable aquatic fauna could have consumed aquatic resources. Further, we have demonstrated that conditions for aquatic exploitation by terrestrial mammals are met in the early Pleistocene on Java: it is plausible that *Homo erectus* on Java consumed aquatic resources. One way to test the hypothesis of aquatic exploitation is to carry out a taphonomic analysis of the aquatic fossils associated with hominin fossils. The observed midden-like characteristics of *Pseudodon* and *Elongaria* shell assemblages from Trinil are an indicator of possible collection by a selective agent for the purpose of aquatic mollusc consumption. These shell assemblages are currently being studied to investigate if any hominin or non-hominin predation traces are present. Also, the role of climate change on hominin prey selection should be investigated. We feel that the possible physiological implications of aquatic resource use for hypotheses on hominin encephalization and cognition merit an active and focused search for possible evidence of aquatic exploitation by early hominins. This study has put forward promising approaches and may trigger new research efforts in this direction.

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