From the Solo to the Madura Strait: Quaternary geology, vertebrate palaeontology and hominin chronology of eastern Java and submerged Sundaland

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The Geological Museum in Bandung, built in 1929 as Geologisch Laboratorium.

Chapter 7

First vertebrate faunal record from submerged Sundaland, the late Middle Pleistocene hominin-bearing fauna of the Madura Strait

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First vertebrate faunal record from submerged Sundaland: the late Middle Pleistocene, hominin-bearing fauna of the Madura Strait

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Abstract

The Sunda Shelf currently holds the world's largest shelf sea. During Pleistocene sea-level lowstands the area emerged, forming a vast landmass called Sundaland. Intermittently exposed Sundaland played an important role in the regional vertebrate biogeography and evolution of species including *Homo erectus* and, in the Late Pleistocene, *Homo sapiens*. So far, our models of the Pleistocene biogeography of Sundaland were based on the distribution of extant species and on island fossil assemblages, notably from Java (Indonesia). Here we present the first vertebrate fossil record from subsea Sundaland. The fossils derive from the sandy fill of a lowstand valley of the Solo River in the Madura Strait, which was OSL-dated to 162±31 and 119±27 ka. The cemented sand was recently extracted and used for a landfill in the port of Surabaya. The assemblage consists of at least 36 species and provides a unique insight into the lowland fauna of emerged Sundaland, during the late Middle Pleistocene. The lowland river had a rich reptile community, consisting of various turtle species, crocodilians, varanids, and pythons. The nearby estuary was frequented by several shark species, including the extinct *Hemipristis serra,* as well as several species of stingrays. Some of these also ascended the river. The lowland plains surrounding the river were populated by herbivores such as Hippopotamidae and several species of Bovidae, Cervidae, and Proboscidea. The terrestrial community represents a grass-dominated environment and is similar to the contemporaneous fossil assemblage of Ngandong (Java). However, on a detailed level, there are conspicuous differences. For example, *Duboisia santeng, Axis lydekkeri,* and *Epileptobos groeneveldtii* are absent in Ngandong and were generally believed to have become extinct by the end of the Middle Pleistocene. Their presence in the Madura Strait assemblage shows that the species persisted on the lowland plains. Interesting is also the presence of more rarely encountered species such as *Varanus komodoensis*, *Macaca* sp. and *Homo erectus* on the lowland plains. Metrically, *Elephas* sp. molars from the Madura Strait site are relatively high-crowned, whereas *Bos palaeosondaicus* is relatively small-statured compared to its Middle Pleistocene relatives from Java. The fossil fauna from the Madura Strait reflects a thus far unknown vertebrate coastal lowland community that lived in and around the lower reaches of the Middle Pleistocene Solo River.

1. Introduction

In 2014 and 2015, sand was dredged from the seabed of the Madura Strait **(Fig. 1A-B)**, in front of the port of Surabaya (Java, Indonesia), and used for the development of a land reclamation west of the city **(Fig. 1C).** The work was assigned by a local port company, Berlian Manyar Sejahtera (BMS), and involved the construction of an artificial island along the coast. Upon completion, the reclamation site turned out to be strewn with vertebrate fossils. Sealand Coastal Consultancy, at this time the engineering consultant of the Surabaya port-operator Pelindo III, recognized the scientific interest of the fossils. After consultation with BMS, Pelindo III, and officials of the Geological Museum Bandung, it was decided to collect and secure the fossils from the site before the construction of port-handling infra-structure. The fossils were stored in the Geological Museum Bandung. In 2017, it was decided to integrate the study of the assemblage in the Indonesian-Dutch research program 'Studying Human Origin in East Java'.

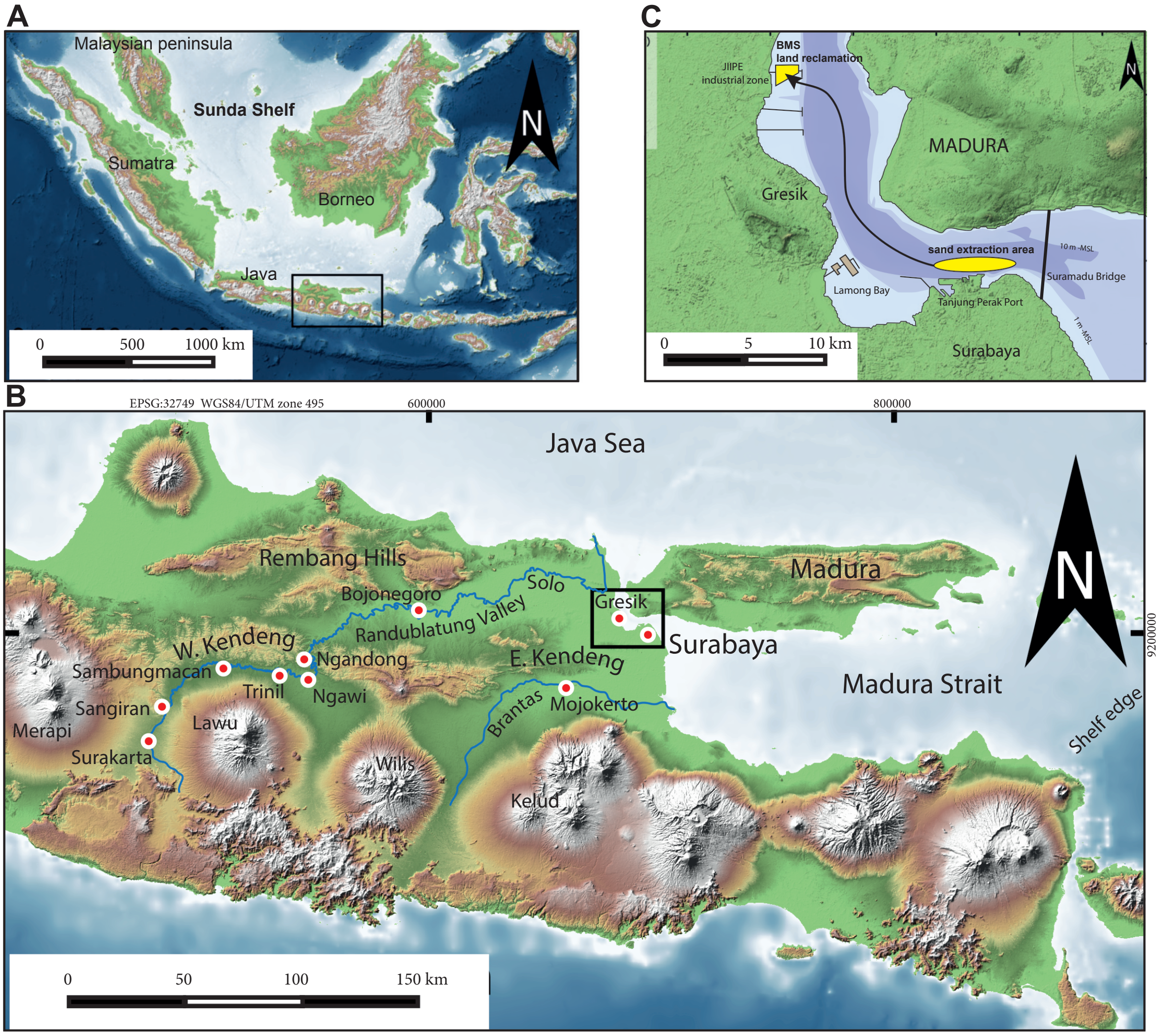


Fig. 1. A: The Sunda Shelf of Southeast Asia, with the Indonesian archipelago. Box indicates the position of map B. **B:** Eastern Java, the Madura Strait, Surabaya, the Solo River, and other sites mentioned in the text. Box indicates the position of map C. **C:** The Madura Strait north of Surabaya, with the sand extraction area and the location of the BMS land-reclamation. Map data: GEBCO and ALOS.

What makes the Madura Strait fossil assemblage special? In the first place, it is one of the largest and most complete vertebrate fossil assemblages collected from this region since the great excavations on Java of the late 19th and early 20th century (Selenka and Blanckenhorn, 1911b; Dubois, 1908). These historic excavations yielded fossil assemblages that, up to today, form the basis of the regional Pleistocene vertebrate taxonomy and shaped our interpretations of the regional biogeography and vertebrate evolution (Hooijer, 1958a, 1955; Janensch, 1911b; Stremme, 1911; Dubois, 1908, 1907). The occurrence of *Homo erectus* in these fossil assemblages makes the region of particular interest for hominin evolution and dispersal (Antón, 2003; Kaifu, 2017). Up to today, palaeontological research teams are working on Java and frequently find new material. However, except for occasional new hominin finds (Widianto et al., 2023; Noerwidi et al., 2021; Zaim et al., 2011), detailed descriptions and measurements of the non-hominin vertebrate fossils are usually not provided. This implies that potentially valuable material remains unrecognized, and that opportunities are missed to build up new comparative data sets and local reference collections. Note in this respect that over the past century, vertebrate taxonomies have been revised and species definitions updated. As a consequence, the existing reference collections and taxonomic literature, although generally of outstanding quality, may be outdated or confusing. The Madura Strait assemblage offers a unique opportunity for a detailed descriptive and metric study, using updated taxonomies and measurement protocols, which may serve as a reference for future finds in the region.

In the second place, the interest of the Madura Strait assemblage lies in its underwater provenance and its relation with the biogeographic region known as Sundaland. Already since the first discovery of vertebrate fossils on Java, the Pleistocene migration of species to the island has been subject of discussion. Initially, it was hypothesized that the dispersal of land vertebrates to Java had taken place via a land bridge over the Andaman and Nicobar Islands. Later, the discovery of ancient drainage systems on the bottom of the Java Sea (Molengraaff and Weber, 1921) showed that this shelf sea must have once been exposed, forming a large landmass that connected Java, Sumatra and Borneo to the Asian mainland. Van Bemmelen (1949) proposed to refer to this Pleistocene landmass as Sundaland, and to the present-day shelf sea as the Sunda Shelf **(Fig. 1A)**. This extensive shelf sea, the largest drowned shelf of the world, was probably widely exposed during most of the Early Pleistocene (Husson et al., 2020). Regional subsidence brought the area into the range of sea-level fluctuations during the Middle Pleistocene, causing intermittent stages of submergence during interglacials (Sarr et al., 2019). During Middle and Late Pleistocene glaciations, Sundaland was exposed (Voris, 2000), providing a pathway for faunal dispersal to Java (Van den Bergh et al., 2001; Van Den Bergh, 1999; De Vos et al., 1982). Meijaard (2003) and Heaney (1991) noted that during glaciations, this exposed land surface may not have been an area over which species could freely pass. The central lowland of the exposed landmass was probably associated with dry climate conditions and open, savannah-like vegetation, forming a barrier for forest-dependent species. However, for open habitat-dwelling herbivores and early hominins, the lowland plains may have formed a corridor for dispersal to Java (Louys and Kealy, 2024; Husson et al., 2022; Louys and Meijaard, 2010; Antón, 2002). The central savannah of emerged Sundaland may even have been a refugium for open-habitat species, in periods when the adjacent Asian mainland became too dry (Louys and Turner, 2012).

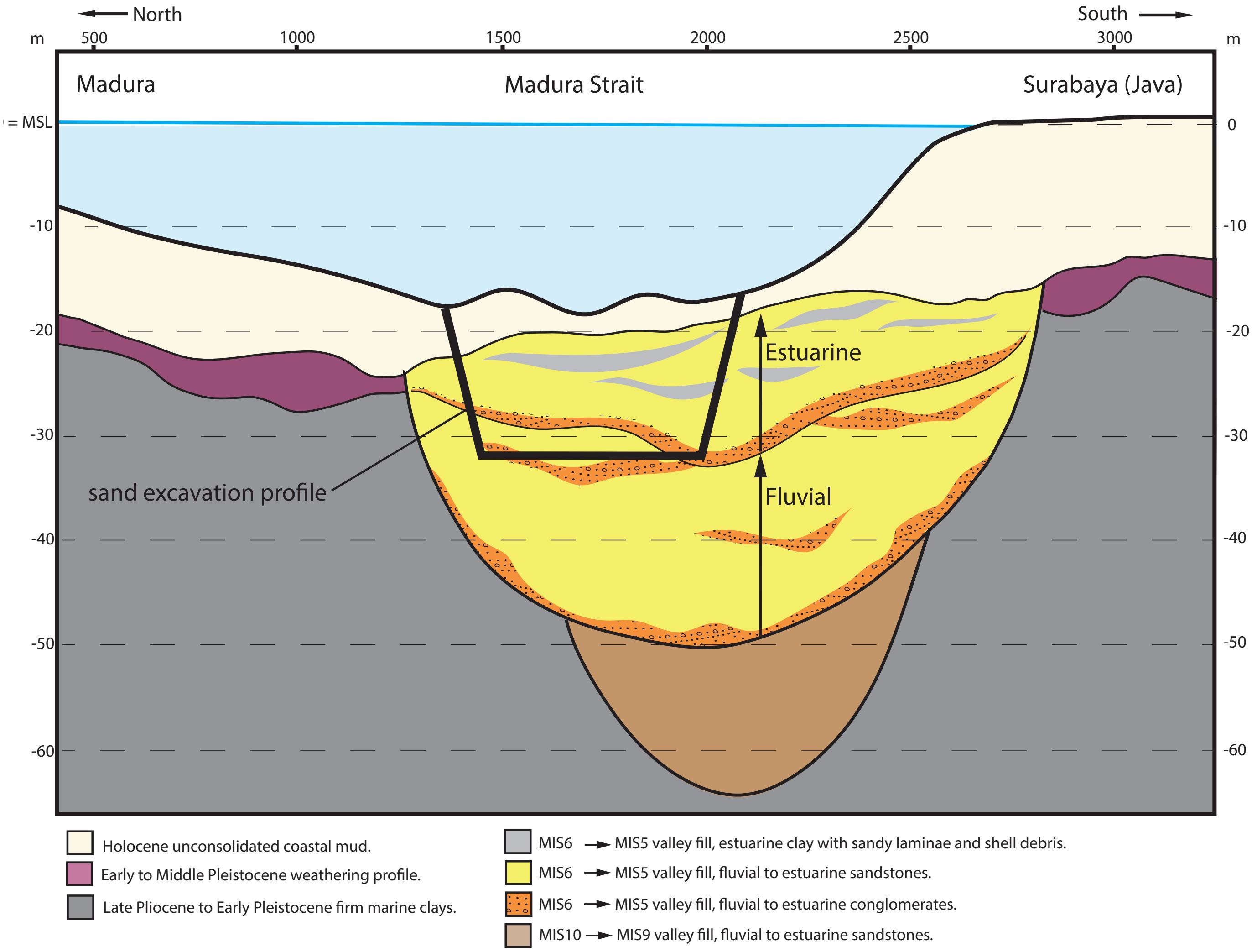


Fig. 2. Schematic cross-section over the Madura Strait north of Surabaya, with a projection of the sand-extraction profile. The local subsoil contains the remnants of two superimposed paleovalleys of the Solo. The extracted material is the sandy fill of the highest paleovalley. Incision of the two paleovalleys has been tied to the lowstands of MIS10 and MIS6 respectively. The valley-fill sequences relate to subsequent transgressive stages. For details, see Berghuis et al. (2025a; 2025c).

Thus far, the models of the Pleistocene biogeography of Sundaland and species dispersal have primarily been based on the distribution of extant species on the islands of Southeast Asia and on the Pleistocene fossil assemblages from Java. Sumatra and Borneo yielded interesting Late Pleistocene cave faunas (De Vos et al., 1982) but relevant older fossil assemblages from open-air sites from these islands are rare. Moreover, there have thus far been no fossil finds from the seabed (Adhityatama and Yarista, 2019). This is remarkable and in great contrast with other shallow shelf seas in the world, such as the North Sea, where seabed dredging and trawling yielded abundant vertebrate fossils (Mol and Bakker, 2022; Kolfschoten and Essen, 2004) including hominin fossils and arftefacts (Niekus et al., 2019; Hublin et al., 2009). The absence of similar finds from the Java Sea or South China Sea may be due to the high fluvial supply of fine terrestrial detritus, blanketing the seabed with Holocene mud. But it is probably also related to a lack of awareness. Note in this respect that large-scale seabed dredging has been carried out in this area, in relation to land reclamation works in Singapore and Jakarta, and that trawling fishing is common in the region.

The Madura Strait assemblage is the first vertebrate faunal record from submerged Sundaland. It offers a unique insight into the fauna of the lowland plains that must have formed the dominant Pleistocene landscape element of Sundaland and therefore forms an important contribution to our understanding of the regional biogeography. In a previous publication (Berghuis et al., 2025a) we described the subsea vertebrate locality as the sandy fill of a submerged lowstand valley of the Solo **(Fig. 2)**. Off the coast of Surabaya, the base of the incised valley lies at a depth of 50 m below mean sea level (MSL). The valley fill has a thickness of ca. 30 m and consists of fluvial sandstones and conglomerates, which change upwards into marine sandstones and marine clay-sand alternations. Two fluvial sandstone samples yielded OSL-ages of 162±31 and 119±27 ka, indicating that the valley fill is associated with MIS6 and with the subsequent transgressive stage in the run-up to MIS5. Consequently, the valley was probably cut during the preceding stage of falling sea-level in the run-up to MIS6. The upwards change to marine strata indicates that the valley was eventually invaded by the sea, changing the valley into an estuary.

The study aimed to provide:

1: a detailed metric and morphological description of the Madura Strait assemblage, which may serve as a reference for future comparative studies of fossil finds in the region.

2: insight into the vertebrate fauna of the lowland plains of Sundaland during the late Middle Pleistocene and into its implications for regional biogeography and faunal dispersal.

This publication presents the results of the palaeontological analysis of the entire Madura Strait assemblage, with the exception of two hominin skull fragments, which are presented separately (Berghuis et al., 2025d).

2. Methods

The first fossil-collecting campaign was carried out between July and September 2015. The entire surface of the site was explored on hands and knees (by H.B.), collecting all vertebrate fossils visible to the naked eye. The work did not include digging trenches or sieving of sediment. Additional searches took place in 2016, 2017, and 2018, collecting in areas that had been subject to erosion by run-off, or where construction-related ground works had exposed new material.

The collected fossils were transported to the Geological Museum Bandung, where the material was cleaned, provisionally ordered, labelled and stored. The total number of collected specimens is 6,372. Most specimens received a separate collection number. In other cases, a collection number was given to a group of related fossils or fossil fragments, which were referred to as specimen A, B, etc. The fossil remains are heavily mineralized and strongly fragmented. A systematic taphonomic analysis has been carried out and is presented separately (Berghuis et al., 2025c).

Morphological description and taxonomical identification of the material was carried out at the Geological Museum Bandung. Measurements were taken with a digital calliper following the guidelines of Von den Driesch (1976). The dental nomenclature is based on Herman (1994) for batoid fish, Cappetta (1987) for sharks, Van den Bergh (1999) for proboscideans and Hillson (2005) for other (mammalian) species. The osteological nomenclature is based on Williston (1925) for reptiles and on Pales et al. (1971) for mammals. Dextral and sinistral positions are indicated as (d), (s) or when unknown as (d/s).

For direct morphological comparison, extensive use has been made of the collection of the Geological Museum Bandung. Other institutes that have been visited for comparative studies are the Trinil Museum (Indonesia), Naturalis Biodiversity Center (the Netherlands), the Zoological Laboratories of Leiden University (the Netherlands) and Tübingen University (Germany) and the Museum für Naturkunde of Berlin (Germany). Identifications have been based on recent and commonly accepted taxonomies of extant and extinct species, with references to relevant publications. For Java, with its long history of palaeontological research, this is not always an easy task, as the taxonomies have been subject to repeated revisions, while abandoned species names are still frequently used.

We followed the hierarchy and taxonomic subdivision of Nelson et al. (2016) for fishes, Pincheira-Donoso et al. (2013) for reptiles and Wilson and Reeder (2005) for mammals. The even-toed ungulates, represented by a large number of taxa within the Madura Strait assemblage, have been referred to as the Order Artiodactyla, thus not following Montgelard et al. (1997) who proposed to revise this order into Cetartiodactyla, a revision which is debated (Prothero et al., 2022).

3. Systematic palaeontology

The Madura Strait assemblage has a high species diversity, representing four taxonomical Classes and eleven Orders **(Table 1)**. In the next sections, the identified species will be discussed per taxonomical Order. The species represent different ecosystems, ranging from terrestrial to fluvial and estuarine. In **Section 4** we will go deeper into the background of the assemblage in terms of vertebrate communities and Sundaland biogeography.

Class Chondrichthyes (Huxley, 1880) - cartilaginous fish		
	Superorder Galeomorphii Compagno, 1973 - galean sharks	
		Order Carcharhiniformes (Compagno, 1977) - ground sharks
	Superorder Batoidea (Compagno, 1973) - rays	
		Order Myliobatiformes (Compagno, 1973) - stingrays
Class Actinopterygii (Klein, 1885) - ray-finned fish		
		Order Siluriformes Cuvier, 1817 - catfish
Class Reptilia Laurenti, 1768 - reptiles		
	Superorder Lepidosauria (Haeckel, 1866) - lepidosaurs	
		Order Squamata (Oppel, 1811) - scaled reptiles
		Order Testudines (Batsch, 1788) - turtles
		Order Crocodilia (Owen, 1842) - crocodilians
Class Mammalia Linnaeus, 1758 - mammals		
		Order Proboscidea (Illiger, 1811) - elephantoids
		Order Primates (Linnaeus, 1758) - primates
		Order Carnivora (Bowdich, 1821) - carnivores
		Order Perissodactyla (Owen, 1848) - odd-toed ungulates
		Order Artiodactyla (Owen, 1848) - even-toed ungulates

Table 1. The vertebrate fauna (Phylum Chordata) of the Madura Strait: subdivision in taxonomic Classes and Orders.

3.1 Order Carcharhiniformes (Compagno, 1973) – ground sharks

Pleistocene shark teeth from Java were first described by Dubois (1907) and Hennig (1911). These teeth were excavated from fluvial strata in Trinil and ascribed to the freshwater shark *Carcharias gangeticus*, a species today referred to as *Glyphis gangeticus* (Nelson et al., 2016). Two morphologically deviant teeth from Trinil were ascribed to *Carcharias taurus* (Joordens et al., 2009; Koumans, 1949), which is an extant coastal species. Yudha et al. (2018) described fossil shark teeth from museum collections in Java, mostly of unknown age or stratigraphic provenience.

Family: Hemigaleidae Hasse, 1878 – weasel sharks
Genus: *Hemipristis* Agassiz, 1843
***Hemipristis serra* Agassiz, 1843**

Available material (N=5). Upper teeth: SBY5050, SBY646. **Lower teeth:** SBY7129A-C.

Description and identification: SBY5050 **(Fig. 3)** is an eye-catching specimen among the shark teeth from the Madura Strait, because of its large size and conspicuous coarse serrations along the cutting edges. The crown is triangular and slightly distally inclined, with a convex mesial cutting edge and a concave distal cutting edge. The labial face of the crown is flat, but the lingual face is arched, which gives it a robust appearance. Also, the root is arched at the lingual side, with a prominent protuberance. The root is bilobate, with a nutritive groove at the lingual side and a prominent concavity between the lobes.

The convex and concave cutting edges with coarse serrations are highly similar to the upper teeth of *Hemipristis elongata,* the extant snaggletooth shark of the Indian Ocean and the western Pacific. However, the size of SBY5050 **(Table 2)** exceeds the range of this species and links it to the extinct sister species *Hemipristis serra* (Kent, 2018). *Hemipristis serra* is known from numerous Miocene to Pleistocene localities worldwide and inhabited shallow tropical seas (Cappetta, 1987). Four other specimens have been assigned to this species. SBY7129B **(Fig. 3)** has a morphology that is highly similar to SBY5050, but is smaller and more inclined. It is slightly weathered, but remnants of the coarse serrations are visible along the concave distal cutting edge. Its size and morphology fall within the range of this species' lower lateral teeth. SBY7129A **(Fig. 3)** is a lower anterior tooth, recognizable by its pointed, unserrated, and hooked morphology**.** They are differentiated from *Glyphis gangeticus* lower anterior teeth (see below) by their larger size, as well as the thicker, strongly bilobate root, with at the lingual face a characteristic rounded protuberance and nutritive groove.

Family: Carcharhinidae Jordan and Evermann, 1896
Genus: *Glyphis* Agassiz, 1843
Glyphis gangeticus (Müller & Henle, 1839) – Ganges shark

Synonyms: *Prionodon gangeticus*, *Eulamia gangetica*; *Carcharias gangeticus*; *Carcharhinus gangeticus*

Available material (N=51). Upper teeth: SBY640A-D, SBY641A-E, SBY5048A-E, SBY5049A-C, SBY7122A-H, SBY7133A-I. **Lower teeth:** SBY654A-E, SBY5047A-F, SBY7123A-F.

Description and identification: The upper teeth have flat, broad, triangular, blade-like cusps with finely serrated cutting edges. Their root is thin and flat, only slightly arched at the lingual side, and lacks a prominent neck, which gives the teeth a tall and slender appearance. We pictured two representative specimens **(Fig. 3)**. SBY5048A is an anterior tooth, with an erect, symmetrical shape. SBY5048B is a lateral tooth, characterized by a semi-oblique, backward-pointing blade, a straight mesial cutting edge, and a slightly notched distal cutting edge. The lower teeth of this species have a different morphology, with a long and pointed crown and unserrated cutting edges. The pictured specimen SBY5047A **(Fig. 3)** has downward projecting, bilobate and rounded roots. This, in combination with its significant length and inward-hooked shape, identifies the specimen as an anterior tooth.

The slender, triangular crowns with finely serrated cutting edges and thin roots are characteristics of the upper teeth of the genus *Glyphis* (Compagno, 2001). *Glyphis* species live in the tidal or freshwater zone of large muddy rivers and occur in an area stretching from the Indian peninsula to northern Australia. The genus holds a number of species, including *Glyphis gangeticus*, *Glyphis glyphis* and *Glyphis garricki* (Compagno, 2001). The latter two species occur in the lowland rivers of Borneo and New Guinea. These two species have a spear-like thickening at the top of the lower anterior teeth, which appears to be absent in the specimens from the Madura Strait. In this respect, the Madura Strait teeth correspond with the extant *G. gangeticus* of India.

Genus: *Carcharhinus* Blainville, 1816
Carcharhinus cf. *leucas,* Valenciennes, 1839 – bull shark

Available material (N=20). Teeth: SBY7124A-C, SBY7125A-F, SBY7126A-B, SBY7132A-I.

Description and identification: The teeth have triangular cusps with finely serrated cutting edges. The crown and the root are relatively thick and rounded, especially at the lingual face. The root is slightly bilobate, with a nutritive groove at the lingual face. There is a prominent neck between the crown and the root at the lingual face, and a prominent distal heel, resulting in a relatively great basal crown width. We pictured two representative specimens: SBY7124A and B **(Fig. 3).**

The teeth may, at first glance, appear similar to those of *G. gangeticus*. However, they differ from this species by their lower crown height **(Table 2)** and rounded lingual face. The specimens correspond well with the teeth of *Carcharhinus leucas* and *Carcharhinus amboinensis* (Compagno, 2001), two species with morphologically identical teeth. Both species are extant in Indonesian waters. We ascribe the specimens to *C.* cf. *leucas* because of their size **(Table 2)**, which is slightly above the reported size range of *C. amboinensis* (Lin et al., 2022; Kocsis et al., 2019). *Carcharhinus leucas* has a coastal habitat, enters shallow bays and estuaries and may ascend rivers. The upper and lower teeth of this species are morphologically similar. We loosely subdivided the Madura Strait specimens into upper and lower teeth by the criteria that the species' upper teeth are slightly larger and thicker, whereas the lower teeth have a slightly more pronounced bilobate root (Compagno, 2001).

Specimen	*Taxonomy*	*Tooth position*	*Crown height (mm)*	*Mesial crown edge length (mm)*	*Basal crown width (mm)*
SBY5048A	*Glyphis gangeticus*	Upper anterior	19.2	21.5	18.1
SBY5048B	*Glyphis gangeticus*	Upper lateral	12.7	18.6	17.7
SBY5047A	*Glyphis gangeticus*	Lower anterior	17.1	18.4	8.9
SBY7124A	*Carcharhinus* cf. *leucas*	Upper lateral	13.9	20.1	18.2
SBY7124B	*Carcharhinus* cf. *leucas*	Lower lateral	12.1	19.4	19.5
SBY5051	*Galeocerdo cuvier*	Upper lateral	16.0	25.1	28.1**
SBY5050	*Hemipristis serra*	Upper lateral	27.3*	31.3*	23.1
SBY7129A	*Hemipristis serra*	Lower anterior	28.4	32.1	15.2
SBY7129B	*Hemipristis serra*	Lower lateral	19.1	21.9	15.7

Table 2. Measurements (mm) Carcharhiniformes teeth (specimens pictured in **Fig. 3**).
* Small part of crown tip broken off, given value is estimate of unbroken state. ** Measurement includes distal cusplet.

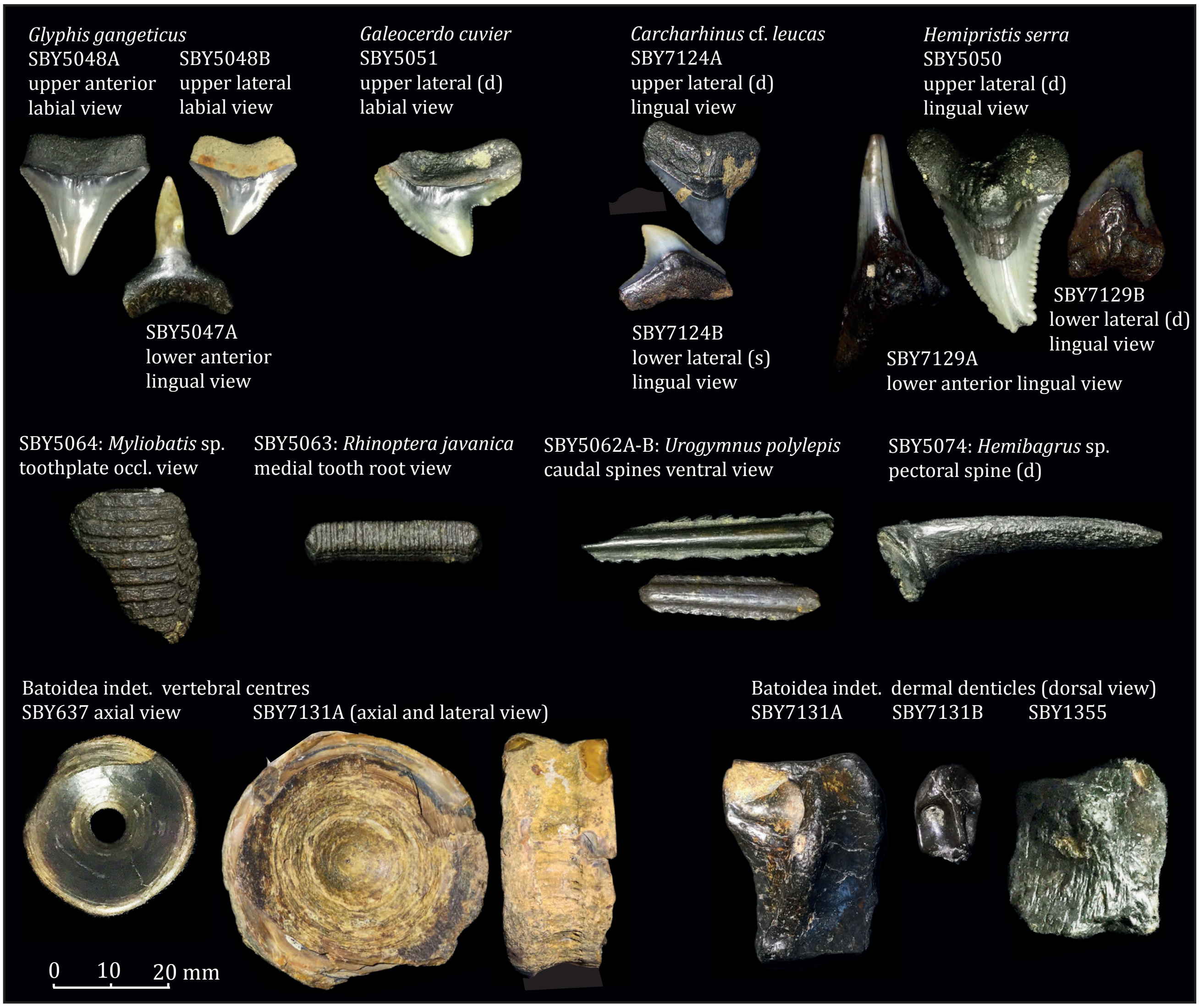


Fig. 3. Fish remains (Myliobatiformes, Carcharhiniformes, Siluriformes) from the Madura Strait assemblage. Selected photographs. For measurements see **Tables 2** and **3**.

Genus: *Galeocerdo* Müller and Henle, 1837
Galeocerdo cuvier (Péron & Lesueur, 1822) – tiger shark

Available material (N=3). Upper teeth: SBY5051, SBY7134A-B.

Description and identification: SBY5051 **(Fig. 3)** is a tooth with a backward-curved crown with a distal cusplet, forming a prominent distal heel. It has coarse serrations along the mesial cutting edge of the main cusp and the distal cusplet. The posterior cutting edge of the main cusp has finer serrations. The root is robust and arcuate. The anterior part of the root is broken off.

The backward-curved crown with the serrated distal cusplet is characteristic of *Galeocerdo cuvier*. The species has similar-shaped upper and lower teeth. However, Compagno (2001) noted that in the upper teeth, the serration pattern on the distal heel increases in height anteriorly toward the notch, a feature which we also observe in SBY5051. *Galeocerdo cuvier* is a common tropical to warm-temperate species with a preference for turbid continental waters and often enters into estuaries.

Specimen	*Taxonomy*	*Tooth position*	*w (mm)*	*l (mm)*	*w/l-ratio*	*h-crown*	*h-root*
SBY5064	*Myliobatis* sp.	medial	17.5	2.3	7.6	0.99	0.71
SBY5063	*Rhinoptera javanica*	medial	29.80	5.71	5.23	1.73	1.39
SBY7121A	*Rhinoptera javanica*	medial	>27.45*	6.84	> 4.01	1.80	1.51
SBY7121B	*Rhinoptera javanica*	medial or 3rd lateral	>13.78*	8.40	--	3.85	2.45

Table 3. Measurements (mm) Myliobatiformes teeth. * Incomplete specimens. Given values are measured (minimum) widths.

3.2 Order Myliobatiformes (Compagno, 1973)

There are no previous records of Pleistocene Myliobatiformes from Java, except for two spine fragments collected in Trinil in the 1890s, which had earlier been referred to as Siluroidea indet. (Koumans, 1949; Dubois, 1908). Joordens et al. (2009) re-interpreted the specimens as caudal spines of the giant freshwater stingray *Himantura chaophraya*, a species nowadays referred to as *Urogymnus polylepis* (Nelson et al., 2016).

Suborder: Myliobatoidei - stingrays
Family: Myliobatidae (Bonaparte, 1838)
Genus: *Myliobatis* Cuvier, 1816
***Myliobatis* sp.**

Available material (N=1). Dental plate fragment: SBY5064.

Description and identification: SBY5064 **(Fig. 3)** is a fragment of a dental plate made up of at least nine teeth rows, each consisting of one laterally enlarged medial (symphysial) tooth and three lateral teeth along both buccal sides. The medial teeth are six-sided, straight, and extremely buccolingually enlarged **(Table 3)**, without significant size variation between the tooth rows. The lateral teeth are not buccolingually enlarged, but square-shaped and placed in an imbricated position, shifted half of a tooth length over the neighbouring rows. The teeth have a smooth occlusal surface. The opposite surface (root view) has a fine pattern of narrow plate elements, directed mesiodistally over the dental plate, separated by grooves.

Pavement-like dental plates are found in Myliobatinae and Rhinopterinae, two subfamilies of Myliobatidae. The described plate architecture, with rows consisting of one laterally enlarged medial tooth sided by three not enlarged lateral teeth, is characteristic of Myliobatinae. The straight, extremely enlarged medial teeth, with little width variation of these medial teeth over the consecutive rows, are indicative of the genus *Myliobatis* (Herman et al., 1994).

The size of the fossil dental plate is indicative of a stingray with a disk width of around 50 cm. Currently, two *Myliobatis* species of this size occur in the Indonesian seas: *M. tobijei* and *M. hamlyni*. However, both are deep-water species, which makes their occurrence in the Madura Strait assemblage unlikely. The fragment is therefore referred to as *Myliobatis* sp.

Family: Rhinopteridae Jordan & Evermann, 1896
Genus: *Rhinoptera* Cuvier, 1829
***Rhinoptera javanica* (Müller & Henle, 1841) – flapnose ray**

Available material (N=3). Teeth: SBY5063, SBY7118A-B.

Description and identification: SBY5063 **(Fig. 3)** is a six-sided, straight, buccolingually enlarged tooth, deriving from a disarticulated dental plate of a stingray. The tooth is larger and more robust than the medial teeth of the articulated dental plate SBY5064 that we ascribed to *Myliobatis* sp., but it has a lower width/length-ratio **(Table 3)**. It has a smooth occlusal surface and a comb-like base (root view), consisting of fine mesiodistally oriented ribs. The position of the root is shifted several mm posteriorly from the crown, which is an interlocking mechanism that makes that crowns partly rest on the root of the adjacent teeth row.

The robustness and relatively low w/l-ratio of the tooth are characteristic of Rhinopterinae dental plates, which are made up of only ca. ten rows of relatively large teeth (Herman et al., 1994). As for Myliobatinae, the teeth rows consist of a medial tooth flanked along both sides by lateral teeth, which are placed in an imbricated pattern. However, in contrast to Myliobatinae, the lateral teeth are hexagonal. Moreover, the lateral teeth are not of uniform size, but become increasingly enlarged toward the medial tooth. The latter is still the widest tooth of the row, but with an enlargement that is not as extreme as in Myliobatinae.

Another difference is that Rhinopterinae dental plates are not as tightly interlocked, which makes that single teeth are found more often (Claeson et al., 2010). There are two extant *Rhinoptera* species in Indonesian waters: *Rhinoptera jayakari* and *Rhinoptera javanica.* The former has highly robust medial teeth, with a w/l-ratio that hardly exceeds 3 (Pradeep et al., 2018). Moreover, it is a deep-water species, which makes its occurrence in the Madura Strait assemblage unlikely. The latter species lives in coastal and estuarine waters and has a dentition that closely matches the Madura Strait specimens, with respect to morphology and size range (Herman et al., 1994). With a width of ~30 mm and a w/l-ratio of ~5, SBY5063 is identified as a medial tooth **(Table 3)**. We therefore ascribe the specimens to *R. javanica*.

Family: Dasyatidae (Jordan, 1888)
Genus: *Urogymnus* (Müller & Henle, 1837)
Urogymnus polylepis (Bleeker, 1852) – giant freshwater stingray

Synonyms: *Himantura polylepis*, *Himantura chaophraya*

Available material (N=3). Caudal spine fragments: SBY 5062A-C.

Description and identification: The specimens **(Fig. 3**) are fragments of straight caudal spines, with symmetrical serrations along both lateral margins and a frequency of nine or ten serrations per cm. The dorsal side of the spines is smooth and convex, whereas the ventral side has a rounded axial rib. In SBY5062A this axial rib is slightly tapering, indicating a position toward the distal end of the spine. With a width between 7 and 8 mm, the fragments must derive from large and robust spines, with an estimated length of around 15 cm, which clearly exceeds the size range of *Myliobatis*. Spines with a length up to ~10 cm are known from *R. javanica* (Schwartz, 2007). Concerning size and morphology, the spine fragments from the Madura Strait compare well with the spines of the giant freshwater stingray *Urogymnus polylepis* (Cuny and Piyapong, 2007), an extant species, living in large lowland rivers and estuaries of Southeast Asia, including Sumatra and Borneo and until recently on Java (Iqbal et al., 2020). The fossils are also highly similar to the Pleistocene specimens from Trinil, ascribed to this species by Joordens et al. (2009).

3.3 Superorder Batoidea, Compagno, 1973

Batoidea indet. - rays

Available material (N=18). Vertebral centra: SBY7130A-G, SBY637, SBY642, SBY662, SBY666 and SBY7130A, SBY7127. **Dermal denticles:** SBY1355, SBY7131A-C, SBY7183.

Description and identification: The vertebral centra are cylindrical and biconcave and have concentric growth bands, which associate them with cartilaginous or bony fish. Compared to their diameter, they have a short anteroposterior length. For example, the pictured specimens SBY637 and SBY7130A **(Fig. 3)** have a diameter of 28 and 40 mm and an anteroposterior length of ~12 and 16 mm respectively. This short anteroposterior length (less than 50% of the radius) is characteristic of Batoidea (Kozuch and Fitzgerald, 1989). Another morphological trait that points to Batoidea is the absence of clear dorsal and ventral foramina along the sides of the vertebral centrum. Because of a lack of diagnostic features and in the absence of useful reference collections or ichthyological descriptions, the specimens have been assigned to Batoidea indet. Referring to their size and to the fluvial to estuarine depositional conditions of the site, the specimens may represent Pristidae (saw fishes), but may also very well derive from the giant stingray *Urogymnus polylepis*.

The Madura Strait assemblage contains several rectangular, flat bony elements with a concave base. SBY1355 **(Fig. 3)** measures 34 mm anteroposteriorly and mediolaterally. Its dorsal surface is ornamented with fine striations that radiate outward from a rounded central keel. Its ventral surface is smooth and slightly convex. SBY7131A and B **(Fig. 3)** have a more elongated outline and a smooth upper surface, with a longitudinal keel that is slightly inclined to one side, running diagonally over the dorsal surface. The specimens have the appearance of crocodilian osteoderms, but they differ from such elements by the absence of a pitted ornamentation on the dorsal surface. We refer to the specimens as Batoidea indet., because of the similarity with the batoid dermal denticles described by Lopes et al. (2016) and Bourbon (2011). Detailed ichthyological descriptions of batoid dermal denticles are unfortunately not available.

3.4 Order Siluriformes (Cuvier, 1817) - catfish

Pleistocene remains of Siluriformes from Java are scarce. Dubois (1908, 1907) mentioned the occurrence of *Clarias magur* among the fossils from Trinil. Hennig (1911) described several pectoral spines and cranium fragments from Trinil as *Clarias* sp. and Siluridae indet. Koumans (1949) re-analysed the material collected by Dubois and recognized three species: *Hemibagrus nemurus*, *Clarias batrachus* and *Clarias leiacanthus,* which was confirmed by Joordens et al. (2009). Yudha et al. (2020) studied museum specimens from of Java, mostly of unknown age and stratigraphic provenience, and recognized several additional species.

Family: Bagridae Bleeker, 1858
Genus: *Hemibagrus* Bleeker, 1862
Hemibagrus sp.

Available material (N=1). Pectoral spine (d): SBY5074.

Description and identification: SBY5074 **(Fig. 3)** is an intact pectoral spine with a length of 53 mm. The specimen is slightly worn and the serrations on the lateral surfaces have largely vanished. The spine has a relatively straight shaft. It slightly bends inwards at the proximal side, which shows that it is a dextral spine. The shaft widens toward the articulation, leaving a prominent and elongated notch (the basal recess) along its posterior face. Its size and morphology are similar to other Pleistocene spines from Java, identified as *Hemibagrus* cf. *nemurus* by Yudha et al. (2020) and Koumans (1949). However, nowadays around 40 extant species are recognized within the genus *Hemibagrus*, most of which live in Southeast Asian drainage systems (Ng and Kottelat, 2013). Lacking clear osteological descriptions, it is not realistic to determine a single fossil spine to species level. SBY5074 is therefore assigned to *Hemibagrus* sp.

3.5 Order Squamata Oppel, 1811 – scaled reptiles

Records of Pleistocene Squamata from Java are scarce. Several dorsal vertebrae of Varanidae were found in Trinil and one in Kedung Brubus (Janensch, 1911a; Dubois, 1908). Hooijer (1972) ascribed most of these to *Varanus salvator*, the Asian water monitor, which is still extant on Java. He ascribed several larger specimens to *Varanus komodoensis*, suggesting that the current occurrences of this species on the islands of Komodo, Rinca, and Flores are relicts of a wider distribution during the Pleistocene.

There is one record of Early to Middle Pleistocene Serpentes, which is a single vertebra from Trinil (Janensch, 1911a). This specimen was only mentioned in the find list, without further details or determination. In the 1990's, a complete skeleton of a Late Pleistocene snake was found in Ciharuman, West-Java, which was ascribed to *Malayopython reticulatus* (Aziz and de Vos, 1999).

Suborder: Lacertilia Günther, 1867
Family: Varanidae Merrem, 1820
Genus: *Varanus* Merrem, 1820
***Varanus komodoensis* Ouwens, 1912 – Komodo dragon**

Available material (N=2). Dorsal vertebrae: SBY533 and SBY7137.

Description and identification: The two vertebrae **(Fig. 4)** have a procoelous centrum and prominent outwards projecting zygapophyses. In both specimens, the posterior part of the centrum and the neural spine are missing. Pre- and postzygapophyses are preserved, although small fragments of the tips are missing. Zygapophysal dimensions could be estimated, using intact varanid vertebrae as a morphological reference **(Table 4)**. Morphologically, the specimens closely match with dorsal vertebrae of recent varanids curated at Naturalis Biodiversity Center and Tübingen University, as well as with the Pleistocene *Varanus* vertebrae from Java presented by Hooijer (1972).

Hocknull et al. (2009) measured a large sample of recent *V. komodoensis* and *V. salvator* vertebrae and provided species-specific size ranges. The measurements of the Madura Strait specimens **(Table 4)** follow the methods of these authors. A bivariate plot **(Fig. 5)** of pre-prezygapophysal width and pre-postzygapophysal length places the two specimens from the Madura Strait in the size range of *V. komodoensis*.

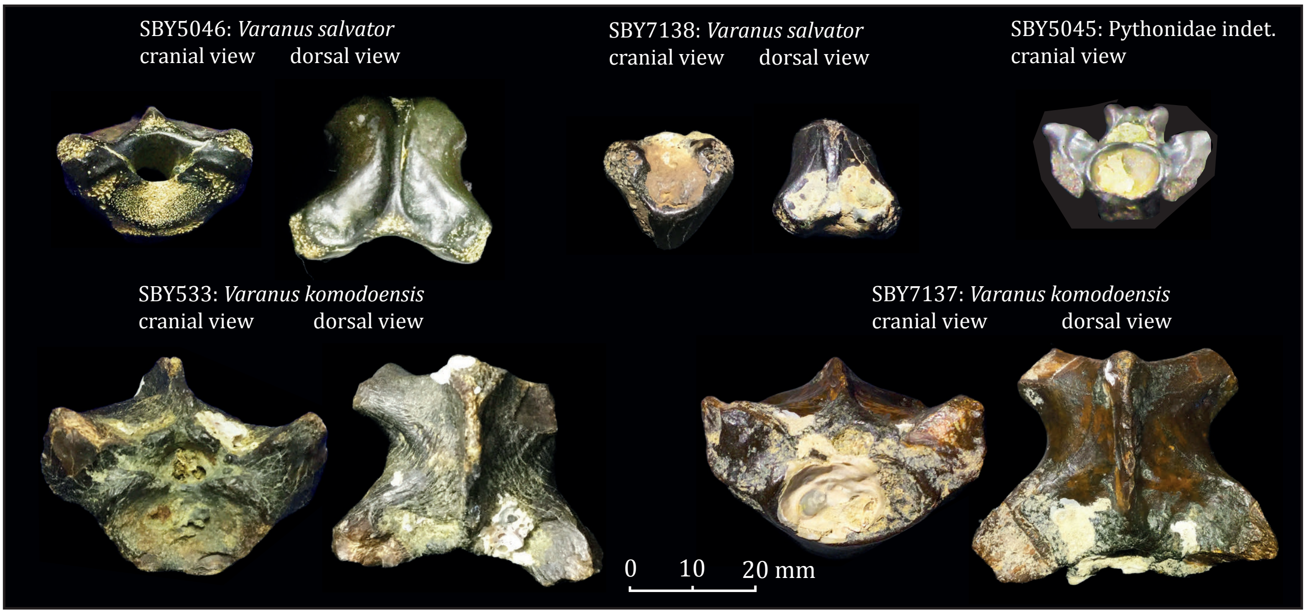


Fig. 4. Dorsal vertebrae of Squamata (Varanidae, Pythonidae) from the Madura Strait assemblage. Selected photographs. For measurements see **Table 4**.

Varanus salvator (Laurenti, 1768) – Asian water monitor

Available material N=2. Dorsal vertebrae: SBY5046, SBY7137.

Description and identification: Morphologically, the two specimens **(Fig. 4)** are similar to the two vertebrae ascribed to *Varanus komodoensis*. Also their state of preservation is similar, with the posterior part of the centrum and the neural arches broken off. SBY5046 has almost complete zygapophyses. In SBY7137, the postzygapophyses are missing. Metrically, the two specimens are significantly smaller **(Table 4).** Note that the postzygapophysal sizes of SBY7137 are estimates. Both specimens plot below the size range of *V. komodoensis* and fall in the range of *V. salvator* **(Fig. 5)**.

Specimen	*Taxonomy*	*Cotylar width (CW) (mm)*	*Pre-pre (mm)*	*Post-post (mm)*	*Pre-post (mm)*	*Zygosphene width (mm)*
SBY533	*Varanus komodoensis*	20.9	48	37	38	
SBY7137	*Varanus komodoensis*	22.4	50	40	41	
SBY5046	*Varanus salvator*	15.1	31	29	28	
SBY7138	*Varanus salvator*	10.0	22		21	
SBY5045	Pythonidae indet.	10.3	25.8			10.4
	*Malayopython reticulatus**	16.2	46.3			16.2

Table 4. Measurements of Varanidae and Pythonidae vertebrae (mm), methods based on Hocknull et al. (2009). Pre-pre = pre-prezygapophysis width; post-post = post-postzygapophysis width; pre-post = pre-postzygapophysis length. Centrum lengths could not be taken, as centra are incomplete. All zygapophysal measurements involve reconstructions of broken tips.
*: Measurements taken from a central trunk vertebra of the Late Pleistocene *Malayopython reticulatus* of West-Java stored in the Geological Museum Bandung.

Suborder: Serpentes Linnaeus, 1758 - snakes

Family Pythonidae Fitzinger, 1826 - pythons

Pythonidae indet.

Available material (N=1). Trunk vertebra: SBY5045.

Description and identification: SBY5045 **(Fig. 4)** is a procoelous vertebra with a prominent zygosphene, which links the specimen to the suborder Serpentes (Holman, 2000). The posterior part of the centrum is broken off and also the postzygapophysis is largely missing. The prezygapophysis is intact, except for a small part of the dextral tip. Both diapophyses have been broken off. Along the dorsal side, the neural spine is broken off. The cotyle is laterally expanded. From an anterior view, the zygosphene has a trapezoid shape and a convex roof, with its lateral edges upturned dorsally. The centrum has a preserved ventral length of 10.6 mm and has a massive, triangular shape, widening anteriorly.

The sizes of the centrum, the cotyle, and the zygosphene **(Table 4)** point to a large snake. The wide, triangular shape of the centrum is characteristic of Boidae and Pythonidae (Ikeda, 2007). Giant Boidae are absent in Southeast Asia and unknown from the regional fossil record. Two large Pythonidae: *Malayopython reticulatus* and *Python bivittatus*, are extant on Java, living in grasslands, marshes and forests. Both are also good swimmers. In the absence of relevant comparison collections or published osteological descriptions, we refer to the specimen as Pythonidae indet.

Morphologically, SBY5045 compares well with the Late Pleistocene *Malayopython reticulatus* of West-Java, which is stored at the Geological Museum Bandung. We took reference measurements of the central trunk vertebrae of this complete skeleton **(Table 4)**, which are above the size of the single vertebra from the Madura Strait.

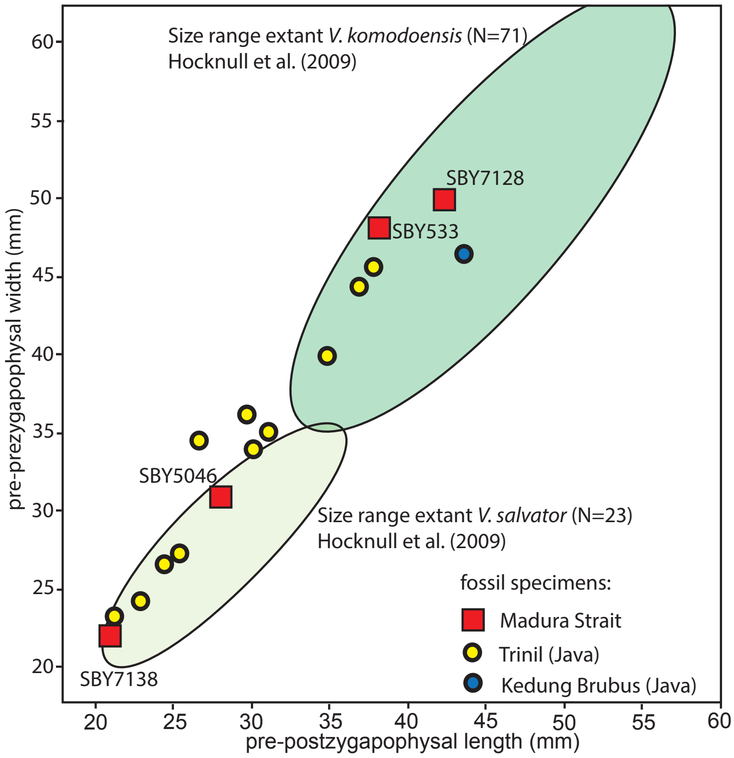


Fig. 5. Bivariate plot of the Varanidae dorsal vertebrae from the Madura Strait (pre-prezygapophysal width and pre-postzygapophysal length) in relation to size ranges of extant *V. salvator* and *V. komodoensis* and sizes of fossil specimens from Trinil and Kedung Brubus. All reference sizes from Hocknull et al. (2009).

3.6 Order Testudines (Batsch, 1788) - turtles

Fossil shell fragments of freshwater turtles are common finds on Java, but they are generally left unidentified. Jaeckel (1911) introduced five new Pleistocene species, based on mostly fragmented material from Trinil. The species were rejected by Karl (1987) and synonymized with extant species. An interesting review of these earlier fossil finds from Java is given by Claude et al. (2024). There are around fifteen extant species of medium to large freshwater turtles in western Indonesia and more in Southeast Asia (Rhodin et al., 2015). For our comparisons, we focussed on the extant, lowland-river turtles of Java, Sumatra, and Borneo.

Family: Geoemydidae (Theobald, 1868) – hard-shelled turtles

Geoemydidae indet.

Available material (N=102). Neural plate fragments (21): SBY5031. **Costal plate fragments (42):** SBY5032, SBY7165. **Peripheral plate fragments (17):** SBY5033, SBY7141. **Plastron fragments (22):** SBY5034.

Description and identification: The shell fragments are smooth-surfaced and have a thickness ranging between several mm and 16 mm. Sutures marking the boundary between the individual plate fragments are not observable and the break surfaces appear to be random, bearing no relation with the original plate boundaries. This points to an advanced state of ossification and fusing of plate elements. The plate fragments have been ordered and grouped by their position in the original shell, distinguishing between neural fragments (with fused vertebrae at the ventral side), costal fragments (with fused ribs), peripheral fragments (preserving parts of the carapace margin) and unarched plastron fragments. Some fragments preserve sulci, which are imprints of seams between the epidermal scutes that covered the ossified plates. In some cases, the sulci provide insight into the original position of the fragment in the turtle shell. For example **(Fig. 6)**: SBY5033A is a peripheral plate fragment preserving the sulci between two marginal scutes and a costal scute. SBY5032A is a fragment of the first sinistral costal plate, preserving the sulci between the first costal scute and the first two vertebral scutes. SBY5033B is a peripheral plate fragment, preserving a sulcus between two marginal scutes and a small part of the sulcus that marks the boundary with the adjacent costal scute. This specimen is special, as it also preserves a fine imprint of the scute's reticulated micro-ornamentation (annuli).

All smooth-plated freshwater turtles of western Indonesia belong to the family of Geoemydidae (Rhodin et al., 2015). Among the Geoemydidae species, there are notable morphological differences of the individual plate elements. However, the strongly ossified and randomly broken fragments offer little clues for species identification based on plate morphology. Nevertheless, some useful taxonomic information can be extracted from the fragmented material. For example, all neural plate fragments have a smooth dorsal surface, which points to the absence of species such as *Siebenrockiella crassicollis*, which have a dorsal keel. Likewise, all peripheral plate fragments have smooth margins, excluding species with serrated carapace margins such as *Heosemys grandis* (Rhodin et al., 2015).

The plate fragments are referred to as Geoemydidae indet. Based on the size and thickness of the plates, we assume that the plate fragments derive from medium to large freshwater species such as *Batagur affinis* and *Orlitia borneensis*, both of which are extant in western Indonesia.

Genus: *Batagur* Gray, 1856

Batagur affinis (Cantor, 1847)

Synonym: *Batagur siebenrocki*

Available material (N=1). Hypoplastron fragment: SBY7139.

Description and identification: SBY7139 **(Fig. 6)** is a lateral fragment of a dextral hypoplastron, preserving the rounded inguinal notch and the transition toward the bridge. Sulci demarcate the margins between the femoral, abdominal, inguinal, and lateral scutes Yudha et al. (2020a, Fig. 8) provided drawings of plastron morphology and sulci patterns for several Geoemydidae. The broad and rounded inguinal notch of SBY7139 links the fragment to the genus *Batagur*. Moreover, the two smoothly curved sulci and their approach to the inguinal notch, as well as the sulci demarcating the inguinal scute, which form an elongated triangle anterior of the inguinal notch, are characteristic of this genus.

The fragment is highly similar to the plate of the southern river terrapin *Batagur affinis,* the extant *Batagur* of Sumatra and Borneo, living in lowland rivers and tidal zones. *B. affinis* is closely related to *Batagur baska* of mainland Asia and has recently been indicated as a separate species (Moll et al., 2021). A carapace from Trinil, described by Jaeckel (1911) as *Batagur siebenrocki*, was re-interpreted by Karl (1987) as *B. baska.* Referring to the geographic proximity of their extant population, *Batagur affinis* is a more appropriate name. Note that there is no osteological difference between both species.

Fig. 6. Geoemydidae and Trionychidae remains from the Madura Strait assemblage. Selected photographs of shell fragments. Carapace fragments in dorsal view and plastron fragments in ventral view.

Genus: *Orlitia* (Gray, 1873)
Orlitia borneensis (Gray, 1873) – Bornean river turtle

Synonym: *Batagur signatus*

Available material (N=1). Xiphiplastron fragment: SBY5031.

Description and identification: SBY5031 **(Fig. 6)** is a fragment of a dextral xiphiplastron with a narrow and triangular shape, pointing posteriorly. Its medial margin is rounded and demarcates a pronounced, semi-circular anal notch. The posterior tip has broken off. Pritchard et al. (2009) provided images of the plastron of relevant turtle species, showing conspicuous morphological differences. A posteriorly pointing xiphiplastron with a large, semi-circular anal notch is characteristic of *Orlitia borneensis*.

Orlitia borneensis is a giant freshwater species of Borneo and Sumatra, with carapaces reaching a length of ~ 80 cm (Rhodin et al., 2015). Probably, the thickest unidentifiable plate fragments from the Madura Strait assemblage also derive from this species. There are two earlier records of this species from the Pleistocene of Java: two small plate fragments from Trinil were described as *Batagur signatus* by Jaeckel (1911) and provisionally re-interpreted by Karl (1987) as *O. borneensis.* Moreover, Setiyabudi et al. (2016) assigned a costal plate from Sambungmacan to this species.

Family: Trionychidae Fitzinger, 1826 – soft-shelled turtles
Genus: *Chitra* Gray, 1844
Chitra chitra Nutaphand, 1986 – Asian narrow-headed softshell turtle

Synonym: *Chitra selenkae*

Available material (N=29). Neural plate fragments (7): SBY5004. **Costal plate fragments (16):** SBY5005. **Plastron fragments (4):** SBY5006.

Description: The plate fragments are relatively thick (5 – 12 mm) and have an ornamentation of thick, vermiform ridges and broad valleys. Three examples are pictured in **Fig. 6.** SBY5005A is an 11 mm thick costal fragment including a section of the lateral margin of the carapace. Note that peripheral plates are absent in Trionychidae. The plate margin is slightly undulating and preserves a small part of the exposed rib tip. The dorsal surface of the plate has an ornamentation of elongate ridges and valleys running parallel to the plate margin. The ridges are coarse and rounded, with a ridge height of ~ 2 mm and an interval of 5 to 10 mm between the ridge crests. SBY5005B is a costal fragment with a similar ornamentation, but on this fragment, it forms a more irregular pattern of open, semi-circular valleys and ridges. SBY5006A is a plastron fragment preserving a lateral margin with three prongs. At its ventral face it has a similar coarse vermiform surface sculpturing, forming parallel and semi-circular ridges and valleys.

The surface ornamentation of thick vermiform ridges and broad valleys is characteristic of *Chitra chitra* (Pritchard et al., 2009). Useful pictures of museum specimens are provided by Gemel and Haring (2011), showing that carapace sculpturing patterns change from irregular and semi-circular ridges on the neural plates and medial zones of the costal plates to parallel ridges and valleys along the plate margins. The undulating outer margin of SBY5005A is characteristic of the anterior two costals. Comparison with the pictured specimens indicates that the fragment derives from the second dextral costal plate. Although surface sculpturing is generally described as a trait of carapaces, the descriptions and pictures of Gemel and Haring (2011) show that the plastron of *C. chitra* has a similar ornamentation. The morphology of the SBY5006A, with its three spiky projections, compares well with the dextral hypoplastron of the museum specimens presented by these authors.

Chitra chitra is a giant freshwater turtle living in large lowland-rivers of Southeast Asia, with a carapace length reaching ~100 cm (McCord and Pritchard, 2002). Pleistocene remains from Java were recorded by Jaeckel (1911), who originally assigned the material to *Chitra selenkae*.

Genus: *Pelochelys* Gray, 1864
Pelochelys cantorii Gray, 1864 – Cantor's giant softshell turtle

Synonym: *Chitra minor*

Available material (N=7). Carapace (5) and plastron fragments (2): SBY5087A-G.

Description and identification: The plate fragments have a thickness of 6 – 10 mm and have a vermiform ornamentation of coarse and rounded ridges. This ornamentation differs from *C. chitra* by the occurrence of irregular ridges with frequent gaps and cross-connections. Pictured examples are costal fragments SBY5087A and B **(Fig. 6)**, the latter preserving a part of the plate margin with an exposed rib tip. As a result of the irregular ridges, the intermediate depressions form wells rather than valleys. These wells have a diameter of around 6 mm and a rounded morphology, with gently sloping walls that grade into the well bottoms.

The surface ornamentation of irregular ridges surrounding rounded wells is characteristic of *Pelochelys cantorii* (Pritchard et al., 2009). Useful descriptions and photographs of museum specimens are provided by Gemel and Haring (2011). *P. cantorii* is a giant freshwater turtle living in lowland rivers and estuaries of Southeast Asia and is extant on Java. There have been no reported finds of this species from Java except for one or two plastron fragments from Trinil that were described as *Chitra minor* by Jaeckel (1911). McCord and Pritchard (2002) suggested that these fragments may represent *P. cantorii*.

Genus: *Amyda* Saint-Hilaire, 1809
***Amyda cartilaginea* (Boddaert, 1770) – black-rayed softshell turtle**

Synonyms: *Trionyx trinilensis*; *Trionyx cartilagineus*

Available material (N=5). Carapace fragments: SBY5000

Description and identification: SBY5000A **(Fig. 6)** is a 6 mm thick costal plate fragment, ornamented with fine, well-defined and vertically oriented ridges, extending ~0.8 mm above the surface of the plate. The ridges form an irregular, angular pattern, leaving flat-bottomed wells with a quasi-hexagonal shape and a diameter of around 3 mm. Discontinuities in the ridges are rare and virtually all wells are closed.

The surface ornamentation of angular, flat-bottomed wells surrounded by thin vertical ridges is characteristic of *Amyda cartilaginea* (Pritchard et al., 2009). Note the great difference with the coarser and rounded ridges of *C. chitra* and *P. cantorii.*

A. cartilaginea is a large Southeast Asian species with a preference for lowland rivers and marshes and is extant on Java. So far, only two other plate fragments of this species are known from the Pleistocene of Java. These are plastral fragments from Trinil, described by Jaeckel (1911) as *Trionyx trinilensis* and re-interpreted by Karl (1987) as *A. cartilaginea*.

Genus: *Dogania* Gray, 1844
***Dogania subplana* (Saint-Hilaire, 1809) – Malayan softshell turtle**

Available material (N=6). Carapace fragments (5): SBY5001. **Hypoplastron fragment:** SBY5002.

Description and identification: SBY5001A-B **(Fig. 6)** are costal plate fragments with a thickness of app. 4 mm. Their dorsal surface is covered with a fine latticework of closely spaced, rounded, punctuate wells with a diameter of around 1.5 mm. This fine, orange- skin-like surface ornamentation of the carapace is characteristic of *Dogania subplana* and compares well with museum specimens described and pictured by Pritchard et al. (2009).

Dogania subplana is a medium-sized freshwater turtle of Southeast Asia, with a carapace length reaching around 35 cm. The species is still present on Java and has a preference for rivers with a gravelly riverbed.

Testudines indet.

Available material (N=24). Ribs: SBY650, SBY1560, SBY1561, SBY1476. **Scapula,** distal fragment: SBY517 (s). **Humerus,** proximal fragment: SBY2122. **Radius**, proximal fragment: SBY1484 (s). **Ulna,** distal fragments: SBY492, SBY497. **Pelvis,** fragment: SBY509, SBY1035, SBY3000. **Femur,** shaft fragments: SBY708, SBY1530. **Metapodial:** SBY1477. **Unidentified limb bones fragments:** SBY506, SBY926, SBY1607, SBY1759, SBY1779, SBY3018, SBY5043A-C.

The identified ribs are the characteristic cone-shaped ribs of the sacral zone. Due to the unavailability of pertinent anatomical descriptions or museum specimens of the relevant turtle species, the anatomical position of smaller limb bone fragments could not always be determined with certainty.

3.7 Order Crocodilia Owen, 1842 - crocodilians

Dubois (1908, 1907) excavated crocodilian skulls from Trinil, which he ascribed to two new species: *Crocodylus ossifragus* and *Gavialis bengawanicus*. Müller (1923) concluded that *C. ossifragus* is synonymous to *Crocodylus siamensis*, the extant freshwater crocodile of Southeast Asia and only recently extinct on Java. Delfino and de Vos (2010) concluded that *G. bengawanicus* is a valid Pleistocene species, differing from the extant *Gavialis gangeticus* by skull morphology and tooth positions.

Family: Crocodylidae Cuvier, 1807
Genus: Crocodylus Laurent, 1768
***Crocodylus siamensis* Schneider, 1801 – Siamese crocodile**

Synonym: *Crocodylus ossifragus*

Available material (N = 24). Teeth: SBY319, SBY328, SBY5068A-F, SBY5069A-G, SBY5081A-B, SBY5071C, SBY7135A-B. **Osteoderms:** SBY1170, SBY5041A-B, SBY5042.

Description and identification: The teeth **(Fig. 7)** are robust and conical and have a relatively blunt tip. Maximum crown height is ~ 45 mm. The teeth have a semi-round cross-section, with faint mesial and distal keels and a maximum (mesiodistal) diameter of ~ 28 mm. They are slightly curved (toward the lingual side). The cones have a thin enamel cover with fine longitudinal striations. The teeth were generally found as loose crowns, only SBY5069A has a significant piece of the root attached. The teeth are identical to the dentition of a recent skull of *C. siamensis* and to a set of Pleistocene teeth from Java, all of which are kept in the Geological Museum Bandung. Moreover, they compare well with the descriptions by Janensch (1911a) and Müller (1923) of *C. siamensis* teeth.

The difference in size of the teeth relates to their position in the tooth row and to growing stage in the tooth-regeneration process. The species develops its largest teeth in the fourth mandibular, fourth premaxillary, and fifth maxillary alveoli. The largest teeth of the Madura Strait assemblage, such as SBY7135A **(Fig. 7)**, probably derive from one of these tooth positions.

SBY5042 **(Fig. 7)** is a fragment of a large rectangular osteoderm with fibrous margins. The lateral or medial half of the osteoderm is missing. It has an anteroposterior length of 39 mm, a mediolateral width of 85 mm (estimated width of complete specimen), and a thickness of 11 mm. It is flat to slightly convex, with a rounded, ca. 8 mm high central keel at the posterior side of the dorsal surface. Its dorsal surface has a pitted ornamentation, whereas its ventral surface is smooth, with fine crisscross striae. Its morphology and measurements compare well with Pleistocene *C. siamensis* osteoderms from Java described and pictured by Delfino and de Vos (2010).

Fig. 7. Crocodilia remains (*Crocodylus*, *Gavialis*) from the Madura Strait assemblage. Selected photographs. Teeth in mesial or distal view. Osteoderms in dorsal view. Vertebrae in lateral view. For measurements of vertebrae see **Table 5**.

Family: Gavialidae Adams, 1854
Genus: *Gavialis* Oppel, 1811 - charial
Gavialis bengawanicus Dubois, 1908

Available material (N=4). Teeth: SBY645, SBY5071A-B. **Osteoderm:** SBY5044.

Description and identification: SBY5071A-B **(Fig. 7)** are slender, pointed teeth with a conical shape. The crowns are labiolingually compressed and strongly curved inwards (lingually). The thin enamel layer is covered with fine striations. Both teeth have a crown height of ~25 mm. The basal crown diameter is 6 mm labiolingually and 8 mm mesiodistally. SBY5044 **(Fig. 7)** is a complete osteoderm with a mediolateral width of 63 mm, an anteroposterior length of 54 mm, and a thickness of around 8 mm. Its dorsal surface is ornamented with large pits, whereas its smooth ventral surface is marked with fine crisscross striae. The osteoderm is slightly convex and has a fine median keel with a height of ca. 3 mm at the posterior side of the dorsal face.

The teeth and the osteoderm match the descriptions of *G. bengawanicus* remains by Janensch (1911a), Delfino and de Vos (2010), and Martin et al. (2012). These authors described teeth with cone heights up to ~30 mm. The osteoderms of this species differ from *C. siamensis* by their lighter build, few but proportionally larger pits, and a thinner medial keel. Based on a comparison with extant *Gavialis* skins, we assume that SBY5044 is a nuchal or mid-dorsal osteoderm.

Crocodilia indet.

Available material (N=4). Vertebral centra: SBY474, SBY511, SBY514, SBY7136.

Description and identification: The vertebral centra are recognized as crocodilian by their cylindrical, elongate corpora and their strongly procoelous morphology, with prominent sub-round condyles and cotyles. Zygopophyses and neural spines have mostly broken off. SBY7136 **(Fig. 7)** has a ventral keel and, based on the fracture surfaces along the side of the corpus, must have had prominent parapophyses, which indicates that the specimen is a cervical vertebra. SBY474 **(Fig. 7)** preserves part of the neural arch. Diapophyses are partly preserved and the fracture surfaces indicate that in a complete state, these must have formed prominent transverse processes. The corpus lacks a ventral keel, but it has small, rounded parapophyses along its sides, which identifies the specimen as one of the anterior dorsal vertebrae. Measurements of the pictured specimens are given in **Table 5**.

The vertebrae compare well with isolated Pleistocene crocodilian vertebrae in the Geological Museum Bandung, both in size and morphology. Chamero et al. (2014) carried out a detailed analysis of crocodilian vertebrae and found no significant morphometric differences between *Crocodylus* and *Gavialis*. Also with respect to body weight and length, there are no significant differences between the extant Southeast Asian populations. We therefore refer to the specimens as Crocodilia indet.

Specimen	*Taxonomy*	*Vertebra*	*Corpus length (mm)*	*Cotylar diameter (mm)*
SBY7136	Crocodilia indet.	Cervical	39	27
SBY474	Crocodilia indet.	Dorsal	40	28

Table 5. Measurements (mm) crocodilian vertebrae pictured in **Fig. 7.**

3.8 Order Proboscidea Illiger, 1811

Proboscidean fossils have been recognized on Java for more than 150 years (Saléh, 1867). This material is dominated by the extinct genus *Stegodon*. Martin (1886) described two species: *Stegodon trigonocephalus* and *Stegodon airawana*. Von Koenigswald (1933) and Hooijer (1955) attributed all Javanese *Stegodon* remains to a single species: *S. trigonocephalus*. Besides *Stegodon*, there are proboscidean remains of the genus *Elephas*. Dubois (1908) ascribed the material to an extinct species, *Elephas hysudrindicus*. It differs from *Elephas maximus,* the extant Asian elephant, by its skull morphology and molar sizes.

For the descriptions and measurements of proboscidean dentition we followed Van den Bergh (1999). Ridges or lamellae are counted in Arabian numbers (anterior to posterior) or Roman numbers (posterior to anterior). Anterior and posterior talons are labelled as 'x'. The lamellar frequency (LF) refers to the number of ridges (for *Stegodon*) or lamellae or plates (for *Elephas*) over a longitudinal distance of 10 cm, measured at the base of a crown. Because of differences in lamellar spacing along the lingual and buccal side of molars, the LF was measured at both sides and the given value is the average.

Family: Stegodontidae (Osborn, 1911)
Genus: *Stegodon* Falconer, 1847
Stegodon trigonocephalus Martin, 1887

Synonyms: *Stegodon airawana* (Martin, 1887; Stremme, 1911); *Stegodon ganesa* var. *javanicus* (Dubois, 1908)

Available material (N= 31). M^1, posterior fragment: SBY83 (d). **M_1,** posterior fragment: SBY81 (d), **M2,** posterior fragment: SBY84, **M2 or M3,** central fragment: SBY82. **Tooth fragments,** unknown position: SBY87, SBY88, SBY89, SBY90, SBY93A-E, SBY95A-G, SBY96A-E, SBY97, SBY98, SBY100, SBY103, SBY2001, SBY3164.

Description and identification: Fragments of *Stegodon* dentition are recognized by their lophodont build of widely spaced, wedge-shaped ridges with a relatively thick, wrinkled enamel cover, each loph terminating in 6 to 15 conelets. For four relatively large specimens **(Fig. 8)**, the tooth position could be determined**.** The relevant measurements of these molars have been listed in **Table 6**.

SBY83 is a fragment of an upper molar, preserving the posterior talon and four intact ridges, none of which are worn. Ridge III has the greatest width, measuring 64.5 mm. This size falls in the range of *S. trigonocephalus* M^1 specimens from Trinil, which have a maximum width of 59 to 66 mm (N=3) (Hooijer, 1955; Janensch, 1911b). SBY81 is a tooth fragment preserving the posterior talon and six and a half ridges. The posterior two ridges are unworn, the other ridges are slightly worn. The slightly concave wear surface in combination with the concave upward crown base identifies the specimen as a lower cheek tooth. The buccally-concave curvature of the crown (in occlusal view) shows that it derives from the right mandible. The widest ridge is number IV and measures 60.4 mm buccolingually. This modest width suggests that the fragment derives from a dP_4 or an M_1. **Fig. 9** shows the width of the individual ridges of SBY81 compared to the measured ridge widths of fossil *Stegodon* dP_4 and M_1 from Trinil and Flores, referring to our measurements of specimens available in Naturalis Biodiversity Center and the Geological Museum Bandung. Note that the dP_4 specimens are not only smaller, but also have a different crown morphology, reaching their maximum width at the posterior or penultimate ridge, whereas the M_1 specimens reach their greatest width further anteriorly. For this feature, SBY81 falls in the M_1 category. The width of SBY81 compares well with the width of the fossil M_1 of *S. trigonocephalus* from Trinil (width range 58.3-66.0 mm, N=4) and exceeds the size range for dP_4 (width range 42.5-54.0 mm, N=7).

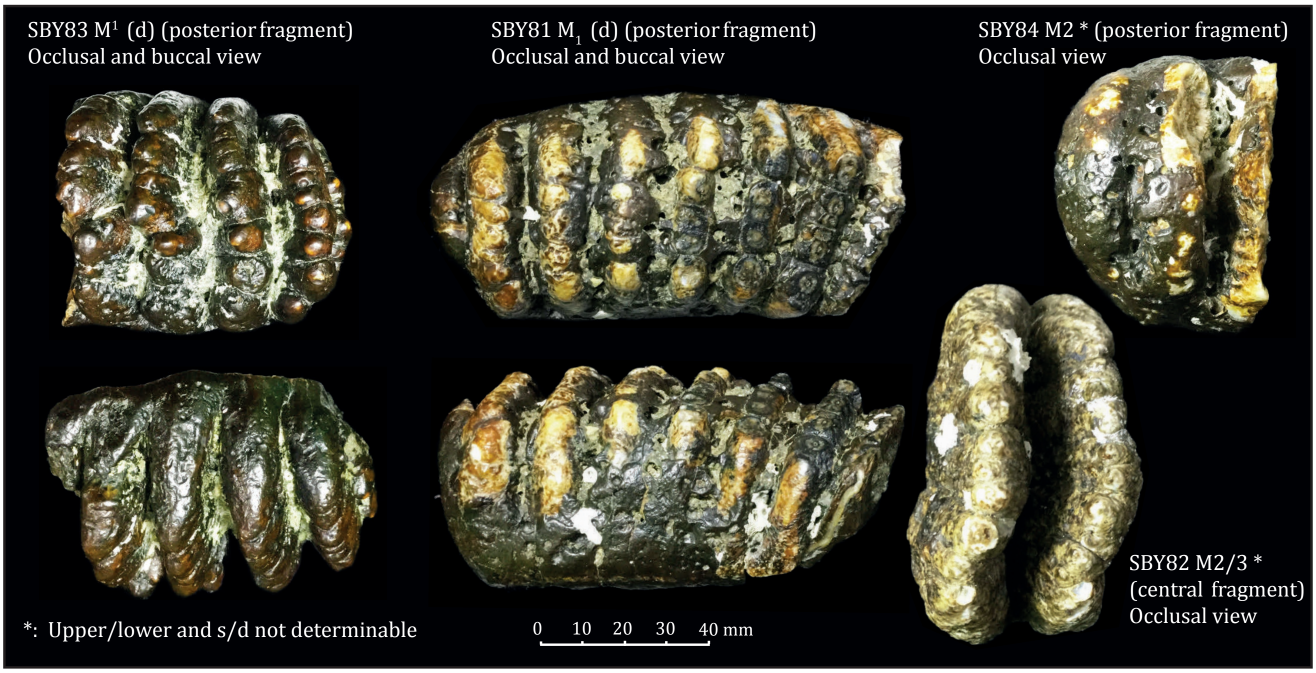


Fig. 8. *Stegodon trigonocephalus* molar fragments from the Madura Strait. Selected photographs. For measurements see **Table 6.**

SBY84 preserves only the posterior talon and 1½ ridges. Ridge II has a width of 74.9 mm; the maximum width of the molar must have been slightly larger. This value falls in the range of second molars, either from the upper or lower teeth row. Hooijer (1954) found a maximum ridge width of 76-94 mm for the M^2 (N=11) and 68–85 mm for the M_2 (N=11), based on molars from various find sites on Java. SBY82 preserves only two unworn ridges from the middle portion of a molar. The cement between the ridges is largely dissolved, leaving the enamel-covered ridges exposed. Small damaged surfaces show an enamel thickness reaching over 6 mm. The ridges have a width of over 94 mm and a height of 60 mm. The fragment may again derive from an (upper) second molar, but a third molar is more likely. Hooijer (1955) provided width ranges of 76–107 (N=19) for the M^3 and 68–98 for the M_3 (N=17).

Specimen	*Element*	*Ridges*	*w (mm)*	*h (mm)*	*h/w-index*	*LF*	*ET (mm)*
SBY83	M^1 (d)	-4x	64.5	41.7	64	6.8	3.1-4.5
SBY81	M_1 (d)	-½6x	60.4	>42	70	7.2	3.7
SBY84	M2	-½1x	74.9	57.0	73	6.2	3.5-4.6
SBY82	M2/M3	-2-	94.3	60.3	64	4.3	4.0-6.4

Table 6. *Stegodon trigonocephalus* molar fragments, measurements of specimens pictured in **Fig. 8**. Ridges: number of preserved ridges, talon is indicated as x. w and h: width and height of largest preserved ridge; if worn the minimum height is indicated as >x. h/w-index: measured or estimated for widest preserved, unworn ridge. LF: ridge or lamellar frequency (average of buccal and lingual values measured at the base of the crown). ET: enamel thickness.

Although all *Stegodon* remains from Java are nowadays referred to as a single species, there are minor differences between the molars of various find sites. Von Koenigswald (1934) and Van den Bergh (1999) proposed a subdivision in subspecies. The specimens from Trinil and Kedung Brubus, forming the largest sample of *Stegodon* molars from Java, are regarded as *S. trigonocephalus trigonocephalus*. For the Madura Strait find site, the youngest subspecies *S.*

trigonocephalus ngandongensis is relevant. This subspecies was defined based on molars from the Solo terrace of Ngandong, with an age that is similar to the fossil fauna of the Madura Strait. The *Stegodon* molars from Ngandong are relatively large, falling in the upper part of the size range of *S. trigonocephalus trigonocephalus*. Moreover, the molars often have one ridge more per homologue element, and tend to have a median cleft.

With respect to crown width, SBY83, SBY84, and SBY82 fall in the size ranges of *S. trigonocephalus trigonocephalus* from Trinil, but for all three specimens, the crown heights are slightly above the recorded ranges. Unfortunately, no homologue elements are available from Ngandong for direct comparison. Looking at SBY81, we find again that the molar width is well within the range of the M_1 of *S. trigonocephalus trigonocephalus*. Hooijer (1955) found an LF of 6 and 7.25 for the Trinil specimens. Upon re-measurement and calculating the measured results to the average of the lingual and buccal values, we found that these values are slightly lower, ranging between 6.0 and 7.0. With an LF of 7.2, SBY81 is slightly above this range. Two complete M_1 specimens of *S. trigonocephalus* from Trinil have x8x ridges while one M_1 from the same locality has a ridge formula of x9x. The comparatively high LF of SBY81 suggests that this specimen may originally have had a ridge formula of x9x or even x10x.

We conclude that the dimensions of the fragmentary Madura Strait molars are in the upper size range of *S. trigonocephalus*, mainly with respect to ridge height. This relatively large height, together with the high ridge frequency of SBY81, links the material from the Madura Strait to the *Stegodon* molars from Ngandong. We tentatively ascribe the material from the Madura Strait to the subspecies *S. trigonocephalus ngandongensis*.

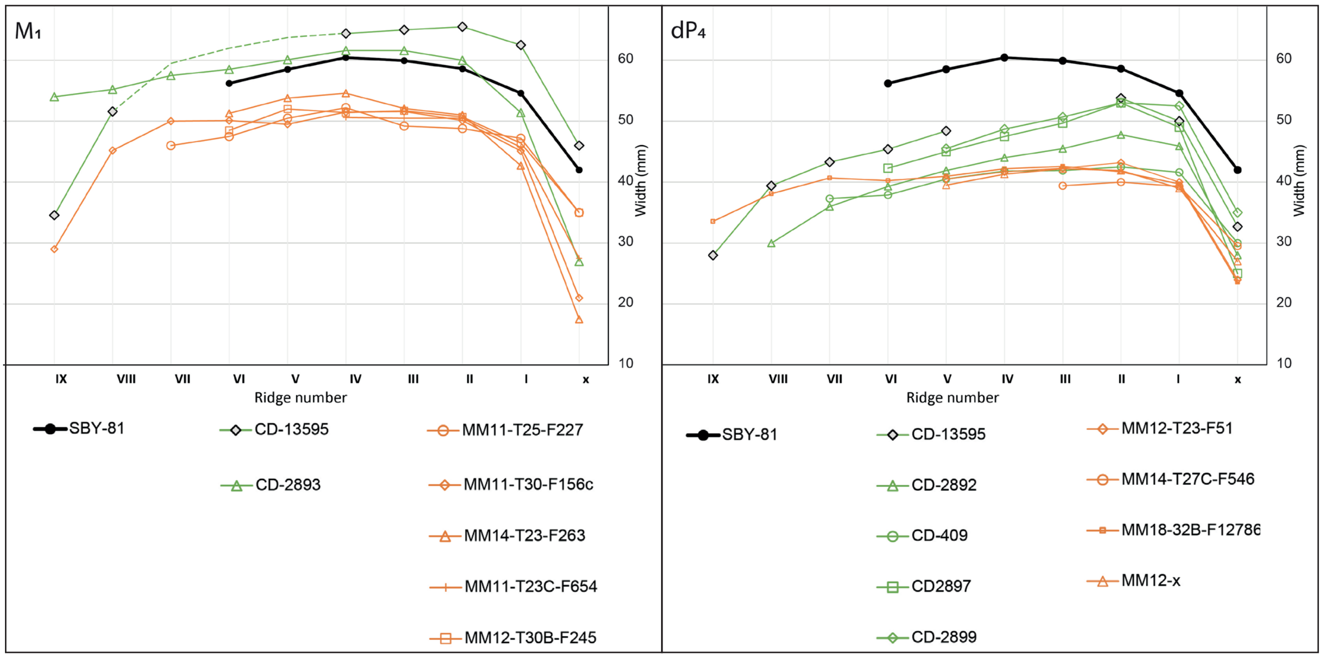


Fig. 9. Ridge-width plot of SBY81 (posterior molar fragment of *Stegodon trigonocephalus*) in comparison with various reference specimens of *Stegodon* dP4 and M1. Orange and yellow plots: *Stegodon florensis* from Flores. Green and grey plots: *Stegodon trigonocephalus* from Trinil. References based on our new measurements of specimens in the Geological Museum Bandung and Naturalis Biodiversity Center. dP4 and M1 CD-13595 derive from a single maxilla.

Family: Elephantidae Gray, 1821

Genus: *Elephas* Linnaeus, 1758

Elephas sp.

Available material (N=15). dM^4, fragment: SBY85 (s/d). **M^3,** posterior fragments: SBY77 (s), SBY7039 (d). **M_2 or M_3,** anterior fragment: SBY79 (s). **Tooth fragments,** unknown position: SBY78, SBY80, SBY86A-E, SBY91, SBY94, SBY99, SBY104.

Description and identification: Fragments of *Elephas* cheek teeth can be recognized by their transverse lophs, which form platy, parallel lamellae with a relatively thin, delicately folded enamel layer, features that clearly differ from the thick and wrinkled ridges of *Stegodon* cheek teeth. Moreover, the lamellae (or plates) reach significantly greater heights than the ridges of *Stegodon.* For four relatively large fragments **(Fig. 10)**, the tooth position could be determined.

SBY77 is a fragment of a high-crowned, rather slender molar, preserving eight lamellae, the anterior two of which are incomplete. Most of the cement has disappeared, leaving the enamel of the lamellae exposed. The width and height of the lamellae decrease posteriorly. Along the tapering posterior end of the molar, only the posterior talon is missing. The posterior tapering identifies the specimen as a third molar. Only the anterior three preserved lamellae are worn, with a plane wear surface forming an angle of ~45 degrees with the lamellae, which is indicative of a third molar from the upper tooth row. From a lateral view, the lamellae are slightly folded, forming a weak S-shape with the apices pointing anteriorly, but they lack the sharp basal bend characteristic of lower third molars. In occlusal view the right side of the crown is convex and the left side slightly concave. In upper molars the convex side is the buccal side, identifying this specimen as an M^3 of the left side. The preserved lamellae are regarded as lamellae I to VIII. The greatest measured width of 61 mm corresponds with plate VI, while plates VII and VIII are too damaged to take width measurements. Plates IV and V have estimated heights of ~140 mm (the tips of the digitations are broken), against a width of 55.2 and 57.7 mm, respectively. This results in H/W-indices of 253 at plate IV and 243 at plate V. The wear figures of the worn plates VI-VII are tripartite and lack pronounced median expansions. The broken digitations of plate V also show a tripartite division, while the most posterior plates have a single median cleft. Enamel thickness varies between 3.27 and 3.79 mm. The enamel is double-layered, with the outer layer occupying approximately 1/3 of the total thickness.

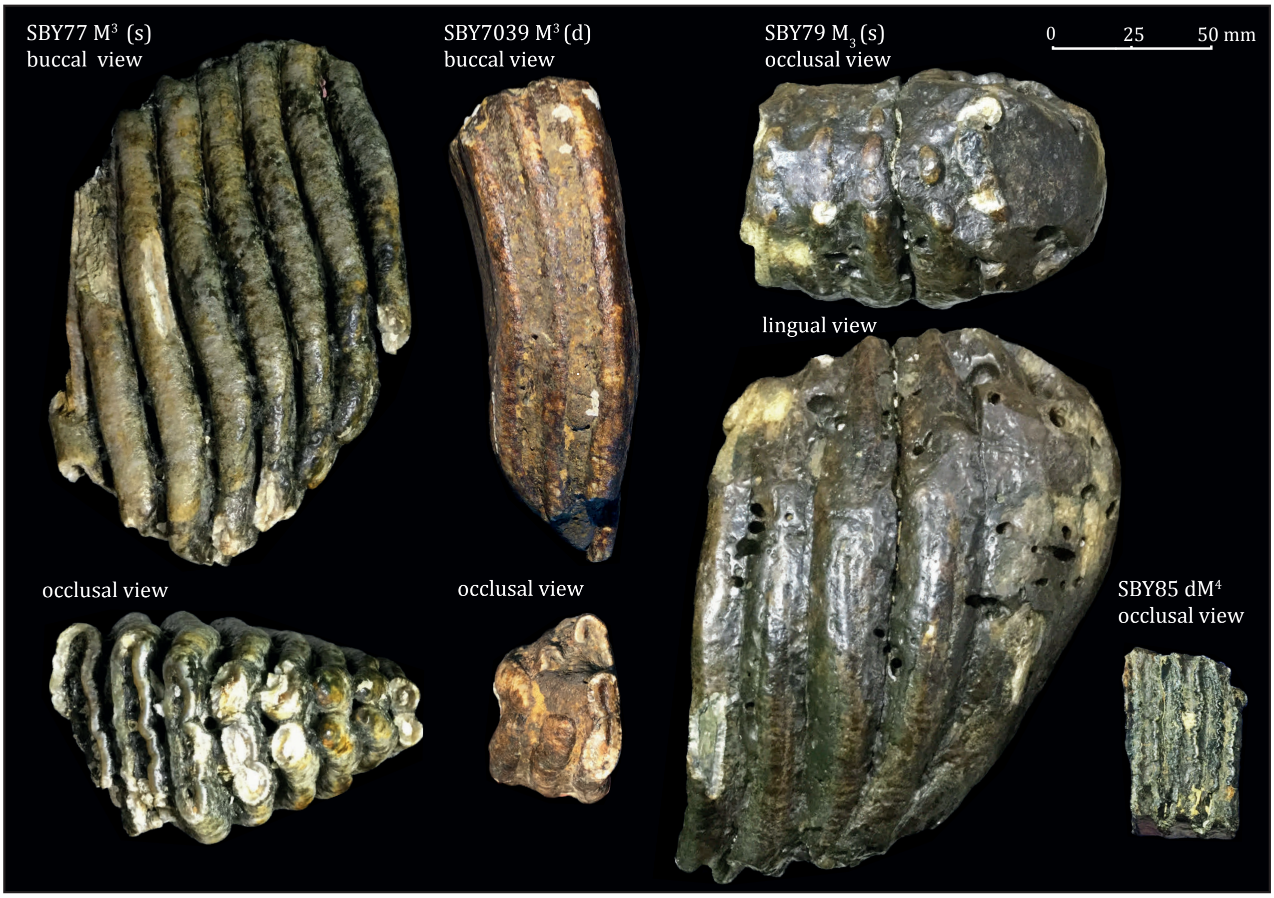


Fig. 10. *Elephas* sp. cheek teeth from the Madura Strait assemblage. Selected photographs. For measurements see **Table 7**.

Specimens and reference	*Element*	*Plates*	*w (mm)*	*h (mm)*	*h/w-index*	*LF*	*ET (mm)*
SBY77	M^3 (s)	8(x)	61.0 (VI)	140 (V)	~253 (IV)	8.1	3.5
SBY7039	M^3 (d)	-3-	62.9 (IV)	136 (III)	~242 (III)	8.4	3.2
E. hysudrindicus$^{\#}$	M^3 (N=9)		80-95	170-180	183-209	6-7 (4.6‡)	(2.4-3.0‡)
E. maximus$^{\#}$	M^3 (N=11)		74-85	165-210	215-269	6-8	--
E. maximus*	M^3 (N=11)		63-98*	170-260*	--	--	(1.8-2.7‡)
SBY85	dM^4	-3-	48	> 57-63	>134	10.1	2.0
E. hysudrindicus$^{\#}$	dM^4 (N=3)		54-58			8-9.5	
E. hysudrindicus$^{\#}$	M^1 (N=1)		58			--	
E. maximus$^{*\#}$	dM^4 (N=18)		41-57			8.5-10$^{\#}$ (N=4)	
E. maximus$^{*\#}$	M^1 (N=13)		53-79			7-7.5$^{\#}$ (N=2)	
SBY79	M_2 or M_3 (s)	x5-	81.2 (V)	176 (III)	218 (IV -V)	5.3	2.6-3.0
E. hysudrindicus$^{\#}$	M_2 (N=4)		67-69	124-145		5-7.5	
E. hysudrindicus$^{\#}$	M_3 (N=15)		70-87	115-150	155-201	5-9$^{\#}$ (4.7‡)	2.6† (3.1-4.55‡)
E. maximus$^{*\#}$	M_2 (N=20)		58-87	155-245	177-209‡	5-8$^{\#}$	2.0-2.3‡
E. maximus$^{*\#}$	M_3 (N=25)		66-100	170-260	153-217$^{\#}$	5-7$^{\#}$ (4.5‡)	1.8-3.2‡

Table 7. *Elephas* sp. molar fragments: measurements of specimens pictured in **Fig. 10** (blue rows) in comparison with published size ranges of *Elephas hysudrindicus* and *Elephas maximus*. Clarification of abbreviations and symbols:

P: Number of preserved plates or lamellae (Given only for the Madura Strait specimens).

w and h: width and height of largest preserved ridge, if worn h = indicated as >x.

h/w-index: measured or estimated for widest preserved ridge. LF: lamellar frequency (average of buccal and lingual values, measured at the crown base).

ET: enamel thickness. * Data from Roth and Shoshani (1988). # Data From Hooijer (1954). ‡ Own measurements. † Data from Maglio (1973).

SBY7039 is a posterior molar fragment consisting of three lamellae. Like in SBY77, the lamellae gradually decrease posteriorly in width and height. The preserved plates are regarded as plates II, III, and IV. The talon and posterior plate (I) are missing. In lateral view the lamellae are very weakly S-shaped, almost straight, and together with the tapering this indicates that we are again dealing with the posterior portion of an M^3. Only plate IV is worn. Plates II and III are unworn and have a medial cleft, while plate IV has a tripartite division. On what is believed to represent the convex buccal side of plates IV and III, the conule is broken. The greatest width (62.9 mm) of the fragment is measured at plate IV. The greatest unworn plate height is measured at plate II and reaches 136 mm. The H/W indices of the unworn lamellae III and II are 242 and 255.

Although Middle Pleistocene *Elephas* material from Java is commonly referred to as *E. hysudrindicus*, the high-crowned and relatively slender appearance of the two M^3 fragments from the Madura Strait is remarkable and resembles the dentition of the extant *E. maximus*. **Table 7** shows the measurements of the two M^3 fragments from the Madura Strait in relation to published size ranges of the same tooth element for the Pleistocene *E. hysudrindicus* from Java and extant Southeast Asian *E. maximus* (data from Roth and Shoshani, 1988; Maglio, 1973; Hooijer, 1955).

As the specimens from the Madura Strait only preserve the tapering posterior plates, a direct comparison of width and height with published size ranges of intact molars is impossible. Looking at the H/W-index and the lamellar frequency, both specimens fall above the range of *E. hysudrindicus* and within the range of *E. maximus*. However, the difficulty with this comparison is that the published species-specific ranges of the H/W-index and lamellar frequency are based on measurements of largely intact molars and were taken at the central zone of the crown, whereas SBY77 and SBY7038 only preserve the posterior zone of the crown. For the lamellar frequency this is probably no problem, as plate thickness usually does not show significant variation within a crown (Van Den Bergh, 1999). But whether an H/W-index measured at posterior fragments is also valid for the central zone of the crown is not clear.

Therefore, for a more profound judgement of the molars, we need to compare the M^3 specimens from the Madura Strait with the posterior zone of relevant reference specimens. Hooijer (1955, table 59) measured the individual plates of four M^3 specimens of *E. maximus*, each with complete and unworn posterior zones. For *E. hysudrindicus* such record was not available. For this reason, we selected and measured five suitable M^3 specimens of *E. hysudrindicus* in Naturalis Biodiversity Center, deriving from various find sites on eastern Java, all with intact and unworn posterior plates (collection numbers CD11656, CD2352, CD2030, CD2501 and CD2359). We also measured the M^3 of the Menden *E. hysudrindicus*, of which a (replica) mounted skeleton is exhibited in the central hall of the Geological Museum Bandung. Its intact M^3 molars are partly concealed in the maxilla, which makes that the given sizes involve minor estimates. Moreover, the posterior plates of the M^3 have not emerged. However, the measurements are particularly valuable, as they derive from a molar that can be ascribed to *E. hysudrindicus* with certainty, based on skull morphology (Rizal et al., 2020).

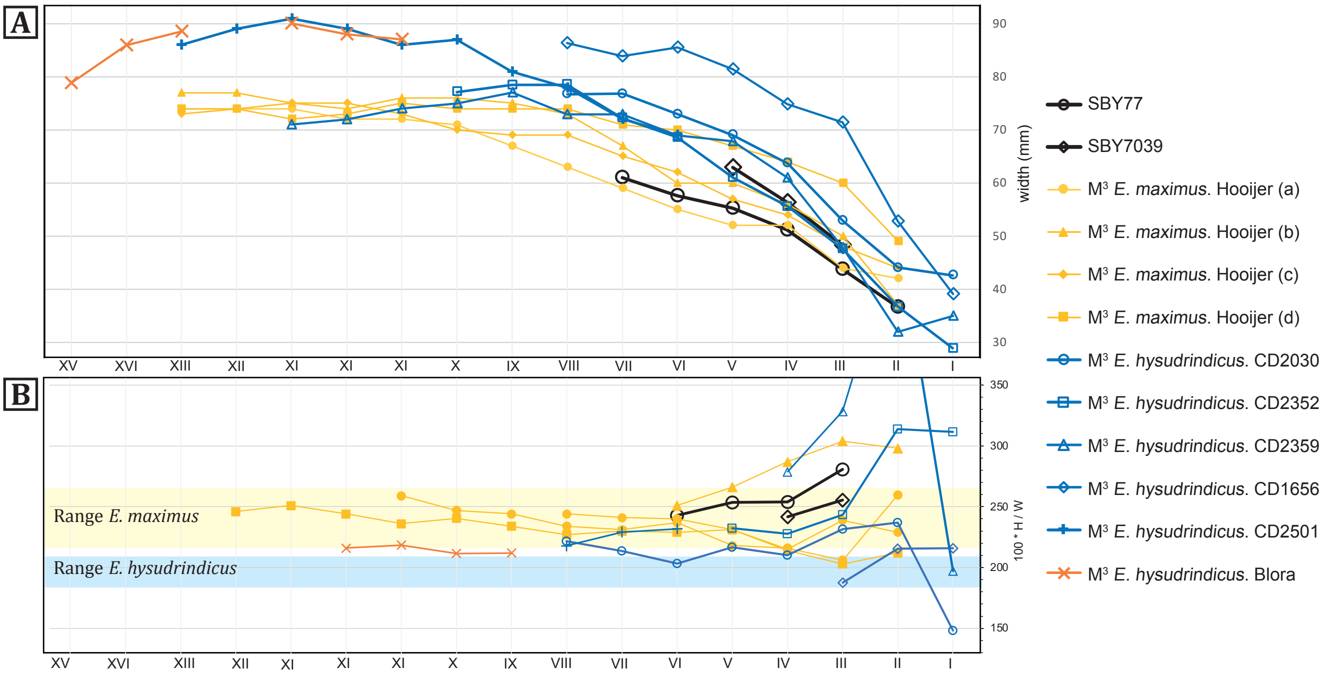


Fig. 11. SBY77 and SBY7039 (posterior fragments of *Elephas* M3) compared to relevant M3 specimens with intact posterior zones. Reference measurements of *Elephas maximus* from Hooijer (1955), indicated as a,b,c,d by this author. Reference measurements of *Elephas hysudrindicus* based on our own new measurements of specimens from Naturalis Biodiversity Center and the Geological Museum Bandung (the Blora specimen).
A: Plate width plot. **B:** H/W-index plot. Indicated H/W-ranges from Hooijer (1955).

Fig. 11A plots the posterior plate widths of the reference M^3 specimens of *E. maximus* and *E. hysudrindicus* in relation to the two specimens from the Madura Strait. The *E. maximus* molars have a uniform build-up, with plate widths of ~ 45 mm in plate II, gradually increasing in anterior direction and reaching their maximum width of 70 to 75 mm around plate IX. The *E. hysudrindicus* upper third molars however show more variation in posterior plate widths. The Menden *Elephas* and two of the molars from Naturalis (CD2501 and CD11656) follow a trend that may be expected from *E. hysudrindicus*, with plate widths plotting above the range of *E. maximus*, reaching a maximum plate width of around 90 mm in plate X or XI. However, the other three specimens, also labelled as *E. hysudrindicus*, have lower plate widths and plot along the upper range of the M^3 of *E. maximus*. The two M^3 fragments from the Madura Strait follow a plate width trend that has most affinity with the *E. maximus* reference specimens.

In **Fig. 11B** we plotted the H/W-indices of the individual (unworn) posterior plates of the same reference specimens in relation to the specimens from the Madura Strait. The yellow and blue bands are the ranges given by Hooijer (1955). The M^3 specimens of *E. maximus* plot close together, with H/W-values ranging between 229 and 259 in the central molar area and with a bit more variation in the posterior four lamellae. As expected, the *E. hysudrindicus* reference specimens have lower H/W-indices in the central molar area, with values ranging between 195 and 232, according to our measurements. Note that the found values are slightly above the range in H/W-indices as reported by Hooijer (1955). However, in their four posterior plates, the *E. hysudrindicus* reference specimens show an extreme variation in the H/W-values. This variation indeed makes it difficult to draw taxonomic conclusions from the H/W-values of the isolated posterior fragments from the Madura Strait. However, looking at the graph, we may still conclude that the two M^3 fragments from the Madura Strait have most affinity with the *E. maximus* reference specimens.

Another interesting molar fragment is SBY85 **(Fig. 10).** It consists of three lamellae, with lamellae missing on both sides. All lamellae have a similar width of 48 mm and an enamel thickness of 2 mm. The wear surface is slightly convex, indicating that the fragment derives from an upper molar. The lamellae are worn and have a height ranging between 57 and 63 mm, giving a H/W-index of >134. The plate widths indicate that the fragment derives from either a dM^4 or an M^1. **Table 7** compares the measurements of the specimen with published size ranges of the dM^4 and M^1 of *E. maximus* and *E. hysudrindicus.* With a width of 48 mm and a laminar frequency of 10.1, the specimen falls in the range of a dM^4 of *E. maximus.* Note, however, the small sample size of the *E. hysudrindicus* comparative specimens, which inhibits firm taxonomic conclusions.

The fourth specimen that is worth discussing is SBY79 **(Fig. 10).** It is an anterior fragment of a high-crowned lower molar, preserving five unworn lamellae and the anterior talon. From a lateral view, the lamellae are weakly curved, with their tips pointing backward. The curvature is most prominent in the talon and anterior two lamellae. Cement covers most of the upper part of the crown, but the tips of the conules are free from cement. The anterior part of the crown bears a flat, steeply inclined oval contact facet developed on the cement surface, where the tooth was in contact with its precursor. The relatively large width of 84.1 mm (at plate 5 from the front), with a slight increase of lamellar width from front to back, indicates that the specimen is the anterior portion of either an M_2 or M_3. The lamellae reach their maximum width at about 1/3 of their height (from the crown base). The slightly curved outline of the crown in occlusal view indicates that the molar derives from the sinistral mandible. The basal lamellar frequency is 5.3. **Table 7** compares the plate dimension of SBY79 with the published size ranges for the M_2 and M_3 of *E. hysudrindicus* and *E. maximus*. Plate width, lamellar frequency, and enamel thickness of SBY79 fall within the overlapping ranges of M_3 of *E. hysudrindicus* and M_2 and M_3 of *E. maximus.* The plate height and H/W-index are slightly above the range of *E. hysudrindicus*. The specimen has therefore most affinity with the M_2 or M_3 of *E. maximus*.

For over a century, it has been the taxonomic practice to regard all Middle Pleistocene *Elephas* remains as *E. hysudrindicus*. A major problem is that the diagnostic criteria for distinguishing between *E. hysudrindicus* and *E. maximus* are based on skull morphology. There are also metric differences between the dentition of both species, but with overlapping ranges. Metrically, the Madura Strait material is closer to the recent *E. maximus* than to most of the Middle Pleistocene material referred to as *E. hysudrindicus.* However, our re-measurements of museum specimens showed that this also applies to some of the Pleistocene molars thus far attributed to *E. hysudrindicus*, and of which the detailed stratigraphic provenance is unknown. To avoid confusion about species identifications, we refer to the material from the Madura Strait as *Elephas* sp.

Proboscidea indet.

Available material (N=54): dI (deciduous tusk): SBY161. **I (tusk fragments):** SBY293A-D, SBY294-300, SBY303, SBY314-318, SBY320, SBY322–227, SBY329–334, SBY343, SBY7050, SBY7051, SBY7190. **Vertebrae:** SBY10, SBY49, SBY57, SBY343, SBY1242, SBY3676. **Rib:** SBY1, SBY2294. **Humerus,** distal fragment: SBY1703 (s/d). **Radius,** distal fragment: SBY344 (s/d). **Lunatum:** SBY578 (s). **Femur,** caput: SBY38, SBY3677. **Patella:** SBY50. **Astragalus,** fragment: SBY7030 (s/d). **Metatarsal 2,** proximal fragment: SBY7199. **Metapodial,** proximal fragments: SBY1069, SBY1601, distal fragment: SBY13.

Description and identification: Proboscidean tusk fragments are recognized by the absence of an enamel layer and the presence of a characteristic pattern of crossing lines (Schreger Pattern) in the dentine. Differences in this dentine pattern have been used to distinguish between the ivory of mammoth and modern elephants (Espinoza and Mann, 1993), but to date there are no publications on Schreger patterns in *Stegodon*. The tusk fragments from the Madura Strait have therefore been left as Proboscidea indet.

The fragmented postcranial remains have been recognized as proboscidean by direct comparison with (mounted) reference specimens in the Geological Museum Bandung. For this material, there are so far no morphological criteria to distinguish between *Elephas* and *Stegodon*.

3.9 Order Primates Linnaeus, 1758 (non-hominin)

The first recorded non-hominin primate fossil from an open-air site on Java is an isolated molar from Trinil, described by Stremme (Stremme, 1911) as *Macacus* sp. Dubois' earlier excavations had also yielded scarce non-hominin primate remains, but the material remained undescribed for several decades. Hooijer (1962) studied this material and assigned several isolated teeth from Trinil as well as a maxilla fragment from Bangle to the genus *Macaca*. Moreover, he assigned a skull from Teguan and a partial palate from Bangle to the genus *Trachypithecus* and a partial palate from Sumber Kepuh to the genus *Presbytis,* both of which are colobine monkeys belonging to the langur group. Recently, a partial femur was described from the Dubois collection, which may be assigned to the Family Hylobatidae (Ingicco et al., 2014).

While primate fossils from the Early to Middle Pleistocene open-air sites of Java are rare, they have been found more frequently at Late Pleistocene to Holocene cave sites on Java and Sumatra. This material, consisting of isolated teeth and occasional mandible or maxilla fragments, has been assigned to the genera *Macaca*, *Trachypithecus, Hylobates, Symphalangus, Nasalis* and *Pongo* (Smith et al., 2021; De Vos et al., 1982; Hooijer, 1962a; Badoux, 1959).

Note that this publication only discusses the non-hominin primates. The taxonomy of two hominin skull fragments from the Madura Strait (attributed to *Homo erectus)* and their relation to the available hominin material from the region, are presented in a separate publication (Berghuis et al., 2025d).

Family: Cercopithecidae Gray, 1821 – Old world monkeys
Tribe: Papionini Burnet, 1828
Genus: *Macaca* Lacépède 1799 - macaque
***Macaca* sp.**

Synonym: *Macacus*

Available material (N=1). Ulna fragment: SBY7174 (d).

Description and identification:

SBY7174 **(Fig. 12)** is a proximal fragment of a dextral ulna, with a total length of 37 mm. The olecranon, trochlear notch and the radial notch are well-preserved. The olecranon is 8.8 mm high. Its proximal surface, where the triceps muscles attach, is rugose and has a prominent groove. Moreover, this proximal surface is slightly inclined, the medial margin being higher than the lateral margin and the anterior margin being higher than the posterior margin.

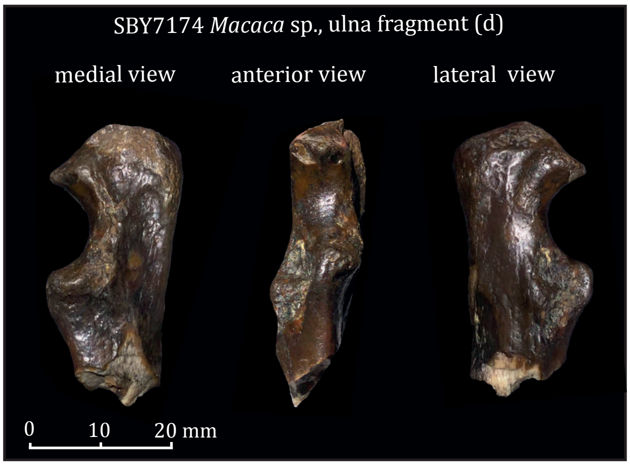


Fig. 12. *Macaca* sp. proximal ulna fragment (d) from the Madura Strait assemblage.

The proximal anteroposterior length of the olecranon is 11.4 mm, but the olecranon projects anteriorly toward the anconeal process, reaching a maximum anteroposterior length of 17.8 mm at the olecranon beak. The opening of the trochlear notch is semi-circular in lateral and medial view and has a proximal-distal length of 11.6 mm, measured from the beak to the coronoid process. The coronoid process is robust and protrudes anteriorly to a similar extent as the olecranon beak, which makes that the opening of the trochlear notch projects anteriorly. The radial notch is well-developed and slightly concave. The preserved part of the shaft is straight, while the posterior side of the olecranon is tilted posteriorly ca. 5 degrees.

The morphology and size of the ulna point to a medium-sized primate. A relation with Hylobatidae (gibbons) can be excluded, as the taxa of this family have a different ulnar morphology, with a strongly reduced height of the olecranon and an upwards-directed opening of the trochlear notch (Nishimura et al., 2022; Harrison, 1989). Referring to the extant and recorded Pleistocene species of Java, a relation with *Macaca*, *Trachypithecus* or *Presbytis* is likely. The relatively great height of the olecranon process compared to the size of the trochlear notch points to *Macaca* rather than *Trachypithecus* and *Presbytis* (Harrison, 1989, 1982). Most of all, the slightly backward tilt of the olecranon is characteristic of *Macaca* and other Papionini taxa. In Colobinae such as the langurs *Trachypithecus* and *Presbytis*, the olecranon is tilted anteriorly relative to the shaft (Milne and Granatosky, 2021; Egi et al., 2007).

There are two extant macaque species of Southeast Asia: *Macaca fascicularis*, occurring on Java and Bali, and the slightly larger *Macaca nemestrina* of Sumatra, Borneo and Malaysia. Hooijer (1962) found that all Pleistocene *Macaca* molars from Java fall in the size range of *M. fascicularis*. For postcranial material, relevant comparison material is not available. We therefore refer to SBY7174 as *Macaca* sp. Extant *Macaca* are quadrupedal, mixed arboreal and semi-terrestrial, with a habitat ranging from forest to scrubland and coastlines.

3.10 Order Carnivora (Bowdich, 1821) - carnivores

Carnivora are scarce in the Pleistocene fossil record of Java (Volmer et al., 2016; Louys, 2014; Brongersma, 1935). The rare finds are dominated by felids such as *Panthera tigris* and *Panthera pardus.* The former only recently became extinct on Java, whereas the latter is still extant on the island. Pleistocene canids are the extant dhole *Cuon alpinus* and the extinct *Cuon trilinensis.* Besides these species, there are extremely rare records of machairodont cats (Kurtén, 1962) and hyenas (Geraads, 1979).

Family: Felidae Fisher von Waldheim, 1817
Genus: *Panthera* Oken, 1816
Panthera pardus (Linnaeus, 1758) - leopard

Available material (N=1). Scapula fragment: SBY1544 (s).

Description and identification: SBY1544 **(Fig. 13)** is a distal fragment of a sinistral scapula with an oval glenoid cavity. The supraglenoid tubercle is well developed and largely intact, only a flake of the facet and the margin with the glenoid cavity is missing**.** The transition toward the supraglenoid tubercle forms a distinct notch along the upper margin of the glenoid cavity. Although the tip of the coracoid process is broken off, it is still recognizable as a slender and downward projecting process. The acromion is broken off, but a small part of its base remains. It is placed centrally on the dorsal surface of the scapula, at a distance of 12 mm from the margin of the glenoid cavity.

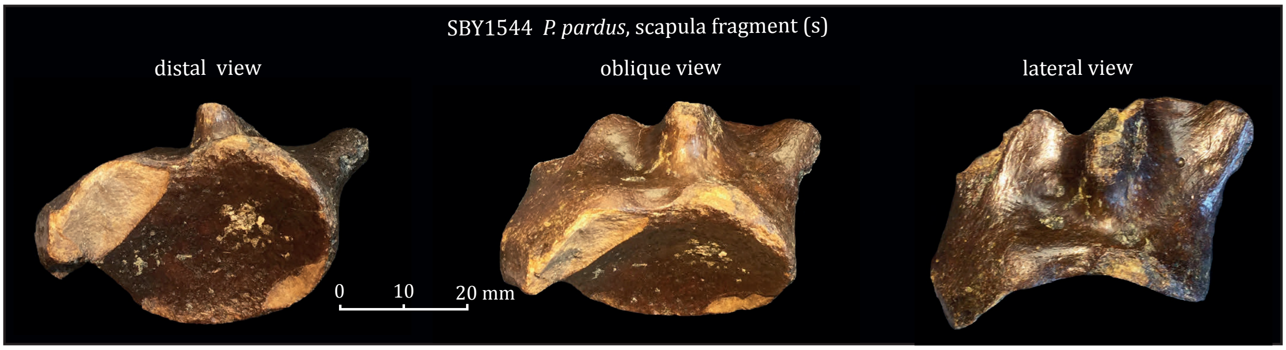


Fig. 13. *Panthera pardus* distal scapula fragment (s) from the Madura Strait assemblage. For measurements see **Table 8.**

The short distance between the base of the acromion and the glenoid cavity, its central position on the scapula surface, and the well-developed supraglenoid tubercle are characteristic features of a carnivore scapula. The morphology and position of the supraglenoid tubercle, forming a notch along the margin of the glenoid cavity and the downward projecting coracoid process, point to a felid rather than to a canid. **Table 8** lists the measurements of the glenoid cavity of SBY1544, compared to the size ranges of *P. tigris* and *P. pardus*. Note that the size ranges are based on measurements of extant adult tigers and leopards from India. SBY1544 is clearly below the size range of *P. tigris* and near the upper margin of the size range of *P. pardus*. A relevant measurement is the distance between the base of the acromion and the margin of the glenoid cavity. This distance is significantly shorter in *P. pardus* than in *P. tigris* and is one of the characteristic traits of this species (Podhade et al., 2019). In SBY1544, this distance is within the range of *P. pardus* and far below the range of *P. tigris*.

Specimen and reference	Sample	*Gleonoid cavity length (mm)*	*Glenoid cavity width (mm)*	*Glenoid cavity to acromion distance (mm)*
SBY1544		38.4	32.8	13
*Panthera tigris**	N=5	55-60	37-40	31-35
*Panthera pardus***	N=4	33-36	23-27	6-21

Table 8. Measurements (mm) of scapula fragment SBY1544 (**Fig. 13)** in comparison with published size ranges of *Panthera tigris* and *Panthera pardus*.
* Tomar et al. (2018). ** Podhade et al. (2019)

3.11: Order Perissodactyla Owen, 1848 – odd-toed ungulates

The Pleistocene Perissodactyla fauna of Java consists of Rhinocerotidae and Tapiridae. Tapir remains are rare finds and mainly associated with forest faunas. *Rhinoceros* remains are more common. Dubois (1907) described two new Pleistocene species: *Rhinoceros sivasondaicus* and *Rhinoceros kendengindicus*. Hooijer (1946) synonymized the former with the extant *Rhinoceros sondaicus* of Java. The latter relates to the extant *Rhinoceros unicornis* of India (Antoine et al., 2022; Antoine, 2012). A third extant species of Southeast Asia is *Dicerorhinus sumatrensis*, the two-horned rhinoceros of Sumatra and Borneo. The species is unknown from the fossil record of Java.

Family: Rhinocerotidae Owen, 1845

Genus: *Rhinoceros* Linnaeus, 1758

Rhinoceros sondaicus (Desmarest, 1822) – Javan rhinoceros

Synonym: *Rhinoceros sivasondaicus*

Available material (N=27). Dentition, dP^3: SBY5076 (d). **P^2:** SBY5075A (d). **M^1:** SBY5073 (d). **M^2:** SBY5077 (s), SBY7142 (d). **M^1 or M^2**, fragment: SBY7181 (d). **P$_3$:** SBY142 (d). **M$_1$:** SBY141 (s), SBY147 (s). **M$_2$:** SBY146 (d). **Tooth fragments,** unknown position: SBY152A-C, SBY7056. **Vertebrae:** SBY7109, SBY463. **Scapula,** distal fragments: SBY7180 (s), SBY7193 (d). **Radius,** proximal fragments: SBY7046 (d), SBY7047 (s/d). **Trapezium:** SBY1313 (d). **Femur,** shaft fragment: SBY33 (d). **Tibia,** shaft fragment: SBY11 (d). Distal fragment: SBY231 (s). **Astragalus,** fragment: SBY251 **Phalanx 3**: SBY7007A-B.

Description and identification: SBY5073 **(Fig. 14)** is a large fragment of a Rhinocerotidae upper molar, showing its characteristic rectangular outline and thick enamel. The crown is broken anteroposteriorly and only the buccal part, with the prominent ectoloph, is preserved. The protolophs and metalophs, making up the mesial and distal parts of the crown, are partly preserved. The preserved buccal face of the crown is smooth and uninterrupted and has an enamel thickness of 0.95 mm. The positions of the paracone fold and parastyle show that the molar derives from the dextral maxilla. The two lingual infoldings, the medisinus and postsinus, are partly preserved. They form smooth, U-shaped valleys with rounded valley-heads and lack a crista.

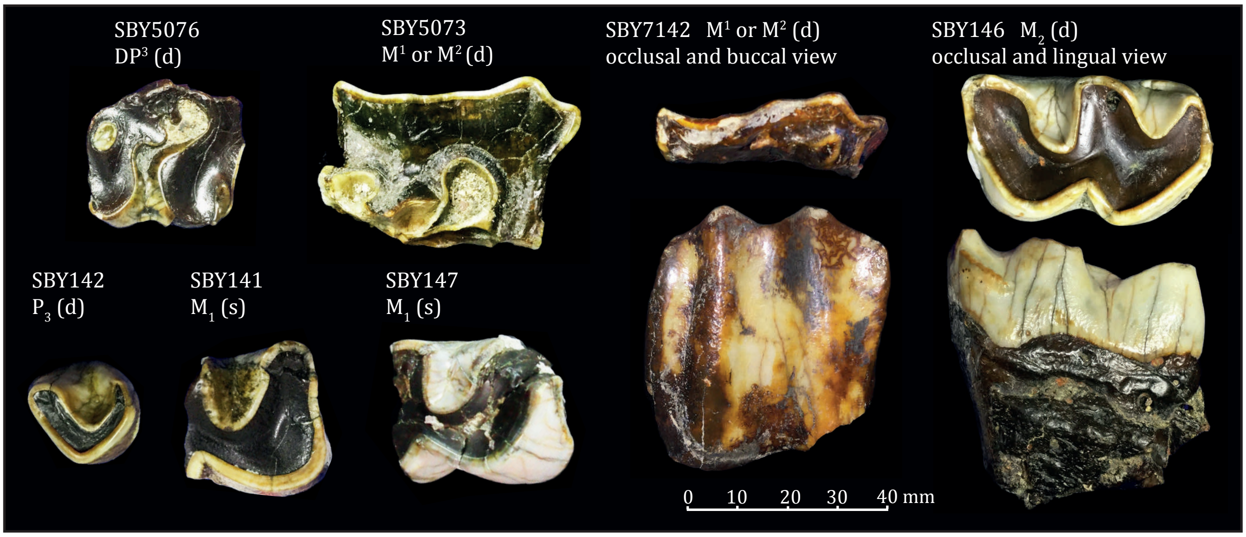


Fig. 14: *Rhinoceros sondaicus* cheek teeth from the Madura Strait assemblage. Selected photographs. For measurements see **Table 9**.

The buccal outline of the crown, with the prominent parastyle is characteristic for both *R. sondaicus* and *D. sumatrensis*. In *R. unicornis*, the parastyle is insignificant (Guérin, 1980). Moreover, the latter species has V-shaped sinuses with cristas at the valley head, both of which are absent in SBY5073. Hooijer (1946) observed that in *D. sumatrensis* upper molars, the postsinus is deeper than the medisinus, whereas in *R. sondaicus* the medisinus is deeper. In SBY5073, the medisinus is clearly deeper than the postsinus, indicating that we are dealing with *R. sondaicus*. Morphologically, there are no notable differences between the last premolar and the first two molars of *R. sondaicus.* Referring to size ranges (Guérin, 1980), SBY5073 derives either from an M^1 or an M^2 **(Table 9)**.

Molar fragment SBY7142 **(Fig. 14)** is highly similar to SBY5073, but preserves only the buccal face of the crown. Referring to its mesiodistal length, it is again an M^1 or an M^2. The fragment is only slightly worn and has a crown height of 50 mm. An interesting specimen is SBY5076 **(Fig. 14)**. It is a strongly worn, almost intact crown with a similar morphology as SBY5073, but with a fine build, a deeply-protruding medisinus and a curved buccal face. It corresponds in size, morphology, and enamel thickness with the dentition of a juvenile maxilla pictured by Guérin (1980) and is probably a dP^3.

Specimens and reference	*Element*	*l (mm)*	*w (mm)*
SBY5076	DP^3 (d)	38.3	35.4
SBY5073	M^1 or M^2 (d)	47.8	--
SBY7142	M^1 or M^2 (d)	46.5	--
D. sumatrensis	M^1	46-51.5	46.6-54
	M^2	47.5-55	48-57
R. sondaicus	**M^1**	46-51	52.6-60
	M^2	44.5-55	53-62.5
R. unicornis	M^1	48-58	62-72
	M^2	53-62	64.5-76
SBY142	P_3	--	23.3
SBY141	M_1 or M_2 (s)	--	29.5
SBY147	M_1 or M_2 (s)	--	29.9
SBY146	M_2 (d)	50.4	32.1
D. sumatrensis	M_1	31-40.5	23-27.5
	M_2	39-47.5	23.5-28
R. sondaicus	**M_1**	41-46.5	26-32
	M_2	40.5-51	27-32.5
R. unicornis	M_1	46-48	28-32.5
	M_2	52-56.5	31-36

Table 9. *Rhinoceros sondaicus* cheek teeth. Measurements of specimens pictured in **Fig. 14** (blue rows) in comparison with published size ranges of relevant Rhinocerotidae. Size ranges from Guérin (1980) based on extant populations, with sample sizes ranging between 4 and 26. In bold: matching size ranges.

SBY146 **(Fig. 14)** is an intact lower molar, with a characteristic morphology of paired, U-shaped lophs, referred to as the trigonid (anterior loph) and talonid (posterior loph). It has a well-developed anterior cingulum and a smaller posterior cingulum. The crown is moderately worn and has a height of 25 mm (buccal) or 18 mm (lingual). The enamel thickness is 1.9 mm. The two valleys at the lingual face of the crown are rounded. Guérin (1980) noted that in *R. unicornis,* both valleys are V-shaped, whereas in *R. sondaicus* and *D. sumatrensis* the valleys are either U- or V-shaped. Therefore, SBY146 belongs to one of the latter species. Guérin (1980) also noted that in *R. sondaicus*, the depth of the two valleys is of similar magnitude, whereas in *D. sumatrensis* there is a great difference in depth. In SBY146, the posterior valley is only slightly deeper than the anterior valley, which again points to *R. sondaicus* as the most likely species. This is confirmed by the size of the crown, which is above the range of *D. sumatrensis* lower molars **(Table 9)**. With a crown length of 50.4 mm, it is probably an M_2 of *R. sondaicus.*

SBY141 and SBY147 are posterior fragments (talonids) of crowns with a morphology that is similar to SBY146. Both fragments have a crown width that is above the size range of *D. sumatrensis* and within the range of the M_1 or M_2 of *R. sondaicus* **(Table 9)**. SBY142 is a single trigonid, which, based on its size, probably derives from a P_3.

3.12 Order Artiodactyla Owen, 1817 – even-toed ungulates

Family Hippopotamidae Gray, 1821

The fossil Hippopotamidae of Southeast Asia belong to the extinct genus *Hexaprotodon,* characterized by six incisors. The genus was first described by Falconer and Cautley (1836), based on a skull from India, which they referred to as *Hexaprotodon sivalensis.* The first record of similar material from Java is by Dubois (1908), who described a calvarium from Kedung Brubus as *Hexaprotodon sivajavanicus*. Von Koenigswald (1933) proposed a taxonomic subdivision of the material from Java in several species. Hooijer (1950) assigned all Pleistocene remains from Java to *Hippopotamus* (*Hexaprotodon*) *sivalensis*. However, De Visser (2008) carried out a biometric study of the Asian fossil material and proposed to maintain the separate species name *Hexaprotodon sivajavanicus* for all Javanese material, which differs from the Asian mainland material by its smaller size.

Genus: Hexaprotodon Falconer and Cautley, 1836

Hexaprotodon sivajavanicus Dubois, 1908

Synonyms: *Hexaprotodon namadicus*, *Hippopotamus* sp., *Hippopotamus simplex*, *Hippopotamus antiquus*, *Hippopotamus sivalensis*

Available material (N=30). Incisors, I_1 or I_3, fragments**:** SBY130A-B, SBY7171. **Canines, lower C,** fragments**:** SBY149 (d), SBY7170 (d). **Upper cheek teeth: M^1 or M^2:** SBY145 (d), SBY156 (s). **Tooth fragments**, unknown position: SBY92A-B, SBY110, SBY131, SBY5055, SBY5056, SBY7182. **Mandibula,** fragment with roots of M_3: SYB108 (s). **Vertebrae:** SBY455, SBY463, SBY465. **Scapula,** distal fragments: SBY4 (d), SBY1689 (s). **Hamatum:** SBY705 (s). **Capitatotrapezoid,** distal fragment: SBY7200 (d). **Metacarpus,** fragment of MC-II: SBY681 (d). **Femur,** shaft fragment: SBY12 (s). **Tibia,** distal fragments: SBY231 (s), SBY1172 (d). **Astragalus:** SBY5089 (s). **Cuneiform:** SBY566 (d). **Metatarsus,** proximal fragment of MTII: SBY1138 (s), proximal fragment of MTIII: SBY551 (s).

Description and identification: SBY7171 and SBY130A **(Fig. 15)** are fragments of incisors with a rounded, slightly laterally-compressed cross-section. Although not well visible, the enamel coating seems to have been present all around the crown. The enamel layer, with a thickness of 1.1 mm, is white and smooth. Within the Pleistocene fauna of Java, only Hippopotamidae have such large, enamel-covered incisors. In the genus *Hexaprotodon*, upper incisors have a circular section, whereas lower incisors are slightly mediolaterally compressed, which indicates that SBY7171 and SBY130A are fragments of lower incisors. Also their size suggests that both specimens derive from the lower tooth row: The two specimens have an estimated anteroposterior diameter of 28 and 26 mm, whereas the maximum recorded diameter of upper incisors of the Javanese *H. sivajavanicus* is 15 mm (de Visser, 2008). Referring to measurements of lower incisors by Hooijer (1950), the fragments probably derive from either an I_1 of I_3, falling in the upper size ranges for these two elements **(Table 10)**.

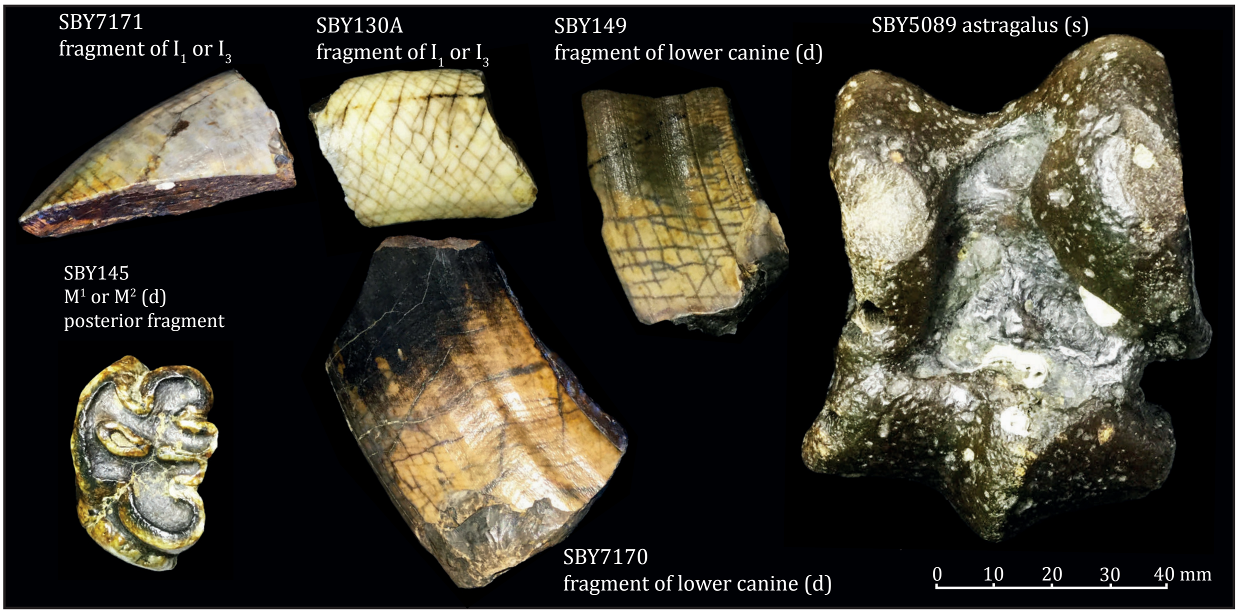


Fig. 15. *Hexaprotodon sivajavanicus* remains from the Madura Strait assemblage. Selected photographs. For measurements see **Tables 10** and **11.**

SBY149 and SBY7170 **(Fig. 15)** are fragments of large canines. They are laterally compressed and have a rounded anterior face and a flat posterior face. SBY7170 preserves a central cavity. The anterior face as well as the lateral faces are covered with enamel, but along the posterior face, in the inside bend of the tooth, enamel is absent and the dentine is exposed. The enamel layer has a thickness of 1.1 mm and has fine longitudinal striations. The large, curved teeth with a U-shaped cross-section, striated enamel and a lack of enamel at the posterior face are characteristic of Hippopotamidae lower canines. A superimposed, smooth longitudinal valley marks the medial face of the tooth, which makes both specimens fragments of dextral canines. The specimens have an anteroposterior diameter of 35 and 44 mm respectively, which corresponds to the size range provided by Hooijer (1950) for *H. sivajavanicus* from Java **(Table 10)**.

SBY145 **(Fig. 15)** is recognized as a Hippopotamidae cheek tooth by its characteristic trefoil-wear pattern and thick and smooth enamel layer, reaching a thickness of ~3 mm. Hippopotamidae molars consist of four relatively high, bunodont cusps. SBY145 is broken buccolingually and only preserves two cusps with an intermediate infundibulum. The fragment is identical to the posterior part of Dub2318a, an isolated upper molar labelled as M^2 by Hooijer (1950, plate VIII-9). The preserved cusps are probably the hypocone and metacone. The specimen has an articular facet along the posterior face and a prominent cingulum at what must be the lingual face, which indicates that the molar derives from the dextral maxilla. In Hippopotamidae, there is considerable overlap between the M^1 and M^2, both in size and morphology. The crown width of 38.7 mm falls in the size range of both tooth positions for *H. sivajavanicus* (**Table 10**), referring to crown measurements of intact fossil maxillae (Hooijer, 1950; Van der Maarel, 1932; Stremme, 1911).

Specimen (SBY) and published size ranges	*Element*	*Diameter (mm) max. (ant-post)*	*l (mm)*	w (mm)
SBY7171	I_1 or I_3	28 (estimate)		
SBY130	I_1 or I_3	26 (estimate)		
I_1 (N=14)*		23-27		
I_2 (N=14)*		16-25		
I_3 (N=14)*		17-26		
SBY149	C lower	35		
SBY7170	C lower	44		
C lower (N=15)*		37-54		
SBY145	M^1 or M^2		--	38.7
M^1 (N=13)$^{\#}$			34-41	31-41
M^2 (N=15)$^{\#}$			38-50	36-48

Table 10: *Hexaprotodon sivajavanicus* incisor, canine and molar fragments. Measurements of specimens pictured in **Fig. 15** (blue rows) in comparison with published size ranges of reference specimens from the Pleistocene of Java.
* From: Hooijer (1950). #: From: Stremme (1911), Van der Maarel (1931) and Hooijer (1950).

An interesting postcranial specimen is the astragalus SBY5089 **(Fig. 15)**. It differs from similar-sized bovid astragali **(Fig. 27)** by its rounded, robust body and its great width compared to its height. It has a distinct Hippopotamidae morphology of the distal articulation, which consists of two rounded facets separated by an obliquely oriented median ridge. Note that in bovid astragali the two condyles are separated by a median groove. Only five other *Hexaprotodon* astragali have been recorded from the Pleistocene of Java. See for reference the pictured specimens in Stremme (1911, Taf. XIX-6) and Hooijer (1950, Plate XX). SBY5089 falls in the size range of these earlier finds, except for a slightly larger lateral height **(Table 11)**.

Specimen (SBY) and published size ranges	*Element*	Lat. h GLl	Mid. h	Med. h GLm	Dist. w Bd	Max. thickness Dl (ant-post)
SBY5089	Astragalus	89.1	77.0	73.0	61.8	48.5
Astragali Java (N=5)		77-85	69-80	--	60-64	--

Table 11: *Hexaprotodon sivajavanicus* astragalus. Measurement of SBY5089 **(Fig. 15)** in comparison with published size range of all known reference specimens from the Pleistocene of Java. Reference measurements from Stremme (1911), Stromer (1914), Hooijer (1950). Measurements methods and codes: Von den Driesch (1976).

Family: Suidae Gray, 1821

Dubois (1908) described two Pleistocene suids from Java: *Sus brachygnathus* and the larger *Sus macrognathus*. Detailed descriptions of skulls and dentition were provided by Stremme (1911), Von Koenigswald (1933), and Hardjasasmita (1987). According to Von Koenigswald (1933), the Pleistocene species may be related to the extant *Sus verrucosus* of Java and to *Sus celebensis* of Sulawesi. *Sus scrofa vittatus*, nowadays the most common species on Java, probably arrived during the Late Pleistocene (Van den Bergh et al., 2001).

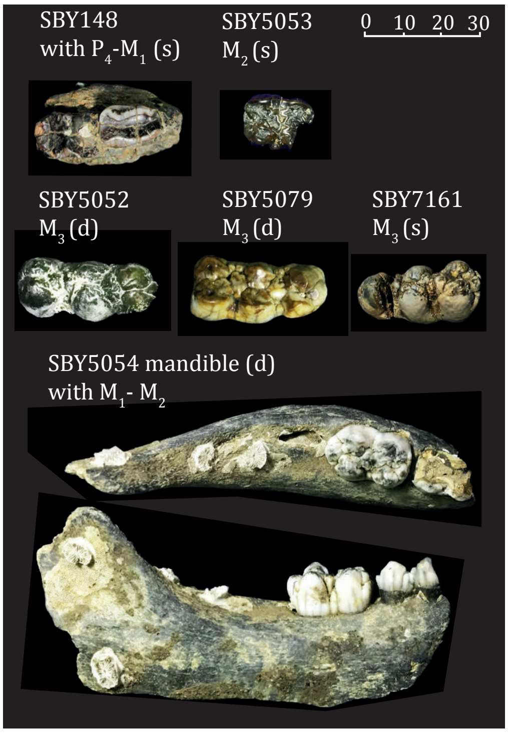
Genus: Sus Linnaeus, 1758
Sus brachygnathus Dubois, 1908

Synonyms: *Sus hysudricus, Sus vatualangensis*

Available material (N=14). Mandibula, fragment with P_2-P_3-P_4: SBY132 (s), fragment with P_4-M_1: SBY148 (s), fragment with M_1-M_2–M_3: SBY5054 (d), fragment with M_3: SBY336 (s), fragment with root of M_3: SBY102 (d). **Lower dentition, M_2:** SBY5053 (s). **M_3:** SBY5052 (d), SBY5079 (d), SBY7161 (s), SBY7162 (d). **Scapula,** distal fragment: SBY7020 (s). **Humerus,** distal fragment: SBY1519 (d). **Radius,** distal fragment: SBY691 (s). **Metatarsus,** MT2: SBY7023 (s).

Description and identification: SBY148 **(Fig. 16)** is a mandible fragment with a heavily worn P_4 and M_1. The P_4 has a characteristic elongate, tricuspid suid morphology. The M_1 preserves the outlines of four bunodont cusps and a median subsidiary cusp, as well as a hypoconulid cusplet. SBY5053 **(Fig. 16)** is an isolated, heavily worn M_2. The wear surface shows the outlines of the four cusps and the median subsidiary cusp. Most of the anterior cingulum and the metaconid are missing.

SBY5054 **(Fig. 16)** is a mandible fragment, preserving a large part of the body and the ramus. It has two unworn molars, a broken M_1 and a complete M_2. The M_2 has a characteristic morphology of 4 bunodont cusps, a median subsidiary cusp, and a strongly developed hypoconulid at the posterior side. The M_3 has not yet emerged, which indicates that the mandible belonged to a juvenile individual. The mandible is broken at the base, which offers a view of the base of the unerupted M_3 and even allows measurement of the crown.



The collection contains three unworn, isolated M_3 specimens, with three rows of bunodont cusps and intermediate subsidiary cusps **(Fig. 16)**. SBY7161 has a pronounced anterior cingulum and anterior subsidiary cusp, both of which are largely absent in SBY5079 and SBY5052. Along the posterior face, all specimens have a well-developed talonid. Note the absence of enamel in SBY5052, which is indicative of a molar that passed the digestive tracts of a crocodilian or another predator (Fisher, 1995).

Metrically, all crowns plot in the size ranges of the Pleistocene *S. brachygnathus* from various Javanese localities as given by Hardjasasmita (1987), Von Koenigswald (1933), and Stremme (1911) and below the size range of *S. macrognathus* **(Fig. 17)**. Most M_3 specimens from the Madura Strait plot close together and have, compared to the reference sample, relatively long and slender crowns. Only SBY7161 is somewhat smaller, plotting along the lower margin of the size range of *S. brachygnathus* M_3.

Fig. 16. *Sus brachygnathus* dental remains from the Madura Strait assemblage. Selected photographs. All molars in occlusal view. SBY5054 in occlusal and buccal view.

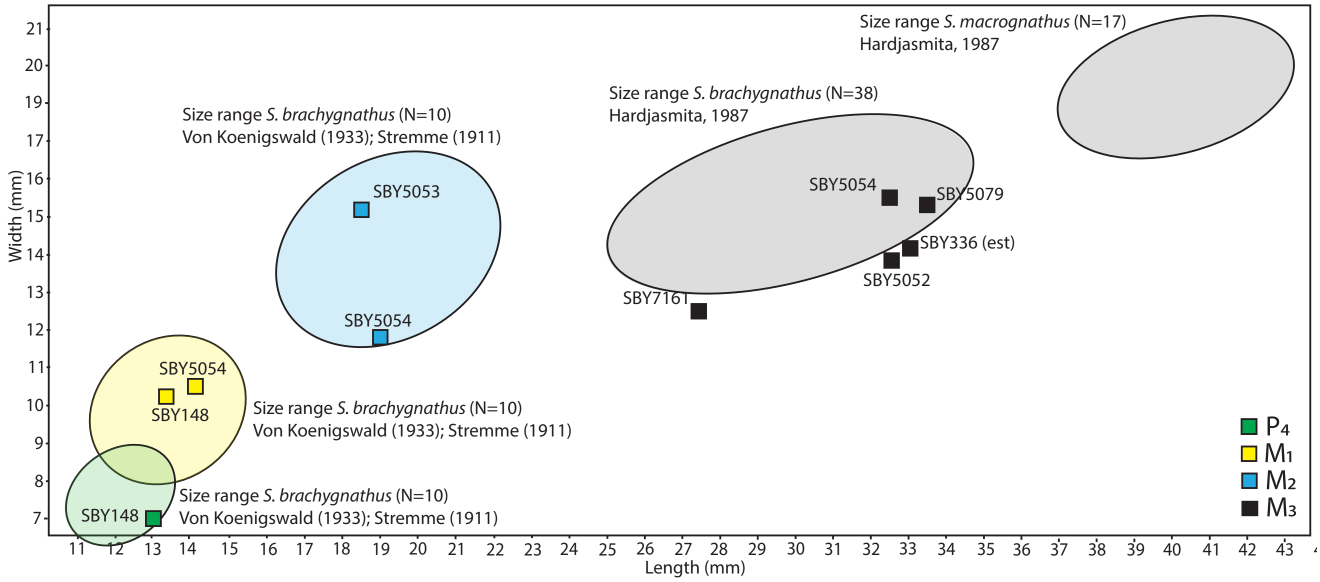


Fig. 17. *Sus brachygnathus* dental remains from the Madura Strait assemblage. Bivariate plot of crown length and width, with published size ranges for *S. brachygnathus* and (for the M_3 only) *S. macrognathus*, based on fossils from various Pleistocene sites on eastern Java.

Sus cf. *macrognathus* Dubois, 1908

Synonym: *Sus terhaari*

Available material (N=2). Phalanx 1: SBY186, SBY193.

Description and identification: Among the sample of Artiodactyla first phalanges, SBY186 and SBY193 stand out by their deviant morphology **(Fig. 28A)**. In comparison to their length, they have a robust shaft with a conspicuous supra-articular inflation directly above the distal articulation. Moreover, they have an asymmetrical, anteriorly-pointing morphology of the proximal articular surface. Both traits are characteristics of suids (Schmid and Garraux, 1972). The size of the proximal articular surface plots in the range of *Bos palaeosondaicus* **(Fig. 28B)**. However, the two specimens have a shorter and comparatively robust shaft. In the bivariate plot of shaft length and width **(Fig. 28C)**, both specimens are easily differentiated from bovid phalanges.

The phalanges, with an articular face that equals those of Bovini, point to a particularly large-bodied suid. Within the Pleistocene fauna of Java, the only candidate species is *Sus macrognathus*. This is an interesting finding, as recorded fossils of this species are rare and only consist of fragmented maxillae, mandibles, and isolated cheek teeth. Postcranial material of this species has never been found or recognized. The two first phalanges from the Madura Strait may therefore be the first postcranial elements to be assigned this species. In the absence of dental material to support the presence of this species within the assemblage, we refer to the specimens as *Sus* cf. *macrognathus.*

Family: Cervidae Goldfuss, 1820

Cervids are common within the Pleistocene fossil assemblages of Java. Species definitions have primarily been based on antler morphology, which resulted in a complex taxonomy with over a dozen species (Von Koenigswald, 1933). A recent morphometric comparison of molars paved the way for a taxonomic simplification (Gruwier et al., 2015). The small Pleistocene species *Axis lydekkeri* (Martin, 1886) is related to the extant *Axis (Hyelaphus) porcinus* of mainland Southeast Asia and *Axis (Hyelaphus) kuhlii* of Bawean Island (Gruwier et al., 2015). The modest-statured *Axis javanicus* (Von Koenigswald, 1933) is not part of the *Hyelaphus* subgenus and probably relates to the extant *Axis axis* of mainland Asia (Meijaard and Groves, 2004). There are also remains of larger deer in the fossil assemblages of Java. Dubois (1908) assigned this material to a new species, *Cervus kendengensis.* In most literature, this large-statured Pleistocene cervid of Java is nowadays referred to as Cervus (*Rusa*) sp. Grubb (2005) raised *Rusa* to genus level, which makes *Rusa* sp. a more appropriate attribution for the fossil material from Java, which is morphologically similar to the extant *Rusa timorensis* of Java and *Rusa unicolo*r of the Asian mainland, Sumatra and Borneo (Gruwier et al., 2015; Meijaard and Groves, 2004).

Genus: *Axis* Smith, 1827

Axis lydekkeri (Martin, 1886)

Synonyms: *Cervus zwaani*, *Cervus oppenoorthi*

Available material (N=36). Antler, antler base with burr and pedicle: SBY7177 (s). Antler base with burr: SBY347 (d), SBY381 (d) SBY387 (d), SBY448 (d), SBY718 (d), SBY721 (d), SBY358 (s), SBY377 (s), SBY446 (s), SBY557 (s), SBY715 (s), SBY791 (s), SBY799 (s), SBY809 (s), SBY857 (s), SBY892 (s), SBY2665 (s), SBY441 (s/d), SBY763 (s/d), SBY888 (s/d), SBY7201 (d). **Mandibula,** fragment with P_3: SBY7172 (d), fragment with M_1 and M_2: SBY7116 (s). **Lower dentition, M_3:** SBY5080 (d). **Radius,** proximal fragment: SBY254 (d). **Os malleolus:** SBY6013 (s). **Astragalus:** SBY182 (d), SBY5099 (d), SBY6008 (s), SBY183 (s), SBY7043 (d). **Scapho-cuboid:** SBY7042 (s). **Phalanx 1**: SBY198, SBY6006. **Phalanx 2:** SBY197.

Description and identification: SBY448 and SBY721 **(Fig. 18)** are antler bases, preserving the burr (coronet), the base of the main beam, and the base of the brow tine. The burr is slightly pearled and the antler base is finely ribbed. The antler base has a diameter of ~30 mm and a height of ~35 mm, measured from the burr to the angle between the brow tine and the main beam. The backward-directed main beam and the forward-directed brow tine both make an angle of ~ 45 degrees with the burr. The preserved lower part of the main beam has a diameter of ~ 20 mm. The antler bases are identical to several complete antlers of *A. lydekkeri* stored in the Geological Museum Bandung (collection nrs. K98 and K105) and correspond with the dimensions and morphological descriptions provided by Stremme (1911) and Von Koenigswald (1933) for this species. Besides the small size (complete specimens have a total beam length of 30 to 35 cm), the antlers of this species are characterized by their fine-ribbed surface and an internal angle of ~90 degrees between the main beam and the brow tine.

SBY7116 **(Fig. 19)** is a fragment of a sinistral mandible with the M_1 and M_2. The mandible is slender, with a height of ca. 24 mm and a thickness of 12.8 mm (measured below the M_2). The molars have a dull, rugose enamel. Both molars are slightly worn and, with a worn height of 14 mm, relatively low-crowned. The crowns have a modest lingual cingulum and narrow toward the apex. The occlusal face has a characteristic cervid morphology of isolated conids and open infundibula. Along the lingual face, the molars have well-developed entostylids and mesostylids, which run obliquely along the crowns. Near the apex of the crown, there is a small metastylid. Along the buccal face, the molars have a small and low ectostylid near the base of the crown. SBY5080 **(Fig. 19)** is an unworn M_3 with a small bone fragment surrounding the root. It has a similar rugose enamel structure as the molars of SBY7116 and shows a similar widening of the crown toward the base. The unworn crown height is ~ 18 mm. It has a prominent metastylid and a small, low ectostylid, but lacks a posterior ectostylid.

Size ranges of *A. lydekkeri* lower molars were provided by Stremme (1911), referring to 12 complete mandibles from Trinil **(Fig. 20)**. The M_1 of mandible fragment SBY7116 plots along the species' upper size margin, whereas the M_2 plots slightly above the size range of the Trinil specimens. Their size is comparable to molars found in Ngebung, which were assigned to the subspecies *A. lydekkeri ngebungensi* based on their relatively large size (Moigne et al., 2004). The M_3 SBY5080 plots well within the size range of *A. lydekkeri* as provided by Stremme (1911).

Limb bones have been assigned to *A. lydekkeri* based on a morphological and metric analysis of ruminant skeletal remains. Relevant, pictured specimens are SBY254, a proximal half of a dextral radius **(Fig. 24)**, SBY183, a sinistral astragalus **(Fig. 27)**, SBY198 and SBY197, first and second phalanges **(Figs. 29 and 30)**.

Fig. 18. Cervidae antler bases from the Madura Strait assemblage. Selected photographs.

Genus: *Axis* Smith, 1827

Axis javanicus Von Koenigswald, 1933

Available material (N=17). Antler, antler base with burr and pedicle: SBY427 (d). Antler base with burr: SBY435 (d), SBY864 (d), SBY368 (s), SBY420 (s), SBY880 (s). **Lower dentition, M_2:** SBY127 (s). **M_3**: SBY7114 (s). **Metacarpus**, proximal fragment: SBY73 (d). Distal fragment: 7153 (d). **Astragalus:** SBY178 (d), SBY7164 (s), SBY179 (s), SBY180 (s). **Calcaneum,** fragment: SBY7052 (s). **Phalanx 1:** SBY7154, SBY201.

Description and identification: SBY427 and SBY435 **(Fig. 18)** are antler bases, preserving the burr, the base of the main beam and the base of the brow tine. SBY427 also preserves a pedicle. The burr is weakly pearled and the surface of the main beam is weakly ribbed. The main beam is directed sharply to the back and has a diameter of 25 - 30 mm. The specimens match the descriptions of *A. javanicus* by Von Koenigswald (1933), who defined the species by its antlers, which are slightly larger than those of *Axis lydekkeri,* have a weak surface ornamentation and have an internal angle between the main beam and the brow tine of more than 90 degrees. The Madura Strait specimens also compare well with several intact antlers assigned to *A. javanicus* stored in the Geological Museum Bandung. The relatively thick, backward-directed main beam of these complete antlers has a strong curvature, curving forward as well as outward, and reaches a length of ~ 50 cm.

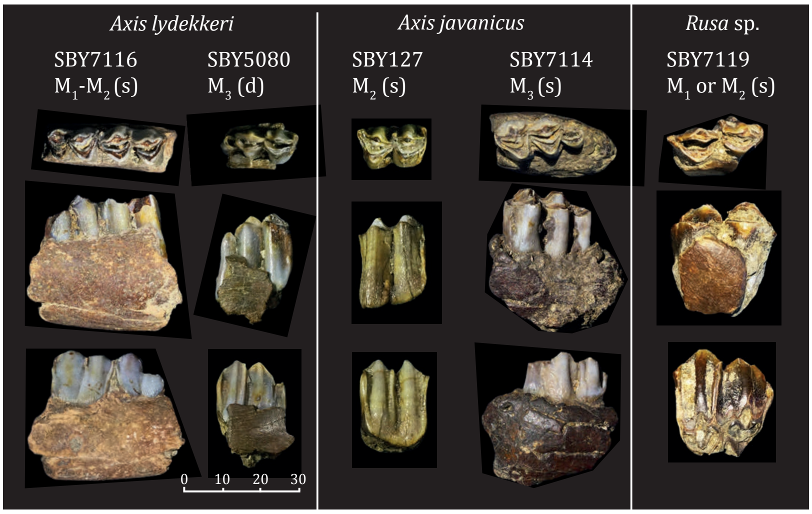


Fig. 19. Cervidae lower molars from the Madura Strait assemblage. Selected photographs in (from top to bottom) occlusal, buccal and lingual view. For crown measurements see **Fig. 20**.

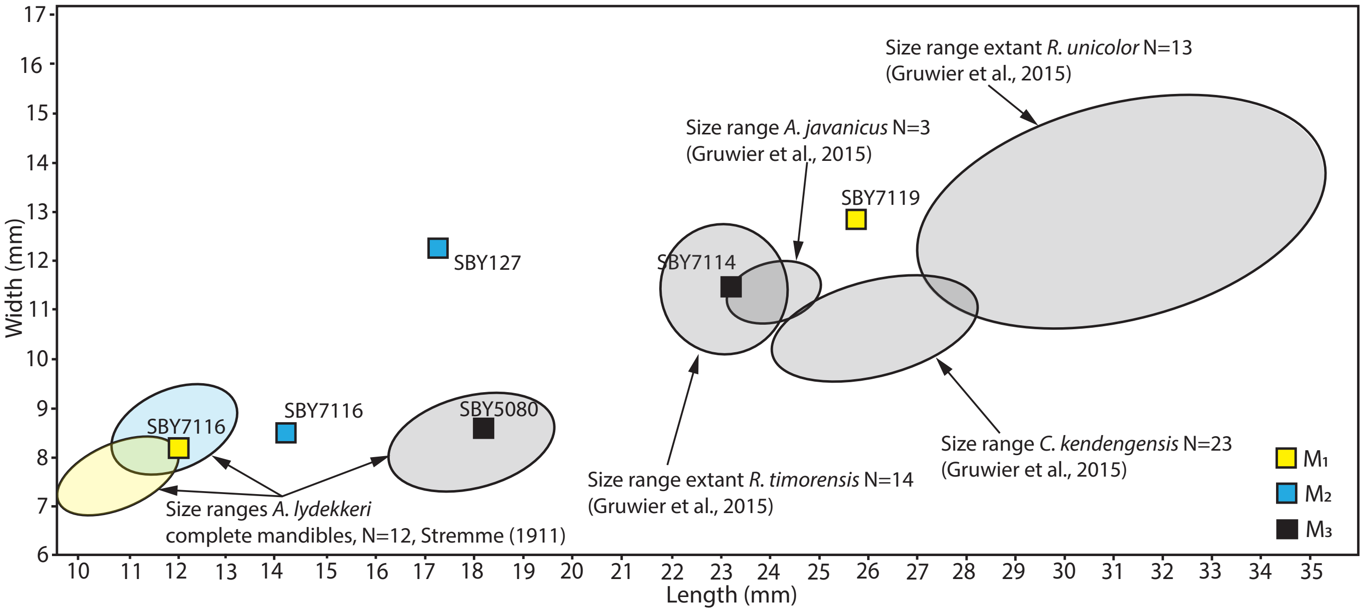


Fig. 20. Cervidae lower molars from the Madura Strait assemblage. Bivariate plot of crown length and width, with published size ranges of extant and fossil species. Note that SBY7119 may also be an M_2.

SBY7114 **(Fig. 19)** is a small fragment of a sinistral mandible with a slightly worn M_3. Below the M_3, the mandible has a thickness of 18.5 mm. The crown has a strongly rugose enamel and thickens toward the base. Its occlusal surface has a cervid morphology of isolated conids and partly connected infundibula. It has a well-developed metastylid and an obliquely, outward-directed mesostylid. An ectostylid is absent or has not yet emerged.

SBY127 is an isolated sinistral M_2 with a similar rugose enamel structure, basal thickening, and an occlusal face of isolated conids. The crown is only slightly worn and has a height of 26 mm. It has a low ectostylid, only present along the crown base. In the bivariate plot of crown length and width, both specimens plot above the range of *A. lydekkeri* **(Fig. 20)**. The M_3 SBY7114 falls in the overlapping size ranges of the fossil *A. javanicus* and the extant *Rusa timorensis*. Gruwier et al. (2015) found that the Pleistocene *Rusa* sp. molars exceed the molars of the extant *R. timorensis* in size. SBY7114 is therefore regarded as *A. javanicus* rather than *Rusa* sp. SBY127 has a similar crown width and is assigned to the same species. Unfortunately, no published size ranges are available for the M_2 of *A. javanicus*.

Two metacarpal fragments SBY73 and SBY7153 have been assigned to *A. javanicus*, based on a morphological and metric analysis **(Fig. 25)**. The specimens represent a medium-sized cervid, plotting above the size range of *A. lydekkeri* and below the range of *Rusa unicolor*. The same applies to several cervid astragali, such as SBY180 **(Fig. 27)**. For the cervid first phalanges only two size groups were found. We tentatively assigned the specimens of the larger size group to *A. javanicus,* as they plot relatively close to *A. lydekkeri* phalanges and appear to be too small to be assigned to *Rusa* sp. **(Fig. 28)**.

Note that the species *A. javanicus* has thus far only been identified by its antlers and isolated dentition. The postcranial bones from the Madura Strait are the first postcranial elements to be ascribed to this species.

Axis sp.

Available material (N=241). Antler: 193 beam fragments labelled as SBY370, SBY441, and SBY7206 and 27 small tines labelled as SBY371 and SBY7203. **Cervical vertebrae:** SBY461, SBY475, SBY476, SBY482, SBY504, SBY513, SBY525, SBY537, SBY7105**. Thoracic vertebrae:** SBY478, SBY488, SBY7103, SBY7106, SBY7107. **Lumbar vertebrae:** SBY185, SBY491, SBY535, SBY538**. Scapula,** distal fragments: SBY682, SBY1641, SBY2111.

Description and identification: The beam fragments are assigned to the genus *Axis* because of their smooth to finely-ribbed surface and small to modest size, with diameters ranging between 10 and 30 mm. The fragments may loosely be assigned to either *A. lydekkeri* or *A. javanicus* based on beam thickness and surface ornamentation. However, as beam diameter and surface ornamentation decrease distally, species allocation becomes more uncertain with decreasing diameter of the fragments. The same applies to the small (up to ~ 50 mm long) tines, which may be brow tines, bez tines or crowns of the main beam.

Scapula fragments and vertebrae have been left out of comparative analyses. All small scapulae and vertebrae with a cervid morphology have been listed as *Axis* sp.

Genus: *Rusa* (Smith, 1827)

Rusa sp.

Synonyms: *Cervus kendengensis, Cervus* (*Rusa*) sp.

Available material (N=95). Antler, antler base with burr and pedicle: SBY367 (s), SBY431 (s/d). Antler base with burr: SBY361 (d), SBY418 (s), SBY422 (d), SBY428 (d), SBY429 (d), SBY433 (d), SBY436 (s), SBY440 (s), SBY443 (s), SBY444 (d), SBY845 (d), SBY7178 (d). 43 beam fragments labelled as SBY372 and 7 tines labelled as SBY373. **Lower dentition, M_1 or M_2:** SBY7119 (s) **Cervical vertebrae:** SBY7187, SBY7188. **Thoracic vertebrae:** SBY1758. **Lumbar vertebrae:** SBY496, SBY505, SBY507, SBY510, SBY519, SBY526, SBY536, SBY7189. **Metacarpus,** proximal fragment: SBY7184 (s). Shaft fragment: SBY58 (s). Distal fragment: SBY5091 (d). **Scaphoid:** SBY1516 (s). **Femur,** proximal fragment: SBY29 (d), SBY30 (s). Caput: SBY3481 (s/d). Distal fragment: SBY221 (d). **Tibia:** Distal fragments: SBY226 (s/d), SBY1600 (s), SBY7204 (d). **Cuneiform:** SBY7202 (d). **Astragalus:** SBY174 (s), SBY176 (s), SBY173 (s), SBY177 (s), SBY7043 (d). **Calcaneum:** SBY7197 (d). **Phalanx 2:** SBY7169.

Description and identification: SBY433 and SBY444 **(Fig. 18)** are bases of large antlers with a pearled burr and a rugged surface ornamentation of longitudinal ribs. The base of the antler, between the burr and the internal angle between the main beam and the brow tine, has a height of 50-60 mm. The main beam is slightly backward-directed and has a basal diameter of 40–45 mm. The forward projecting brown tine has broken off in both specimens. SBY431 derives from a similar, large and strongly ornamented antler and preserves a ca. 55 mm long pedicle. The antler fragments compare well with the antlers of the extant *Rusa timorensis* and *Rusa unicolor* and with several mounted Pleistocene antlers kept in the Geological Museum Bandung, most of which are labelled as *Cervus kendengensis*. Due to a lack of diagnostic features to differentiate between these species based on fragmented antler remains, and following the current taxonomical practice for the Pleistocene cervids of Java, the material is assigned to as *Rusa* sp.

SBY7119 **(Fig. 19)** is a worn sinistral M_1 or M_2 preserving some of the surrounding bone. It has rugose enamel and a cervid morphology, with an occlusal surface characterized by isolated conids and open or connected infundibula. Along the lingual face, it has an oblique, outward-directed mesostylid and entostylid and a well-developed metastylid. Along the buccal face, it has straight and well-defined ribs, lacking a visible ectostylid. Its crown size plots far above the size ranges of *Axis lydekkeri* and also above the sizes of the two molars from the Madura Strait that we assigned to *Axis javanicus* **(Fig. 20)**. For the extant or fossil species of *Rusa*, reference size ranges are only available for the M_3. SBY7119 has a higher crown width than the Pleistocene M_3 specimens that were assigned to C*ervus kendengensis*. Its crown width is more comparable to the M_3 of the extant *Rusa unicolor*. We therefore assign SBY7119 to *Rusa* sp., noting that it is relatively large compared to the available Pleistocene *Rusa* molars from Java. Lacking useful references, it is impossible to make out whether the specimen is an M_1 or an M_2.

Postcranial remains have been assigned to *Rusa* sp. based on a morphological and metric analysis of ruminant material. An interesting specimen is the distal metacarpal fragment SBY5091 **(Fig. 25)**. From an anterior view, its median groove continues distally along the shaft until ca. 20 mm above the distal condyle, which identifies the specimen as a cervid (Heintz, 1970). With a distal width of 49 mm, the specimen is remarkably large, approaching the size of bovid species such as *Bos palaeosondaicus*, which shows that the *Rusa* sp. of the Madura Strait must have been particularly large-statured. *Rusa* sp. astragali are well-represented in the assemblage **(Fig. 27)**. Metrically, these astragali are comparable to two fossil astragali from Sangiran attributed to *Rusa* sp. (Moigne et al., 2004). SBY7169 **(Fig. 29)** is a cervid second phalanx that plots slightly below the size range of *B. palaeosondaicus,* again pointing to a particularly large posture.

Family: Bovidae Gray, 1821

Dubois (1908) distinguished three large bovid species from the Pleistocene of Java: *Bos (Bibos) palaeosondaicus, Bubalus palaeokerabau* and *Leptobos groeneveldtii.* The former two are common Pleistocene species and related to the extant *Bos javanicus* and *Bubalus bubalis* of Southeast Asia. *Leptobos groeneveldtii,* later revised to *Epileptobos groeneveldtii* (Hooijer, 1958a) is a rare Pleistocene species, only recorded by two skulls and scarce horncore fragments. Besides these three species, all of which are Bovini, Dubois recognized a small bovid, which he named *Anoa santeng* (Dubois, 1891). The species, which was renamed *Duboisia santeng* (Brongersma, 1937; Stremme, 1911), belongs to the Boselaphini and relates to the extant *Tetracerus quadricornis* and *Boselaphus tragocamelus* of India (Rozzi et al., 2013). There are also scarce fossil records of *Capricornis sumatraensis,* the extant serow of Sumatra and mainland Southeast Asia. This material, consisting of isolated teeth, derives from Late Pleistocene caves of Sumatra and Java (Badoux, 1959; Hooijer, 1958a).

Species definitions have primarily been based on the morphology of skulls and horncores. Metric details were provided by Hooijer (1958) and Stremme (1911). With respect to the dentition, these authors found no morphological or metric differences between the two most common bovid species *B. palaeokerabau* and *B. palaeosondaicus*, except for a slight size reduction of the P_2 in *B. palaeosondaicus.* Isolated cheek teeth from the Javanese find sites are therefore generally referred to as Bovidea indet. With respect to limb bones, the authors concluded that *B. palaeokerabau* and *B. palaeosondaicus* exceeded their extant descendants in size. Moreover, the authors noted that in the extant as well as fossil species, *Bubalus* differs from *Bos* by having more expanded articular facets in the limb bones. Yet measurement data are scarce and bovid postcranial material from Java has mostly been identified as Bovidae indet.

The Madura Strait assemblage is rich in bovid remains and forms an interesting sample for a comparative study. For molars and limb bones, an extensive morphological and metric comparison has been carried out.

Tribe: Bovini Gray, 1821
Genus: *Bubalus* Smith, 1827
Bubalus palaeokerabau Dubois, 1908

Synonyms: *Bubalus buffelus*, *Buffelus palaeokerabau*

Available material (N=101). Horncore fragments: SBY301 (d), SBY304 (s/d), SBY348 (d), SBY558 (s/d), SBY369 (d), SBY564 (s/d), SBY5084 (d), SBY5085 (d), SBY5093 (s), SBY7045 (s/d), SBY7195 (s), SBY7198 (s/d). **Upper dentition, M^1**: SBY117A, SBY117E, SBY126A, SBY126D, SBY126F, SBY7143A, SBY7143B. **M^2:** SBY126C, SBY3402. **M^3:** SBY124D, SBY124G, SBY125A, SBY137A, SBY137C, SBY137E, SBY137F, SBY7145A, SBY7145E. **Lower dentition, M_1:** SBY135A, SBY135C, SBY135E. SBY7147A. **M_2:** SBY116B, SBY118, SBY123B, SBY123F, SBY124A, SBY124C, SBY124D, SBY124G, SBY125B, SBY125C, SBY129B. **M_3:** SBY122A, SBY122B, SBY122C, SBY122D, SBY7149A-B, SBY7151. **Humerus,** distal fragments: SBY2 (s), SBY7 (s/d), SBY221 (s/d), SBY468 (s/d), SBY577 (s/d), SBY680 (s/d), SBY7014 (d). **Radius,** proximal fragments: SBY17 (s), SBY28 (s). Distal fragments: SBY227 (s), SBY1201 (s). **Scaphoid:** SBY520 (s). **Lunatum:** SBY203 (s). **Pyramidal:** SBY7001 (d). **Hamatum:** SBY1633 (d). **Metacarpus,** proximal fragment: SBY19 (s/d). Shaft fragment: SBY22 (s). Distal fragments: SBY53 (d/s), SBY5090 (d). **Femur,** shaft fragment: SBY18 (s). **Tibia,** distal fragments: SBY15 (d), SBY16 (d), SBY45 (d), SBY7035 (d). **Os malleolus:** SBY3440 (d), SBY6009 (d), SBY6011 (d), SBY7185. **Astragalus:** SBY163 (s), SBY164 (s), SBY165 (d), SBY169 (d), SBY170 (d), SBY464 (d), SBY5094 (s), SBY5096 (s), SBY7156 (d). **Naviculo-cuboid:** SBY456 (d). **Metatarsus,** proximal fragments: SBY20 (s), SBY 51 (s/d). Distal fragments: SBY222 (s/d), SBY225 (d). **Phalanx 1**: SBY62, SBY6004. **Phalanx 2:** SBY190, SBY1571, SBY7158, SBY7175.

Description and identification: In the absence of complete crania, species identification has in the first place been based on horncore morphology. Horncores of *B. palaeokerabau* have a smooth outer surface and a characteristic subtriangular cross-section, with one flat face and two more rounded faces (Hooijer, 1958a). Even in a fragmented state, such horn cores can easily be recognized. A good specimen is SBY5084 **(Fig. 21)**. The fragment has a maximum diameter of 69 mm and derives from the central part of a dextral horn core. The flat side is the superior face of the horn core, with a sharp angle at its anterior edge.

Upper and lower molars have provisionally been assigned to *B. palaeokerabau* based on a metric and morphological analysis of all isolated bovid molars and a comparison with museum specimens **(Fig. 22 and 23,** further explanation on the figures). Note that the taxonomic conclusions are indicative only. Overlap between the large bovid species is significant, both in crown size and morphology. Together with Khurniawan (2019), our work forms a first attempt for a systematic analysis of isolated bovid molars from the Pleistocene of Java or surrounding submerged Sundaland.

For the identification of bovid long bones, a similar strategy was followed, using a metric analysis in combination with scarce morphological evidence and comparisons with published size ranges of extant and fossil species (**Fig. 24-26,** further explanation on the figures). Ordering of long bone fragments with intact articulations provides distinct size groups. The specimens of the largest size group, with pronounced laterally-expanded articular facets, have been assigned to *B. palaeokerabau*, which is confirmed by reference measurements of extant and fossil *Bubulus*.

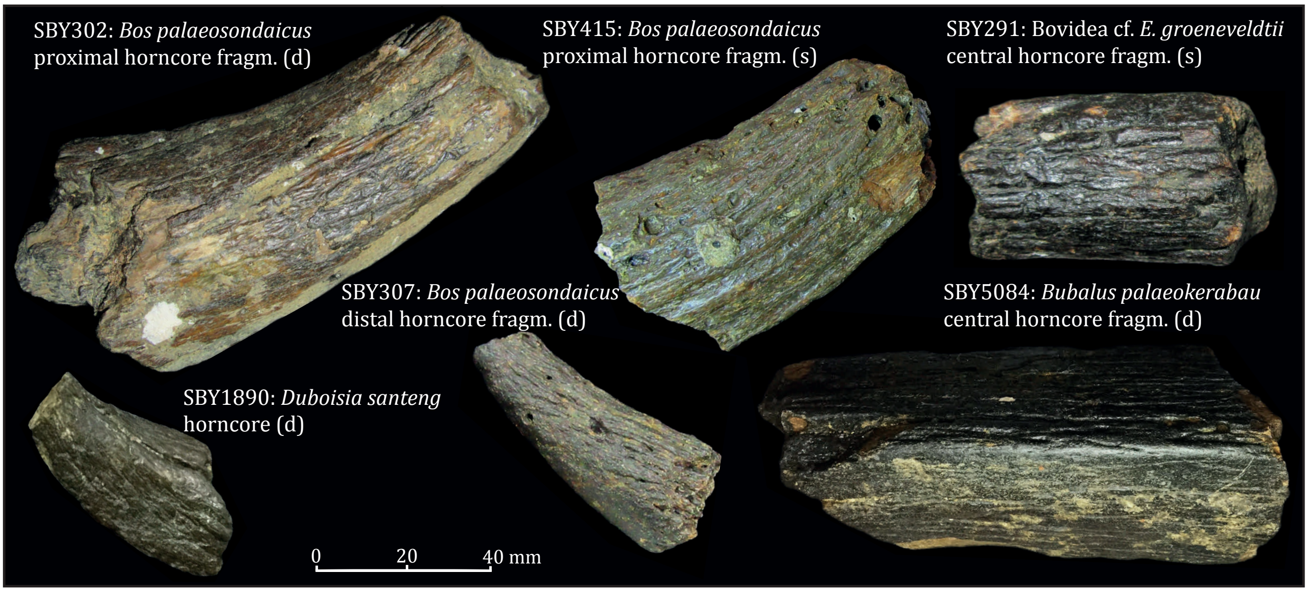


Fig. 21. Bovidae horn cores from the Madura Strait assemblage. Selected photographs. SBY302 in posterior view. SBY307, SBY415, and SBY5084 in anterior view. SBY1890 in lateral view. SBY291: view direction not determinable.

Small and massive bone elements, such as astragali and phalanges, have been found in relatively large numbers and are often intact. Hooijer (1958) noted that the size differences between *Bubalus* and *Bos* are most pronounced in the distal zones of the extremities, which makes these elements an interesting subject for size analyses. The astragali from the Madura Strait cluster in distinct size groups **(Fig. 27**, further explanation on the figure). Published size ranges for fossil or extant *Bubalus* are not available. The largest astragali from the Madura Strait roughly correspond in size with the largest astragali of Kedung Brubus (Weinand, 2005) and are provisionally assigned to *B. palaeokerabau*. The specimens articulate well with the largest tibiae, assigned to the same species.

For the first and second phalanges, similar size analyses have been carried out **(Fig. 28 and 29,** further explanation on the figures). Again, the largest specimens form a distinct size group, with robust shafts and proportionally wide articulations. Reference measurements in related extant species are not available, but the specimens significantly exceed the extant *Bos taurus* in size (Ocal et al., 2004). We tentatively assigned the specimens of this size group to *B. palaeokerabau.* First phalanx SBY6004 articulates well with the largest metacarpals and metatarsals of the assemblage, which were assigned to the same species.

Genus: *Bos* Linnaeus, 1758
***Bos (Bibos) palaeosondaicus* Dubois, 1908**

Synonyms: *Bison sivalensis*, *Bibos banteng*, *Bibos protocavifrons*

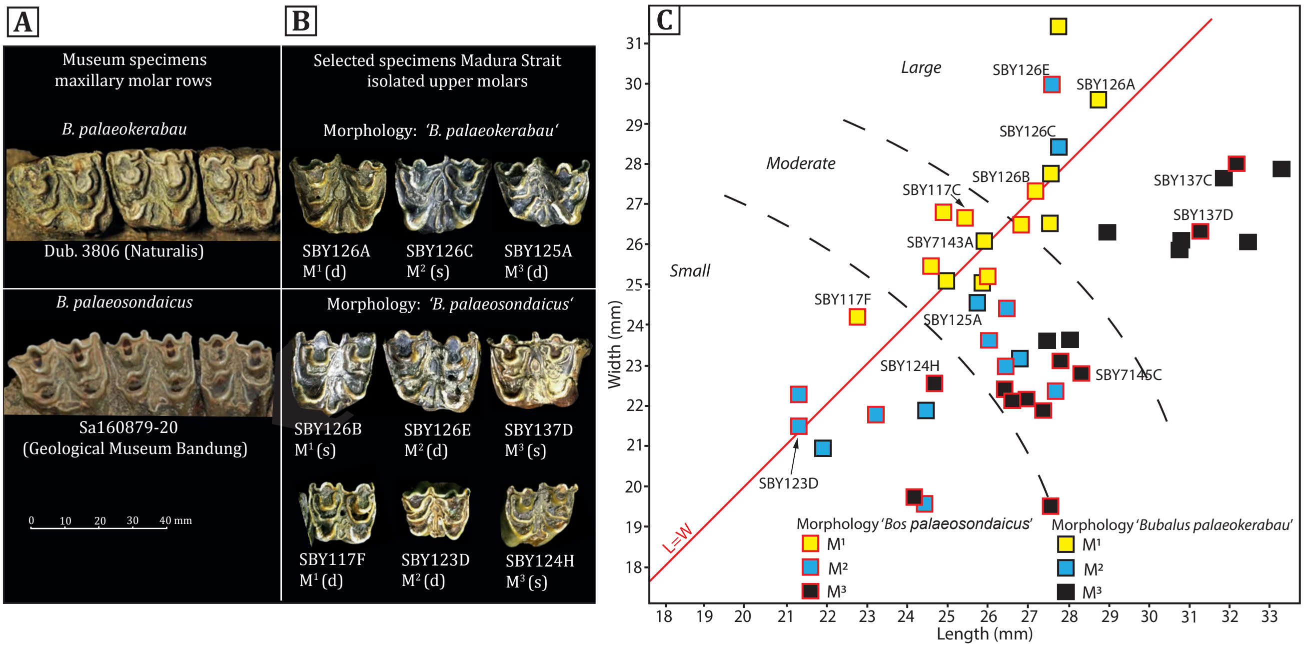
Available material (N=129). Horncore fragments: SBY302 (d), SBY307 (d), SBY308 (s/d), SBY310 (d), SBY311 (s), SBY312 (s/d), SBY313 (s/d), SBY415 (s), SBY7194 (s/d). **Upper dentition**, **M^1:** SBY116A, SBY116C, SBY117B, SBY117C, SBY117D, SBY117F, SBY126B. **M^2:** SBY121, SBY124B, SBY126E, SBY129A. **M^3:** SBY124A, SBY124C, SBY124E, SBY124F, SBY124H, SBY137B, SBY137D, SBY7145B, SBY7145C. **Lower dentition, M_1:** SBY120, SBY135B, SBY135D, SBY155, SBY7160. **M_2:** SBY115A, SBY115B, SBY115C, SBY115D, SBY123D, SBY123E, SBY124B, SBY7148B, SBY7148C. **M_3:** SBY119, SBY122E-G, SBY125C, SBY139, SBY157A, SBY157B, SBY157C, SBY157D. **Humerus,** distal fragments: SBY3 (s), SBY23 (d), SBY1272 (d). **Radius,** proximal fragments: SBY37 (d), SBY1205 (d), SBY7152 (s), SBY7159 (s). Shaft fragments: SBY34 (d), SBY68 (s/d). Distal fragments: SBY483 (d), SBY42 (s/d), SBY48 (s), SBY7024 (s), SBY7025 (s). **Ulna,** shaft fragment: SBY534 (s/d). **Scaphoid:** SBY208 (d), SBY210 (d). **Lunatum:** SBY205 (d), SBY206 (d), SBY207 (d), SBY212 (d), SBY211 (s), SBY215 (s), SBY7186 (d). **Capitato-trapezoid:** SBY1728 (d). **Hamatum:** SBY209 (d), SBY2159 (s). **Metacarpus,** proximal fragments: SBY21 (s), SBY24 (d), SBY53 (s). Distal fragments: SBY220 (s), SBY223 (s/d). **Femur,** proximal fragment: SBY5072 (d). Shaft fragment: SBY31 (s). Distal fragment: SBY686 (s/d). **Tibia,** distal fragments: SBY26 (d), SBY25 (s), SBY226 (s), SBY229 (d), SBY230 (d). **Os malleolus:** SBY6010 (d), SBY6012 (d). **Astragalus:** SBY166 (d), SBY167 (s), SBY171 (d), SBY172 (s), SBY5095 (d), SBY5097 (s), SBY7155 (s). **Calcaneum:** SBY27 (s), SBY1200 (d), SBY7021 (d), SBY7196 (s). **Naviculo-cuboid:** SBY218 (s), SBY224 (d). **Cuneiform:** SBY1461 (s), SBY1790 (d). **Metatarsal,** shaft fragment: SBY59 (d). Distal fragment: SBY6002 (s/d). **Phalanx 1**: SBY187, SBY188, SBY189, SBY191, SBY192, SBY194, SBY672, SBY7155. **Phalanx 2**: SBY195, SBY200, SBY202, SBY204, SBY1575, SBY6005, SBY7053, SBY7192. **Phalanx 3:** SBY7169.

Description and identification: Just as for the other bovid species, the identification of *B. palaeosondaicus* among the fragmented material from the Madura Strait has in the first place been based on horncores. SBY302 and SBY415 **(Fig. 21)** are large fragments of relatively thick horncores with a rugged outer surface. The fragments closely match the taxonomical descriptions by Hooijer (1958), by their oval cross-section, strong curvature, and rough longitudinal grooves. The latter are slightly twisted in a spirally pattern. The fragments have a maximum diameter of 67 and 58 mm respectively and show a strong distal tapering. The longitudinal grooves are twisted posteriorly, which indicates that SBY302 derives from a dextral and SBY415 from a sinistral horn core. SBY307 **(Fig. 21)** is the distal tip of a dextral horn core, with a similar oval cross-section and twisted longitudinal grooves. It has a faintly flattened surface on the inside of the curvature, which is also recognized in the distal-most zones of the horn cores of the available museum specimens.

Isolated molars have been assigned to *B. palaeosondaicus* based on an analysis of size ranges and morphology and our comparison of museum specimens **(Fig. 22 and 23,** further explanation on the figures). As noted earlier for the molars assigned to *B. palaeokerabau*, the taxonomic conclusions are indicative only.

Bovid long bones assigned to *B. palaeosondaicus* are large and robust, but lack the extreme lateral inflation of the articular facets that is characteristic for *B. palaeokerabau* **(Fig. 24-26)**. Based on an analysis of bovid material, most of which derives from Trinil and Kedung Brubus, Hooijer (1958) and Stremme (1911) found that *B. palaeosondaicus* limb bones slightly exceed those of the extant *Bos javanicus* in size. For the Madura Strait assemblage this could not be confirmed. The limb bones assigned to *B. palaeosondaicus* are similar in size to those from the extant *Bos javanicus*. Note that morphologically, the Pleistocene and extant species are identical (Hooijer, 1958a; Von Koenigswald, 1933). The taxonomic subdivision between the Pleistocene species *Bos palaeosondaicus* and the recent or Holocene species *B. javanicus* is based on palaeontological tradition rather than on morphological or metric distinction. We therefore prefer to use the species name *Bos palaeosondaicus* for the late Middle Pleistocene material from the Madura Strait.

Within the sample of Bovini astragali **(Fig. 27)** there is a distinct cluster of medium-sized specimens, which has tentatively been assigned to *B. palaeosondaicus.* The size group overlaps with the medium-sized bovid astragali from Kedung Brubus (Weinand, 2005), which probably also represents this species. Reference measurements of the extant *B. javanicus* are not available. Note that the size group falls apart into two sub-clusters, which may reflect sexual dimorphism within the species. Also within the sample of first and second phalanges **(Fig. 28 and 29)**, there is a distinct



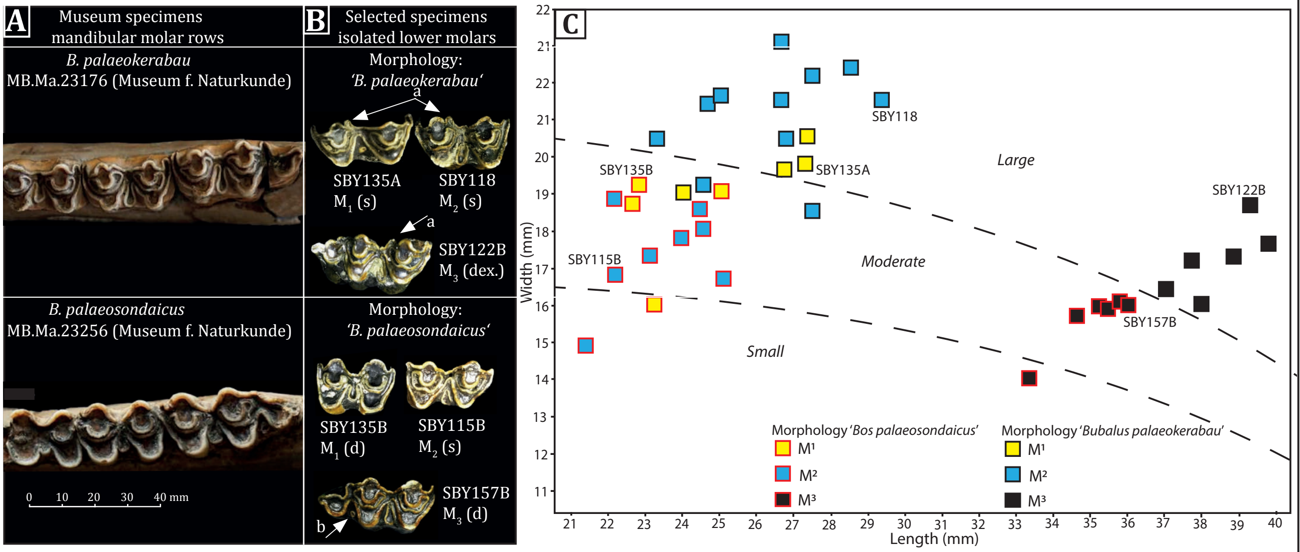
The bovid (Bovini) upper molars from the Madura Strait roughly plot in three size groups (large, moderate and small). Direct metric comparison with museum specimens is difficult, because upper molars with an undisputed taxonomy are as a rule concealed in intact maxillae. Measurements of concealed molars are taken higher up the crown and are dependent on wear stage. However, a rough metric inquiry of museum specimens indicates that the molars of size groups 'large' and 'moderate' are similar to the dentition of *B. palaeokerabau* and *B. palaeosondaicus*. *B. palaeokerabau* molars seem to reach slightly larger sizes, but size ranges overlap. Intra-species size variation may relate to sexual dimorphism. Reliable distinction between the two species based on size is therefore not possible.

With respect to crown morphology, Stremme (1911) and Hooijer (1958) found no reliable morphological differences between *B. palaeokerabau* and *B. palaeosondaicus,* or on a more basic level between the genera *Bos* and *Bubalus.* Bacon et al. (2011), working on fossil assemblages from Thailand, noted more complex folds of the infundibula and more voluminous cones and conids in *Bubalus* than in *Bos*. We carefully checked these traits in the available museum collections from Java. With respect to the infundibula, the morphological differences are not convincing. The anterior infundibulum can be U-shaped or Y-shaped, whereas the posterior infundibulum has a twisted Y- or X-shape. The occlusal morphology of the infundibula varies with wear, which makes it a difficult basis for species identification. However, with respect to cone size and morphology there indeed appears to be a difference between the two species. In *B. palaeosondaicus*, the protocone and hypocone tend to form rounded, wide ribs, whereas in *B. palaeokerabau* the ribs are often thinner. Sukiato (2019) found that these thinner ribs are visible on the occlusal face as narrow, U-shaped lobes, especially in the protocone (see **A:** reference specimens). Ordering the Madura Strait molars based on protocone morphology, we noted another morphological difference: the crowns with the more voluminous protocones, presumably representing *B. palaeosondaicus*, have prominent and often bilobed entostyles, which fill up most of the area between the protocone and hypocone ribs. The crowns with the narrow protocones, presumably representing *B. palaeokerabau*, generally have a thinner and unbilobed entostyle, leaving a larger open area between the protocone and hypocone, which is mostly filled with cement (see **B**: selected Madura Strait specimens). We used these morphological traits to subdivide the crowns from the Madura Strait in two groups. The size plot **(C)** shows that the molars of both morphological groups are distributed over the size ranges 'large' and 'moderate', with a slight overrepresentation of the molars assigned to *B. palaeokerabau* in the size group 'large'.

The molars of the size group 'small' are slightly below the size ranges of the available museum specimens of *B. palaeokerabau* and *B. palaeosondaicus*. Morphologically, they are similar to the crowns that we assigned to *B. palaeosondaicus,* i.e. with rounded protocone and hypocone ribs. Possibly the specimens derive from small females of this species. It is also possible that there are *Epileptobos groeneveldtii* molars among the size group 'small'. As was noted by Hooijer (1958), the molars of this rare species are relatively small and morphologically similar to *B. palaeosondaicus*.

Fig. 22. Bovidae (Bovini) upper molars from the Madura Strait assemblage. **A:** Reference maxillary molar rows in occlusal view. **B:** Selected specimens from the Madura Strait in occlusal view. **C:** Metric and morphological analysis. Crown measurements were taken 10 mm above the crown base. Numbered specimens are pictured in B.

size group of medium-sized Bovini. Reference measurements of relevant extant or fossil Bovini are not available. The specimens are similar in size to the phalanges of the extant *Bos taurus* (Ocal et al., 2004). We tentatively assigned the phalanges to *B. palaeosondaicus*.



The bovid (Bovini) lower molars from the Madura Strait roughly plot in 3 size groups (large, moderate and small). As noted for bovid upper molars **(Fig. 22)**, direct metric comparison with reference material is difficult, because all taxonomically identified museum specimens are intact mandibular molar rows. A metric inquiry of museum specimens indicates that *B. palaeokerabau* and *B. palaeosondaicus* crowns are similar to the size groups large and moderate of the Madura Strait.

Looking at the available reference mandibles of these two species, we found no significant difference in volume or roundness of the conids that might serve as a similar taxonomical marker, such as used for bovid upper molars. Suraprasit et al. (2016), working on a Middle Pleistocene assemblage from Thailand, noted that *Bubalus* lower molars generally have a distinct metastylid, whereas in *Bos* this stylid is absent or only developed near the apex of the crown. Moreover, the authors noted a posterior ectostylid in the M_3 of the genus *Bos*, while this stylid is generally absent in *Bubalus*. The latter was noted earlier by Colbert and Hooijer (1953), who found this trait not sufficiently reliable to serve as a taxonomic marker. Upon comparison with reference mandibles, we conclude that the observations by Suraprasit et al. (2016) are mostly valid for the Middle Pleistocene species of Java and may be used as indicative taxonomic markers to distinguish between *B. palaeokerabau* and *B. palaeosondaicus*, at least within a larger sample of isolated molars (see **A**: reference specimens and **B**: selected specimens from the Madura Strait. a = metastylid in *B. palaeokerabau*. b = posterior ectostylid in the M_3 of *B. palaeosondaicus*.

We subdivided the lower molars from the Madura Strait using these tentative morphological criteria, assigning the crowns with a metastylid to *B. palaeokerabau* and the crowns lacking a clear metastylid to *B. palaeosondaicus*. As expected, none of the M_3's with a metastylid has a posterior ectostylid. In a few M_3's, both the metastylid and the posterior ectostylid appeared to be absent or not observable. These specimens have provisionally been assigned to *B. palaeosondaicus*, thus giving priority to the absence of the metastylid as taxonomic marker. Within the size plot **(C),** the size groups 'large'and 'moderate' largely overlap with this tentative morphological distinction: most crowns with a *B. palaeokerabau* morphology fall in the size group 'large'; most crowns with a *B. palaeosondaicus* morphology fall in the size group 'moderate'.

Fig. 23. Bovidae (Bovini) lower molars from the Madura Strait assemblage. **A:** Reference mandibular molar rows in occlusal view. **B:** Selected specimens from the Madura Strait in occlusal view. **C:** Metric and morphological analysis. Crown measurements were taken 10 mm above the crown base. Numbered specimens are pictured in B.

Genus: *Epileptobos* Hooijer, 1956

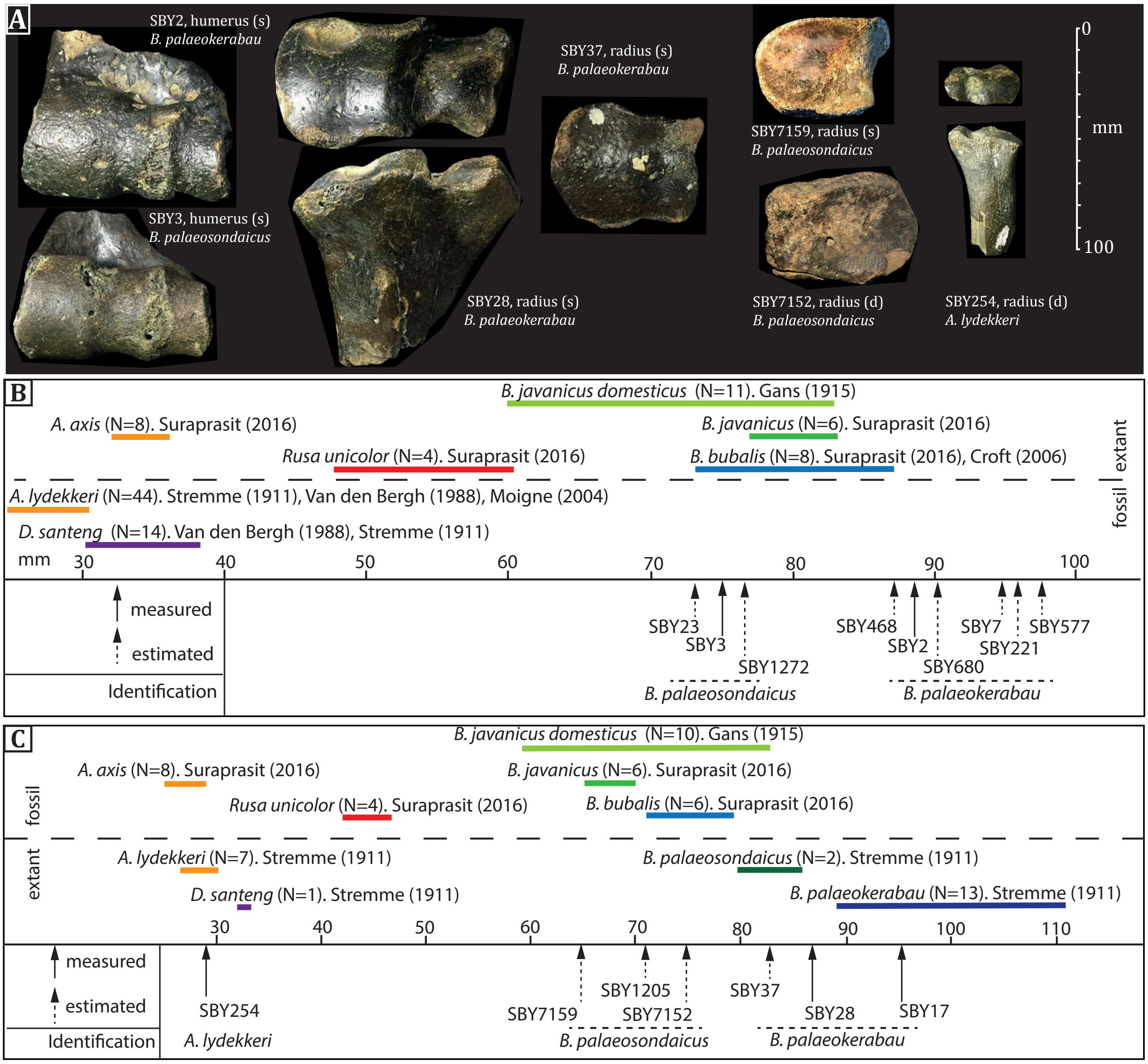
Epileptobos groeneveldtii (Dubois, 1908)

Synonyms: *Leptobos groeneveldtii*, *Leptobos cosijni*

Available material (N=4). Horncore fragments: SBY291 (s/d), SBY305 (s/d), SBY306 (s/d), SBY7038 (s/d).

Description and identification: Among the horncore fragments from the Madura Strait, four specimens have a slightly deviant morphology. Their ribbed surface is similar to *B. palaeosondaicus,* but the fragments lack the robust, oval-shaped cross-section, the strong distal-tapering, and the strong curvature. SBY291 **(Fig. 21)** is a fragment of a ribbed horncore with a circular cross-section and a diameter of ~50 mm at both sides. Its curvature is insignificant, and this absence of curvature is accentuated by the straight, untwisted longitudinal grooves. SBY7038 is a larger fragment, with a preserved length of 17 cm. The fragment has break surfaces at both sides, with a diameter of 44 mm at the proximal side and 37 mm at the distal site.

The fragments resemble the descriptions of *E. groeneveldtii* horn cores by Hooijer (1958) and fit well with the relatively long and only gently curved horn cores of the two crania of this species that are stored at Naturalis Biodiversity Center (collection numbers Dub. 2765 and 2766). SBY291 is probably the central portion of a horncore, SBY7038 represents a more distal zone, with the tip broken off. In the absence of curvature, tapering or twisted grooves, it is

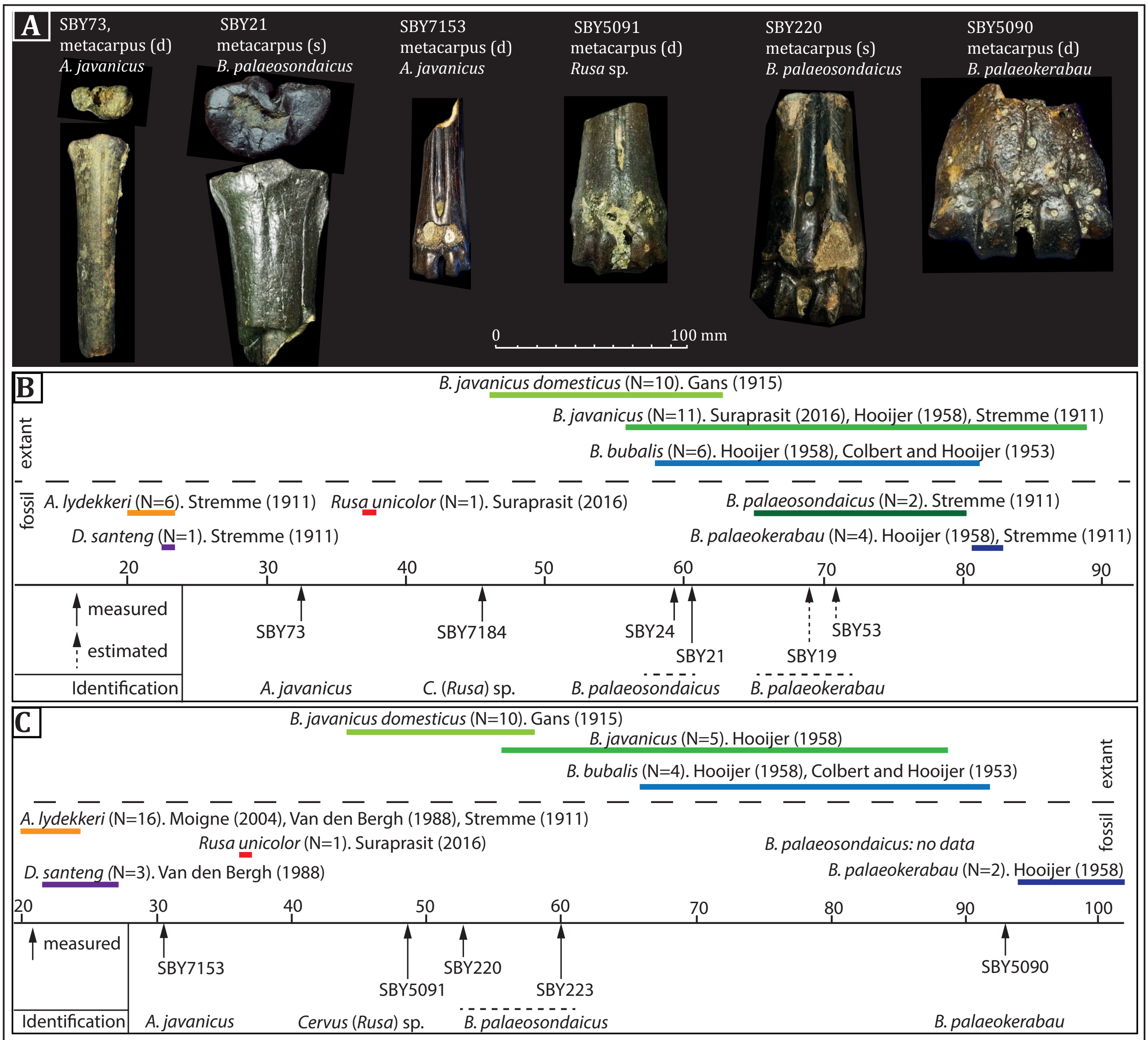


The Madura Strait assemblage contains 9 distal humeri of ruminants, characterized by a rounded and downward-projecting median trochlea, bordered by a sharp lateral condyle and a relatively small capitulum **(A)**. The specimens cluster in two size ranges **(B)**. Unfortunately, size ranges of fossil specimens are not available. We tentatively assigned the smaller specimens to *B. palaeosondaicus.* The elements are similar in size to the extant and Late Pleistocene *B. javanicus*. The larger specimens are assigned to *B. palaeokerabau*, based on the general notion that this species has wider articulations in the limb bones.

The assemblage contains 7 radius heads with a ruminant morphology of a mediolaterally expanded, flat articular surface, separated in two by the fovea capitis radii, with a relatively wide medial articular surface, which articulates with the trochlea of the humerus (5 specimens pictured in **A**). Most plot in the size range of extant and fossil Bovini **(C)**. Stremme (1911) noted that *B. palaeokerabau* has pronounced notches along the margin of the radius head, whereas in *B. palaeosondaicus* the radius head has a smooth outline. Based on this morphological trait, the largest 3 radius heads are assigned to *B. palaeokerabau*. Radius head SBY28 articulates well with distal humerus SBY2, supporting its attribution to *B. palaeokerabau.* Likewise, radius head SBY7152, attributed to *B. palaeosondaicus*, articulates well with humerus SBY3. Note that the size of the radii attributed to *B. palaeosondaicus* plot slightly below the published size ranges of this species, which are mainly based on finds from Trinil. SBY254 is a small radius head, plotting in the size range of *A. lydekkerii* and close to the size range of *D. santeng*. The specimen is recognized as cervid rather than bovid by its gentle medial tuberosity and the relatively greater elevation of the posterior margin of the articular surface (Schmidt, 1972).

Fig. 24. Ruminant humeri and radii from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs in frontal view (humeri) and proximal view (radii). Radii SBY2 and SBY254 also in anterior view. **B:** Metric analysis humeri: width of distal articulation (BT) and published size ranges (mm). C: Metric analysis radii: width of proximal articulation (Bfp) and published size ranges (mm). Measurements and codes based on Von den Driesch (1976).

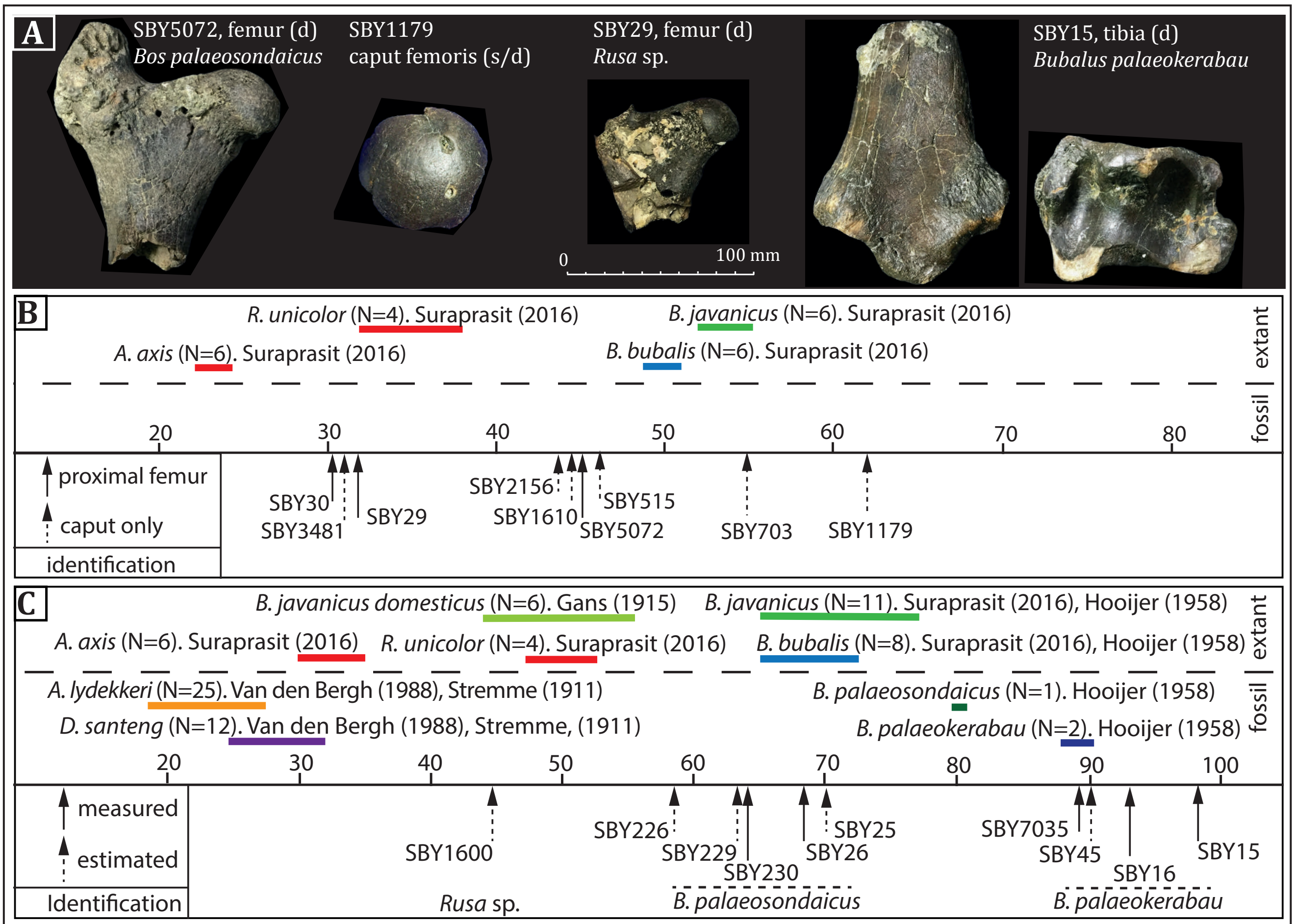
impossible to decide whether the specimens derive from sinistral or dextral horncores. The other two specimens, SBY305 and SBY306, are distal tips of slender horncores with a round cross-section.



In absence of *Equus* in the Pleistocene of Java, all fused metacarpals derive from ruminants. Among the proximal fragments **(A)**, SBY73 stands out by its small size. It is recognized as a cervid rather than the small bovid *D. santeng* by the course of the median ridge at the articular surface, which is interrupted by the central cavity (Van den Bergh, 1988). Its size is intermediate to reference specimens of *A. lydekkeri* and *Rusa* sp. **(B)**. We therefore assigned the specimen to the medium-sized cervid *A. javanicus*. The other proximal fragments fall in the size range of Bovini. All have a well-preserved articular surface of two facets separated by a ridge. The medial facet, articulating with the unciform, continues further anteriorly than the lateral facet. Stremme (1911) noted that in *Bos*, this medial facet is significantly larger, whereas in *Bubalus* both facets are of similar size. Based on this morphological marker, we assigned SBY21 and SBY24 to *B. palaeosondaicus.* SBY19 and SBY53 have a wider proximal articulation. Their facets are damaged, but appear to be of similar size. The specimens have provisionally been assigned to *B. palaeokerabau*. All proximal fragments plot slightly below the published size ranges of the fossil species, which are primarily based on specimens from Trinil.

Among the distal fragments, only SBY7153 is small-sized. It is recognized as a cervid by the median groove along the anterior face of the shaft, which ends ca. 2 cm proximal of the distal epiphysis, whereas in bovids it continues to the epiphysis (Heinz, 1971). The specimen plots above the published size range of *A. lydekkeri* and is assigned to *A. javanicus* **(C)**. Remarkably, also SBY5091 has this cervid morphology of the median groove. The specimen, which comes close to the size range of Bovini, must be assigned to *Rusa* sp. and is illustrative of this species' large size. SBY220 and SBY223 have a median groove continuing to the distal epiphysis. They are assigned to the Middle Pleistocene *B. palaeosondaicus*, noting that again the specimens appear to be relatively small. Reference sizes from the Pleistocene of Java are not available, but the Madura Strait specimens plot in the lower size range of the extant *B. javanicus.* SBY5090 is laterally expanded, characteristic of *Bubalus*, and similar-sized as two reference specimens of *B. palaeokerabau* from Trinil.

Fig. 25. Ruminant metacarpalia from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs in anterior view. Proximal fragments also in proximal view. **B:** Metric analysis proximal fragments: width of proximal epiphysis (Bp) and published size ranges (mm). **C:** Metric analysis distal fragments: width of distal articulation (Bd) and published size ranges (mm). Measurements and codes based on Von den Driesch (1976).



Three proximal femora are recognized as ruminants by the elongate trochanter major, which extends (proximally) significantly beyond the caput. Eight loose capita femoris with a well-developed, round fovea capitis femora in the centre of the caput probably also derive from ruminant species (Schmidt, 1971), but a relation with suids or hippos cannot be excluded. The specimens have been ordered by diameter of the caput **(B)** and form three size groups. Size ranges of fossil species are not available. A comparison with scarce measurement data of extant bovid and cervid taxa provides a basic insight into the taxonomic background of the Madura Strait specimens. A taxonomic identification has only be given for the three intact proximal femora. SBY29 and 30 probably derive from *Rusa* sp., noting that they may also represent the medium-sized cervid *Axis javanicus.* SBY5072 is assigned to *B. palaeosondaicus.* Most of the loose capita femoris have been listed as Bovidae indet. in the find list.

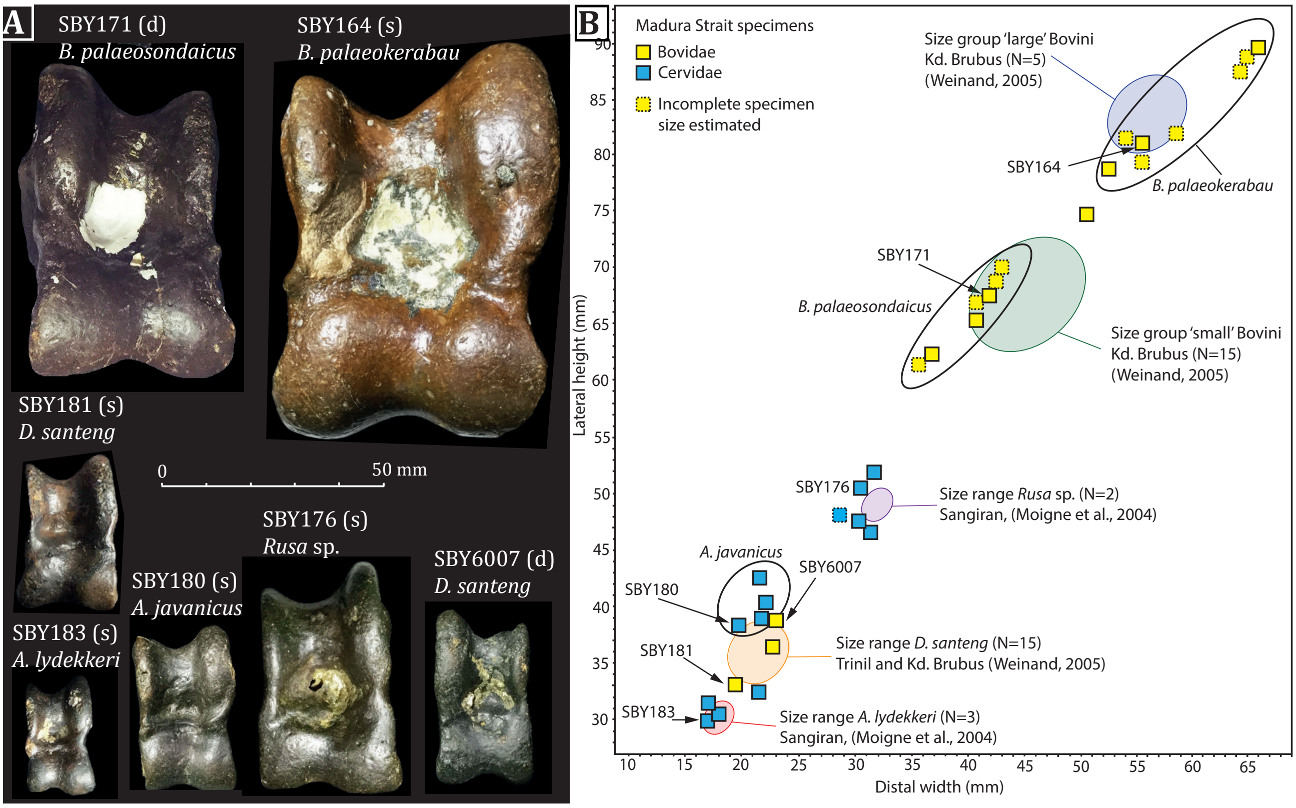
Ten distal epiphyses of tibiae have a characteristic ruminant morphology with two parallel furrows, which form the contact facet with the proximal condyles of the astragalus. The distal widths of the specimens form 3 distinct size groups **(C)**. In comparison with published size ranges of fossil and extant species, the size groups have been assigned to *Rusa* sp., *B. palaeosondaicus* and *B. palaeokerabau*.

Fig. 26. Ruminant femora and tibiae from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs. Femora SBY29 and SBY5072 in frontal view. Caput femoris SBY1179 in articular view. Tibia SBY15 in frontal and distal view. **B:** Metric analysis femora: diameter (depth) caput femoris (DC) and published size ranges (mm). **C:** Metric analysis tibiae: width of distal epiphysis (Bd) and published size ranges. Measurements and codes based on Von den Driesch (1976).

Bovini indet.

Available material (N=88). Palladium, fragment: SBY7002. **Maxilla,** fragment with DP^4: SBY7160 (d). **Mandibula,** fragment with dP$_4$-M$_1$: SBY7149 (d), fragment with dP$_4$: 7150 (s), fragment with P$_3$ –P$_4$: SBY133 (d), fragment with M$_2$ and M$_3$: SBY5067 (s). **Deciduous dentition, dP^3:** SBY120. **dP^4:** SBY123A and C. **dP$_3$:** SBY5059. **dP$_4$:** SBY5057. **Incisor:** SBY162. **Premolars, P^2:** SBY153A, SBY153B, SBY5078. **P^3:** SBY144A-B, SBY3403A-C. **P^4:** SBY128A-F, SBY144C. **P$_2$:** SBY158A. **P$_3$:** SBY138A-B, SBY158B-C, SBY5061, SBY7167. **P$_4$:** SBY3401. **Cervical vertebrae:** SBY498, SBY451, SBY457, SBY461, SBY470, SBY1204, SBY1208, SBY7012, SBY7031, SBY7032, SBY7102. **Thoracic vertebrae:** SBY451, SBY454, SBY458, SBY460, SBY467, SBY479, SBY7034, SBY7015, SBY7033, SBY7036, SBY7101, SBY7111. **Lumbar vertebrae:** SBY459, SBY466, SBY472, SBY473, SBY481, SBY495, SBY508, SBY522, SBY528, SBY529, SBY534, SBY7027. **Caudal vertebra:** SBY216. **Scapula,** distal fragments: SBY9 (d)**,** SBY56 (d), SBY1532 (d), SBY7057 (s), SBY7179 (s). **Humerus,** distal fragments: SBY7011A-B (s/d). **Radius:** shaft fragment: SBY7006 (s). **Femur,** caput (s/d) small: SBY703, SBY1610, SBY2156, SBY5125, caput (s/d) large: SBY1179 (s/d), SBY7044 (s/d), SBY7110. **Tibia,** proximal fragment: SBY7005 (s). Distal fragment (juvenile): SBY7013 (d).

Description and identification: The Madura Strait assemblage contains several deciduous premolars, one incisor, and a large number of (fragmented) premolars of Bovini. Published accounts on the metrics or morphology of this mate-



The Madura Strait assemblage contains 31 (mostly) complete ruminant astragali. Cervid and bovid astragali can be separated by the morphology of the distal condyles (Heintz, 1971). In cervids, the lateral condyle is larger than the medial condyle and the median valley separating the two condyles is slightly off-centre, shifted medially. In bovids both condyles are almost equal in size, with a smooth median valley in the centre. This trait is important to separate *D. santeng* from similarly-sized cervids.

The astragali fall apart in several well-marked size groups **(B)**. The smaller size groups can be linked with published size ranges of *A. lydekkeri*, *D. santeng* and *Rusa* sp. Four specimens with a cervid morphology plot slightly above the size range of *D. santeng.* We assign these to *A. javanicus,* as we know from the molar analysis that this cervid species must have been intermediate in size between *A. lydekkeri* and *Rusa* sp.

The larger bovid astragali from the Madura Strait roughly plot in two size ranges. Previous researchers did not differentiate such large astragali into separate species. Weinand (2005) measured large bovid astragali from Trinil and Kedung Brubus available in Naturalis Biodiversity Center. For the specimens from Kedung Brubus, he found two size ranges, which compare well with the two size ranges from the Madura Strait. Among the specimens from Trinil he found a dominance of larger astragali, comparable to the largest specimens from Kedung Brubus.

Referring to the repeatedly found pattern of more robust limb bones in *Bubalus* compared to *Bos*, both in fossil and in extant species, we provisionally separated the bovid astragali in *B. palaeosondaicus* and *B. palaeokerabau* based on size groups. The size differences within these groups may reflect sexual dimorphism.

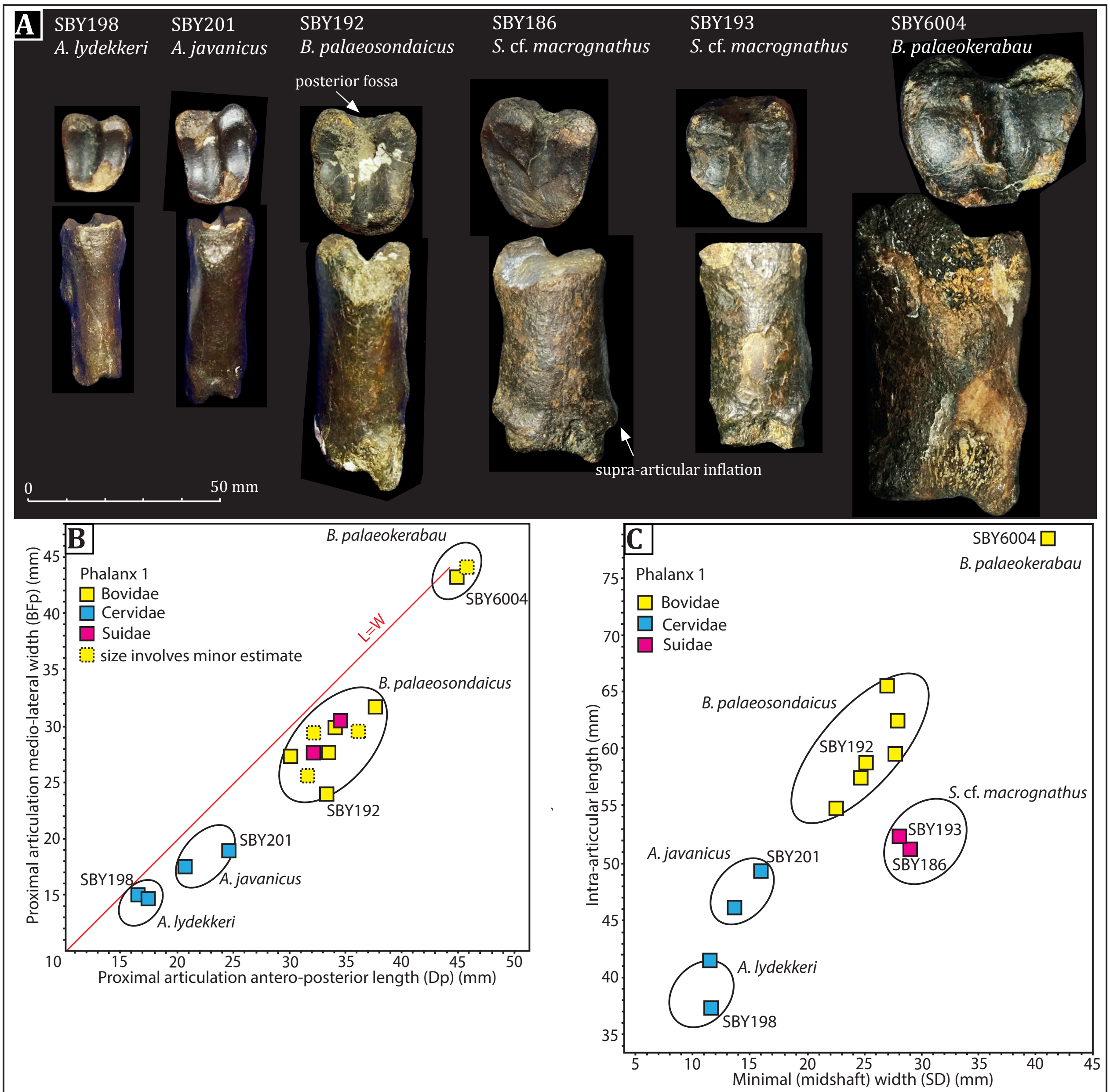
Fig. 27. Ruminant astragali from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs in anterior view. **B:** Metric analysis: bivariate plot of distal width DW) and lateral height (LH) and published size ranges. Measurements and codes based on Von den Driesch (1976).

rial are scarce. Colbert and Hooijer (1953) noted a reduced size of the P_2 in *Bos* compared to *Bubalus.* However, there is no intact bovid P_2 in the collection. The sample size of intact specimens is not sufficient to carry out a meaningful metric or morphological comparison of premolars. Bovid scapulae and vertebrae have been left out of the comparative analysis of the larger bovid postcranial material. All these elements have been referred to as Bovini indet.

Tribe: Boselaphini Knottnerus-Meyer, 1907
Genus: *Duboisia* Stremme, 1911
Duboisia santeng (Dubois, 1891)

Synonyms: *Anoa santeng*, *Tetracerus kroesenii*, *Duboisia kroesenii*, *Antilope mojokertensis*

Available material (N=7). Horncore: SBY1890 (d). **Mandibula,** fragment with M_1, M_2 and M_3: SBY105 (d). **Lower dentition:** M_2: SBY101 (d). **Astragalus:** SBY181 (s), SBY5098 (d), SBY6007 (d). **Phalanx 2**: SBY7041.



Ruminant first phalanges are characterized by the median groove at the proximal articular surface, a feature which they share with suids. In cervids, the posterior fossa only affects the outlines of the articular face, but in bovids it continues proximally into the articular surface, where it forms a notch between the two sesamoid facets (Heintz, 1971). See for example in **(A)** the well-developed posterior fossa in SBY192 and SBY6004. Based on this morphological trait, all smaller specimens of the assemblage are cervid rather than bovid, which implies that *D. santeng* is probably not represented among the first phalanges.

SBY186 and SBY193 have a different outline of the proximal surface, which is slightly asymmetrical and pointed anteriorly. Their deviant morphology among the sample of first phalanges is more pronounced in the shaft, which is relatively wide and has an inflation directly above the distal articulation. This is a characteristic trait of suids (Schmidt, 1974). The only large suid known from the Pleistocene of Java is *Sus macrognathus*. The specimens are tentatively referred to as *Sus* cf. *macrognathus.*

Metrically, the phalanges plot in distinct size ranges. Published size ranges of relevant fossil and extant species are not available. The size groups have been assigned to species based on direct comparison with museum specimens and articulation with metapodials. With respect to the size of the proximal articular face **(B)**, the 2 suid phalanges fall in the size range of *B. palaeosondaicus*. However, looking at the metrics of the shaft **(C)**, they form a distinct group, with a shorter length and a relatively great width.

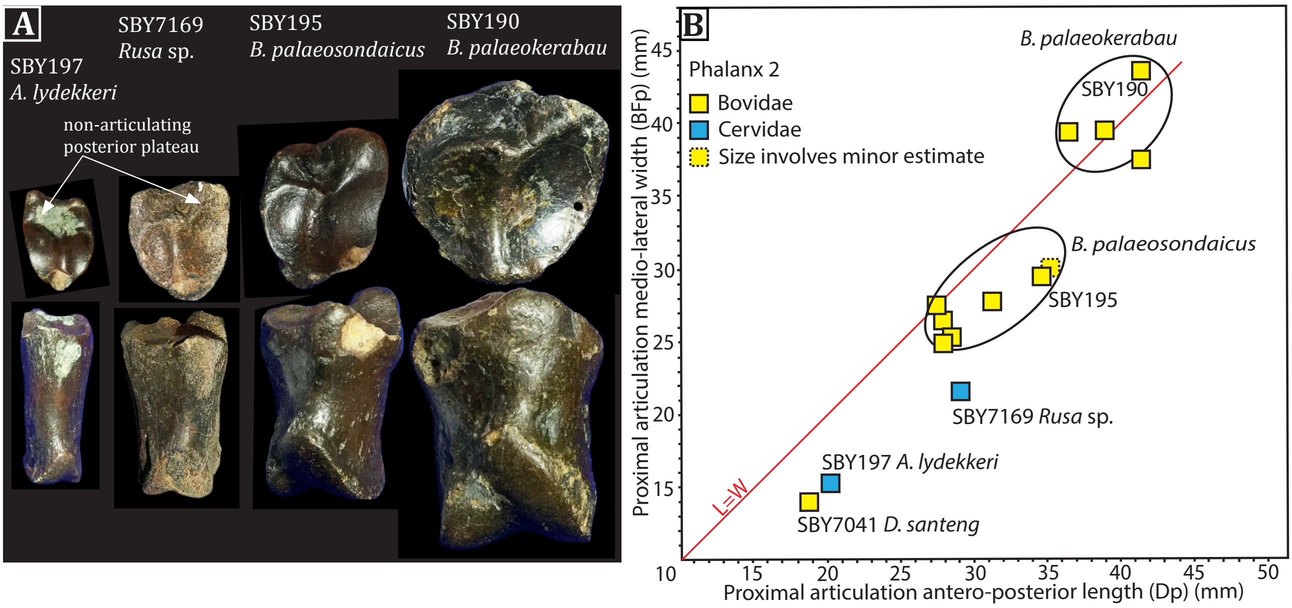
Fig. 28. Ruminant and suid first phalanges from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs in proximal and anterior view. **B:** Metric analysis; bivariate plot of length (Dp) and width (BFp) of the proximal articular face. **C:** Metric analysis; bivariate plot of shaft width (SD) and length. No distinction has been made between phalanges from the forelimb and hindlimb. Measurements and codes based on Von den Driesch (1976) except for intra-articular shaft length: callipers placed in median groove.

Description and identification: SBY1890 **(Fig. 21)** is an almost complete dextral horncore, only missing the distal tip. It is slightly antero-posteriorly compressed, with a trapezium-shaped cross-section. Its anterior face is flattened, whereas its wider posterior face is rounded. Also the lateral face is flattened, forming a keel at the transition to the anterior face. The horncore has a maximum (proximal) diameter of 30 mm and tapers over a short distance. The horncore is strongly curved upward and forward. Total preserved length is 45 mm. The horncore compares well with several intact skulls in the Geological Museum Bandung and Naturalis Biodiversity Center (collection nrs. Dub. 2037-2039.) The base of the specimen from the Madura Strait must have broken off close to the skull. Total missing length of the horn core tip is 15 to 20 mm, which gives an estimated complete length of the horn core of around 65 mm.

SBY105 **(Fig. 30A)** is a fragment of a dextral mandibular ramus. The lower margin of the ramus is damaged, but the molar row is intact, preserving the M_1, M_2 and M_3. Below the M_2, the mandible has a height of 29.0 mm and a thickness of 14.2 mm. The molars are slender and relatively high-crowned. The enamel is smooth, white and shiny and lacks a cement cover. In buccal view, the protoconids and hypoconids form prominent, straight ribs.

The M_2 has a low basal pillar (ectostylid). The molars are slightly worn and have an occlusal morphology with merged conids and two isolated, U-shaped infundibula. SBY101 **(Fig. 30A)** is an isolated, unworn lower molar with a slender crown morphology lacking a cingulum or basal thickening. It has shiny white enamel and straight ribs, highly similar to the molars of mandible fragment SBY105 and a size comparable to the M_2 of this specimen.

Although the crown sizes are similar to cervids, the crown morphology is indicative of a bovid. Note in this respect the absence of basal thickening, the straight protoconid and hypoconid ribs, the smooth and shiny enamel, and the isolated infundibula. See **Fig. 19** for a direct comparison with cervid lower molars. The only small-sized Pleistocene bovid species of Java are *Duboisia santeng* and *Capricornis sumatrensis*. Metrically, SBY105 is below the size range of *C. sumatrensis,* but it compares well with several mandibles of *D. santeng* stored at the Trinil Museum, the Geological Museum Bandung, and Naturalis Biodiversity Center (collection nrs. Dub. 2053 and 2068d), with respect to mandibu-



Ruminant (and suid) second phalanges are characterized by a median ridge at the proximal articular surface and a groove at the distal articulation. Heintz (1971) noted two morphological markers at the proximal articulation surface that may be used for differentiation between relevant genera. 1) The articulation consists of two facets, of which the lateral facet is slightly longer (anteroposteriorly). In bovids, this size difference between the two facets is significant, whereas in cervids there is a modest size difference. In the Madura Strait assemblage, this morphological difference is not always easy to recognize. Based on its similar-sized facets, SBY7169 is regarded as a cervid, whereas the larger phalanges SBY195 and SBY190 are clearly bovid. 2) Cervids have a non-articulating plateau along the posterior margin of the proximal face, whereas in bovids the corresponding zone is an irregularly sloping transitional surface towards the posterior face. This plateau is well-developed in SBY197 and SBY7169, identifying the specimens as cervids. Metrically, the second phalanges fall apart in distinct size groups **(B)**. The two cervid phalanges have been assigned to *A. lydekkeri* and *Rusa* sp. based on size comparison and articulation with available metapodials, which for example indicates that SBY7169 is too large for *A. javanicus*. Among the bovid specimens, *B. palaeokerabau* stands out by its larger size and considerable lateral expansion. Size differences within the bovid size groups may represent sexual dimorphism as well as differences between forelimb and hindlimb.

Fig. 29. Ruminant second phalanges from the Madura Strait assemblage. Morphological and metric analysis. **A:** Selected photographs in proximal and anterior view. **B:** Metric analysis; bivariate plot of length (Dp) and width (BFp) proximal articular face. Measurements and codes based on Von den Driesch (1976).

lar size, molar morphology, and molar sizes. The smooth and shiny enamel is a characteristic trait of the species, a feature which it shares with other Boselaphini (Moigne et al., 2016). The molar sizes plot within the published size ranges of *D. santeng*, which are mostly based on specimens from Trinil **(Fig. 30B)**.

The unworn M_2 SBY101 has a crown height of 25.2 mm and a H/W-index of 2.80. There is only one record of an unworn lower molar of *D. santeng*, found in Trinil and stored in Naturalis Biodiversity Center (numbered Dub. 2509A). Hooijer (1958) described it as an M_1, but we note that it may also be an M_2. With a crown width of 10 mm and a crown height of 26.5 mm, it has a H/W-index of 2.65, similar to the specimen from the Madura Strait.

We carefully examined all small-sized ruminant postcranial material for the presence of *D. santeng* remains, using the morphological criteria provided by Van den Bergh (1988) and Heintz (1970). The only postcranial elements that could be assigned to this species are three astragali: SBY181, SBY5098, SBY6007 **(Fig. 27A)**. They are distinguished from cervid astragali by their similar-sized distal condyles, separated by a smooth median valley. The attribution of the three astragali to *D. santeng* is supported by their sizes, plotting in the size range of this species as provided by Weinand (2005) **(Fig. 27B)**. The astragalus sizes are intermediate between *A. lydekkeri* and *A. javanicus*, the two small cervids of the Madura Strait assemblage.

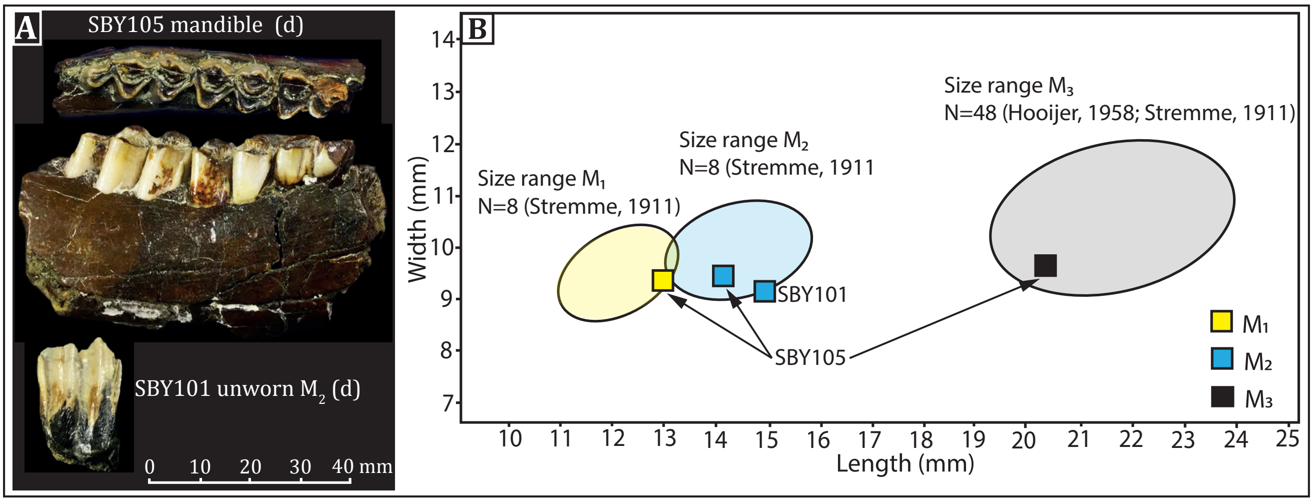


Fig. 30. *Duboisia santeng* lower molars from the Madura Strait assemblage. **A:** SBY105 in occlusal view and buccal view and SBY101 in lingual view. **B:** Bivariate plot of crown lengths and widths with published size ranges.

4. Discussion

4.1 The Madura Strait assemblage as a reference for regional palaeontological studies

4.1.1 First records and rare specimens

The Madura Strait assemblage yielded several vertebrate species that were thus far unknown from the Middle Pleistocene fossil record of Java or the Sundaland region. Moreover, it contains rare specimens, most of which were thus far not available in Indonesian museum collections.

The shark *Carcharhinus* cf. *leucas* was previously unknown from the Pleistocene of the Sundaland region. Recently, several teeth from the museum collection of Naturalis Biodiversity Center, excavated in Sangiran in the 1930s, were ascribed to this species (Kocsis, 2024). Another shark, *Galeocerdo cuvier*, was only known from rare teeth in Late Pliocene marine strata near Sangiran (Yudha et al., 2018). Interesting is also the occurrence of *Hemipristis serra,* an extinct species known from various Late Oligocene to Pleistocene sites worldwide (Cappetta, 1987). We could find no fossil records of this species from the Sundaland region, except for several teeth pictured by Yudha et al. (2018) and assigned to *Hemipristis* sp., which possibly represent this same extinct species. Relevant Southeast Asian records come from Taiwan (Lin et al., 2022) and Sulawesi (Hooijer, 1958b, 1954), both probably dating from the Early Pleistocene. The late Middle Pleistocene *H. serra* teeth from the Madura Strait may very well be the youngest recorded occurrence worldwide of this extinct species.

Two stingrays, *Rhinoptera javanica* and *Myliobatis* sp., were previously unknown from the Pleistocene of Sundaland, although the former was recently also reported in the museum collection of Naturalis (Kocsis, 2024), again deriving from a 1930s excavation in Sangiran. Three spine fragments of the giant stingray *U. polylepis* are very rare specimens. There are two similar specimens from the Pleistocene of Java, both excavated in Trinil in the 1890s and today housed at Naturalis Biodiversity Center (Joordens et al., 2009).

Other highly rare Pleistocene specimens are varanid and snake vertebrae. There are several specimens from Trinil and Kedung Brubus (Hooijer, 1972; Janensch, 1911a; Dubois, 1908), all of which are stored in Naturalis Biodiversity Center or the Museum für Naturkunde Berlin. Two of the Madura Strait specimens fall in the size range of *Varanus komodoensis.* There is one record of an Early to Middle Pleistocene snake vertebra from Java, found in Trinil (Janensch, 1911a). The specimen, which was never described or pictured, is probably housed in the Museum für Naturkunde Berlin. The Madura Strait assemblage contains one Pythonidae trunk vertebra, which is the first described Middle Pleistocene snake fossil from Java.

A new record for the Pleistocene of Indonesia is the freshwater turtle *Dogania subplana*. The species is extant in Southeast Asian rivers and was recorded in the Late Pleistocene fossil record of Sarawak, Malaysian Borneo (Pritchard et al., 2009). Highly rare is the *Macaca* ulna fragment from the Madura Strait. There are only a few records of non-hominin primate remains from the Middle Pleistocene of Java, most of which are dental elements. Thus far, only one postcranial fossil had been described. This is a femur from Trinil assigned to Hylobatidae (Ingicco et al., 2014), which is kept at Naturalis Biodiversity Center. Another rare specimen is the astragalus of *Hexaprotodon sivalensis*. There are five earlier records of similar specimens from Java, all of which are housed in Naturalis Biodiversity Center or the Museum für Naturkunde Berlin.

4.1.2 Species-specific morphological traits

Our morphological analyses of the Madura Strait assemblage provided new insights into species-specific morphological traits, which may also be of use for the identification of other, fragmentary fossil remains from the region. The most important contributions relate to turtle plate fragments and bovid molars.

Morphological distinction between Geoemydidae (hard-shelled turtles) is difficult, due to a scarcity of diagnostic features. The plates are often fused and the breaks are random. However, we showed that it is possible to get a general insight into the species composition of an assemblage. For the Madura Strait assemblage, several potential species could be discarded by the absence of serrated margins or crested cervical plate fragments. Moreover, we could find species-specific matches for a limited number of plate fragments, referring to sulci patterns and the morphology of plate margins, which in the case of the Madura Strait assemblage point to the presence of *Orlitia borneensis* and *Batagur* sp. Our identification procedure is therefore useful for large samples of fragmented Geoemydidae shells and gives a general indication of represented species. For Tryonychidae (soft-shelled turtles), identification of plate fragments has been based on plate ornamentation, following the morphological subdivision of Pritchard et al. (2009). It appeared to be relatively straightforward to organize the fragments into four morphological groups, representing *Chitra chitra*, *Pelochelys cantorii*, *Amyda cartilaginea* and *Dogania subplana*.

For our study of bovid molars, we compared the dentition of *Bubalus* and *Bos*, both in extant and fossil species. Despite morphological overlap, it proved to be possible to make a tentative subdivision between *Bubalus palaeokerabau* and *Bos palaeosondaicus*, based on morphological traits. The identifications are supported by metric control: the crowns with a *Bubalus* morphology are overall slightly larger than the crowns with a *Bos* morphology. Moreover, the ratio *Bubulus* to *Bos* within the molar sample is similar to the ratio among horn core fragments or postcranial fragments. We conclude that our morphological identification procedure is a valuable tool in large samples of bovid molars and gives a reasonable insight into the composition of the fossil bovid fauna. Note that for the molar analysis, we left the rare and extinct taxon *Epileptobos* out of consideration, due to a scarcity of reference specimens.

4.1.3 Species-specific size ranges

A large fossil sample such as the Madura Strait assemblage offers opportunities for metric analyses. We measured dental and postcranial elements of various genera and species, and compared the measurement results to published size ranges or new reference measurements of museum specimens. The metric data have been combined in tables and graphs, forming an easy reference for future palaeontological studies in the region. For *Elephas* cheek teeth and Artiodactyla postcranial elements, our metric analyses provided new insights into species-specific size ranges or local evolutionary trends.

The *Elephas* teeth from the Madura Strait are relatively slender, high-crowned, and metrically closer to the extant *Elephas maximus* than to the Middle Pleistocene *E. hysudrindicus.* The difficulty is that the diagnostic criteria for distinguishing the extinct *E. hysudrindicus* from the extant *E. maximus* are primarily based on skull morphology. Hooijer (1955) also found metric differences between the dentition of the two species, but with overlapping ranges. We measured several Middle Pleistocene museum specimens attributed to *E. hysudrindicus* from various sites on Java and found that also among this material there are slender and high-crowned specimens, with plate sizes similar to *E. maximus.* The taxonomic implications of this finding are unclear (see also **Section 4.4**).

The fragmented limb bones from the Madura Strait are dominated by Artiodactyla. Within comparable fossil assemblages from Java, this material is generally left unidentified, or identified up to genus only. We selected cervid and bovid specimens based on the morphological criteria provided by Schmid and Garroux (1972), Heintz (1970) and

Van den Bergh (1988) and measured the sizes of the articular surfaces. The elements fall apart in distinct size ranges, which compare well with published size ranges of relevant extant and Pleistocene species. Interestingly, the limb bones of the intermediate-sized cervid *Axis javanicus* form a distinct, well-defined size range. This is the first time that postcranial material of this species, formerly only known from antlers (Von Koenigswald, 1933) and molars (Gruwier et al., 2015) has been identified. The larger bovid material forms at least two size groups, which could be assigned to *Bos palaeosondaicus* and *Bubalus palaeokerabau* based on a greater medio-lateral width of the articulations in the genus *Bubalus*. The limb bones assigned to *Bos palaeosondaicus* are small compared to fossil reference specimens from Java. The material falls in the size range of the extant *Bos javanicus*, which is on the average slightly smaller than its Pleistocene ancestor (see also **Section 4.4**).

4.2 Fauna list and translation to vertebrate communities

The total find list consists of 6,372 specimens, from which 19% could be identified **(Table 12**). We recognized a total of 36 vertebrate species, divided over 11 orders. One of the most conspicuous characteristics of the assemblage is its ecological mixture. In order to get a better idea of the ecological context of the species, the assemblage has been subdivided into three vertebrate communities or habitats: estuarine, fluvial and terrestrial. For each habitat, we provided relative abundances of the available taxa. To this end, we equated the number of specimens with the number of individuals per taxon, which is an appropriate method for highly dispersed fossil assemblages (Badgley, 1986).

Order	*Family*	*Species*	*NISP*	*%*
Carcharhiniformes	Hemigaleidae	*Hemipristis serra*	5	0.08
	Carcharhinidae	*Glyphis gangeticus*	51	0.8
		Carcharhinus cf. *leucas*	20	0.31
		Galeocerdo cuvier	3	0.05
Myliobatiformes	Myliobatidae	*Myliobatis* sp.	1	0.02
		Rhinoptera javanica	3	0.05
	Dasyatidae	*Urogymnus polylepis*	3	0.05
Batoidea (Superorder)*	Indet.		18	0.28
Siluriformes	Bagridae	*Hemibagrus* sp.	1	0.02
Squamata	Varanidae	*Varanus komodoensis*	2	0.03
		Varanus salvator	2	0.03
	Pythonidae	indet.	1	0.02
Testudines	Geoemydidae	Geoemydidae indet.	102	1.6
		Batagur affinis	1	0.02
		Orlitia borneensis	1	0.02
	Tryonychidae	*Chitra chitra*	29	0.46
		Pelochelys cantorii	7	0.11
		Amyda cartilaginea	5	0.08
		Dogania subplana	6	0.09
	indet.		24	0.38
Crocodilia	Crocodylidae	*Crocodylus siamensis*	24	0.38
	Gavialidae	*Gavialis bengawanicus*	4	0.06
	indet.		4	0.06
Proboscidea	Stegodontidae	*Stegodon trigonocephalus*	31	0.49
	Elephantidae	*Elephas* sp.	15	0.24
	indet.		54	0.85
Primates	Hominidae	*Homo erectus*	2	0.03
	Cercopithecidae	*Macaca* sp.	1	0.02
Carnivora	Felidae	*Panthera pardus*	1	0.02
Perissodactyla	Rhinocerotidae	*Rhinoceros sondaicus*	27	0.42
Artiodactyla	Hippopotamidae	*Hexaprotodon sivajavanicus*	30	0.47
	Suidae	*Sus brachygnathus*	14	0.22
		Sus cf. *macrognathus*	2	0.03
	Cervidae	*Axis lydekkeri*	36	0.56
		Axis javanicus	17	0.27
		Axis indet.	241	3.78
		Rusa sp.	95	1.49
	Bovidae	*Bubalus palaeokerabau*	101	1.59
		Bos palaeosondaicus	129	2.02
		Epileptobos groeneveldtii	4	0.06
		Bovini indet.	88	1.38
		Duboisia santeng	7	0.11
Total determined			1212	19.02
Total indetermined			5160	80.98
TOTAL			6372	100

Table 12: Vertebrate taxonomy, identified and unidentified specimens; Madura Strait assemblage. Specimen counts and percentages (rounded to two decimaplaces) of the entire assemblage.* The specimens listed as Batoidea indet. may (partly) be Myliobatiformes.

The estuarine community **(Table 13)** consists of large fish species, which is obviously a sampling bias. The estuaries of Southeast Asia are rich in smaller fish (Kottelat, 2013). Finding remnants of these species, if preserved, requires sediment sieving and microscope analysis, which was outside the scope of this study. The abundance of shark teeth relates to their excellent preservation potential, but also to their frequent shedding, which may reach several thousand teeth in a lifetime. Any assessment of species abundances based on shark teeth must therefore be made with caution and merely has significance in comparison with other shark species. Most of this fossil material probably derives from the estuarine deposits that form the top of the valley fill. A few species, such as the river shark *Glyphis gangeticus,* the giant stingray *Urogymnus polylepis*, and the catfish *Hemibagrus* sp. have an estuarine to lowland-river habitat. This implies that their remains may also have been part of the fluvial sandstones that form the basal part of the valley fill. In the case of *G. gangeticus*, this probably contributed to the high abundance of its fossil remains in the assemblage.

Order	*Species*	*%*
Carcharhiniformes	*Hemipristis serra*	4.8
	Glyphis gangeticus	48.6
	Carcharhinus cf. *leucas*	19
	Galeocerdo cuvier	2.9
Batoidea (superorder)	Batoidea indet.	17.1
Myliobatiformes	*Myliobatis* sp.	1
	Rhinoptera javanica	2.9
	Urogymnus polylepis	2.9
Siluriformes	*Hemibagrus* sp.	1
TOTAL		100

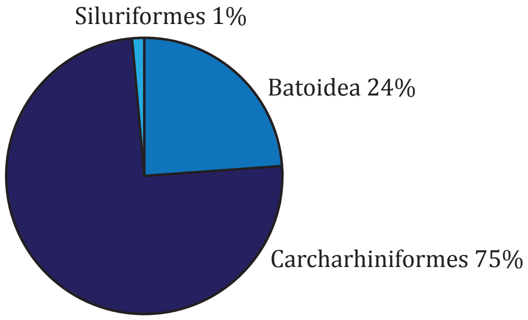


Table 13. The estuarine community: estuarine and lowland-river fishes. Madura Strait assemblage. Percentages (rounded to one decimal place) of total identified specimens for this community. Pie diagram shows the community per taxonomical order or (for Batoidea) superorder.

The fluvial community **(Table 14)** consists of reptiles and mammals tied to the river as their main habitat. Besides one caudal spine attributed to *Hemibagrus* sp. (added to the estuarine community), we found no remnants of fluvial fish, which relates to the applied sampling methods. The abundance of turtles partly relates to the high preservation potential of turtle shells and to their fragmentation, causing sample inflation. The crocodilians are mainly represented by teeth. Just as we noted for sharks, this may lead to an overestimate of crocodilian abundances, caused by shedding of teeth. On the other hand, crocodilian postcranial material is probably underrepresented in the find list, as we did not have access to a collection of relevant comparative skeletal material.

Order	*Species*	*%*
Squamata	*Varanus salvator*	0.8
	Pythonidae sp.	0.4
Testudines	Testudines indet.	10
	Geoemydidae indet.	42.5
	Batagur affinis	0.4
	Orlitia borneensis	0.4
	Chitra chitra	12.1
	Pelochelys cantorii	2.9
	Amyda cartilaginea	2.1
	Dogania subplana	2.5
Crocodilia	Crocodilia indet.	1.7
	Crocodylus siamensis	10
	Gavialis bengawanicus	1.7
Artiodactyla	*Hexaprotodon sivajavanicus*	12.5
TOTAL		100

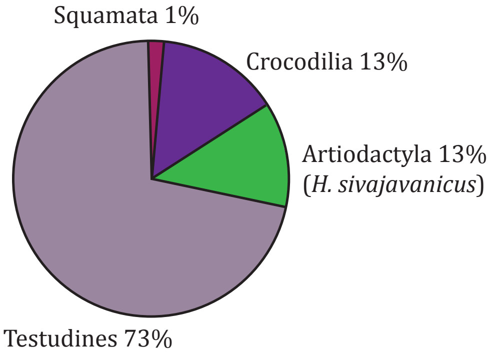


Table 14. The fluvial community: reptiles and mammals tied to the river. Madura Strait assemblage. Percentages (rounded to one decimal place) of total identified specimens for this community. Pie diagram shows the community per taxonomical order.

The terrestrial community **(Table 15)** is dominated by mammals, most of which are herbivores. There is probably a bias against small- to medium-sized animals, which again relates to not-implementing sediment sieving, but also to the higher susceptibility of small bones to carnivore mastication and chemical or physical destructions (Behrensmeyer et al., 1979). Small animals like rodents were not found. Medium-sized animals, with body weights of around 60 kg, are scarce and their abundances are probably underestimated. This concerns species such as *Sus brachygnathus, Duboisia santeng* and *Axis lydekkeri.*

Order	*species*	*%*
Squamata	*Varanus komodoensis*	0.2
Proboscidea	*Stegodon trigonocephalus*	3.6
	Elephas sp.	1.7
	Proboscidea indet.	6.2
Primates	*Homo erectus*	0.2
	Macaca sp.	0.1
Carnivora	*Panthera pardus*	0.1
Perissodactyla	*Rhinoceros sondaicus*	3.1
Artiodactyla	*Sus brachygnathus*	1.6
	Sus cf. *macrognathus*	0.2
	Axis lydekkeri	4.2
	Axis javanicus	2
	Axis sp.	27.8
	Rusa sp.	11
	Bubalus palaeokerabau	11.6
	Bos palaeosondaicus	14.8
	Epileptobos groeneveldtii	0.5
	Bovini indet.	10.1
	Duboisia santeng	0.8
TOTAL		100

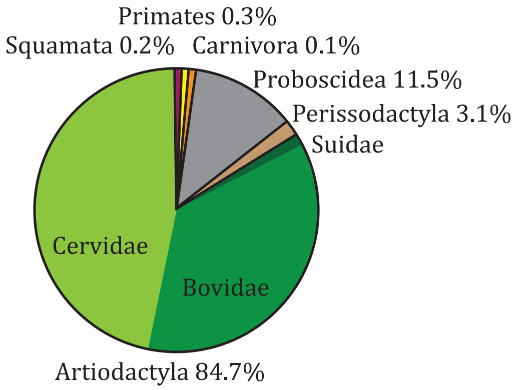


Table 15. The terrestrial community: mammals and reptiles of the lowland plains. Madura Strait assemblage. Percentages (rounded to one decimal place) of total identified specimens for this community. Pie diagram shows the community per taxonomical order, with Artiodactyla subdivided in families.

Cervidae make up 45% of the terrestrial assemblage, however, their great representation is primarily accounted for by antler fragments. If we focus only on other elements such as molars, astragali, or phalanges, the representation of cervids is much lower and bovids are always in the majority. Taking a closer look at the material, we found most antlers to be shed antlers. Out of 13 antler bases of the genus *Rusa,* only 2 preserve a pedicle. For the genus *Axis* this is even more extreme: out of 26 antler bases, only 1 preserves a pedicle. This great dominance of shed antlers results in an overestimate of cervid presence. We therefore recalculated the occurrence of cervids within the population by only including antler bases with a pedicle, which are in fact frontal fragments. This changes the relative abundances of all terrestrial species and brings up a dominance of bovids **(Table 16)**. The occurrence of proboscideans within the terrestrial community is probably somewhat underestimated. Proboscideans were mainly recorded by their dentition, including fragmented tusks. Remnants of limb bones are scarce, which is probably also a taphonomic bias, as fragments of such large bones often do not preserve recognizable articulations, complicating their determination.

4.3 The vertebrate biostratigraphy of Java and age overlap with the Ngandong Fauna

The Pleistocene terrestrial vertebrate assemblages of Java are generally discussed in terms of faunal units, which were defined by Von Koenigswald (1934, 1933) and later revised by de Vos et al. (1982). The units are regarded as records of intermittent dispersal waves of new species to Java, and as records of local evolution and extinction (Van den Bergh et al., 2001, 1996; Leinders, 1985; Sondaar, 1984). Moreover, the faunal units have commonly been used as chronostratigraphic markers (Zaim, 2010; Duyfjes, 1938a). Relevant Pleistocene faunal units are the Trinil HK Fauna, Kedung Brubus Fauna, Ngandong Fauna, and Punung Fauna.

Recent studies provided new insights into the age and (lack of) homogeneity of the faunal units. The Trinil HK Fauna primarily derives from two stacked fluvial channels, dated to 830-773 ka and 540–380 ka respectively, but probably also contains fossils from the younger Solo terrace deposits (Hilgen et al., 2023; Pop et al., 2023a). The younger channel may contain fossils that were locally reworked from the older channel, and both channels may contain fossil mate-

Order	*species*	*%*
Squamata	*Varanus komodoensis*	0.4
Proboscidea	*Stegodon trigonocephalus*	5.5
	Elephas sp.	2.7
	Proboscidea indet.	9.7
Primates	*Homo erectus*	0.4
	Macaca sp.	0.2
Carnivora	*Panthera pardus*	0.2
Perissodactyla	*Rhinoceros sondaicus*	4.8
Artiodactyla	*Sus brachygnathus*	2.5
	Sus cf. *macrognathus*	0.4
	Axis lydekkeri	2.7
	Axis javanicus	2.1
	Axis sp.	3.8
	Rusa sp.	5.9
	Bubalus palaeokerabau	18.1
	Bos palaeosondaicus	23.1
	Epileptobos groeneveldtii	0.7
	Bovini indet.	15.7
	Duboisia santeng	1.3
TOTAL		100

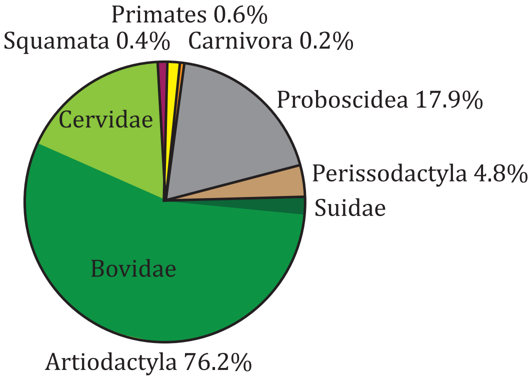


Table 16. The terrestrial community: mammals and reptiles of the lowland plains. Madura Strait assemblage. Similar to **Table 15**, but with a correction for shed antlers. Percentages (rounded to one decimal place) of total identified specimens for this community. Pie diagram shows the community per taxonomical order, with Artiodactyla subdivided in families.

rial reworked from the underlying older strata. The Ngandong Fauna derives from a fluvial terrace that has been dated to 140 – 92 ka (Rizal et al., 2020). The age and stratigraphic background of the Kedung Brubus Fauna is not fully understood, but is generally assumed to be intermediate to the Trinil HK and Ngandong Faunas. However, it may very well have a complex depositional background and a temporally mixed composition. The Punung Fauna derives from cave breccias that have been dated to 128 – 115 ka (Westaway et al., 2007). Kaifu et al. (2022) provided an updated stratigraphy and updated species list for the Punung Fauna.

With an OSL age of 162±31 and 119±27 ka, and a most likely age range of 146 – 131 ka (Berghuis et al., 2025a), the Madura Strait fossiliferous valley fill overlaps in age with the Ngandong terrace and with the Punung cave breccias. Looking at the composition of the fossil faunas from these three sites, there is a great similarity between the Madura Strait assemblage and the Ngandong Fauna. Both are dominated by open-grassland herbivores and both contain the archaic mammal species that characterize the Early and Middle Pleistocene of Java, such as *Stegodon* and *Homo erectus.* The Punung Fauna is a different fauna, which includes modern and rainforest-dependent taxa such as *Pongo* sp. (orang-utan). Note, however, that the rainforest dependency of the latter species has recently been questioned (Louys et al., 2022; Spehar et al., 2018). The transition to the Punung Fauna is regarded as a major faunal turn-over, representing a change from dry and open conditions to humid and forested conditions during MIS5 (Van den Bergh et al., 2001). The Ngandong Fauna, as well as the Madura Strait assemblage, predates this faunal turnover and may be tied to MIS6.

The Ngandong assemblage was excavated between 1931 and 1934, unearthing ~25,000 fossils including twelve hominin calvaria and two hominin tibia (Huffman et al., 2010; Weidenreich, 1951; Oppenoorth, 1932). The non-hominin collection was never investigated in detail. Von Koenigswald (1933) provided a list of species, which has become the basis of the Ngandong Fauna. In later years, the species list was updated, following taxonomical revisions and brief inquiries of the stored material (Van den Bergh et al., 2001; Van Den Bergh, 1999; De Vos et al., 1982). Unfortunately, detailed specimen counts and metric data of the Ngandong assemblage are not available. Moreover, the non-hominin collection is poorly catalogued and possibly partly lost, which makes it difficult to carry out re-investigations or to take new measurements.

4.4 The faunal records of Ngandong and Madura Strait compared: implications for the late Middle Pleistocene vertebrate biogeography of Sundaland

Not only are the assemblages from Ngandong and the Madura Strait of similar age, they also have a shared relation with the Pleistocene Solo River. However, there may have been a relevant difference in landscape setting. Ngandong lies along the uplifted middle reach of the Solo, bordering the volcanic highland of Java, whereas the Madura Strait site represents the lower reach of this river, in the lowland plains of Sundaland that had become emerged during MIS6. It is interesting to see whether there are faunal differences between the two fossil assemblages that may be linked to this difference in landscape setting.

A conspicuous difference between the two fossil assemblages is the wealth of shark and stingray remains among the fossils from the Madura Strait, none of which were recorded in Ngandong. It shows that the river shark *Glyphis gangeticus* was a common species in the lower reach of the late Middle Pleistocene Solo. Other sharks such as *Carcharias leucas*, *Galeocerdo cuvier*, and *Hemipristis serra* roamed the estuary. The former two species are still extant in Indonesian coastal waters and are known to occasionally ascend lowland rivers. Another fish of the lowland Solo was the giant stingray *Urogymnus polylepis*. Today, this species is extant in lowland rivers of Southeast Asia, but extinct on Java. Two other stingrays, *Rhinoptera javanica* and *Myliobatis* sp. were present in the estuary. The former is still extant in Indonesian coastal waters. The latter is unknown from present-day Indonesian coasts. It may have been related to the extant *Myliobatis aquila* of the western Indian Ocean or *Myliobatis australis* of Australia, both of which are modest-sized stingrays with a coastal habitat. This suggests a wider geographic range of the ancestors of either of these species in the late Middle Pleistocene.

The absence of such shark and stingray remains in Ngandong suggests that these species did not ascend the Solo this far inland. However, it is very well possible that occasional shark teeth in the Ngandong terrace deposits have remained unnoticed or undocumented. Note in this respect that Dubois found 16 *G. gangeticus* teeth as well as two *U. polylepis* stingrays in Trinil. Later, Selenka discovered another 12 shark teeth in Trinil (Joordens et al., 2009). Their exact stratigraphic provenance is unknown. It is possible that these species occurred naturally in the Trinil area at certain times, but it is also possible that all or some of these specimens were actually brought to the site by *Homo erectus* for use as tools (Gilson et al., 2021; Joordens et al., 2015).

Another faunal difference between the assemblages is the richness of river-related reptiles in the Madura Strait assemblage and their scarcity in the assemblage from Ngandong. Von Koenigswald (1933) noted rare remains of *Crocodylus siamensis* among the fossils from Ngandong, but none of *Gavialis bengawanicus*. He also briefly mentioned the occurrence of turtle shell fragments, including 'rare Trionychidae'. The Madura Strait assemblage is extremely rich in turtle shell fragments, moreover, it contains teeth and osteoderms of *Crocodylus siamensis* and *Gavialis bengawanicus* and vertebrae of *Varanus salvatori* and Pythonidae. Just as we noted for sharks and stingrays, the abundance of river-related reptiles in the Madura Strait assemblage must be related to lowland conditions, with a wide and slowly moving river. The species diversity among the fresh water turtles from the Madura Strait is unique compared to other regional Pleistocene sites and is similar to the turtle community in Southeast Asian lowland rivers that have not been affected by environmental degradation.

When it comes to large terrestrial herbivores, there are important similarities between the assemblages from Ngandong and the Madura Strait. Both assemblages are dominated by the large bovids *Bos palaeosondaicus* and *Bubalus palaeokerabau*. In the Madura Strait assemblage, we noted a reduced body size of *B. palaeosondaicus* compared to the older assemblages of Trinil and Kedung Brubus. Whether this reflects a late Middle Pleistocene evolutionary trend towards reduced body size or dispersal of new bovid groups across Sundaland is unknown. Unfortunately, me- tric data of *B. palaeosondaicus* remains from Ngandong are not available. The presence of *Epileptobos groeneveldtii* in the Madura Strait assemblage is interesting, as this species is absent in Ngandong and was thus far regarded to have gone extinct in the course of the Middle Pleistocene. It may reflect a slightly older age of the Madura Strait assemblage, or an enduring presence of *E. groeneveldtii* on the lowland plains of Sundaland in the late Middle Pleistocene.

Also with respect to proboscideans, the Ngandong and Madura Strait assemblages appear to be similar. *Stegodon trigonocephalus* is the most common proboscidean species on both sites. We also noted a metric similarity of the dentition of this species from both sites, pointing to the same subspecies: *S. trigonocephalus ngandongensis.* The genus *Elephas* is also part of both assemblages, although the genus appears to be rare in Ngandong. Von Koenigswald (1933) mentioned only one incomplete cheek tooth from Ngandong and Rizal et al. (2020) reported two additional *Elephas* tooth fragments from the original fossil assemblage. In the Madura Strait assemblage, the genus is represented by a much larger number of tooth fragments. This different abundance of *Elephas* remains probably reflects a difference in geographic distribution, but it is difficult to say whether this can be explained by a preference of *Elephas* for the lowland plains. Note that *Stegodon* and *Elephas* must have been competing for grassy resources and probably avoided habitat overlap (Puspaningrum et al., 2020). The fact that the two proboscidean taxa are both well-represented in the Madura Strait assemblage may relate to migration of herds of proboscideans from different grazing areas to the river during dry seasons, or it may reflect time-averaging of the assemblage. The late Middle Pleistocene *Elephas* of the Madura Strait has, on average, more slender and high-crowned cheek teeth than the Middle Pleistocene *E. hysudrindicus* from Trinil and Kedung Brubus. Whether this also accounts for the scarce *Elephas* teeth from Ngandong is unknown. Metrically, the teeth from the Madura Strait are similar to the extant *E. maximus*. It is generally thought that the dispersal of *E. maximus* from the Asian mainland to the Sundaland area occurred in the Late Pleistocene, with a find near Cipeundeuy (West-Java) as the oldest known occurrence on Java, bracketed by radiocarbon ages of 35.5 ka and 29.6 ka (Van Den Bergh, 1999; Dam, 1994). The taxonomical significance of the high-crowned *Elephas* molars of the Madura Strait is unknown. It may for example reflect a late Middle Pleistocene evolutionary trend within *Elephas hysudrindicus* towards greater hypsodonty, or an early dispersal wave of *Elephas maximus* across the plains of Sundaland. Taxonomical interpretation can only be based on metric analyses of intact skulls, which are not available among the assemblages from Ngandong and the Madura Strait. To avoid confusion about species identifications, we referred to the material from the Madura Strait as *Elephas* sp.

In general, we may conclude that the large bovid and proboscidean taxa that dominated the hills of Middle Pleistocene Java also dispersed over the emerging plains during sea-level lowstands, at least during MIS6. The same accounts for other large species such as *Rhinoceros sondaicus*, *Hexaprotodon sivajavanicus*, all of which are part of the fossil assemblages of Ngandong and the Madura Strait. However, there are some interesting differences among the smaller terrestrial species, which probably have biogeographic significance. One of these relates to the small bovid *Duboisia santeng.* This species is represented in the Madura Strait assemblage by a horn core, a mandible, an isolated molar, and several astragali. The species is commonly regarded as endemic to Java, with a small body size that reflects insular isolation (Rozzi et al., 2013). Its fossil remains are abundant in the older faunal assemblages from Trinil and Kedung Brubus, but absent in Ngandong, which has thus far been regarded as evidence of its extinction in the course of the Middle Pleistocene. The occurrence of this species in the Madura Strait assemblage is surprising and points to an enduring presence of *D. santeng* during the late Middle Pleistocene. Moreover, it shows that the species dispersed over the exposed Sundaland plains during lowstands, which seems to contradict its assumed prolonged isolation. The occurrence of *D. santeng* on the lowland plains of Sundaland also sheds a new light over possible fossil finds of this species in Thailand (Nishioka and Vidthayanon, 2018) and mainland Malaysia (Hooijer, 1962b).

Another interesting difference between the assemblages from Ngandong and the Madura Strait relates to the genus *Axis.* The small-bodied *Axis lydekkeri* is a common species in the older faunal assemblages from Trinil and Kedung Brubus, but there is confusion over its presence in the assemblage from Ngandong. Note in this respect the differences between the faunal descriptions of De Vos et al. (1982), Van den Bergh et al. (2001), and Gruwier et al. (2015). In his original descriptions, Von Koenigswald (1933) noted an absence of *Axis lydekkeri* in the assemblage from Ngandong, and the presence of a new, medium-sized species, which he named *Axis javanicus.* The taxonomic confusion partly relates to the fact that later authors did not regard *Axis javanicus* as a valid species. However, Gruwier et al. (2015) confirmed the validity of the species by a comparative study of molars. Interestingly, both *A. lydekkeri* and *A. javanicus* are common in the Madura Strait assemblage. For *A. lydekkeri* this implies a continued presence up to the latest Middle Pleistocene and dispersal over the exposed Sundaland plains. The species is probably ancestral to the extant *Axis kuhli*, a species only found on the small island of Bawean in the Java Sea. In this respect, the dispersal and survival of herds of *A. lydekkeri* on the lowland plains of Sundaland is not surprising. The presence of *Axis javanicus* in the Madura Strait assemblage confirms the age overlap with the Ngandong Fauna. According to Gruwier et al. (2015), the species is related to the extant *A. axis* of the Indian mainland. Its presence in the fossil assemblages of Ngandong and the Madura Strait reflects a period of great geographic dispersal of this medium-sized *Axis* species over Sundaland during the lowstand of MIS6.

The large-statured *Rusa* sp. is common in the assemblages from Ngandong and the Madura Strait. In the Madura Strait assemblage, we found particularly large sizes of postcranial elements. Whether this also accounts for the fossil remains from Ngandong is unknown. There is uncertainty over the ancestral relation between the Middle Pleistocene *Rusa* sp. and the two extant species *Rusa timorensis* of Java and *Rusa unicolor* of Sumatra. Gruwier et al. (2015) noted that the fossil molars from Java are metrically similar to the extant *R. timorensis.* However, the postcranial remains from the Madura Strait fall in the size range of the larger *R. unicolor.* The implications of this finding with respect to evolutionary lineages and dispersal of *Rusa* deer over Sundaland are unknown.

Also among the predators, there are some noteworthy differences between the assemblages from Ngandong and the Madura Strait. The Madura Strait assemblage is extremely poor in mammalian carnivores, with only one specimen attributed to *Panthera pardus.* The Ngandong assemblage is richer in carnivore remains, which have been ascribed to three species: *Megacyon merriami*, *Panthera pardus* and *Panthera tigris* (Volmer et al., 2016). Especially *P. tigris* is well-represented in this fossil assemblage, by a complete skull, diverse skull fragments, isolated teeth, and several postcranial elements (Brongersma, 1935; Von Koenigswald, 1933). Surely, the greater abundance of carnivore remains partly relates to a larger sample size (the original Ngandong assemblage consisted of around 25,000 fossil specimens), but also in relative terms, the difference in representation of carnivores is remarkable. A possible explanation for the scarcity of carnivore remains in the Madura Strait might be that the death assemblage relates to stages of drought. Ferreira and Viljoen (2022) noted that in such assemblages, carnivore remains may be scarce, as these species have high survival rates under drought conditions, profiting from an abundance of weakened herbivores.

The scarcity of carnivore fossils within the Madura Strait assemblage may also be an actual reflection of the ancient faunal community. There may for example be a relation with the presence of the predatory reptile *Varanus komodoensis* in the Madura Strait assemblage. In its current territories, such as the island of Flores, this species is the only large predator of the terrestrial food chain, but on Middle Pleistocene Sundaland there must have been a niche overlap with felid and canid carnivores. Possibly, the predator community of the upland region was dominated by carnivores, whereas *V. komodoensis* was dominant on the lowland plains. In this respect, it is interesting that Volmer et al. (2016) and Hertler and Volmer (2008) noted a sharply increased body mass of the tigers from Ngandong compared to earlier tigers from Java. The authors related this to niche overlap and 'unusually intense competition among carnivores'. Possibly, this was not (only) an inter-carnivore competition, but also a competition between tigers and Komodo dragons. Unfortunately, the limited availability of fossil material from carnivores and Komodo dragons makes it impossible to draw detailed conclusions on this subject.

Finally, the presence of *Homo erectus* in Madura Strait assemblage has interesting implications for hominin dispersal over Sundaland in the late Middle Pleistocene (Berghuis et al., 2025d).

4.5 Climate, vegetation and biogeography

The Middle Pleistocene of Java is characterized by a climate of long and intense dry seasons and a grass-dominated vegetation (Sémah et al., 2010). This probably accounted also for the greater Sundaland region, especially during glacial stages (Dennell, 2009). A pollen study of a lacustrine core in West-Java revealed exceptionally dry conditions during the latest Middle Pleistocene (Van der Kaars and Dam, 1995).

We have no direct data on the climate or vegetation of the exposed Madura Strait shelf area during the late Middle Pleistocene lowstand of MIS6. However, analogous to the current situation, in which eastern Java is significantly dryer than western Java, climate conditions in this part of the Sundaland region may have been particularly dry. The herbivore-dominated assemblage of the Madura Strait indeed suggests open vegetation conditions. Possibly, remnant forests or swamp forests remained along the course of the perennial rivers. In Berghuis et al. (2024a) we showed that the late Middle Pleistocene Madura Strait Shelf had two of such large rivers: the Solo and the Brantas. During the long dry seasons, the swampy riversides may have attracted herds of herbivores from the surrounding plains.

Compared to the lowland plains, the volcanic highland of present-day Java probably had a higher precipitation rate and slightly cooler conditions. There is evidence that patches of remnant forests remained on the hills of Java throughout the Middle Pleistocene (Morley et al., 2020; Sémah and Sémah, 2012; Polhaupessy, 1990). Clear evidence for anthropic impact and clearance of the forest does not occur until late in the Holocene, after the rise of the ancient kingdoms on Java at the end of 1st millennium A.D.

The history of landscape change in Java over the last 2.5 million years appears to have been highly complex and may be described as a repeated expansion and fragmentation of the rain forest. The extent of rain forest throughout the Holocene appears to have been quite sensitive to small perturbations, making it somewhat difficult to reconstruct, especially for relatively ancient Holocene forest recessions. This distribution of climate and vegetation over Java and the surrounding Sundaland plains must have played an essential role in the geographic distribution of species. *Varanus komodoensis* may for example have preferred the hot and dry lowland plains. On the other hand, the occurrence of *Duboisia santeng* on the lowland plains is unexpected, as this species is thought to have preferred forests over grassland (Rozzi et al., 2013). Possibly, the species dispersed over lowland Sundaland through remnant forests along the main rivers, or through mangrove forests along the coast.

5. Conclusions

The Madura Strait assemblage provides a unique insight into the late Middle Pleistocene vertebrate fauna of the lowland plains of Sundaland. The fossils derive from the fill of a large paleovalley of the Solo River, the incision of which relates to the lowstand of MIS6. The lowland river was rich in fluvial reptiles, such as various turtle and crocodilian species. Herds of large herbivores roamed the surrounding plains, pointing to a grass-dominated vegetation. Among these were *Stegodon trigonocephalus* and *Elephas* sp., as well as the bovids *Bubalus palaeokerabau, Bos palaeosondaiucus* and *Epileptobos groeneveldtii.* Other species, such as the smaller bovid *Duboisia santeng*, *Rhinoceros sondaicus* and *Macaca* sp. point to the presence of patches of forest or open woodland, possibly along the river course. Among the predators of the lowland plains was *Varanus komodoensis*. The only carnivore of the assemblage is *Panthera pardus*. The nearby estuary was rich in sharks and stingrays, some of which also ascended the lowland river.

The terrestrial species composition is highly similar to the contemporary Ngandong Fauna of Java, and differs markedly from the slightly younger Punung Fauna, which represents a more humid, forested habitat. The Ngandong assemblage derives from an upstream terrace of the Solo River and therefore forms an upland equivalent of the Madura Strait assemblage. As may be expected, the lowland fauna of the Madura Strait is richer in fluvial reptiles and estuarine fish than the Ngandong assemblage. Among the terrestrial herbivores, the presence of *Duboisia santeng,* *Epileptobos groeneveldtii* and *Axis lydekkeri* in the lowland fauna of the Madura Strait is interesting. These species are absent in the Ngandong assemblage and were thus far regarded to have gone extinct on Java in the second half of the Middle Pleistocene. Their occurrence in the Madura Strait assemblage shows that the species persisted on the lowland plains, up to the latest Middle Pleistocene. Another interesting difference with the Ngandong assemblage is the scarcity of carnivores in the lowland fauna of the Madura Strait and the absence of *Panthera tigris*. A possibility is that in the lowland plains, the tigers were outcompeted by *Varanus komodoensis*.

The Madura Strait assemblage is among the richest Pleistocene vertebrate assemblages of the region. It contains several species thus far unrecorded for the Pleistocene of Java or Indonesia. Moreover, it contains rare specimens, thus far not available in Indonesian museum collections. Our morphometric analyses provided valuable new insights into species-specific morphological features and size ranges. For example, the *Elephas* sp. cheekteeth of the Madura Strait are relatively slender and high-crowned compared to the cheekteeth of the Middle Pleistocene *Elephas hysudrindicus* from Java. And the common bovid *Bos palaeosondaicus* is on the average slightly smaller-statured than its Middle Pleistocene relatives from Java. In both cases, these metric differences may represent a regional evolutionary trend or geographical variation. Our metric analysis of cervid postcranial bones made it possible to demonstrate the presence of the intermediate-sized species *Axis javanicus,* a species thus far only known from dentition or antlers. The species probably relates to the *Axis axis* of India, and its presence in the assemblages from the Madura Strait and Ngandong probably represents a short dispersal wave over Sundaland during the late Middle Pleistocene.

In general, the results of our taxonomical analyses underline the importance of studying complete fossil assemblages (rather than ‘cherry-picking’) and building up local reference collections from various Pleistocene sites in the region. Such ‘complete-assemblage’ studies can be carried out for newly excavated material. Also, an inquiry of thus far undescribed fossil material from previous excavations, abundantly available in Indonesian museums, is highly promising.