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Insular dwarfism in canids on Java (Indonesia) and its implication for the environment of *Homo erectus* during the Early and earliest Middle Pleistocene

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ABSTRACT

Several canid fossils, which were originally discovered and described in the early 20th century, are known from Early and earliest Middle Pleistocene of Java (Indonesia). Here we revise the taxonomy and relative age of the Javanese canid fossils in light of recent developments in the taxonomy and phylogeny of Canidae, and new insights in the evolution of island mammals. Results show that *Cuon* was absent during the Early and earliest Middle Pleistocene while the large-sized *Xenocyon* (previously *Megacyon*) was present in the Early Pleistocene and replaced by the small-sized *Xenocyon* (previously *Mececyon*) during the earliest Middle Pleistocene. The latter is probably an anagenetic dwarf derived from the larger form of the preceding period. The change in body size of *Xenocyon* on Java over time is likely the effect of increased competition within the carnivore guild within the restricted boundaries of the island. Simultaneously with a pronounced body size shift, a dietary shift from large-sized prey to much smaller prey must have taken place in order to meet energetic constraints. The degree of endemism of terrestrial mammals of the earliest Middle Pleistocene horizon of the site Trinil, which has also yielded *Homo erectus* fossils, indicates that during this period, Java was marginally isolated which allowed for a corridor dispersal to the island with subsequent vicariance. The nature and degree of isolation may have been similar to that of Late Pleistocene Sicily, but of a longer duration, given the higher degree of dwarfism of the stegodon, antilope and canid. The following continentalisation enabled the invasion by mainland terrestrial mammals, as is seen in younger layers at Trinil, and eventually by *Homo sapiens* and *Cuon* in the Late Pleistocene / Holocene.

1. Introduction

Towards the end of the 19th century, the island of Java (Indonesia) became famous for its Pleistocene hominin record of *Homo erectus* after the discovery by Eugène Dubois in 1891–1892 of a hominin calvaria, third molar and a femur in river deposits along the Bengawan Solo River near the abandoned village of Trinil, East Java (Dubois, 1894). He described the remains as *Pithecanthropus erectus*, an ancestral human that he considered to be intermediate between humans and apes (Dubois, 1894). The species name was inspired by shape and size of the femur (field number Trinil 3), which was similar to that of modern humans. Based on stratigraphy and absolute dating, the deposits with the hominin fossils are about 1.0–0.9 million years old (Leinders et al., 1985; Suzuki et al., 1985; van den Bergh, 1999).

About 400,000 more mammalian remains were unearthed at Trinil and other sites along the Bengawan Solo River and at the Sangiran dome (Central Java) by Dubois (1907, 1908) and later expeditions (e.g. Selenka and Blanckenhorn, 1911; Von Koenigswald, 1935), informing us about the environment and ecology of our early ancestors. Amongst the many mammalian fossils are a few scattered hypercarnivorous canid remains that have been attributed to two different extinct genera: *Megacyon merriami* (Merriam's dog) by Von Koenigswald (1940) and *Mececyon trinilensis* (Trinil dog) by Stremme (1911). Based on its small size, the Trinil dog has regularly been attributed to the extant genus *Cuon* (Hertler and Volmer, 2008; Hertler et al., 2007; Louys, 2014; Louys et al., 2007; Rozzi et al., 2013; van der Made, 2011), whereas others maintained the genus *Mececyon* (Von Koenigswald, 1933, 1939, 1940; Schütt, 1973; van den Bergh et al., 2001; Hertler and Rizal, 2005; Lyras et al., 2010; van der Geer et al., 2010; Ingicco et al., 2014; Volmer et al., 2016), based on the presence of a lower third molar, which is

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never present in *Cuon* (Tedford et al., 1995, 2009). Merriam's dog and the Trinil dog are endemic to the Pleistocene of Java; however, the systematic position and the precise relation between these two canid species remain, however, unresolved. Lyras et al. (2010) suggested that they form an anagenetic lineage, and should thus be attributed to a single genus. They further argued that their evolution is a typical example of insular dwarfism. These canids are thus crucial to our understanding of the degree of insularity of Java during the time frame when the first hominins entered the stage. The degree and nature of insularity has implications for the ecology of *H. erectus* on Java, including resource availability.

One of the reasons behind the taxonomical confusion of the Pleistocene canids of Java was the lack of knowledge on hypercarnivorous canids early in the 20th century. Since then, several studies have been published on systematics and phylogeny of this polyphyletic group (e.g. Tedford et al., 2009), and more findings are now known from Asia (e.g. Tong et al., 2011), the source area for Javanese mammals. Most importantly, forms like *Cuon dubius* and *Cuon stehlini* have been reconsidered and attributed to either the extinct genus *Xenocyon* (e.g. Echassoux et al., 2008; Sotnikova, 2001) or that of the African wild dog, *Lycaon* (Martínez Navarro and Rook, 2003). Furthermore, the biostratigraphy of Java has been resolved in more detail (e.g. van den Bergh et al., 2001). Based on these new insights and data, a revision of the Javanese canids is finally feasible.

Here we provide a detailed and updated description of the late Early-early Middle Pleistocene canid material of Java, revise the systematics and put our findings in the broader context of evolution in isolation of hypercarnivorous dogs. Our findings have implications for our understanding of the insular episodes of Java, during which the first hominids entered the scene.

2. Geological context

The geological history of Java (Fig. 1a) is complex; it originated as a calc-alkaline volcanic arc whose growth culminated in the Late Miocene when parts of Java emerged as palaeo-islands (van den Bergh, 1999). Tectonics, the buildup of volcanic cones and the filling of shallow basins and lagunas by lahars and clays originating from the erosion of volcanic ashes not only led to the gradual growth of these palaeo-islands, but also to its lesser isolation from Sumatra. The central and eastern parts of Java, the focal region of this study, emerged after c. 2.6–2.0 Ma (Bandet et al., 1989). Eventually, Java became periodically part of the mainland (Sunda Shelf) during periods of low sea level in the Late Quaternary as recently as 10 kya (Voris, 2000). Holocene sea level rise restored Java as an island, albeit with minimal isolation.

Between the de novo origin of the island and its final continentalisation as part of the Sunda Shelf, subsequent mammalian colonisations, in situ evolution and extinctions took place, which we here summarise. Generally, the successive Pleistocene faunas are classified as follows in three main divisions based on proboscidean fossils: the Early Pleistocene *Mastodon – Geochelone* fauna, the late Early to Middle Pleistocene *Stegodon – Homo erectus* fauna and the Late Pleistocene to Holocene *Elephas – Homo sapiens* fauna (van der Geer et al., 2010). Subdivisions (Fig. 1b) are named after their respective type locality name. The earliest of these is the Satir faunal unit (c. 2–1.5 Ma; van den Bergh, 1999; van den Bergh et al., 2001), which is represented by a highly endemic, typical insular fauna consisting only of dwarf elephantoids (including the mastodon *Sinomastodon bumiajuensis*), dwarf hippos (*Hexaprotodon simplex*), giant tortoises (*Geochelone*), murids (*Mus* sp., *Rattus* sp.) and lacking carnivores (Sondaar, 1984). Pollen samples indicate the development of immense mangrove forests (Sémah, 1984, 1986), The first *Stegodon – Homo* erectus fauna is the Cisaat fauna (Early Pleistocene; 1.2–1.0 Ma; van den Bergh et al., 2001), which also is a typical island fauna, again consisting only of taxa able to pass marine filters like deer (*Muntiacus muntjak, Axis lydekkeri*), hippos (*Hexaprotodon sivajavanicus*), elephants (*Stegodon trigonocephalus*), tigers (*Panthera* sp.) (de Vos and Sondaar, 1994; Huffman et al., 2006; van der Geer et al., 2010), murids (*Chiropodomys gliroides*, *Rattus* sp.; van der Meulen and Musser, 1999) as well as the oldest *Homo erectus* fossils (Indriati and Antón, 2008). Scattered dwarfed elephantoids without clear faunal context (dwarf *Stegodon* from Cirebon and Sambungmacam, *S. elephantoides*, *Stegoloxodon indonesicus*) may belong to this or an earlier layer (van den Bergh et al., 2001), and/or originate from different isolated subregions. Mangrove and tropical rain forests or open, seasonal forests now dominate the vegetal formation, coinciding with wetter and drier periods respectively (Sémah et al., 2016), After the Cisaat zone, Java became gradually easier to reach, albeit through a filtered corridor traversable only for a limited number of taxa (Larick et al., 2001; Meijaard, 2004), which includes the canids that comprise the focus of this study. The successive faunal stages are Trinil H.K. (1.0–0.9 Ma in van den Bergh (1999) or 0.8 Ma in Saleki (1997)) (Fig. 1b), Kedung Brubus (0.8–0.7 Ma; Leinders et al., 1985; van den Bergh et al., 2001) and Ngandong faunal levels (possibly c. 135 ka; van den Bergh et al., 2001), and are characterized, apart from *Homo erectus* and *Stegodon*, by an increasing number of taxa (van den Bergh et al., 2001; van der Geer et al., 2010) (see Section 2.1.2). These three faunas are characteristic for open woodland environments; this is confirmed by the dominance of grasses in the pollen samples (Sémah, 1982). Finally, during the Late Pleistocene, starting with the Punung Fauna (110–70 ka in van den Bergh et al. (2001) or 128–118 ka in Westaway et al. (2007)), Java became part of the continental Sunda Shelf and its fauna did not differ from that of neighbouring Sumatra. The Punung fauna represents rainforest conditions (e.g. with *Pongo pygmaeus*, *Hylobates moloch*), and witnesses the first arrival of *Homo sapiens* to Java (Storm et al., 2005) (for fauna list, see Westaway et al., 2007). Climatic changes associated with the last glacial maximum likely resulted in impoverishment of the Javanese fauna as elements like *Pongo* have not been retrieved from Holocene sites (van den Bergh et al., 2001). Palynological data confirm drier conditions and increased seasonality (Morley and Flenley, 1987). The Holocene sea level rise, perhaps combined with anthropogenic habitat disturbance, led to further local extinctions, including *E. maximus*.

2.1. Stratigraphy and biostratigraphy

The material attributed to *Megacyon merriami* was retrieved from the black clays of the Sangiran Formation of the Kendeng Group (Fig. 1c). Findings of *Mececyon trinilensis* are restricted to Trinil H.K. ("Hauptknochenschicht" or main bone layer) of the site Trinil (Fig. 1b). The material was excavated during the Selenka field campaigns and derives from layers that are equivalent to Trinil H.K. as excavated by Dubois (Selenka and Blanckenhorn, 1911).

2.1.1. Sangiran Formation

The Sangiran Formation of the Kendeng Group is one of four that are exposed in the Sangiran region of central eastern Java, an anticline formed between the stratovolcanos Mount Merapi and Mount Lawu. These formations are, from lower to upper stratigraphic levels, the Puren (or Upper Kalibeng) Formation, the Sangiran (or Pucangan) Formation, the Bapang (or Kabuh) Formation, and the Pohjajar (or Notopuro) Formation (Indriati and Antón, 2008) (Fig. 1c). The Sangiran Formation, preceded by the largely marine Puren Formation, consists of two members, the Lower Lahar Unit and the upper black clays (Bettis III et al., 2004). The Lower Lahar Unit, dated to 1.90 ± 0.02 Ma ($^{40}Ar/^{39}Ar$ on hornblende; Bettis III et al., 2004), stems from a massive lahar-type debris flow and incorporates fossils from various environments, but no hominids. The black clay member derives from sediments deposited in shallow marine, brackish-water and marsh environments, interspersed with thin tuff layers (Yoshikawa and Suminto, 1985), and contains fossils of terrestrial vertebrates adapted to lake-margin and marshy environments (Aimi and Aziz, 1985) and with sporadic *Homo erectus* findings in the uppermost part (Indriati and Antón, 2008). The