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Palaeoenvironments at the *Homo erectus* type locality of Trinil (Java, Indonesia): the artiodactyl evidence

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Abstract:

In this study we assess the artiodactyl fossil record of the *Homo erectus* type locality of Trinil (Indonesia) and explore the paleoenvironmental implications for the site and for our understanding of early hominin paleoecology. Combining ecomorphological analyses on postcranial elements of cervids from Trinil (N=43) with a range of existing paleobiological and paleoecological data on the bovids and cervids, a holistic reconstruction is made of the ecology of the artiodactyl community. The ecomorphological analyses indicate that the cervid *Axis lydekkeri* was adapted to relatively open environments with wet substrate. In combination with evidence of the other families, these results are compared in a correspondence analysis with the artiodactyl communities of contemporary Asian nature reserves. Trinil was shown to be similar to a number of mainland Southeast Asian sites and reconstructed as an open woodland habitat with a wet component, possibly in the form of alluvial grasslands. The paleoenvironmental conditions reconstructed for Trinil, indicate that *Homo erectus* was present in relatively open environments, but that it still had a significant degree of environmental flexibility and was able to persist in wet and dry environments with a vegetation structure ranging from grassland to open woodland.

Keywords: Trinil, Pleistocene, paleoecology, *Homo erectus*, artiodactyls, ecomorphology

1. Introduction

Although it is currently the consensus that *Homo erectus* (sensu lato) was the first hominin to disperse out of Africa into parts of Asia, and possibly Europe, the nature and chronology of this biogeographic dispersal event have long been a matter of debate (Larsen et al. 1998, Dunsworth & Walker 2002, Anton 2003, Anton et al. 2016). In the last few decades increasingly robust evidence has surfaced for an early dispersal, with sites such as Dmanisi (1.78-1.85 Ma) (Ferring et al. 2011) and Sangiran (1.6-1.8 Ma) (Swisher et al. 1994; Indriati & Anton 2008; Matsu'ura et al. 2020; Husson et al. 2022), showing a quick expansion of the species after its first occurrence at Koobi Fora (1.8-1.9 Ma) (Leakey & Walker 1976) or possibly Drimolen (2.0-1.95 Ma) (Herries et al. 2020). Despite this changing paradigm, the underlying processes driving this biogeographic expansion remain poorly understood. While it is generally accepted that ecological factors during the Plio-Pleistocene played a role in this event (Anton & Swisher

2004, Lahr 2010, Agusti & Lordkipanidze 2011, Carotenuto et al. 2016), there is disagreement whether this expansion was primarily driven by extrinsic (i.e. changing environmental conditions) or intrinsic factors (i.e. the increased capacity of *H. erectus* to adapt to certain conditions) (Tappen 2009). Adherents of the first model have suggested that the development of open, savannah-like environments across Africa and Asia facilitated this process and have pointed out that early hominin dispersal out of Africa was part of a larger ecosystem expansion (Vrba 1996, Dennell & Roebroeks 2005, Tappen 2009, Dennell 2010). Others have proposed that intrinsic factors, such as the appearance of bipedalism or encephalization, were decisive and led to an increased capacity for ecological flexibility, driving early *Homo* dispersal (Potts 1998, Bobe & Behrensmeyer 2004, Carotenuto et al. 2016). While intrinsic and extrinsic factors are not mutually exclusive and may well have both contributed to the success of *Homo erectus* (Carotenuto et al. 2016), understanding how they articulate requires a more nuanced understanding of the environmental conditions that were encountered by this hominin during the Early and Middle Pleistocene.

Unfortunately, the currently available paleoenvironmental data are unequally distributed in time and space and come from a range of different proxies that can sometimes seem contradictory. One region that has been comparatively neglected from a paleoecological perspective is Southeast Asia. Java especially, in spite of its wealth of *Homo erectus* fossils (Simanjuntak 2001), has received far less attention than East Africa in this sense. Sites such as Trinil and Sangiran have yielded large amounts of vertebrate fossils (Van den Bergh et al. 2001) and have a high potential to improve our understanding of early hominin paleoecology and biogeography. However, some of the most prolific sites in this region, including Kedung Brubus and Trinil, were excavated more than a century ago, and lack detailed stratigraphic, micropaleontological and sedimentological data, useful for paleoenvironmental reconstruction (De Vos et al. 1994; Van den Bergh et al. 2001; Selenka et al. 2011). As a result, paleoecological reconstructions of these sites have relied heavily on the vertebrate fauna (e.g. De Vos et al. 1994; Van der Meulen & Musser 1999; Van den Bergh et al. 2001).

In most Early to Middle Pleistocene sites from Java, including the *Homo erectus* type locality of Trinil, the vertebrate fossil record is dominated by artiodactyl remains (Van den Bergh 2001, Storm 2012). Although the evolution, taxonomy and biostratigraphic relevance of the different artiodactyl families in Java have been dealt with in a number of studies (e.g. Hooijer 1958; Hardjasasmita 1987; Gruwier et al. 2015), far less attention has been given to their ecology and role in ancient hominin environments. Paleoecological studies on bovids and suids have, nevertheless, contributed considerably to our understanding of the ecological context of early hominin evolution in Africa (e.g. Vrba 1980; Kappelman 1988; Bishop 1994; Bishop et al. 2006). Especially with the advent of techniques, such as ecomorphology (e.g. Kappelman 1988; Van Valkenburgh 1988; Kovarovic & Andrews 2007, Forrest et al. 2018), microwear and mesowear studies (Ungar & Grine 1991; Ungar 2004; Rivals et al. 2018; Uno et al. 2018) and stable isotope analyses (e.g. Leslie et al. 2016), researchers have been able to explore the ecology of extinct artiodactyls with increasing detail. In this sense, the Trinil artiodactyl record can be considered a largely untapped source of paleoenvironmental data, which can be used to increase our understanding of *Homo erectus* ecology in the region.

In this paper we review the bovid, cervid and suid fossil record of Trinil and discuss its paleoenvironmental implications. In addition to synthesizing the available taxonomic, paleoecological and contextual data on the different taxa at the site and analysing this by means of a canonical analysis, we present new, ecomorphological analyses on a sample of cervid elements. Finally, we integrate the existing data and the new results and assess the implications for Trinil and discuss how this informs contemporary models of *Homo erectus* paleoecology and dispersal.

1.1. *Background*

Trinil is a Pleistocene site discovered in 1891 by Dutch paleoanthropologist Eugène Dubois, on the banks of the Solo River in East Java (Jacob 1973) (Fig. 1). In addition to the discovery of the famous *Homo erectus* fossils, Dubois also discovered thousands of animal remains in a series of fluvial terrace deposits (Berghuis et al. 2021; Storm 2012). Follow-up expeditions, most notably by Emil and Margarethe Selenka (Selenka et al. 1911), added to this already large collection, making it one of the richest assemblages of vertebrate fossils in Southeast Asia. Although the taphonomic conditions under which this conglomeratic bone bed was deposited are not well understood, a study by Hill et al. (2015) pointed out that the collection consists mainly of disarticulated remains of large terrestrial mammals, with limited traces of pre-burial weathering or transportation damage. Based on the lithological and palaeontological features of the site, the assemblage probably accumulated from muddy flood waters originating as a lahar flow on a stratovolcano some kilometers to the south of Trinil, and resulted from a catastrophic mass death accumulation (Hill et al. 2015). The faunal remains from Trinil (Table

1) consist primarily of mammals of six different orders: proboscideans, artiodactyls and perissodactyls, and to a lesser extent carnivores, primates and rodents (Van den Bergh et al. 2001; Storm 2012). In addition, small numbers of fish, reptiles and birds are also present (Van den Bergh et al. 2001; Joordens et al. 2009; Storm 2012), as well as a range of terrestrial and aquatic molluscs (Joordens et al. 2009).

'Figure 1'

The age of Trinil has for a long time been a topic of debate. Having always played an important role in the biostratigraphy of the region, the site and its fauna were placed in the Middle Pleistocene in Von Koenigswald's (1933; 1934) classical biostratigraphic scheme for the island. Adjustments to the scheme in the 1980's only considered the main fossiliferous layer, also called the "Trinil Haupt-Knochen Schicht" or "Trinil H.K.", as contemporaneous, and placed it around 800-900 Ka, at the transition from the Early to the Middle Pleistocene (De Vos & Sondaar 1982; De Vos 1985). Although this improved scheme has generally been accepted (e.g. Van den Bergh et al. 2001; Louys et al. 2007; Storm 2012; Rozzi et al. 2013), some recently obtained $^{40}Ar/^{39}Ar$ and paleomagnetic dates partially contradict this, with an age of either 1.1 to 1.3 Ma from the supposedly contemporaneous Kabuh formation at Sangiran (Larick et al. 2001) or respectively 830 to 773 Ka and a maximum of 450 ±110 Ka from two different bone bearing channel fills at the original Trinil excavation site (Hilgen et al. 2023). For the purposes of this study we focus on the material from "Trinil H.K" and accept an age around the beginning of the Middle Pleistocene, as proposed in the generally used biostratigraphic scheme (De Vos & Sondaar 1982; De Vos 1985) and partially confirmed by the most recent reevaluation of the site's chronology (Hilgen et al. 2023). However, as suggested in the latter study, we acknowledge that younger materials from the later (Middle) Pleistocene may also be present.

'Table 1'

While the physiographic features around Trinil are generally considered to have been similar to those found in the area now (Huffman 1997, 1999), there is still debate about the nature of its environments. In the work of Selenka and colleagues (1911) Trinil was reconstructed as a forested environment. Some researchers have followed this interpretation (e.g. Pope 1995), but more recent reconstructions have suggested the presence of an open woodland, based on the predominance of bovids, cervids and proboscideans (de Vos et al. 1994, van den Bergh et al.

2001). The small number of rodents, as well as the species of birds confirm this (Van der Meulen & Musser 1999; Meijer 2014). While the aquatic and semi-aquatic taxa, including the fish, molluscs and reptiles, indicate a wet component (Joordens et al. 2009), it remains unclear if this merely indicates the presence of the Solo River, or reflects the wider environment. No pollen records are available from Trinil, but palynological analyses of the presumably contemporaneous Grenzbank and lower Kabuh formation at nearby Sangiran indicate an open vegetational cover with seasonal forest rapidly evolving into a more grassland dominated landscape (Sémah et al. 2010; Sémah & Sémah 2012).

1.2. *The Trinil artiodactyl record*

The Hippopotamidae in the Selenka collection are probably of a younger age and are not part of the Trinil (H.K.) fauna (Van den Bergh et al. 1996). We can therefore conclude that three artiodactyl families are present at Trinil: Cervidae, Bovidae and Suidae (see Table 1). The Bovidae are the best represented family at Trinil (see table 1). In total, they make up approximately 47% (NISP) of all the mammalian remains discovered at the site. This is followed by the Cervidae, making up about 36% of all mammal fragments. Represented by only 2% of the fragments at Trinil, the Suidae are the rarest of the three families.

1. 2.1. *Suidae*

The taxonomy, evolution and biostratigraphic significance of the suids have been extensively reviewed by Hardjasasmita (1987). Although other forms have been described for the Pleistocene of Java (Von Koenigswald 1933), it is thought that only one suid species is present at Trinil: *Sus brachygnathus* Dubois, 1908 (Stremme 1911; Hardjasasmita 1987). It concerns a relatively small pig, similar in morphology to extant *Sus verucosus*, to which it may be ancestral. Outside of Trinil it is present at a number of other Pleistocene sites in Java, such as Kedung Brubus and Watualang, and persisted until the Late Pleistocene (Hardjasasmita 1987). Isotope analyses on tooth enamel of *Sus brachygnathus* from Trinil, showed $\delta^{18}O$ values between -5.31 to -7.49, and a broad range of $\delta^{13}C$ values between -1.96 and -12.77 (Janssens et al. 2016). These values indicate a diet consisting of a combination of plants with C3 (i.e. parts of shrubs or trees) and C4 (i.e. tropical grasses) photosynthetic pathways, or animals that feed on this type of vegetation (Janssens et al. 2016). Similar to most extant Southeast Asian suids (Francis 2008), *S. brachygnathus* was probably a generalist adapted to a wide variety of habitats.

1.2.2. *Bovidae*

Even though several Pleistocene bovids from Java were described in the 19th and early 20th century (e.g. Martin 1888; Von Koenigswald 1933), Hooijer's (1958) synthesis is the most authoritative work on this group. Three bovid species are recognized to have been present at Trinil: two large species *Bibos palaeosondaicus* Dubois, 1908 and *Bubalus palaeokerabau* Dubois, 1908, and one smaller species *Duboisia santeng* Dubois, 1891 (Hooijer 1958; Van den Bergh et al. 2001; Storm 2012).

Although many of the large bovid remains have not been identified to species, *Bibos palaeosondaicus* is the least common form at Trinil (Table 1). The morphology of this animal is close to that of the living banteng (*Bos javanicus*), which was previously incorrectly placed under the nomen *Bibos javanicus* (Nowak 1991). Probably *Bibos palaeosondaicus* was closely related to the banteng (Hooijer 1958). According to Von Koenigswald (1933) it is a subspecies of this form, but Hooijer (1958) distinguishes it from the latter by its cranial morphology, which is generally wider, has a continuous sagittal ridge extending from just behind the nasals to the vertex, has deeper supraorbital grooves, and a wider diverging angle of the horncores (Hooijer 1958). Although an earlier isotope analysis was conducted on 21 unidentified large bovid teeth from Trinil (Janssens et al. 2016), no specimens specifically identified as *Bibos palaeosondaicus* were included. However, as the oxygen ($\delta^{18}O$: -1.89 to -6.73) and carbon values ($\delta^{13}C$: -3.32 to 2.79) for all the unidentified large bovids fell in the range of C4 plant consumers (Janssens et al. 2016), and if we assume that at least some of these specimens are *B. palaeosondaicus*, it is conceivable that this species fed primarily on tropical grasses. *B. palaeosondaicus* persisted in Java until the Ngandong faunal stage at the end of the Middle Pleistocene (Van den Bergh et al. 2001).

Bubalus palaeokerabau is the most common bovid present at Trinil (Hooijer 1958). It is also found elsewhere in Java, including at Sumber Kepuh, Teguan and Kedung Brubus, and persisted at least until the Ngandong faunal stage (Hooijer 1958). Morphologically, it is similar to the wild Asian buffalo (*Bubalus arnee*) and its domesticated counterpart the water buffalo (*Bubalus bubalis*) (Hooijer 1958). It is probably closely related to both these forms, but only the domesticated water buffalo (*B. bubalis*) is currently known from Java (Hooijer 1958; Francis 2008). *B. palaeokerabau* is primarily distinguished from the two extant forms by its relatively wider skull behind the orbits and its longer, heavier horncores (Dubois 1908; Hooijer 1958). In comparison with *B. palaeosondaicus, B. palaeokerabau* has an atlas with transverse processes further extended medio-laterally and posteriorly, and shorter metacarpals expanded further in the distal plane (Hooijer 1958). Although its premolars and molars are similar to those of *B. palaeosondaicus*, its second premolar is less reduced, and its mandible comparatively longer and more gracile (Hooijer 1958). No functional explanations were given to these morphological differences by Hooijer (1958), but other studies have demonstrated a relationship between the relative depth of the mandibular corpus and feeding behavior in bovids (Forrest et al. 2018). Extrapolating this to the large bovids from Trinil, the more gracile mandibles of *B. palaeokerabau* could indicate that it was less of an obligate grazer than *B. palaeosondaicus*. This is partially corroborated by carbon ($\delta^{13}C$: -8.63 to 0.8) and oxygen ($\delta^{18}O$: -2.52 to -5.37) isotope analyses conducted on eleven *B. palaeokerabau* specimens from Trinil (Janssens et al. 2016). Although the majority of the specimens gave values that indicate a reliance on grazing of C4 grasses, at least one specimen gave lower carbon isotope values ($\delta^{13}C$: -8.63), suggesting a greater reliance on browsing.

An ecomorphological analysis was also conducted on the astragali of the large bovids from Trinil (Weinand 2005), which did not distinguish between *Bibos palaeosondaicus* and *Bubalus palaeokerabau*, given that no identification criteria for the astragalus are currently available. Using a linear model based on a relatively small comparative dataset, Weinand (2005) showed, seemingly contradictively, that the large bovid specimens from Trinil had a morphology similar to either heavy cover or open vegetation species. As the isotope analyses (Janssens et al. 2016) indicate that the more common *B. palaeokerabau* may have been a less obligate grazer, perhaps the larger sample of specimens giving a heavy cover signal (Weinand 2005), belongs to the latter species. The smaller number of fossils that were morphologically more typical of open vegetation species, could belong to the rarer *B. palaeosondaicus*. In any case, it is evident that the morphology of both large bovids is different from that of closed, forested vegetation species.

The smaller bovid species, *Duboisia santeng* Dubois 1891, was extensively described by Hooijer (1958), but its taxonomic status and ecology were later revised by Van den Bergh (1988) and Rozzi et al. (2013). In addition to Trinil, it is found at several other Early and Middle Pleistocene sites, including Sangiran, Kedung Brubus and Bumiaju in Java, and possibly at Tabun in Malaysia (Hooijer 1958, 1963). The general consensus is that this species is a member of the Boselaphini tribe and related to the extant four-horned antelope (*Tetracerus* *quadricornis*) and the nilgai (*Boselaphus camelus*), both known from the Indian subcontinent (Hooijer 1958; Van den Bergh 1988; Rozzi et al. 2013). While its cranial morphology is reminiscent of *Boselaphus*, its dental characteristics are closer to *Tetracerus* (Hooijer 1958). In contrast with the two extant species, in *D. santeng* both males and females are horned (Hooijer 1958). With an estimated body mass of 53.75 kg on average, it is intermediate in size between *Boselaphus* and *Tetracerus* (Hooijer 1958; Rozzi et al. 2013).

The ecology of this species has been a matter of debate. Isotope analyses on three *D. santeng* specimens from Trinil show carbon ($\delta^{13}C$: -0.10 to -0.30) and oxygen values ($\delta^{18}O$: -5.10 to -2.70) typical of a C4 grazing diet (Janssens et al. 2016). This was, however, contradicted by mesowear analyses by Rozzi and colleagues (2013), who reconstructed it as a browser with some abrasive components in its diet. Furthermore, an ecomorphological analysis of the femur and astragalus, by the same authors (Rozzi et al. 2013), suggested a morphology typical of forest adapted species. Weinand's (2005) ecomorphological analysis of the astragalus was less conclusive about *D. santeng*. Depending on the different models he tested, *D. santeng* was reconstructed as either an animal adapted to open or closed vegetation, although the author considered the latter interpretation more likely (Weinand 2005). In any case, it was clear from his study (Weinand 2005), that this species had a substantially different postcranial morphology than the large bovids from Trinil. Considering that this was independently demonstrated for the femur by Rozzi et al. (2013), it is likely that this species was more adapted to saltatorial locomotion in closed environments than the large bovids. This does not necessarily preclude it from having been primarily a grazer, a notion also suggested by the fact that its teeth are more hypsodont than those of *Boselaphus*, a mixed feeder (Hooijer 1958; Haque 1990).

1.2.3. *Cervidae*

In terms of their evolution and taxonomy, the cervids of Southeast Asia are poorly understood. Over the course of the late 19th and 20th century a large number of taxa have been proposed, based on Pleistocene finds from Java (Dubois,1907; Stremme, 1911; von Koenigswald, 1933, 1934). Although a brief synthesis of the members of the Cervini tribe is provided by Gruwier et al. (2015), no comprehensive revision of the cervid family has been undertaken so far. It is generally thought that during the Pleistocene three types of cervids were present in Java: large sized deer of the genera *Rusa* or *Cervus*, medium sized deer of the genus *Axis* and small sized deer of the genus *Muntiacus* (Gruwier et al. 2015; Amano et al. 2016). Only representatives of the latter two are present at Trinil: *Muntiacus kendengensis* Stremme 1911 and *Axis lydekkeri* Martin 1888.

Of the small species *Muntiacus kendengensis* practically nothing is known. It is only represented by a few antler fragments from Trinil and Pandejan (Stremme 1911, von Koenigswald 1933). According to Stremme (1911) the antlers are sufficiently different in shape and size to separate it from the extant *Muntiacus muntjak*. Von Koenigswald (1933), on the other hand, considered it merely a subspecies of the latter (*Muntiacus muntjak kendengensis*). Although no specific information is available on its habits or ecology, all extant muntjacs are known to be small, slinker type deer, adapted to browsing in dense vegetation (Geist 1998). It is plausible that this was also the case for *M. kendengensis*.

More common at Trinil, is the medium sized species *Axis lydekkeri*. This form was described on the basis of an almost complete, smooth, groove-less antler with a typical lyre-shape (Martin 1888, Zaim et al. 2003). In addition to Trinil, it is also found at other Early and Middle Pleistocene sites in Java, such as Kedung Brubus, Watualang and Sangiran (Von Koenigswald 1933, 1934, Moigne et al. 2004). Based on morphological and morphometric analysis, most authors place this species in the genus *Axis*, possibly in the subgenus *Hyelaphus* (Dubois 1908; Meijaard & Groves 2004; Gruwier et al. 2015). It is similar in size to the extant *Axis porcinus* and somewhat smaller than *Axis axis*, two species currently restricted to continental South and Southeast Asia. Little investigation has been done into the ecology of this species. However, isotope analyses on a sample of six *A. lydekkeri* teeth from Trinil gave carbon (δ^{13}C: -2.15 to 0.85) and oxygen values (δ^{18}O: -5.36 to -3.03) consistent with a grazing diet reliant on C4 plants (Janssens et al. 2016). Based on its supposed relatedness to *Axis porcinus* (Meijaard & Groves 2004; Gruwier et al. 2015), it has been proposed that *A. lydekkeri* was a species adapted to marshes and wet grasslands like its modern conspecific (Gruwier et al. 2015; Huffman et al. 2022). This is potentially confirmed by its common presence in the Perning paleodelta and in the swamp deposits that formed under wet climatic conditions at Sangiran (Huffman et al. 2022).

2. Materials and methods

We employed a synecological and autecological approach. Using the relevant paleozoological evidence on the Trinil artiodactyls detailed above, the autecological characteristics were constructed for each species present at the site. For the bovids and suids, this was based exclusively on the evidence available from the literature. For the cervids (i.e. *Axis lydekkeri*) we conducted new 3D morphometric ecomorphological analyses on the calcaneus and intermediate phalanx to predict their habitat preferences. The reconstructed autecological characteristics for each taxon, were then used to identify the synecological structure of the artiodactyl community at Trinil. We acknowledge that these characteristics were inevitably established using different proxies and methodologies, which can complicate comparison but nevertheless follow Bishop et al. (2006) that this is outweighed by the advantage of looking at different ecological aspects in order to obtain a more holistic reconstruction of the site's ecosystem.

2.1. *Cervid postcranial ecomorphology*

For the 3D ecomorphological analyses on the cervid bones, we selected the calcaneus and intermediate phalanx, as established methodologies are available for these elements and because they are often found in a relatively complete state in fossil collections. We used the modern comparative data and methodologies developed by Gruwier and Kovarovic (2022, 2023), which in turn were based on Curran (2009, 2012) for the calcaneus, and focus on the morphology of the cervid intermediate phalanx (N=131) and calcaneus (N=129) as proxies for habitat preference. Ecomorphology is based on the principle that the shape of these elements is mainly constrained by environmental parameters, as they relate to differences in locomotion and predator evasion strategy (Leinders 1979, Köhler 1993, Degusta & Vrba 2005, Polly 2007, Curran 2009, 2012, Barr 2014, Gruwier & Kovarovic 2022, 2023). Gruwier and Kovarovic (2022) found that the morphology of the calcaneus is mainly a predictor of the vegetation structure in which cervids habitually locomote. Cursorial animals adapted to open vegetation have tuber calcanei that are longer and more vertically positioned relative to the hock joint and a longer articular surface supporting the malleolus. Saltatorial animals adapted to closed vegetation, have shorter tuber calcanei, placed more horizontally relative to the hock joint and a shorter articular surface supporting the malleolus (Curran 2009, 2012; Gruwier & Kovarovic 2022). The morphology of the intermediate phalanx, on the other hand, was found to be a reliable predictor of the substrate on which cervids locomote. Forms adapted to wet, yielding substrate have more gracile phalanges with shallower proximal articulations relative to species adapted to locomotion on dry, firm substrate (Köhler 1993; Gruwier & Kovarovic 2023). Open vegetation was defined in this study as an area with open canopy of 40% or less closure (Thomas

& Packham 2007). Wet environments were defined in a broad sense, as areas where a significant part of the surface was continuously covered with water, or at various periods of time during the year (Chen et al. 2010). We used a geometric morphometric approach on the cervid bones, as established by Curran (2009, 2012), but the landmarking schemes used in this study were adopted unadjusted from the work of Gruwier and Kovarovic (2022, 2023). These were constructed to capture those morphological aspects of the bones, thought to be correlated with the ecological parameters, while at the same time keeping the number of variables low enough for robust statistical analysis on smaller (fossil) sample sizes (Gruwier & Kovarovic 2022, 2023).

We scanned 28 fossil calcanei and 15 intermediate phalanges using a NextEngine laser scanner (model 2020i). After 3D-objects were generated using the associated software package 'Scanstudio HD v. 1.3.2', six landmarks (Fig. 2b) were digitally placed on the calcaneus, and eight on the intermediate phalanx (Fig. 2a) using Landmark Editor 3.0 (Wiley et al. 2005). After the cartesian coordinate data were exported, the morphometric data were compiled with those of the comparative datasets from Gruwier and Kovarovic (2022, 2023). Next, a Generalized Procrustes Analysis (GPA) was conducted on the datasets to exclude all information irrelevant to shape differences (Zelditch et al. 2004), followed by a between group Principal Component Analysis (PCA) to explore morphological variation. Thin plate spline deformation grids were used to visualize shape changes along the axes. To test for statistically significant between-group differences, a permutational MANOVA (perMANOVA) was conducted on the relevant principal components, followed by pairwise perMANOVA's between all pairs of groups, as a post-hoc test (Gruwier & Kovarovic 2022, 2023). We followed Gruwier and Kovarovic (2022, 2023) and considered those principal components relevant that cumulatively explained 70% of the variation in the dataset, a commonly used cutoff point in PCA (Jolliffe & Cadima 2016). Uncorrected and Bonferroni corrected p-values were reported to account for family-wise error rate (Dunn 1961). All fossil cervid specimens included in the analysis belonged to the species *Axis lydekkeri* and are kept at the Naturalis Biodiversity Center in Leiden (The Netherlands) and the Museum für Naturkunde in Berlin (Germany) (Table 2). Because of the difficulty of distinguishing between forelimb and hindlimb phalanges, both were included in the model, as is done in most similar ecomorphological studies (e.g. Degusta & Vrba 2005, Curran 2012). Incomplete and pathological specimens were excluded from the fossil dataset. All statistical analyses were conducted using PAST 2.17 (Hammer et al. 2001) and Procrustes transformed raw coordinate data are provided in appendix A.

'Figure 2'

'Table 2'

2.2. *Artiodactyl community analysis*

Using the autecological characteristics of the different taxa, the structure of the Trinil artiodactyl community was explored. This approach is based on the principle that mammalian communities and their members' adaptations are informative about the environments in which they subsist (Reed 1997; Kovarovic et al. 2018). We compared Trinil's artiodactyl record with that of a series of contemporary ecosystems in the wider region using correspondence analysis (CA) (Legendre & Legendre 1998). CA is an ordination method which allows for associations in a data matrix to be explored (Legendre & Legendre 1998) and has been used to compare the properties of archaeological and paleontological sites (e.g. Sargeant 2014; Reynolds et al. 2017; Galán-de-Mera 2020). It relies on chi-squared tests to analyze relationships between row and column data and calculates the axes of maximum variation in a multidimensional cloud of data points (Reynolds et al. 2007). Here we conducted a CA on three categorical variables organized into 13 categories (including body size class, taxonomic representation and ecological affinity) pertaining to the artiodactyl communities of Trinil and 20 nature reserves in South and Southeast Asia (Table 3). As all of the Trinil artiodactyls are extinct and are difficult to directly compare to extant taxa, we only made use of broad taxonomic and size classes (e.g. small bovid or large cervid) and assigned these to a preferred vegetation structure (e.g. open or closed) and, where known, to a substrate type (wet, intermediate or dry) (Appendix B). In this sense, it is important to note that by including family level taxonomic categories in the CA, our analysis should not be considered a purely ecological community analysis. In such a "taxon free" approach one would make use of more strictly functional/ecological categories, irrespective of taxonomic affinities. While this approach has been successfully applied on African Plio-Pleistocene sites in the past (e.g. Reed 1997, 2008; Fara et al. 2005), it remains difficulty to untangle the complex relationship between taxonomy and ecology (Szalay 2000), particularly for Asian communities where cervids and bovids are found together in the same ecosystems but their niches often only overlap partially (Ahrestani et al. 2012). As these family level differences have some ecological significance, and because our approach is mainly descriptive and intended to broadly compare sites, this taxonomic information was retained in the community analysis.

Following Bellmaker (2010, 2018) our analysis was restricted to presence or absence of the different categories, in part because the proportional representation of taxa at Trinil is presumably biased by taphonomic factors (Hill et al. 2015; see section 1.1), complicating comparison with abundances in modern ecosystems. In addition, the different categories were sufficiently specific, so that so that there was almost never more than one taxon present in each category within a single site (although this would not always be the exact same species). The ecological characteristics of the contemporary nature reserves and the habitat preferences of the extant artiodactyls were taken from the literature (see Appendix B). Body sizes were based on average weights from the literature (see Appendix B) and placed in broad categories. The relationship between artiodactyl body size and ecology is closely tied to locomotion, dietary requirements and metabolic rate, and is generally considered a valuable ecological parameter (Geist 1998; Andrews & Hixon 2014; Kovarovic et al. 2018). Therefore, we defined three size classes for the bovids in our analysis: more than 500 kg (large sized), 100 to 500 kg (medium sized) and less than 100 kg (small sized). The cervids were also placed in three size classes: more than 100 kg (large sized), 50 to 100 kg (medium sized) and less than 50 kg (small sized). The suids were not divided in different ecological and size categories, as the (extant) species diversity is relatively low in this family in the region, and the majority of the taxa tend to be habitat generalists of broadly similar size (Francis 2008). Only their presence/absence was included as a categorical variable.

'Table 3'

3. Results

3.1. *Cervid ecomorphological analysis*

In our ecomorphological analysis of the calcaneus, the *Axis lydekkeri* specimens from Trinil grouped with extant specimens adapted to (cursorial) locomotion in open vegetation (Fig. 3). In morphological terms this can be translated to *A. lydekkeri* having a relatively long tuber calcanei that is more vertically positioned relative to the hock joint, and a comparatively long articular surface supporting the malleolus. With the exception of the difference between the closed/saltatorial and intermediate group, the perMANOVA ($p<0.001$) and associated pairwise comparisons confirmed the significance of the differences between all other habitat groups (Table 4). The Trinil specimens were significantly different from all habitat groups, but most similar to the open vegetation group.

'Figure 3'

'Table 4'

The group affinities of *A. lydekkeri* were less clear in the ecomorphological analysis of the intermediate phalanges (Fig. 4). A substantial number of specimens appeared to fall outside of the normal shape variation of the extant species. The reason for this was unclear but could potentially be due to the presence of morphological traits uncommon in extant cervids. It is, however, clear that on the first axis, the *A. lydekkeri* specimens tended to group with the modern forms adapted to wet substrate. The perMANOVA (p<0.001) and associated pairwise comparisons indicated that most habitat groups were significantly different from each other, except that the wet adapted group did not differentiate well from the intermediate group (p=0.149). All groups were significantly different from the Trinil specimens (Table 5). Nevertheless, as was already indicated by visual assessment of the scatterplot, the differences between *A. lydekkeri* and the wet substrate group were least pronounced. In morphological terms this implies that the Trinil specimens have relatively slender phalanges, and in some cases less shallow proximal articulations, as is typically found in modern forms adapted to wet, open substrate. Although a number of specimens had relatively deep proximal articular surfaces, more typical of dry adapted forms, the overall gracile shape of its phalanges was probably a more reliable indicator of substrate type (Degusta & Vrba 2005; Kovarovic et al. 2021). This would indicate that *A. lydekkeri* was a species probably adapted to wet, fairly open environments.

'Figure 4'

'Table 5'

3.2. *The artiodactyl community*

Based on our synthesis and the new analyses on the cervids, the autecological characteristics were described for the artiodactyl taxa from Trinil (Table 6). While *Sus brachygnathus* was considered a habitat generalist, our review of the available evidence indicated that the large bovids were either adapted to a mixed environment with heavy cover or open environment. *Bibos palaeosondaicus* was probably adapted to somewhat more open vegetation, with a diet focused on grazing. For our CA it was categorized as a mixed to open adapted large bovid (B_L_MO). *Bubalus palaeokerabau* was presumably adapted to somewhat more closed vegetation and included more browse in its diet. For the CA this species was categorized as a large bovid adapted to mixed vegetation (B_L_M). Our medium sized bovid *Duboisia santeng* was reconstructed as an animal adapted to closed vegetation, but possibly more reliant on grazing. For reasons of consistency, we focused primarily on the characteristics of the habitats in which this animal lived, and therefore considered it a closed vegetation species (B_M_C). *Axis lydekkeri* was reconstructed as an animal adapted to more open vegetation, with wet substrate. Based on the isotope data (Janssens et al. 2016), it probably relied primarily on grazing. For the CA it was categorized as a mixed to open adapted medium sized cervid, preferring wet substrate (C_M_MO_W). Based on our general understanding of extant muntjac ecology, *Muntiacus kendengensis* was categorized as a small cervid adapted to closed vegetation with intermediate to wet substrate (C_S_C_IW). Based on these autecological profiles, a contingency table was constructed that served as a base for the CA (Table 7).

'Table 6'

'Table 7'

The results of the CA of the artiodactyl communities show a clustering of the contemporary localities according to geographic location and ecosystem (Fig. 5). Five major clusters could be discerned in the plot of the first two axes of variation (together explaining 56.7% of the variation). In the upper right corner, the only semi-arid site (Gir, India) is well separated, mainly by the presence of small and large bovids adapted to mixed or open environments (yellow ellipse). All sites from the Indian subcontinent give low values on the second axis (orange ellipse). This is mainly driven by the presence of large, mixed environment bovids and medium sized cervids, either adapted to dry, open woodland or wet, open woodland. Drier sites in this cluster appear to give a higher score on the first axis. In the upper left corner, a cluster of Sundanese rainforest sites can be observed (green ellipse). These sites tend to be characterized by a lower diversity of large bovids, but a presence of medium sized, closed environment bovids and large cervids. Close to this cluster, but somewhat lower on the second axis, are a number of drier woodland sites, from the Sundanese and Indochinese subregion (purple ellipse). These localities tend to be richer in large bovids, adapted to mixed to open environment. A fifth cluster is found in between that of Indochinese woodland sites and the more wet sites in the Indian cluster (blue ellipse). The sites in the blue ellipse are mainly from the Indochinese subregion, but in addition to being open woodland habitats, they are characterized by a wet component, usually in the form of alluvial grasslands. They are typically richer in large bovids adapted to mixed-to-closed environments, and medium sized cervids adapted to wet, relatively open environments. The Trinil artiodactyl community clearly groups with the latter cluster of sites. In terms of its composition, the CA indicates that it is similar to the communities of Cat Tien National Park (Vietnam) and Phnom Prich Wildlife Sanctuary (Cambodia).

'Figure 5'

4. Discussion

Based on our study of the artiodactyl record at Trinil, certain conclusions can be drawn about the nature of its paleoenvironments. The presence of suids seems to be of little consequence to reconstructions of the site. Similarly, almost all Asian sites included in our CA, had muntjacs (small cervids adapted to closed, often wet environments) in their species list. Keeping in mind that our analysis did not take relative proportions of taxa into account, it seems clear that, despite its association with closed, wet environments, the (limited) presence of *Muntiacus kendengensis* at Trinil is not a good predictor of habitat.

The more diverse bovids and medium-to-large sized cervids, on the other hand, are responsible for the variation in our correspondence analysis. While it is important to stress that uncertainties remain about the autecological characteristics of some of the Trinil taxa, and that with our presence/absence-based ordination method some of ecological information may have been missed, the results suggested a close affinity between Trinil and a number of continental Southeast Asian sites, characterized by open woodland environments and alluvial grasslands. Especially a similarity to the Phnom Prich wildlife sanctuary in Cambodia was noted. This is not necessarily surprising, as during glacial stages in the Pleistocene, large parts of the Sunda shelf were exposed, connecting the major islands, Borneo, Sumatra and Java, to the Asian mainland (Voris 2000, Bird et al. 2005). Based on geomorphological, palynological and biogeographical evidence, some workers (Heaney 1991; Bird et al. 2005) have suggested that there was even a dry savannah corridor stretching from Indochina to Java, allowing mammals from continental Asia, including hominins, to disperse to the southern limits of the Sunda shelf.

Although our study does not refute that Trinil was part of such a corridor of relatively open environment; the results indicate that it should not be characterized as a dry savannah habitat. In fact, our analyses of the artiodactyls are in line with reconstructions by Joordens and colleagues (2009), who argued for the presence of a regional environment consisting of grasslands, floodplains, swamp forest and rivers. Based on a re-evaluation of the terrestrial fauna and a number of aquatic biota in the Trinil assemblage, the authors drew an analogy with the Sundarban swamp forests of Southern India and Bangladesh (Joordens et al. 2009). As Joordens et al. (2009) correctly point out, there is a high degree of similarity between the faunal list of Trinil and that of the Sundarbans. This is also seen in our CA, where (on the first axis) this locality plots close to Trinil in respect to its artiodactyl community.

However, even if we consider the wider mammalian composition of Trinil (see Table 1), the similarities with the Sundarbans are matched by those with Phnom Prich. If, in addition to the artiodactyls, we take all mammals above 10 kg into account, Trinil shares 13 taxa (or their closely related extinct counterparts) with the Sundarbans (Joordens et al. 2009), but 15 with Phnom Prich (Gray & Phan 2011). Phnom Prich is part of Cambodia’s northern and eastern plains, that are dominated by open deciduous, dipterocarp woodland, alternated by seasonally wet grasslands (Packman et al. 2013). Probably this type of ecosystem is the closest modern analogue to Trinil. Not only does this match well with the presumably contemporaneous pollen records from Sangiran, suggestive of open vegetation with seasonal forest rapidly evolving into a grassland dominated landscape (Sémah et al. 2010; Sémah & Sémah 2012), but it also offers a plausible explanation why some of the different proxies applied to the Trinil fauna have sometimes given contradictory results (see section 2). It explains the predominant C4 signals measured in the isotope analyses on most of the artiodactyl remains, as well as the mixed vegetation and wet substrate signals picked up by the ecomorphological analyses. This wet signal should probably not be considered merely a reflection of a localized aspect in the landscape. Given that the remains of the wet adapted *Axis lydekkeri* make up about a third of the large Trinil assemblage (Storm 2012), it is unlikely that they represent an uncommon form that was adapted to local wet conditions present in the immediate vicinity of the Solo riverbed. This point was further strengthened by the fact that this taxon is also found at other localities, such a Pitu and Watualang (Von Koenigswald 1933), where there was no evidence of a large river in the immediate vicinity (Gruwier et al. 2015).

Most other paleoenvironmental reconstructions of Early and Middle Pleistocene sites in Java have supported the idea that *Homo erectus* was primarily associated with relatively open environments (e.g. Moigne 2004; Bouteaux 2005; Indriati & Anton 2008; Sémah 2010; Janssens et al. 2016). This is, for example, the case for Ngandong (De Vos et al. 1994; Van den

Bergh et al. 2001; Huffman et al. 2010) and Kedung Brubus (De Vos et al. 1994; Van den bergh et al. 2001). It has been argued that this is because *Homo erectus* focused its hunting strategies on following large savannah mammals at a time during which hominins underwent a shift from occupying a niche focused on occasional hunting and scavenging to becoming top predators (Turner 1999; Carotenuto et al. 2016). In dense forests this strategy would be more challenging, as resources in such environments are scarce, unevenly distributed and difficult to access (Bailey et al. 1989). This seems to be confirmed by the absence of *Homo erectus* from the Early- to Middle Pleistocene *Stegodon-Ailuropoda* fauna, which is found on continental Southeast Asia and associated with closed forest (Kahkle 1961; Ciochion 2010). Clear evidence for human presence in closed, forested environments does not appear before the Late Pleistocene in Southeast Asia. At sites such as Niah cave in Borneo (Barker et al. 2009) and Punung (Badoux 1959) in Java, hominins were evidently present in rainforest habitats, but these are all associated with *Homo sapiens*. Together, these observations fit with the extrinsic explanation that the expansion of open environments in Asia and Africa during the Plio- Pleistocene was an important driver of early hominin dispersal (Bonnefille 1984; Prentice & Denton 1988; Vrba 1996; Dennell & Roebroeks 2005; Tappen 2009; Dennell 2010). In this so-called Savannahstan model, open landscapes would have become especially prominent around 1.8 Ma, coinciding with the appearance and range expansion of *Homo erectus* across large parts of the Old World (Dennell & Roebroeks 2005; Dennell 2010).

As pointed out, our reconstructions of the Trinil paleoenvironment are in line with this model, to the extent that *Homo erectus* was probably not found in closed, forested environments. However, it also adds a layer of nuance, as Trinil appears to have been characterized by a wetter habitat than what is commonly proposed in the Savannahstan model (Dennell & Roebroeks 2005; Dennell 2010; but see Huffman 1999). This could suggest that other environmental factors may have also played a role in early hominin dispersal and that *Homo erectus* had a greater ecological flexibility than sometimes given credit for. Indeed, the presence of a wet component might have been an important factor in itself, facilitating hominin dispersal. Some researchers have even pointed out that wet environments provided habitat corridors, rich in resources, allowing hominins to ‘coast’ their way out of Africa (Cohen et al. 2012; Joordens et al. 2009; Stringer 2000). When looking at *Homo erectus* paleoecology on a wider scale, it does appear that many other sites, including Sangiran, Dmanisi, Koobi fora, Olorgesaillie, Kocabas and Ternifine, had a substantial wet component (Watanabe & Kadar 1985; Geraards et al. 1986; Behrensmeyer et al. 2002; Bobe et al. 2007; Ferring et al. 2011; Lebatard et al. 2014). The existence of lacustrine environments and marshes at the Pucangan formation at Sangiran (Watanabe & Kadar 1985; Bettis et al. 2009), was even recognized by Dennell (2010), a major proponent of the Savannahstan model. Nevertheless, he argued that the hominin remains must have washed down from a drier region upstream (Dennell 2010). The presence of similarly wet conditions at Trinil demonstrates that this should not necessarily be the case. There are no indications at the latter site that the processes of sedimentation, accumulation, and preservation were any different for the hominin fossils than for the other faunal remains (Hill et al. 2015). It is likely that *Homo erectus* had a certain flexibility and was well equipped to cope with dry and wet habitats. Although not explicitly tested here, this would lend some support to the idea that intrinsic changes in this species may also have contributed to its biogeographic expansion (Potts 1998; Bobe & Behrensmeyer 2004, Carotenuto et al. 2016).

5. Conclusions

Our analysis of the Trinil artiodactyl record allowed us to improve our understanding of the environments that were present in the vicinity of the site. As such, it demonstrated the value of using a multi-proxy approach for paleoecological studies. Based on a range of different proxies, mainly applied on the cervids and bovids from Trinil, its paleoenvironment was reconstructed as an open woodland alternated by seasonally wet grasslands. A similarity to the ecosystems currently found in Cambodia's northern and eastern plains is proposed.

Placing Trinil within a wider paleoanthropological context, a picture emerges where *Homo erectus* was largely confined to relatively open environments, but that the ecological reality on a regional level was probably one of considerable variation. In addition to dry, savannah-like environments, our reconstructions suggested that this hominin was equally capable of dealing with wet environments, with a somewhat more closed vegetation. The results, nevertheless, lend support to the idea that the species was absent from closed forested environments.

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Figures:

Figure 1: Map of Java and the surrounding Greater Sunda Islands (names in white), with the location of Trinil (diamond).

Figure 2: Three dimensional landmarks used in the ecomorphogical analyses of the cervid intermediate phalanx (A) and calcaneus (B), with landmark numbers and description of landmarks(adapted after Gruwier & Kovarovic 2022 and 2023).

Figure 3: First two components of a bgPCA on calcanei of A. lydekkeri and extant cervid species of known habitat preference. Shape changes along the axes are visualized with thin plate spline deformation grids showing hypothetical values at the end of the axes. Eigenvalues are given in parenthesis (dots=Trinil, squares=open/cursorial, crosses=intermediate, plusses=closed/saltatorial and diamonds=open/wet).

Figure 4: First two components of a bgPCA on intermediate phalanges of A. lydekkeri and extant cervid species of known habitat preference. Shape changes along the axes are visualized with thin plate spline deformation grids showing values at the end of the axes and hypothetical

3D renderings of the shape changes in the phalanges at both ends of the two axes (adapted after Gruwier & Kovarovic 2023). Eigenvalues are given in parenthesis. (dots=Trinil, squares=dry, plusses=intermediate en diamonds=wet).

Figure 5: Correspondence analysis (CA) using presence/absence of artiodactyls at Trinil and contemporary nature reserves, with eigenvalues in parenthesis. Row data are represented as black dots and column data as blue dots. The colored ellipses are interpretative and represent wider ecosystems in the broad region of South and Southeast Asia. See table 3 for an explanation of the codes in the columns.

Tables:

Table 1: Mammalian taxa found at Trinil, with number of identified specimens (NISP) for the collections in Leiden and Berlin, based on Ingicco et al. (2014), Joordens et al. (2009), Selenka et al. (2011), Storm (2012), and the inventory list of the Selenka collection at the Museum für Naturkunde. Note that the Hippopotamidae mentioned by Selenka and colleagues (1911) and *Lutrogale palaeoleptonyx* listed by Joordens and colleagues (2009) are excluded as they are most likely part of the younger Kedung Brubus fauna (Van den Bergh et al. 1996, 2001).

Table 2: List of fossil *Axis lydekkeri* specimens included in the ecomorphological analysis (RMNH= Naturalis Biodiversity Center, Leiden; MFN= Museum für Naturkunde, Berlin).

Table 3: Categorical variables used in Correspondence Analysis.

Table 4: Permutational MANOVA on the first two component scores of a PCA on morphometric data of cervid calcanei, with significant values (<0.05) in bold. Uncorrected p-values are given in the upper right triangle of the matrix, Bonferroni corrected values in the lower left triangle.

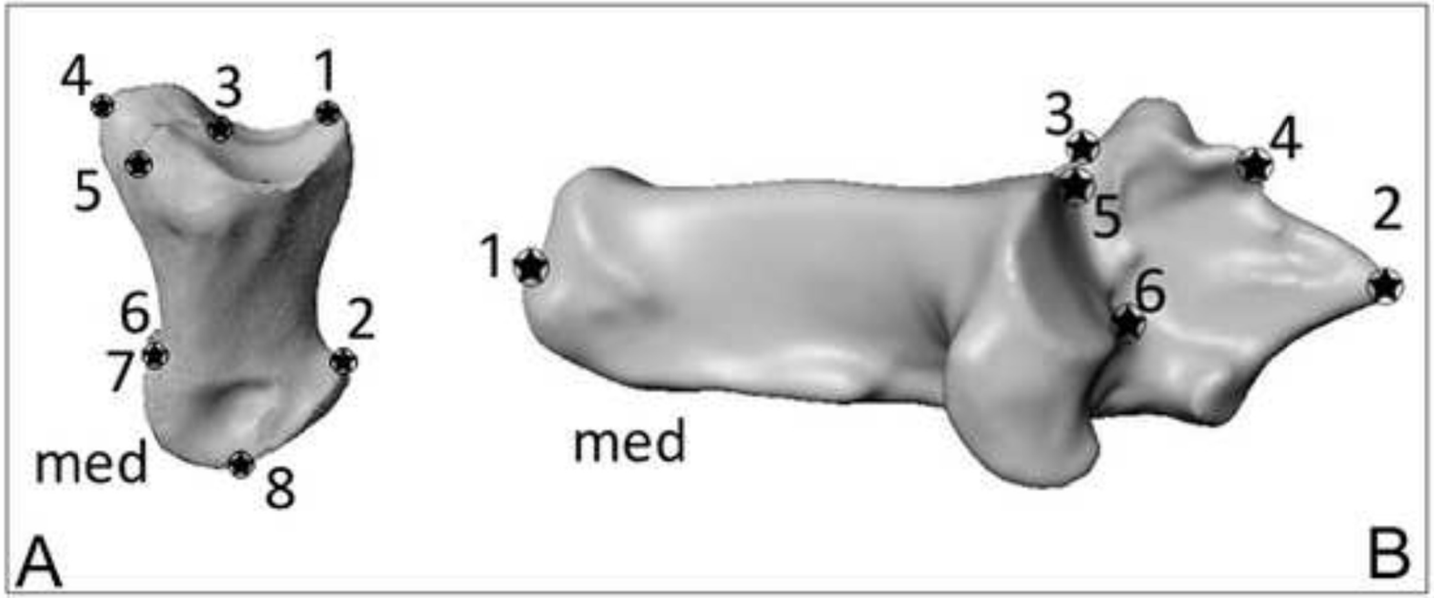
Table 5: Permutational MANOVA on the first two component scores of a PCA on morphometric data of cervid phalanges, with significant values (<0.05) in bold. Uncorrected p-values are given in the upper right triangle of the matrix, Bonferroni corrected values in the lower left triangle.

Table 6: Reconstructed habitats and habitat assignments of the Trinil artiodactyls for the CA analysis.

Table 7: Contingency table for correspondence analysis of the Trinil artiodactyl community. See table 3 for the explanation of the codes in the columns.

Figure 1

Figure 2



Element	Number	Description
Phalanx II	1	Most anterior point of the proximal articular surface.
	2	Most proximal point of the anterior extensor process.
	3	Apex of the proximal articular surface at the junction between the left and the right facet.
	4	Most posterior point of the lateral extension on the posterior side of the plateau postarticulaire.
	5	Most posterior point of the medial extension on the posterior side of the plateau postarticulaire.
	6	Proximal apex of the lateral palmar extension on the posterior shaft.
	7	Proximal apex of the medial palmar extension on the posterior shaft.
	8	Apex and most distal point of the medial ridge of the distal articular surface.
Calcaneus	1	Most posterior point of the tuber calcanei.
	2	Most anterior point of the cubonavicular articular surface.
	3	Most posterior point of the articular surface supporting the os malleolus.
	4	Most anterior point of the os malleolus articular surface.
	5	Most superolateral point of the posterior astragalar articular surface.
	6	Most inferolateral point of the posterior astragalar articular surface.

Figure 3

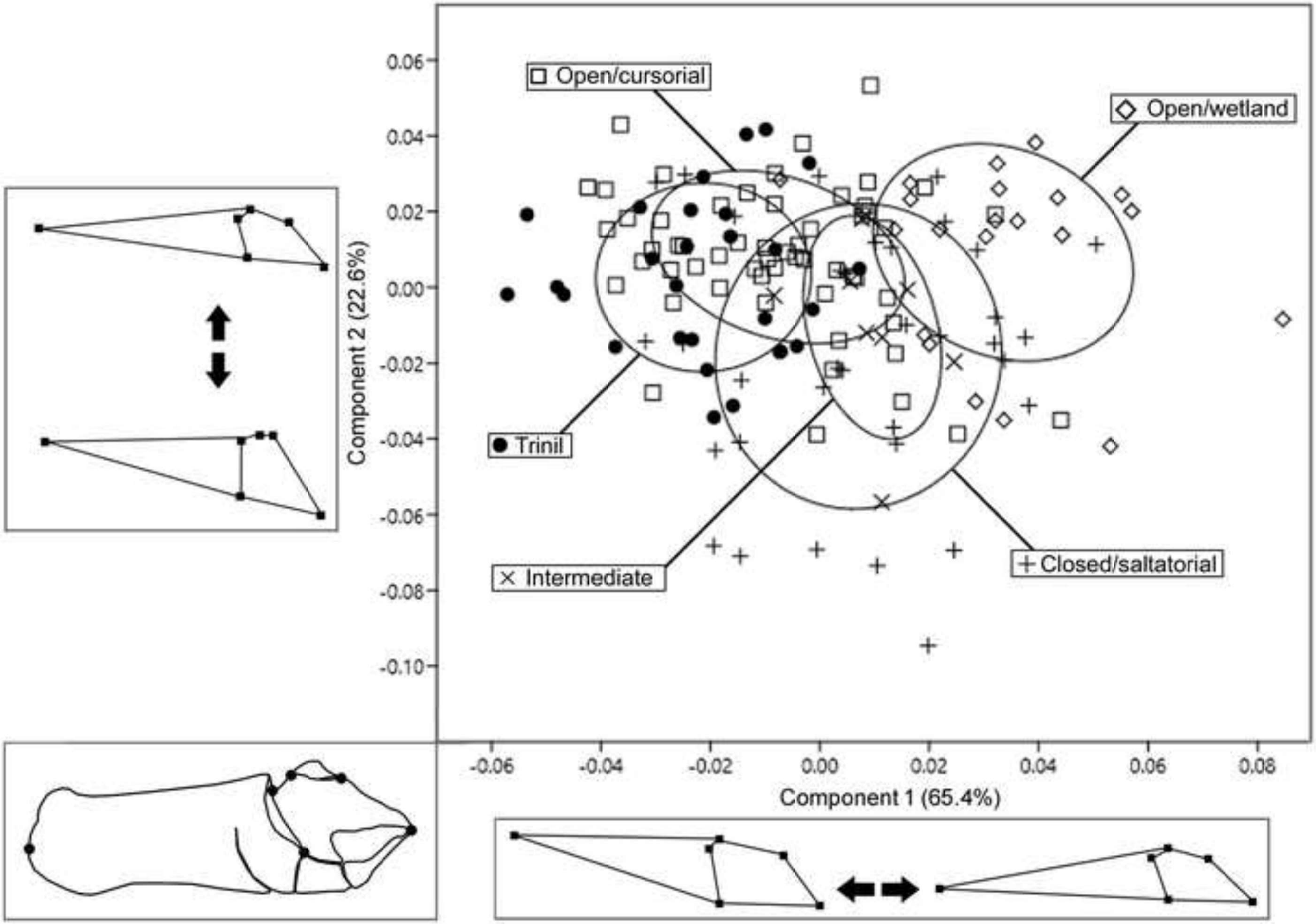
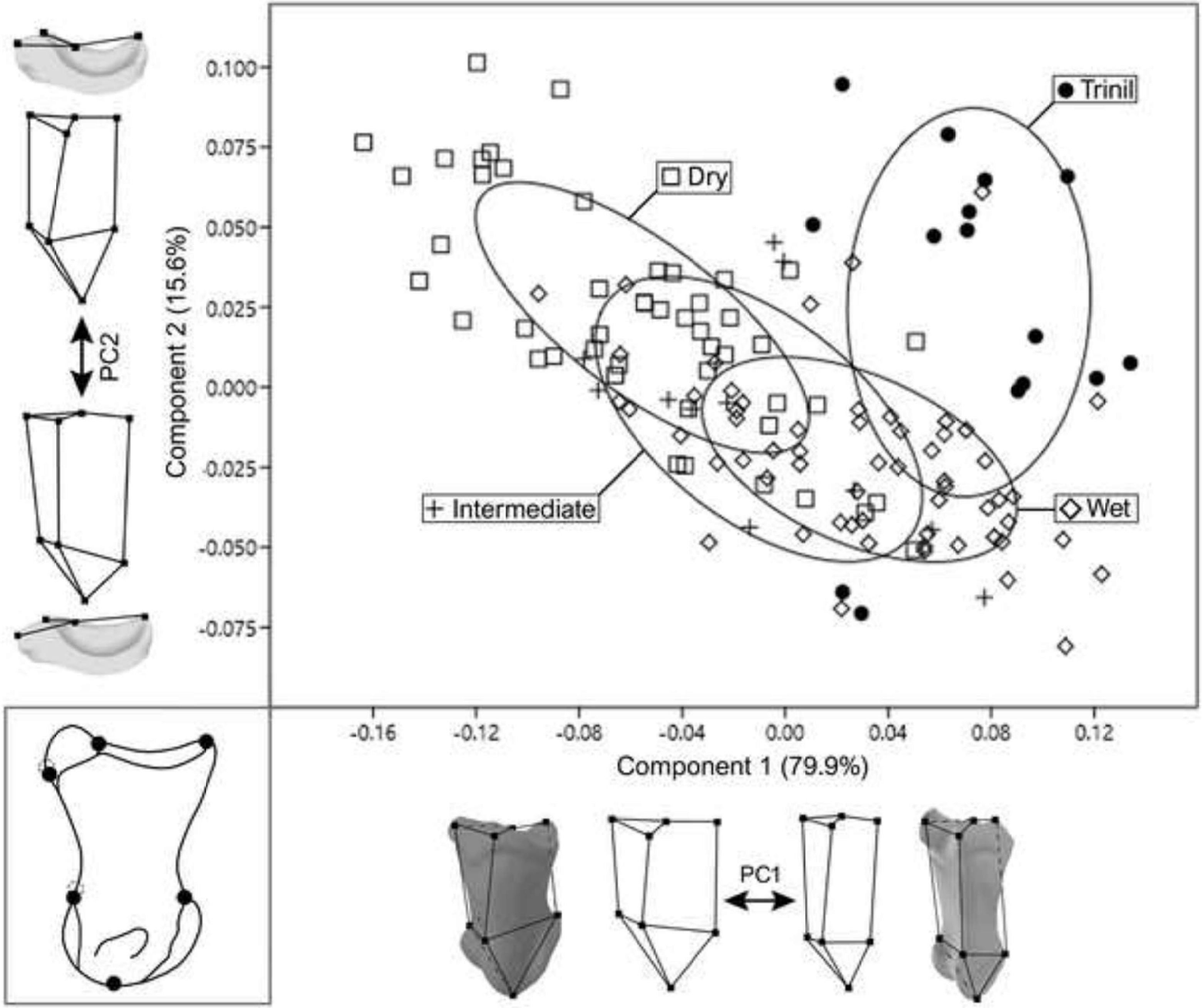

Open/cursorial
Open/wetland
Trinil
Intermediate
Closed/saltatorial
Component 2 (22.6%)
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
Component 1 (65.4%)
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08

Figure 4



● Trinil
□ Dry
+ Intermediate
◇ Wet
Component 2 (15.6%)
0.100
0.075
0.050
0.025
0.000
-0.025
-0.050
-0.075
Component 1 (79.9%)
-0.16
-0.12
-0.08
-0.04
0.00
0.04
0.08
0.12
PC2
PC1

Figure 5

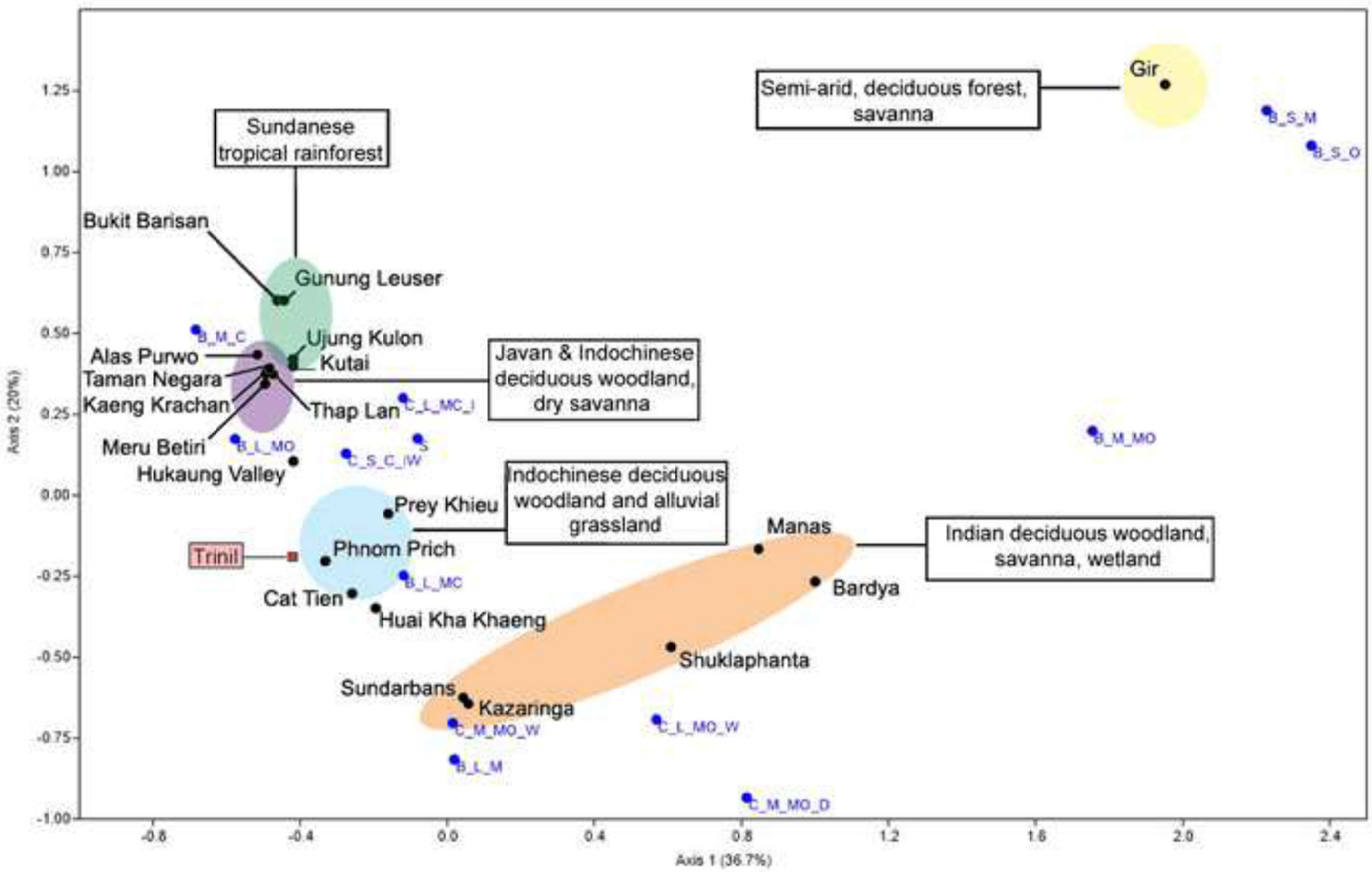

Sundanese tropical rainforest
Semi-arid, deciduous forest, savanna
Gir
B_S_M
B_S_O
Bukit Barisan
Gunung Leuser
B_M_C
Ujung Kulon
Kutai
Alas Purwo
Taman Negara
Kaeng Krachan
Thap Lan
C_L_MC_I
Javan & Indochinese deciduous woodland, dry savanna
B_M_MO
Meru Betiri
B_L_MO
S
C_S_C_IW
Hukaung Valley
Indochinese deciduous woodland and alluvial grassland
Prey Khieu
Trinil
Phnom Prich
B_L_MC
Manas
Indian deciduous woodland, savanna, wetland
Bardya
Cat Tien
Huai Kha Khaeng
Shuklaphanta
Sundarbans
Kazaringa
C_M_MO_W
C_L_MO_W
B_L_M
C_M_MO_D
Axis 2 (20%)
Axis 1 (36.7%)
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
-0.8
-0.4
0.0
0.4
0.8
1.2
1.6
2.0
2.4

Table 1

Order	Family	Species	Leiden	Berlin	Total:
Rodentia	Hystricidae	*Hystrix lagrelli*	2	-	2
		Hystrix sp.	-	1	1
	Muridae	*Rattus trinilensis*	2	-	2
		Muridea indet.	1	-	1
Primates	Hominidae	*Homo erectus*	7	-	7
	Hylobatidae	*Hylobates* sp.	1	-	1
	Cercopithecidae	*Macaca fascicularis*	11	-	11
		Trachipithecus cristatus	1	-	1
		Colobinae indet.	1	-	1
Carnivora	Canidae	*Xenocyon trinilensis*	-	1	1
	Felidae	*Panthera tigris*	10	-	10
		Panthera sp.	3	-	3
		Prionailurus bengalensis	1	-	1
Artiodactyla	Cervidae	*Axis lydekkeri*	1075	664	1739
		Muntiacus kendengensis	-	2	2
	Bovidae	*Duboisia santeng*	231	60	291
		Bibos palaeosondaicus	51	24	75
		Bubalus palaeokerabau	94	373	467
		Bovidae indet.	1406	17	1423
	Suidae	*Sus brachygnathus*	78	32	110
Perissodactyla	Rhinocerotidae	*Rhinoceros sondaicus*	44	-	44
		Rhinoceros sp.	6	9	15
Proboscidea	Stegodontidae	*Stegodon trigonocephalus*	499	1	500
		Stegodon sp.	-	69	69
		Proboscidea indet.	1	19	20

Table 2

Institution	Collection	Inv. nr.	Element	Institution	Collection	Inv. nr.
RMNH	Dubois coll.	5648	calcaneus	RMNH	Dubois coll.	5918a
RMNH	Dubois coll.	5649	calcaneus	RMNH	Dubois coll.	5918b
RMNH	Dubois coll.	5651	calcaneus	RMNH	Dubois coll.	5918d
RMNH	Dubois coll.	5652	calcaneus	RMNH	Dubois coll.	6245d
RMNH	Dubois coll.	5952	calcaneus	RMNH	Dubois coll.	5918f
RMNH	Dubois coll.	5998	calcaneus	RMNH	Dubois coll.	5918i
RMNH	Dubois coll.	6045	calcaneus	MFN	Selenka coll.	22490
RMNH	Dubois coll.	6046	calcaneus	MFN	Selenka coll.	22491
RMNH	Dubois coll.	6049	calcaneus	MFN	Selenka coll.	22492
RMNH	Dubois coll.	6149	calcaneus	MFN	Selenka coll.	22493
RMNH	Dubois coll.	6150	calcaneus	MFN	Selenka coll.	22495
RMNH	Dubois coll.	6156	calcaneus	MFN	Selenka coll.	22496
RMNH	Dubois coll.	6157	calcaneus	MFN	Selenka coll.	22497
RMNH	Dubois coll.	6160	calcaneus	MFN	Selenka coll.	22447
RMNH	Dubois coll.	6867	calcaneus	MFN	Selenka coll.	22448
RMNH	Dubois coll.	6880	calcaneus	MFN	Selenka coll.	22635
RMNH	Dubois coll.	6881	calcaneus	MFN	Selenka coll.	22636
RMNH	Dubois coll.	6884	calcaneus	MFN	Selenka coll.	22641
RMNH	Dubois coll.	6885	calcaneus	MFN	Selenka coll.	22642
RMNH	Dubois coll.	6886	calcaneus	MFN	Selenka coll.	22643
RMNH	Dubois coll.	6887	calcaneus	MFN	Selenka coll.	22644
RMNH	Dubois coll.	5918e	Phalanx II			

Element
Phalanx II
Phalanx II
Phalanx II
Phalanx II
Phalanx II
Phalanx II
calcaneus
calcaneus
calcaneus
calcaneus
calcaneus
calcaneus
calcaneus
Phalanx II
Phalanx II
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Phalanx II
Phalanx II
Phalanx II
Phalanx II

Table 3

Categories	Code
Bovid large: mixed vegetation	B_L_M
Bovid large: mixed to open vegetation	B_L_MO
Bovid large: mixed to closed vegetation	B_L_MC
Bovid medium: mixed to open vegetation	B_M_MO
Bovid medium: closed vegetation	B_M_C
Bovid small: open vegetation	B_S_O
Bovid small: mixed vegetation	B_S_M
Cervid large: mixed to open vegetation/wet substrate	C_L_MO_W
Cervid large: mixed to closed vegetation/intermediate substrate	C_L_MC_I
Cervid medium: mixed to open vegetation/wet substrate	C_M_MO_W
Cervid medium: mixed to open vegetation/dry substrate	C_M_MO_D
Cervid small: closed vegetation/intermediate to wet substrate	C_S_C_IW
Suid	S

Table 4

	Closed/saltatorial	Intermediate	Open/cursorial	Trinil
Closed/saltatorial	-	0.7298	**<0.001**	**<0.001**
Intermediate	1	-	**0.0045**	**<0.001**
Open/cursorial	**0.001**	**0.045**	-	**0.0044**
Trinil	**0.001**	**0.001**	**0.044**	-
Open wetland	**0.001**	**0.026**	**0.001**	**0.001**

Open wetland
<0.001
0.0026
<0.001
<0.001
-

Table 5

	Trinil	Dry	Intermediate	Wet
Trinil	-	**<0.001**	**<0.001**	**<0.001**
Dry	**<0.001**	-	**0.008**	**<0.001**
Intermediate	**<0.001**	**0.05**	-	**0.024**
Wet	**0.001**	**<0.001**	0.149	-

Table 6

Family	Species	Reconstructed habitats	Habitat assignment
Suidae	*Sus brachygnathus*	Generalist adapted to wide variety of habitats	S
Bovidae	*Bibos palaeosondaicus*	Primarily grazer, adapted to mixed to open vegetation	B_L_MO
	Bubalus palaeokerabau	Mixed browser/grazer, adapted to mixed vegetation	B_L_M
	Duboisia santeng	Browser/grazer, more reliant on grazing, adapted to closed vegetation	B_M_C
Cervidae	*Axis lydekkeri*	Grazer, adapted to open vegetation with wet substrate	C_M_MO_W
	Muntiacus kendengensis	Browser adapted to closed vegetation with intermediate to wet substrate	C_S_C_IW

Table 7

Site	Location	Habitats	B_L_M	B_L_MO	B_L_MC	B_M_MO	B_M_C	B_S_O	B_S_M	C_L_MO_W	C_L_MC_I	C_M_MO_W	C_M_MO_D	C_S_C_IW	S
Kazaringa	India	Alluvial grassland, savanna woodland	1	0	1	0	0	0	0	0	1	1	1	1	1
Manas	India	Alluvial grassland, savanna woodland	1	0	1	1	0	0	1	1	1	0	1	1	1
Gir	India	Semi-arid savanna woodland	0	0	0	1	0	1	1	0	1	0	0	0	1
Bardiya	Nepal	Savanna grassland, riverine forest	0	0	1	1	0	1	0	1	0	1	1	1	1
Shuklaphanta	Nepal	Grassland, wetland, riverine forest	0	0	0	1	0	0	0	1	1	1	1	1	1
Huai Kha Khaeng	Thailand	Seasonal forest, riverine forest	1	1	1	0	1	0	0	1	1	1	0	0	1
Kaeng Krachan	Thailand	Seasonal evergreen forest	0	1	1	0	1	0	0	0	1	0	0	1	1
Thap Lan	Thailand	Dry evergreen forest	0	1	1	0	1	0	0	0	1	0	0	1	1
Sundarbans	Banglad.	Mangrove forest	1	1	1	0	0	0	0	1	1	1	1	1	1
Meru Betiri	Java	Mangrove forest	0	1	0	0	0	0	0	0	0	0	0	1	1
Alas Purwo	Java	Savannah, mangrove forest	0	1	0	0	0	0	0	0	1	0	0	1	0
Ujung Kulon	Java	Lowland rainforest	0	1	0	0	0	0	0	0	1	0	0	1	1
Gunung Leuser	Sumatra	Lowland and montane rainforest	0	0	0	0	1	0	0	0	1	0	0	1	1
Bukit Barisan	Sumatra	Lowland rainforest	0	0	0	0	1	0	0	0	1	0	0	1	1
Kutai	Borneo	Lowland rainforest	0	1	0	0	0	0	0	0	1	0	0	1	1
Taman Negara	Malaysia	Lowland and montane rainforest	0	1	1	0	1	0	0	0	1	0	0	1	1
Phnom Prich	Cambodia	Open woodland, alluvial grassland	0	1	1	0	0	0	0	0	0	1	0	1	1
Prey Khieu	Cambodia	Semi evergreen forest	0	1	1	0	0	0	0	1	1	0	0	1	1
Cat Tien	Vietnam	Open woodland, alluvial grassland	1	1	1	0	0	0	0	0	1	1	0	1	1
Hukaung Valley	Myanmar	Woodland, riverine forest, grassland	0	1	1	0	1	0	0	0	1	1	0	1	1
Trinil	**Java**	-	**1**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**1**

Appendix A

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Appendix B

Citation on deposit: Kovarovic, K., & Gruwier, B. (in press). Palaeoenvironments at the Homo erectus type locality of Trinil (Java, Indonesia): the artiodactyl evidence Acknowledgements. Journal of Human Evolution