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The taphonomy of the Madura Strait fossil assemblage, a record of selective hunting and marrow processing by late Middle Pleistocene Sundaland hominins

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ABSTRACT

The Madura Strait assemblage is the first vertebrate faunal record of submerged Sundaland. The material derives from an ancient valley of the Solo River, which was cut during the lowstand of MIS6. The geological background of the site and the taxonomy of the fossils have been described in previous publications. However, the significance of the assemblage within the Pleistocene biogeography of Southeast Asia can only be understood if we have insight into its accumulation history and homogeneity, and into the representativeness of the OSL-dated sediment for the fossils it contains. Moreover, the presence of hominin fossils raises questions on hominin subsistence strategies, which may have left traces in the fossil record. Over the past decades, similar questions have successfully been addressed by systematic taphonomic studies of fossil assemblages, notably from Africa and Europe. However, such studies are rare in Southeast Asia. Moreover, taphonomic studies of assemblages from subsea sites lag behind. Here we describe the results of a systematic taphonomic study of the Madura Strait assemblage. The fossils of terrestrial species form a homogenous assemblage, representing a steady supply of skeletal elements to the river, presumably during yearly flooding stages. OSL-dated fluvial sandstone samples point to a most likely age range of 146–131 ka. The material has been subject to fluvial size-sorting, but the absence of significant rounding points to short transportation distances and a local provenance. The skeletal remains accumulated in the fluvial valley fill or became concentrated in an overlying marine lag, as a result of tidal scour during the subsequent transition to estuarine conditions. Fossils of estuarine species derive from the estuarine sediment overlying this basal marine lag and are linked to peak-highstand conditions around MIS5e (~123 ka). The bone remains of terrestrial species have been subject to two fracturing stages: a green-state fracturing stage prior to fluvial uptake and a sub-fossil-state fracturing stage during later marine reworking. Extensive green-state fragmentation of ruminant limb bones points to hominin bone battering and marrow processing. The age-at-death frequency distribution of bovids is indicative of selective hunting of prime adult prey. Cut marks on turtle bones show that hominins also fed on these aquatic species.

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1. Introduction

Since the classic taphonomic publications of the late 20th century (Lyman, 1994; Behrensmeyer, 1984; Binford, 1981) and the ‘hunting or scavenging’ discussions of the eastern African hominin sites (Domínguez-Rodrigo et al., 2021; Egeland et al., 2007; Domínguez-Rodrigo, 2002; Blumenschine, 1995, 1986; Selvaggio, 1998; Bunn et al., 1986), systematic taphonomic studies have become an essential part of zoo-archeological research (Sala et al., 2024; Wang et al., 2022; Stewart et al., 2020; Fourvel et al., 2018). This research has strongly improved our understanding of past ecosystems and the role of hominin populations therein. Remarkably, systematic taphonomic studies have never been carried out for the assemblages from Java.

Another area where taphonomic research lags behind is submarine zoo-archeology (Louys, 2018). Flooded continental shelfs may contain valuable faunal and archaeological records of past terrestrial vertebrate faunas (Bailey and Cawthra, 2023; Flemming, 2021; Kolfschoten et al. 1995). Shelfs that have been subject to subsidence may even preserve a stacking of buried landscapes, representing subsequent Pleistocene sea-level cycles, potentially holding multiple faunal or archaeological records (Hijma et al., 2012). However, despite the relevance of these submerged landscapes, systematic taphonomic studies of fossil assemblages from subsea sites are rare (Smith and Smith, 2003). This is a missed opportunity: submarine sites are difficult to access and their detailed stratigraphic and sedimentary background can often not be studied by direct observations, which leaves taphonomy as an important tool for studying past ecological and geographical conditions.

The Sunda Shelf (Fig. 1A) is the world’s largest shelf sea. During the Pleistocene, the shelf was intermittently exposed, forming a wide continental area known as Sundaland (van Bemmelen, 1949), connecting the current islands of western Indonesia with the Asian mainland. This regime of intermittent shelf-exposure played an important role in the regional evolution and dispersal of vertebrate species (Louys and Meijaard, 2010; Van den Bergh et al. 2001), which included *Homo erectus* and, from the Late Pleistocene onward, *Homo sapiens* (Louys and Kealy, 2024; Husson et al., 2022; Antón, 2003).

Early and Middle Pleistocene vertebrate and archaeological records from this region are primarily known from Java (Indonesia). Localities as Sangiran, Trinil, Mojokerto and Ngandong yielded rich fossil assemblages (Von Koenigswald, 1935, 1933; Oppenoorth, 1932; Selenka and Blanckenhorn, 1911; Dubois, 1908, 1907), which reflect a long and complex history of local evolution and regional dispersal of species (Van Den Bergh, 1999; De Vos et al., 1982). *Homo erectus* presence on Java probably goes back to at least 1.3 Ma (Matsu’ura et al., 2020). The skulls from Ngandong, dated to 140–92 ka (Rizal et al., 2020), are the youngest known fossil remains assigned to this hominin species.

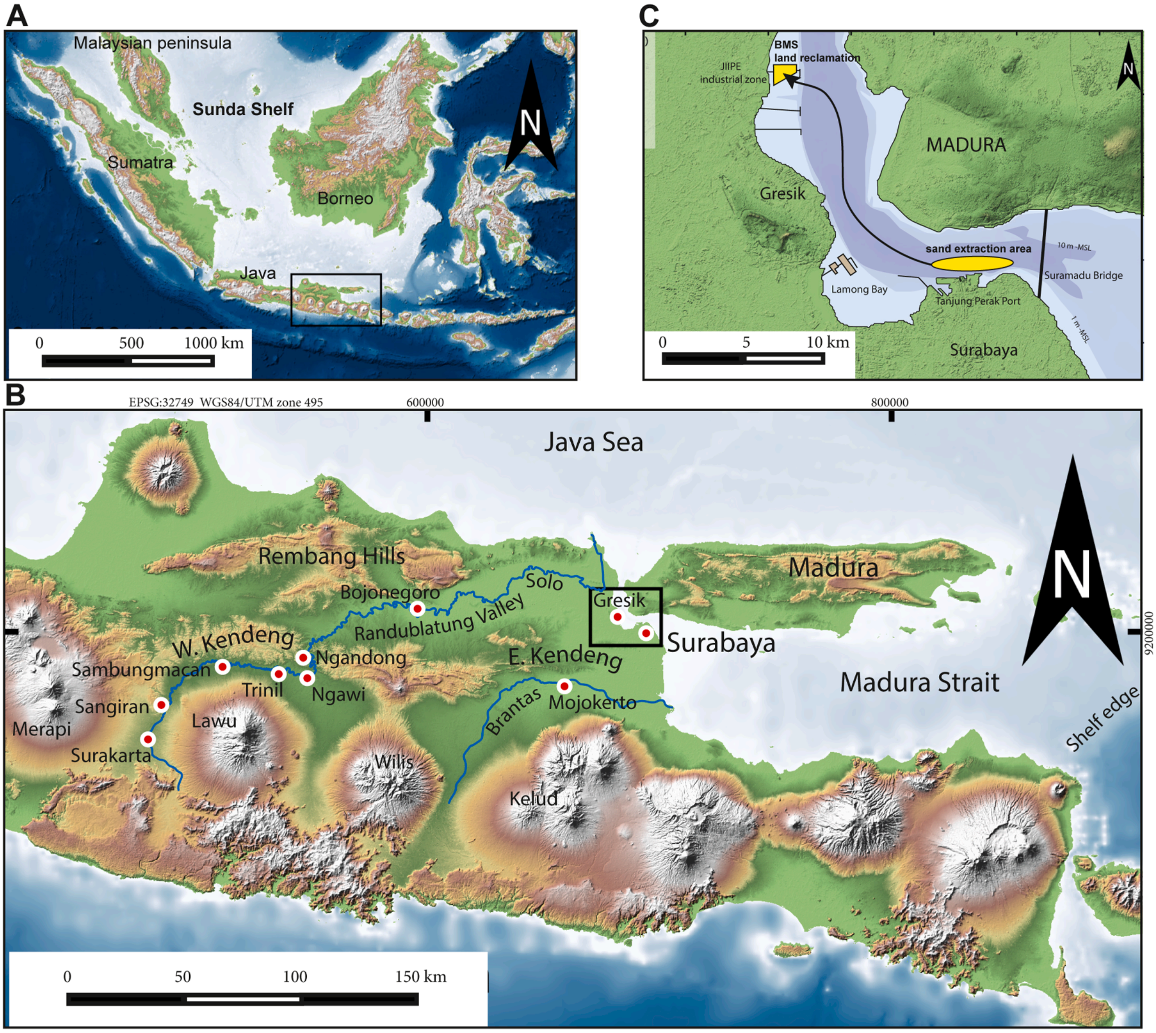


Fig. 1. A: The Sunda Shelf of Southeast Asia, with the Indonesian archipelago. Box indicates the position of map B. **B:** Eastern Java, the Madura Strait, Surabaya, the Solo River, and other sites mentioned in the text. Box indicates the position of map C. **C:** The Madura Strait north of Surabaya,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

The Sunda Shelf is a subsiding shelf (Husson et al., 2020; Sarr et al., 2019) with a great and thus far unexplored potential for faunal and archaeological records (Adhityatama and Yarista, 2019). Recently, a large vertebrate fossil assemblage was dredged from the Madura Strait, the sea strait between Java and Madura, along the southeastern margin of the Sunda Shelf (Fig. 1B). It consists of 6372 specimens (Table 1) and is the first faunal record from submerged Sundaland, consisting of estuarine fishes, river-related reptiles and terrestrial, mostly mammalian species (Berghuis et al., 2025b), which include ancient hominins (Berghuis et al., 2025d). The material derives from the sandstone fill of a lowstand valley of the Solo River, which was excavated during a submarine sand-extraction work and used for the reclamation of an artificial island in the port area of Surabaya. Two samples of the fluvial sandstones in which the fossils were embedded were OSL-dated to 162 ± 31 and 119 ± 27 ka (Berghuis et al., 2025a).

The Madura Strait assemblage offers an unprecedented insight into the vertebrate fauna of late Middle Pleistocene Sundaland. The geological background of the fossil-bearing strata is well-understood, thanks to a wealth of deep-drilling data from construction works in the adjacent port of Surabaya (Berghuis et al., 2025a). Nevertheless, several important questions have remained unaddressed. For example, has there been extensive hydraulic transport? How did the skeletal remains from terrestrial vertebrates become mixed with the remains of fluvial and estuarine vertebrates? Does the assemblage represent a single accumulation event or a longer period of accumulation? Are the OSL-ages of the sediment representative for the fossils it contains? These questions, which relate to the accumulation history and homogeneity of the assemblage, cannot be addressed by direct geological observations of the submarine excavation site. However, a systematic taphonomic study, in combination with the available geological data, may offer important new insights. Besides these accumulation-related aspects, a systematic taphonomic study may also provide relevant insights into the past ecosystem, and into the role that hominins played in this ecosystem.

This study, therefore, aims for a detailed reconstruction of the taphonomic pathways that the Madura Strait vertebrate fossils have been through, from mortality and disarticulation to accumulation, preservation and sampling. More specifically, the study aims to address three main research questions:

1. What is the history of accumulation, ecological mixing and sampling of the fossil remains and to what extent are the OSL-ages of the sediment representative of the ages of the fossil remains?
2. To what extent does the assemblage represent living populations and what does it tell us of past ecosystems and landscapes?
3. Can we find indications of hominin behavior, such as foraging and food processing behavior?

2. Geological background of the site and fossil excavation

At the sandstone extraction site, the Madura Strait has a depth of ca. 20 m. The seabed is made up of firm, massive marine clays of Pliocene to Early Pleistocene age. North of the Surabaya port area, a submerged valley of the Solo can be traced over the seabed for several kilometres. It was cut into the clayey subsoil, down to a depth of ca. 50 m –MSL (= local mean sea level) and has a fill of fluvial sandstones with lenses of fine conglomerate, which change upwards into marine clay-sand alternations with fine shell debris (Fig. 2). For more geological details, reference is made to Berghuis et al. (2025a).

In 2014–2015, sand was extracted from the valley fill by submarine dredging and used for the reclamation of an artificial island in the Surabaya port area (Fig. 1**C**). The work was commissioned by Berlian Manyar Sejahtera (BMS), a local port company, which today operates the reclamation site for port logistics. For the sand extraction, use was made of a trailing suction hopper dredger, a vessel that collects bottom sediment by dragging a suction pipe over the seabed. The suction pipe was mounted with a drag head, penetrating and loosening the sandstones and mixing the loosened material with water. The loosened and water-saturated material was sucked up and stored in the vessel's hopper. A 30/30 cm grid at the dredge head prevented the uptake of larger fragments. When fully loaded, the vessel sailed to the land reclamation site, where it was connected to a floating pipeline for discharge. Dredging was carried out in east-west trails and proceeded down to a depth of 32 m –MSL. A projection of the dredging profile is shown in the geological cross-section (Fig. 2), indicating that most of the extracted sand derives from the upper part of the fill, which consists of estuarine sandstones and claystones. Sand extraction only penetrated several meters into the underlying fluvial strata.

The reclamation material of the BMS-island is a poorly sorted mixture of sand, shell fragments and dispersed fine gravel. Fossils were mostly found as isolated specimens on the surface. The more than 100 ha wide reclamation area was meticulously searched on hands and knees (by H.B.), collecting vertebrate remains visible to the naked eye. Sediment sieving or trenching was not carried out.

Of interest is the occurrence of sediment blocks at the reclamation site, which passed the dredging process intact, and which provide a semi-direct insight into the sedimentological background of the site and into the distribution of fossils in their original sedimentological context. The blocks have a maximum size of ca. 30/30 cm, which relates to the grid on the dredge head. In Berghuis et al. (2025a) we subdivided these sediment blocks into five genetically significant facies (Fig. 3). The original stratigraphic position of these facies could be reconstructed through a comparison with the deep-drilling-based cross-section over the excavation site (Fig. 2). The two fluvial facies represent the basal part of the valley fill. The marine sandstones and claystones represent the estuarine top of the valley fill and mark the drowning of the valley, during peak highstand-conditions. The marine conglomerates derive from a ca. 1 m thick bed at the boundary between the fluvial and estuarine parts of the valley fill. In Berghuis et al. (2025a) we described the bed as a tidal lag deposit, mantling the transgressive surface. Vertebrate fossils were found to be associated with the fluvial sandstones and conglomerates and with the marine conglomerate.

OSL-ages are available from two samples of the excavated fluvial sandstones. One sample was taken from a block of uncrushed fluvial sandstone found on the reclamation site. Another sample was taken from the fluvial sandstone fill of the neural canal of a cervid vertebra found on the reclamation site. The found OSL-ages, of 162 ± 31 and 119 ± 27 ka, suggest that fluvial backfilling relates to the lowstand of MIS6 and the subsequent transgression in the run-up to MIS5. Valley incision probably relates to the preceding stage of falling sea-level, prior to peak lowstand conditions of MIS6 (Berghuis et al., 2025a). The change from fluvial to estuarine strata shows that, in the course of the transgression, the valley was invaded by the sea. A marine sandstone sample from the reclamation site, which was expected to be representative of this estuarine top of the valley fill, was OSL-dated to ≥ 462 ± 71 ka. This old and unexpected OSL-age suggests that the sample derives from a block of older sediment, which was hit upon by the dredger, or which had become reworked in the valley fill. It may for example originate from the marine sandstone top layer of the MIS10 valley fill that underlies the large MIS6 paleovalley (Fig. 2).

Table 1
The Madura Strait assemblage, total specimens and total identified specimens (NISP).

	Nr	%
Total specimens	6372	100
Total identified (NISP)	1212	19.02
Total unidentified	5160	80.98

3. Methods

The quantification of taxa and skeletal elements, as well as the analysis of post- and perimortem bone modification, were carried out in

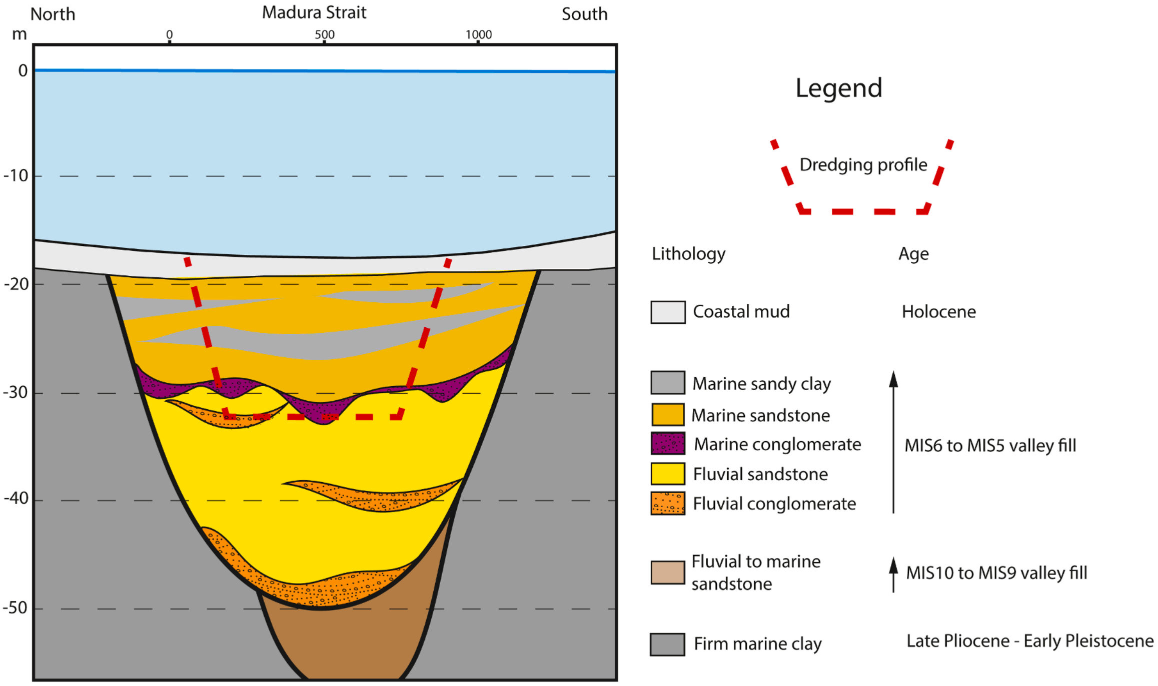


Fig. 2. Schematic cross-section of the Madura Strait paleovalley north of Surabaya. Based on deep drilling data of the Suramadu Bridge. For details, see Berghuis et al. (2025a).

the Geological Museum Bandung, which houses the assemblage. Whenever possible, we used published and commonly accepted procedures, classes and terminology, with references added. Quantifications have been expressed as NISP (number of identified specimens), MNI (minimum number of individuals) or MAU (minimum animal units), following the definitions of Binford (1981) and Lyman (1994).

Observations were made by the naked eye or by using a hand-held lens. Microscope or stereomicroscope analyses have, at this stage, not been conducted, as we aimed for the analysis of large numbers of specimens rather than a detailed inquiry of specific specimens.

Specimen sizes have been based on the measurement protocol provided by Von den Driesch (1976). Fragment sizes (mm) are the largest linear size of a specimen, measured in any direction. The size distribution analysis of the assemblage is based on a random subsample (N = 500).

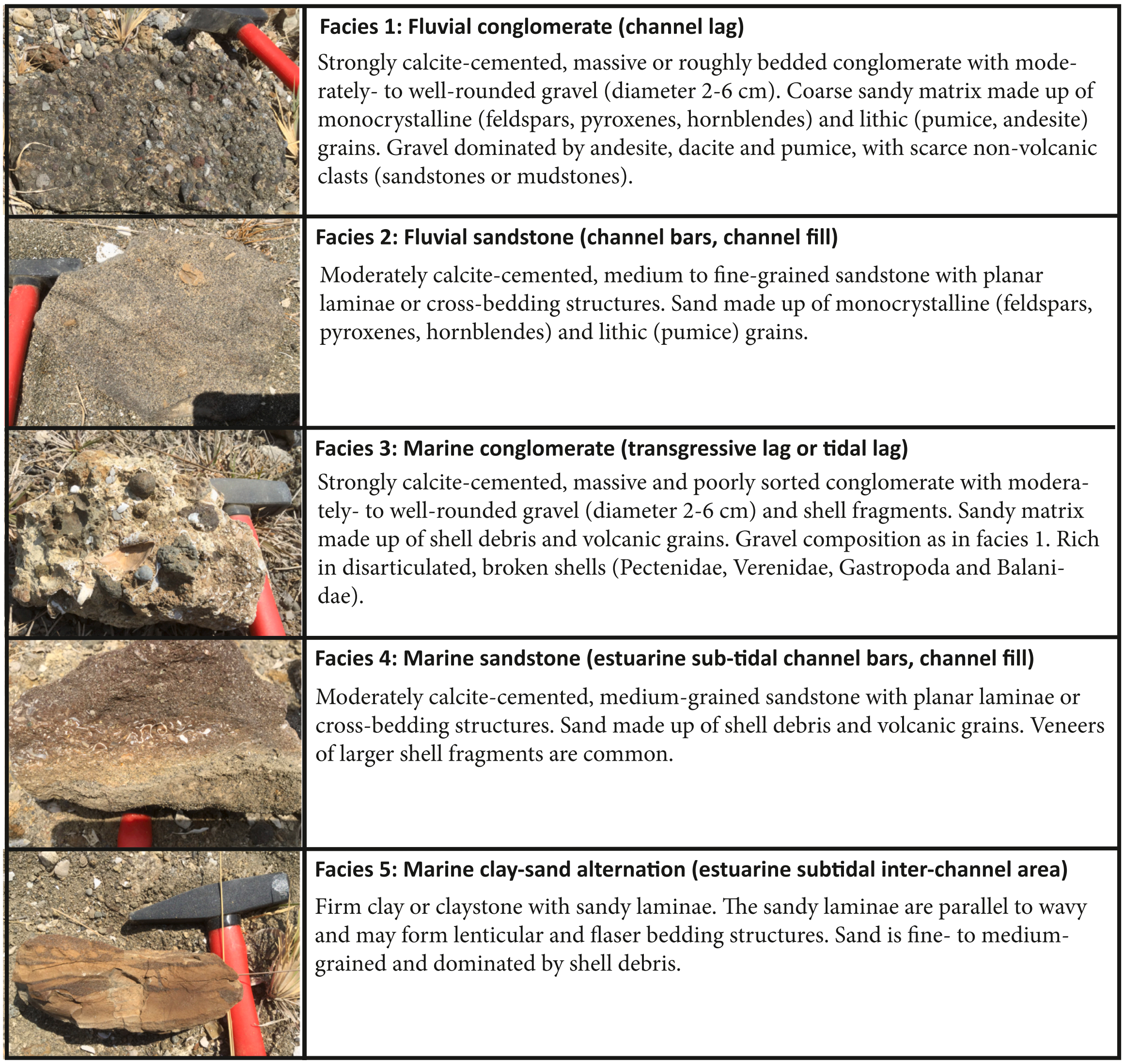
The weathering analysis follows the guidelines of Behrensmeyer (1978). The subdivision in 'weathering stages' has been based on an analysis of the cortical surface of long-bone shafts. Bone weathering rates differ among taxa, with the bones of smaller taxa being more susceptible to weathering. In our analysis, we only included bones of medium to large species. As weathering stages are indicative of surface exposure prior to fluvial uptake and deposition, we only included bone remains of terrestrial species. A difficulty is that the available shaft remains are strongly fragmented and that it is not always clear whether the fragments derive from a fluvial reptile or a terrestrial mammal. We randomly selected 100 shaft fragments from the assemblage, omitting material that has a reptilian morphology. We regard this as a representative sample of long-bone shaft fragments of medium to large terrestrial species. Note in this respect that among the entire assemblage, there is a dominance of skeletal remains of terrestrial mammals, whereas the remains of fluvial reptiles, other than turtle shells, are relatively scarce (Table 2). Looking only at postcranial bone remains, excluding dentition, horns, antlers or turtle shell, the ratio between the number of identified specimens of fluvial and terrestrial species is ca. 1:10.

Fracturing, fragment types and fracture morphology have been analyzed for long-bone remains from medium to large ruminants, which in the Madura Strait assemblage are mostly Bovidae or Cervidae. The analyses have been based on the criteria of Johnson (1985) and Villa and Mahieu (1991), distinguishing between spiral fractures, straight transverse fractures, straight diagonal fractures, longitudinal fractures and jagged fractures. The analyses of cylindrical shaft fragments and epiphyseal fragments have been based on all available specimens within the assemblage. Cylindrical fragments have two fracture faces, which have been counted separately. For the analysis of non-cylindrical shaft fragments, we selected a random subsample (N = 100). Following Villa and Mahieu (1991), only the proximal and distal sides of these non-cylindrical fragments were considered, thus giving two counts per specimen. Note that for these latter fragments, the assignment to ruminants has been based on cortical thickness, estimated shaft circumference and the presence of a well-developed medullar cavity. Undoubtedly, this sample is somewhat commingled with, for example, similar-sized hippopotamid or suid bone remains. However, referring to teeth and identified post-cranial remains, these taxa are much less common and it may confidently be assumed that they only form a minor part of the sample of the non-cylindrical shaft fragments.

The analysis of bone surface marks has been based on an inquiry of the entire assemblage, excluding the dental elements. The same applies for the analysis of marine bioerosion and encrustation.

A skeletal part analysis has been conducted for large Bovidae (Bovini) and Cervidae. For this purpose, the skeletal parts of individual species within these families have been lumped together. This is necessary, as not all skeletal parts were determined up to the same level of detail (Berghuis et al., 2025b). For example, bovid and cervid limb bones could often be identified to species or genus level based on metric analyses, but vertebrae were mostly assigned to Bovidea or Cervidae indet. Moreover, lumping skeletal parts in larger taxonomic groups creates more adequate sample sizes. Obviously, this obscures potential differences among the individual species in terms of biogeographic ranges, differential survivorship of skeletal parts or hunting / predation pressure. On the other hand, the composite samples are useful for exploring differential hydraulic transport of skeletal parts, or potential transport decisions of body parts by hominins.

An age-mortality profile could only be made for large bovids, as this is the taxon from which dental elements are available in sufficient



Facies 1: Fluvial conglomerate (channel lag)

Strongly calcite-cemented, massive or roughly bedded conglomerate with moderately- to well-rounded gravel (diameter 2-6 cm). Coarse sandy matrix made up of monocrystalline (feldspars, pyroxenes, hornblendes) and lithic (pumice, andesite) grains. Gravel dominated by andesite, dacite and pumice, with scarce non-volcanic clasts (sandstones or mudstones).

Facies 2: Fluvial sandstone (channel bars, channel fill)

Moderately calcite-cemented, medium to fine-grained sandstone with planar laminae or cross-bedding structures. Sand made up of monocrystalline (feldspars, pyroxenes, hornblendes) and lithic (pumice) grains.

Facies 3: Marine conglomerate (transgressive lag or tidal lag)

Strongly calcite-cemented, massive and poorly sorted conglomerate with moderately- to well-rounded gravel (diameter 2-6 cm) and shell fragments. Sandy matrix made up of shell debris and volcanic grains. Gravel composition as in facies 1. Rich in disarticulated, broken shells (Pectenidae, Verenidae, Gastropoda and Balanidae).

Facies 4: Marine sandstone (estuarine sub-tidal channel bars, channel fill)

Moderately calcite-cemented, medium-grained sandstone with planar laminae or cross-bedding structures. Sand made up of shell debris and volcanic grains. Veneers of larger shell fragments are common.

Facies 5: Marine clay-sand alternation (estuarine subtidal inter-channel area)

Firm clay or claystone with sandy laminae. The sandy laminae are parallel to wavy and may form lenticular and flaser bedding structures. Sand is fine- to medium-grained and dominated by shell debris.

Fig. 3. The five facies of the extracted material, based on uncrushed sediment blocks on the BMS reclamation site. (From: Berghuis et al., 2025a).

numbers to allow for this analysis. Just as for the skeletal part frequency analysis, we lumped together all available dental remains of Bovini. This creates a larger sample and makes it possible to include deciduous dentition, which could only be identified to family level. This procedure provisionally assumes that the individual bovid species were subject to similar mortality and that the timing of teeth eruption and wear was similar among the species. Our analysis has been based on four mandibular dental elements: DP_4, M_1, M_2 and M_3. We focused on crown height, which forms the most practical and reliable basis for age estimates (Klein and Cruz-Uribe, 1983; Voorhies, 1969; Kurtén, 1953). Given crown heights (CH) represent the distance between the base of the enamel and the occlusal face, measured at the anterior lobe along the buccal face. For mandible fragments with molars in place, crown heights were estimated.

4. Results

4.1. Assemblage description

The Madura Strait assemblage consists of 6372 specimens. It is dominated by small skeletal remains with linear sizes up to 80 mm (Fig. 4). As the specimens were hand-picked from the reclamation site (Berghuis et al., 2025b), without sieving or microscope analyses, the lower size limit of the available specimens is around 5 mm. In the size classes above 80 mm, abundances quickly reduce. Maximum specimen size is ca. 20 cm. This is below the grid size of 30/30 cm as used on the dredging head during sand excavation, which indicates that the maximum specimen size is not a sampling bias caused by the dredging process.

The fossils have been through strong diagenetic alteration. Bone remains have a dark brown to black colour and are heavily mineralized. The open spaces of cancellous bone are mostly filled with calcite. The fossils lack attached ferrous or calcareous concretions. The bone

Table 2
Vertebrate taxonomy Madura Strait assemblage, from: Berghuis et al. (2025b). Percentages are rounded to two decimal places.

Order	*Family*	*Species*	*NISP*	*%*	*Community*
Carcharhiniformes	Hemigaleidae	*Hemipristis serra*	5	0.41	Estuarine
	Carcharhinidae	*Glyphis gangeticus*	51	4.21	Estuarine
		Carcharhinus cf. *leucas*	20	1.65	Estuarine
		Galeocerdo cuvier	3	0.25	Estuarine
Myliobatiformes	Myliobatidae	*Myliobatis* sp.	1	0.08	Estuarine
		Rhinoptera javanica	3	0.25	Estuarine
	Dasyatidae	*Urogymnus polylepsis*	3	0.25	Estuarine
Batoidea*	Indet.		18	1.49	Estuarine
Siluriformes	Bagridae	*Hemibagrus* sp.	1	0.08	Estuarine
Squamata	Varanidae	*Varanus komodoensis*	2	0.17	Terrestrial
		Varanus salvator	2	0.17	Fluvial
	Pythonidae	indet.	1	0.08	Fluvial
Testudines	Geoemydidae	Geoemydidae indet.	102	8.42	Fluvial
		Batagur affinis	1	0.08	Fluvial
		Orlitia borneensis	1	0.08	Fluvial
	Tryonychidae	*Chitra chitra*	29	2.39	Fluvial
		Pelochelys cantorii	7	0.58	Fluvial
		Amyda cartilaginea	5	0.41	Fluvial
		Dogania subplana	6	0.50	Fluvial
	indet.		24	1.98	Fluvial
Crocodilia	Crocodylidae	*Crocodylus siamensis*	24	1.98	Fluvial
	Gavialidae	*Gavialis bengawanicus*	4	0.33	Fluvial
	indet.		4	0.33	Fluvial
Proboscidea	Stegodontidae	*Stegodon trigonocephalus*	31	2.56	Terrestrial
	Elephantidae	*Elephas* sp.	15	1.24	Terrestrial
	indet.		54	4.46	Terrestrial
Primates	Hominidae	*Homo erectus*	2	0.17	Terrestrial
	Cercopithecidae	*Macaca* sp.	1	0.08	Terrestrial
Carnivora	Felidae	*Panthera pardus*	1	0.08	Terrestrial
Perissodactyla	Rhinocerotidae	*Rhinoceros sondaicus*	27	2.23	Terrestrial
Artiodactyla	Hippopotamidae	*Hexaprotodon sivajavanicus*	30	2.48	Fluvial
	Suidae	*Sus brachygnathus*	14	1.16	Terrestrial
		Sus cf. *macrognathus*	2	0.17	Terrestrial
	Cervidae	*Axis lydekkeri*	36	2.97	Terrestrial
		Axis javanicus	17	1.40	Terrestrial
		Axis sp.	241	19.88	Terrestrial
		Rusa sp.	95	7.84	Terrestrial
	Bovidae	*Bubalus palaeokerabau*	101	8.33	Terrestrial
		Bos palaeosondaicus	129	10.64	Terrestrial
		Epileptobos groeneveldtii	4	0.33	Terrestrial
		Bovini indet.	88	7.26	Terrestrial
		Duboisia santeng	7	0.58	Terrestrial
Total			1212	100	

Note: the allocation to vertebrate communities is slightly arbitrary (see text).

* : Superorder. The specimens are possibly Myliobatiformes.

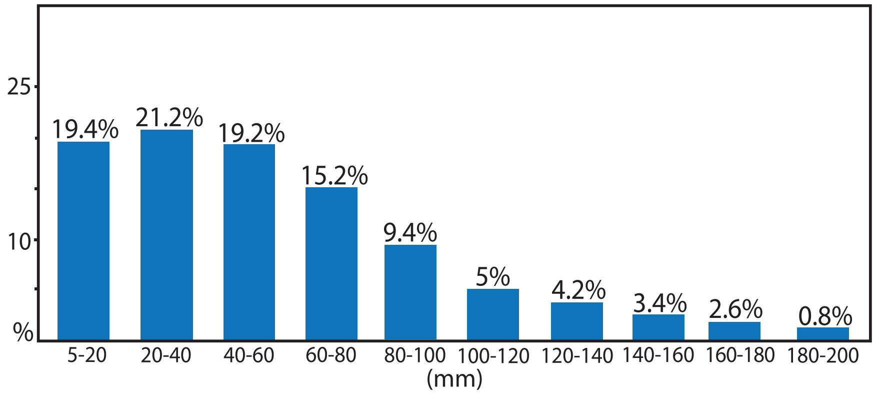


Fig. 4. Size distribution of the Madura Strait assemblage. Shown sizes (in mm) are the largest linear size of a specimen, measured in any direction. Analysis based on a random subsample (N = 500) from the entire assemblage.

fragments have a smoothly polished surface, which, in combination with their mineralized state, gives the material a shiny appearance. All-sided polishing of a fossil bone is generally associated with smooth abrasion by fine, moving sediment particles in flowing water (Behrensmeyer, 1988; Shipman and Rose, 1988). Note, however, that this abrasion must have been modest. None of the specimens may be referred to as rounded and the bone contours are always sharp, with well-recognizable articulations and protuberances.

Only around 4 % of the specimens is more or less intact. These are mostly dental elements or small and robust postcranial bones such as vertebrae, carpalia, tarsalia or phalanges. The other 96 % of the assemblage consists of fragmented skeletal material, mostly with multiple break surfaces. Approximately 19 % of the specimens could be identified to skeletal element and taxon, mostly to species or genus level.

A total of 36 vertebrate species was recognized, divided over 11 orders (Table 2). One of the conspicuous characteristics of the assemblage is its ecological mixture. In Berghuis et al. (2025b), we subdivided the species into three vertebrate communities: estuarine, fluvial and terrestrial. The allocation of species to these vertebrate communities is, in some cases, slightly arbitrary. Estuarine fish ascend rivers, whereas the fluvial reptiles also occur along the estuary. Likewise, terrestrial species come to the riverbank for water and food resources, while hippopotamids, added to the fluvial community, come on land at night for grazing.

4.2. *Weathering*

Weathering of bones gives an indication of their post-mortem surface exposure prior to burial. For the Madura Strait assemblage, this post-mortem weathering history varies between the species from different ecosystems. Skeletal remains from the estuarine community consist of shark and ray teeth and vertebrae of batoid fish. As may be expected from the aquatic living conditions, their fossil remains are always unweathered. Remains from the fluvial community consist of turtle shell fragments, crocodilian teeth and postcranial remains of fluvial reptiles and hippopotamids. The material is generally unweathered, although some specimens do bear traces of weathering. Such specimens may have become stranded on the riverbank, or they may derive from body parts that were taken ashore by predators (including hominins).

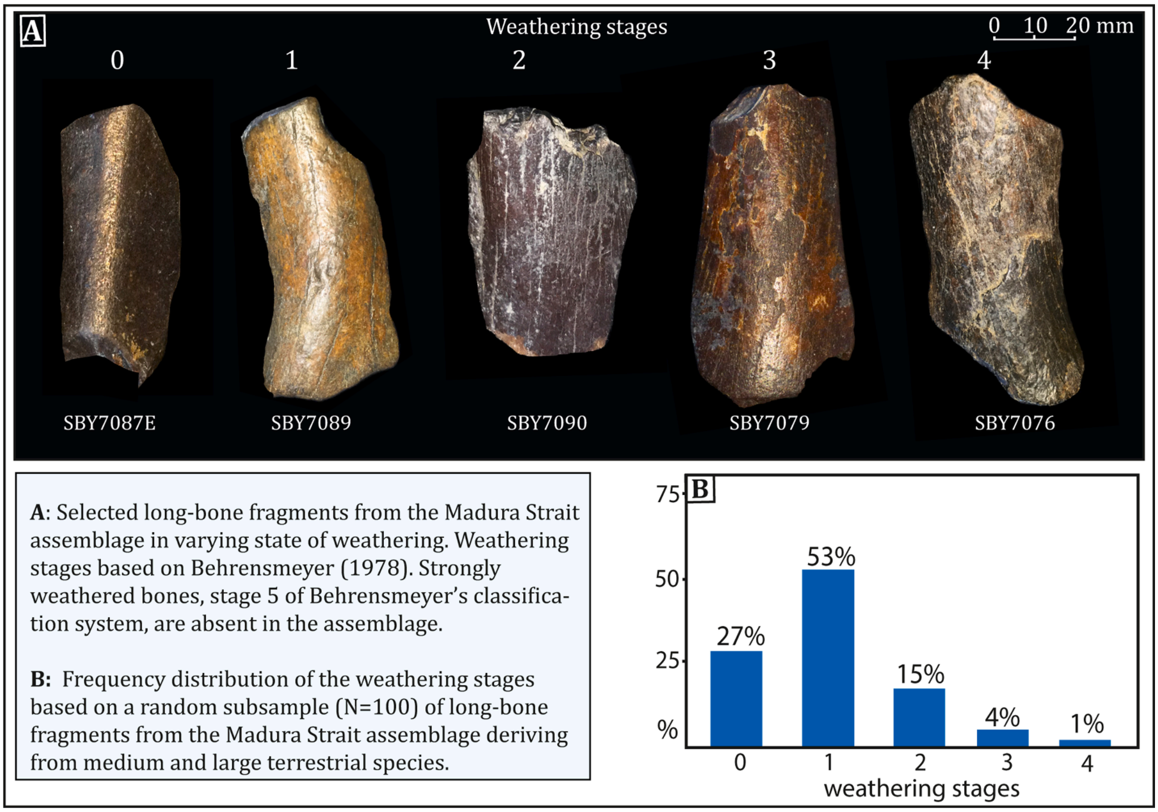
The analysed shaft fragments of medium to large terrestrial mammals are mostly unweathered or slightly weathered, most specimens falling in weathering stages 0 or 1 (Fig. 5). These are specimens with a smooth cortical surface or with few fine surface cracks. Ca. 20 % of the specimens show more drying cracks and exfoliation of outer bone layers and fall in weathering stages 2, 3 and 4.

4.3. *Fracturing*

The skeletal remains from the Madura Strait assemblage are highly fragmented. The vast majority of the fracture surfaces on the bone remains has the same dark colour and shiny, mineralized appearance as the bone's unbroken cortical surface, showing that breakage predates bone diagenesis. Recent fractures, related to the dredging process, are easily recognized by their light brown colour. Such recent fractures generally form minor damage only, such as broken tips or edges (Fig. 6).

Among the available long-bone fragments of medium to large ruminants, cylindrical shaft fragments are extremely scarce, only represented by 10 specimens, with preserved lengths of 3–14 cm. Epiphyseal fragments are much more common and represented by 60 specimens. These generally preserve a few centimeters of the adjacent shaft. Non-cylindrical shaft fragments are abundant, with a total of ~650 specimens. They generally preserve < 25 % of the shaft diameter and are elongated in outline, with a common W/L-ratio of ~0.4.

We analyzed the fracture morphology based on the criteria of Johnson (1985) and Villa and Mahieu (1991), distinguishing between spiral fractures, straight transverse fractures, straight diagonal (oblique) fractures, longitudinal fractures and jagged fractures (Fig. 6). Spiral fractures have a concave or convex outline and cut through the shaft with an angle of ~45 degrees with the axis of the shaft. Straight transverse fractures cut perpendicularly through the shaft. Straight diagonal fractures cut through the shaft with an angle of < 45 degrees with the axis of the shaft. Zooming in on the fracture, spiral and diagonal fracture faces run obliquely from the cortical surface to the medullar cavity, forming an acute or obtuse angle with the cortical surface. Straight transverse fractures run straight to the medullar cavity and form a right angle with the cortical surface. Fracture surfaces are smooth for spiral



A: Selected long-bone fragments from the Madura Strait assemblage in varying state of weathering. Weathering stages based on Behrensmeyer (1978). Strongly weathered bones, stage 5 of Behrensmeyer's classification system, are absent in the assemblage.

B: Frequency distribution of the weathering stages based on a random subsample (N=100) of long-bone fragments from the Madura Strait assemblage deriving from medium and large terrestrial species.

Fig. 5. Weathering analysis of long-bone fragments of terrestrial species, Madura Strait assemblage. See Section 3 for sample selection procedure. Weathering stages based on Behrensmeyer (1978).

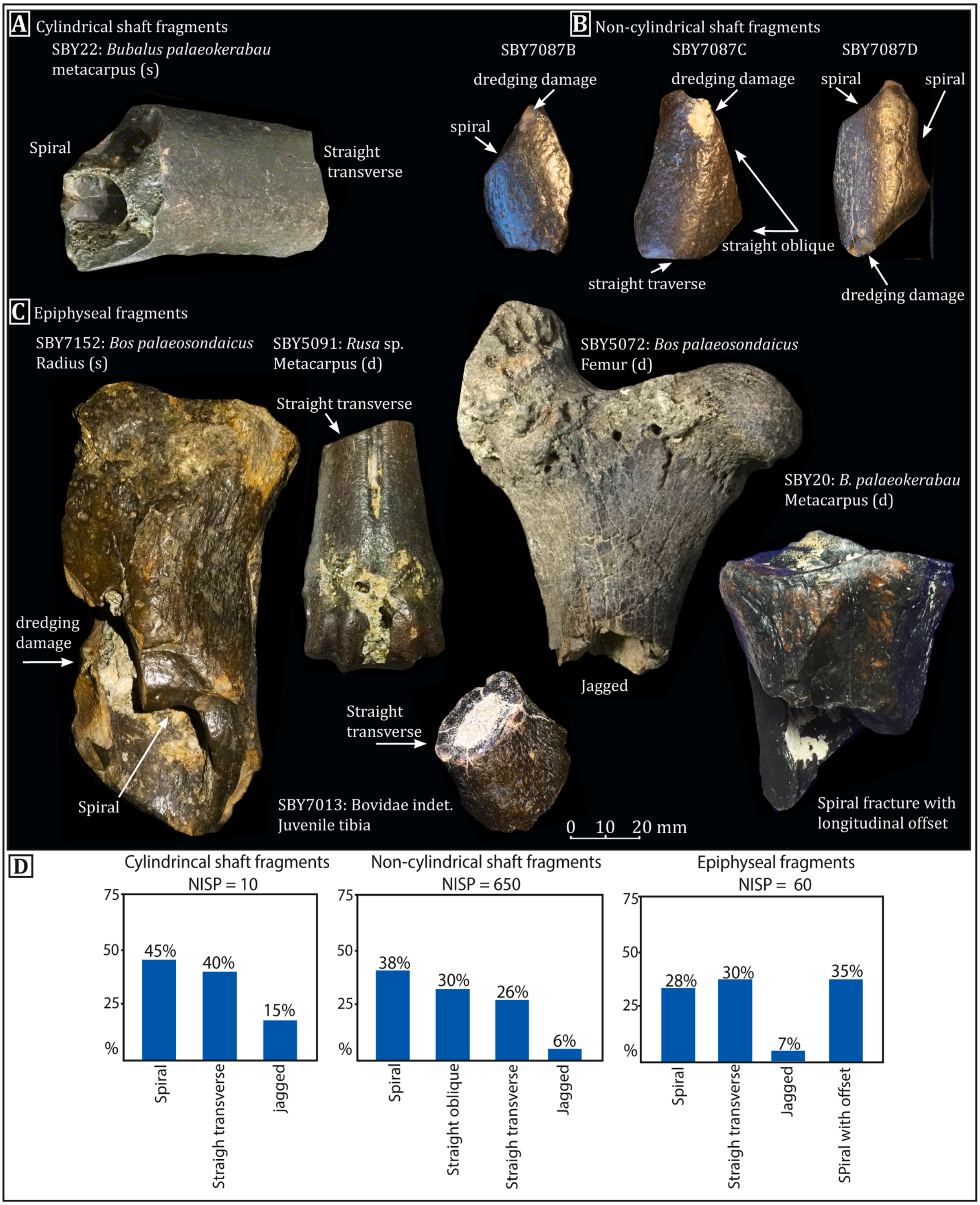


Fig. 6. Fracturing of long bones of medium to large ruminants, Madura Strait assemblage. **A-C:** Selected photographs of cylindrical shaft fragments, non-cylindrical shaft fragments and epiphyseal fragments. **D:** Fracture types for each of these fragment types. Fracture analyses based on all identified specimens (for cylindrical and epiphyseal fragments) and on random subsample of 100 specimens (for the non-cylindrical specimens).

and straight diagonal fractures, smooth and sharp for straight transverse fractures, and rough for jagged fractures.

Among the cylindrical fragments, there is a dominance of spiral and straight transverse fracture faces (Fig. 6D). Jagged fracture faces are uncommon. Fragments may have different fracture morphologies at either side. For example, bovid metacarpal fragment SBY22 (Fig. 6A) has a spiral fracture at the distal side and a straight transverse fracture at the proximal side. Also, among the epiphyseal fragments, spiral and straight transverse fractures are most common. Jagged fractures, with small right-angle offsets along the fracture face, are scarce and only observed in strongly weathered specimens such as the proximal bovid femur SBY5072 (Fig. 6C). A few specimens, such as the proximal bovid metacarpal SBY20 (Fig. 6C), have an intermediate fracture morphology, consisting of a spiral face with a longitudinal offset. The smaller shaft fragments have multiple fracture faces. Among the non-cylindrical shaft fragments, there is a dominance of spiral and straight oblique fractures.

The dominance of spiral and diagonal (oblique) fractures points to breakage in a fresh (green) state, while the bones were still moist, rich in collagen and contained marrow in the medullary cavity (Lyman, 1994; Villa and Mahieu, 1991; Johnson, 1985). The intermediate fractures, consisting of a spiral fracture face with a longitudinal offset, may be indicative of breakage after some drying had taken place, with a spiral fracture front hitting an incipient drying crack. However, it is also possible that breakage took place in a green state, with the longitudinal offset following the internal bone structure, as was noted specifically in metapodials by Blumenshine (1988). The rare occurrence of jagged fractures is in line with the low degree of weathering. Only rare, weathered bone elements may have stepped fracture faces, pointing to breakage of dry bone.

The frequent occurrence of straight transverse break surfaces does not comply with this model of fresh-bone breakage. Straight transverse fractures are sometimes associated with breakage of dry bone, but this is, in this case, not very likely, considering the fact that straight transverse breaks are observed in unweathered bone. They are, however, also common in bones that experienced incipient mineralization (Lyman, 1994; Johnson, 1985; Morlan, 1980). Note in this respect the sharp fracture face of SBY7013 (Fig. 6), which resembles broken glass rather than broken bone tissue.

4.4. Bone surface marks

4.4.1. Gnawing and chewing marks

Traces of gnawing by carnivores or rodents are rare. Among the sample of ruminant cylindrical shaft fragments, carnivore-gnawed edges are absent. Small-scale gnawing marks are observed on ca. 5 % of the limb-bone epiphyses, such as distal scapula SBY9 (Fig. 7). There are only

Fig. 7. Surface marks on bone fragments. Madura Strait assemblage.

two examples of more intense gnawing in the assemblage, which is the distal bovid femur SBY31 (Fig. 7), from which the epiphysis is gnawed off, with characteristic ragged edges along the distal margins (Jalvo and Andrews, 2016; Binford, 1981). Also the adjacent shaft of this specimen shows irregular scores. Several circular perforations resemble tooth punctures, but are recognized as *Gastrochaenolites* borings by their downward-increasing diameter (Section 4.5). The other bone fragment with intense gnawing traces is SBY7013 (Fig. 7), a juvenile bovid tibia from which most of the distal end has been gnawed off. This specimen also has some poorly preserved, rather coarse marks at the adjacent shaft, which may be carnivore or crocodile tooth pits but may also be hominin chop marks or percussion pits. Among the hundreds of smaller shaft fragments, we found no evidence of significant gnawing.

4.4.2. *Curved marks*

SBY7075 is a small rib fragment of unknown taxonomical origin. It has three shallow striations with a curved outline and a similar orientation, roughly parallel to the bone axis, and a length of around 20 mm (Fig. 7). Two scores have a width of ca. 1.5 mm, the third one (lowest on the picture) is slightly wider, but possibly consists of two superimposed scores. Curved striations are uncommon for human butchery or carnivore tooth dragging. However, they have been described from carcasses foraged by *Varanus komodoensis* (D’Amore and Blumenschine, 2009), crocodilians (Njau and Gilbert, 2016) and vultures (Fisher, 1995), all of which use repetitive, side-wards-directed strokes of the head when defleshing carcasses, which may produce curved marks.

4.4.3. *Linear marks*

Linear marks have been found on three specimens. SBY5067 is a sinistral mandible fragment assigned to *Bos palaeosondaicus*, which has fine, parallel linear marks running obliquely over the medial surface below the M_2 (Fig. 7). They have similar lengths of around 11 mm and a cross-sectional width of 1 mm. The marks have a V-shaped section, which is most clearly observed on the lowest mark on the mandible. Micromorphological details such as Hertzian cones or fine striations, within or directly beside the main cuts, are absent or not preserved. SBY517 is a sinistral scapula of a large turtle, with fine linear marks at its dorsal side, running parallel to the bone axis (Fig. 7). They have a length of 10 mm and a cross-sectional width of $<$ 1 mm. SBY650 is a rib from the sacral zone of a turtle. It has parallel linear marks at its ventral side, running parallel to the bone axis (Fig. 7). The marks are relatively short (4–8 mm) and wide ($>$ 1 mm).

Linear marks may be associated with trampling, carnivore tooth-dragging or hominin butchery (Jalvo and Andrews, 2016; Andrews and Jalvo, 1997; Fisher, 1995; Lyman, 1994). For the described specimens, a relation with trampling is unlikely, as trampling-related marks generally occur in greater numbers, as irregular scratches with varying orientations and lengths (Behrensmeyer et al., 1986). The V-shaped section of the marks, as well as their isolated occurrence lacking surrounding traces of carnivore gnawing or gripping, points to hominin butchery rather than carnivore foraging (Costamagno et al., 2019; Lyman, 1994; Shipman and Rose, 1988; Bunn et al., 1986; Binford, 1981). For the two turtle bones with linear marks, no direct equivalents are known from hominin butchery sites. However, their fine, V-shaped outline, parallel position and the absence of surrounding tooth scores are indicative of hominin butchery rather than trampling or carnivore-tooth dragging. Their longitudinal orientation probably reflects defleshing activity (Costamagno et al., 2019).

4.4.4. *Predator ingestion*

SBY5052 (Fig. 7) is a lower third molar of *Sus brachygnathus.* The molar is unworn and its occlusal morphology is well-preserved. However, it completely lacks its enamel cover. Note the difference with SB5079, a highly similar specimen but with enamel. The complete dissolution of enamel is indicative of a molar that passed the digestive tract of a predator, most likely a crocodilian (Fisher, 1995). SBY7080 (Fig. 7) is a shaft fragment, probably deriving from a small herbivore. It has rounded edges and a strongly polished surface that might relate to digestive etching by a carnivore or crocodilian (Andrews and Jalvo, 1997).

4.4.5. *Percussion marks*

The spiral and oblique fractures, as described for ruminant long bone fragments, point to intense, green-state fragmentation. This makes it relevant to search for indications of hominin battering, in the form of percussion pits, percussion notches with negative flake scars or impact flakes (Blumenschine and Selvaggio, 1988). Such features, however, appear to be scarce or disputable. A number of small shaft fragments, such as SBY7074 (Fig. 7), have small pits along the fracture edges, which might be regarded as impact pits. Note however that similar pits along fracture edges were attributed to trampling by Blasco et al. (2008) and to hyena mastication by Coil et al. (2020). Larger pits that may relate to percussion were only found on the bovid tibia SBY7013 (Fig. 7).

Some of the turtle shell fragments show semi-circular notches (indentations) along the fracture edges. Note, for example, SBY7165A and B, both being Geoemydidae carapace fragments (Fig. 7). They have semi-circular notches with diameters of 15 and 19 mm, which may relate to hammerstone breakage. However, they lack other characteristic features of hammerstone impact, such as a negative flake scar, or impact pits surrounding the notch. Another possibility is that the notches are crocodilian tooth punctures (Njau and Gilbert, 2016; Milan et al., 2011).

Specimen is SBY7210 (Fig. 7) is a Geoemydidae carapace fragment with ca. 3 mm wide, irregular grooves and scratches. These may be crocodilian tooth scores, but the marks may also have been caused by slippage of the turtle shell over a stone anvil during battering (Blumenschine and Selvaggio, 1988; Fisher, 1995).

4.5. *Marine bioerosion and encrustation*

A conspicuous taphonomic feature of the assemblage is the rich occurrence of small sub-circular boreholes of the trace fossil *Gastrochaenolites* (Leynerie, 1842). Among the bone remains with linear sizes over 30 mm, ca. 80 % of the specimens has been affected by this type of marine bioerosion. Dental elements and smaller bone specimens are mostly unaffected. The boreholes have an aperture of 2–4 mm and are oriented perpendicular to the bone surface. They continue downward into a circular or oval chamber, which is slightly wider than the aperture (Fig. 8).

The trace fossil is associated with rock-boring bivalves, mostly of the genera *Lithophaga* Röding, 1798 and *Gastrochaena* Spengler, 1783 (Kleemann, 1980). Both are common in Southeast Asian coastal waters and occur in the intertidal and subtidal zone. They make their borings in hard substrates, which may be rocky shorelines, coral, other shells and in rare cases fossil bones (Lopes, 2012). In several bone specimens from the Madura Strait assemblage, shell fragments of the boring bivalve have remained in the chamber.

The boreholes are generally found on all sides of the specimens, which shows that the specimens have been subject to rolling and reorientation by waves or tidal currents. The internal walls of the bored chambers are strongly mineralized and have the same dark color as the bone surface surrounding the boreholes, indicating that marine exposure and bioerosion predate diagenesis. Break surfaces, especially those exposing cancellous bone, are often particularly rich in boreholes, which shows that, at least in these cases, fragmentation preceded bioerosion.

Besides bioerosion, the Madura Strait bone remains show scarce traces of encrusting Ostreida Fërussac, 1822 and Cirripedia Burmeister, 1834 (Fig. 8). The ostreid and cirriped crusts are mainly found in sheltered cavities along the bone surface and along break surfaces. The thin and scarce shell crusts on the bones suggest that conditions at the sea bed did not allow for prolonged encrustation. This may relate to frequent remobilization of the bone fragments at the seabed (Taylor and

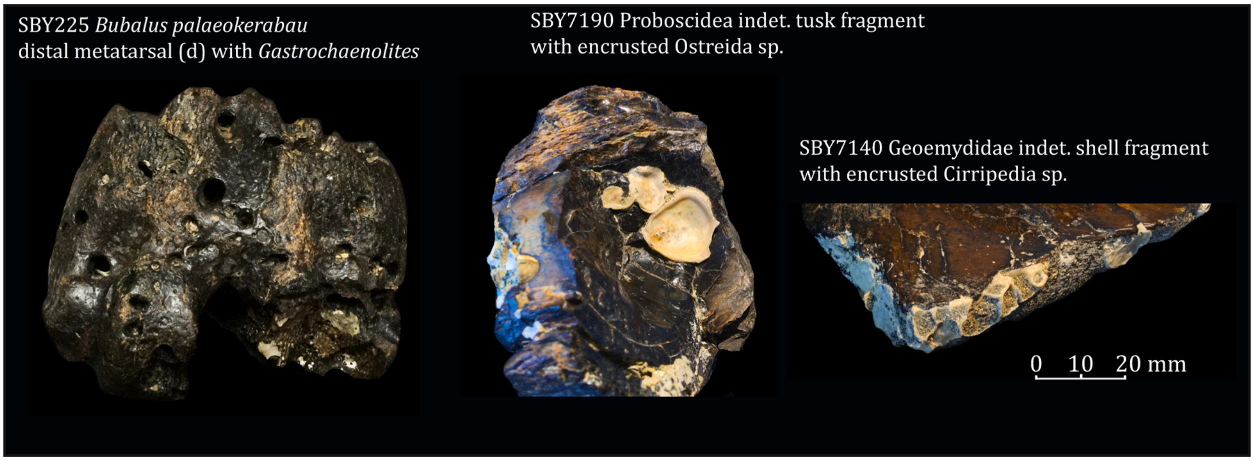


Fig. 8. Marine bioerosion and bioencrustation, selected photographs. Madura Strait assemblage.

Wilson, 2003). Cirriped shells are often damaged and partly eroded. Their shells have a calcite fill, indicating that marine encrustation predated diagenesis.

4.6. Skeletal part frequency

A skeletal part analysis has been conducted for large Bovidae (Bovini) and Cervidae. Skeletal parts have been expressed as NISP and, if possible, as MAU (minimal animal units), which is the minimum number of individuals (MNI) represented by specimens per skeletal part, without taking into account left or right position. For extensively mixed assemblages, MAU is a more useful unit than MNI. The use of MAU also has the advantage that it makes it possible to include elements for which the sidedness could not be determined. Moreover, for analysing the survival rates or susceptibility to hydraulic transport of individual skeletal elements, sidedness is not relevant.

Among the remains of Cervidae (Table 3) there is a dominance of antler fragments. Their abundance among the identified specimens is caused by fragmentation in combination with a characteristic morphology, which makes the material easy to recognize even in a fragmented state. Moreover, most of the antlers are shed antlers. From all available antler bases (N = 42), only 3 preserve a pedicle, indicating that these actually derive from dead individuals. This gives an MAU of only two, based on antlers with a pedicle.

Also for other cervid body parts, the representation as MAU is very low. Note the extreme scarcity of dental elements. Clearly, cervids only form a modest part of the death assemblage, an aspect that is masked by the great abundance of antler fragments. In this context, the high NISP of cervid astragali forms an anomaly.

Compared to Cervidae, the skeletal part frequency distribution of Bovidae fossil remains (Table 4) is more proportional to their anatomical distribution. Nevertheless, there are some relevant differences among the different body parts. Elements with high structural densities and low surface-to-volume ratios, such as molars, carpalia and tarsalia are dominant. Among the long bones, cylindrical shaft fragments are very scarce, whereas epiphyseal fragments are common. The survivorship of individual epiphyseal parts is proportional to bone density, with the distal humerus, proximal radius and distal tibia being the epiphyseal areas of highest structural density in bovids (Kreutzer, 1988). Phalanges are common within the assemblage, but expressed as MAU, their occurrence is low. The same accounts for vertebrae. For example, a total of 12 thoracic vertebrae only represents an MAU of 1.

4.7. Mortality profile of Bovini

An age-mortality profile could only be made for large bovids, as this is the taxon from which dental elements are available in sufficient numbers to allow for such analysis (Table 4). Fig. 9B plots the measured crown heights of all measured specimens. The DP_4 is only represented by 3 specimens, each in different wear stages. Their low occurrence compared to permanent lower molars reflects a scarcity of young individuals among the death assemblage. The available M_1 specimens occur in various wear stages, with a slight dominance of half-worn crowns. Among the M_2 and M_3, there is a clear dominance of unworn or slightly worn specimens, with rare occurrences of half-worn or strongly worn specimens. The M_3 erupts around the beginning of sexual maturity. Therefore, the large numbers of unworn or slightly worn M_3 specimens point to a dominance of prime-age (or young adult) individuals within the death assemblage.

To get an indicative insight into the age-at-death distribution, we converted the measured crown heights to age estimates, using the equation by Spinage (1973):

Table 3
Cervidae specimen counts per skeletal element, Madura Strait assemblage.

Antler, skull, dentition, vertebrae	*NISP*	*MAU*	*Forelimb*	*NISP*	*MAU*	*Hindlimb*	*NISP*	*MAU*	*Foot*	*NISP*	*MAU*
Antler base	*38*	19	Scapula distal	3	2				Phalanx 1	4	1
Antler shaft fr. / tine	*270*		Humerus prox.	-		Femur prox.	2	1	Phalanx 2	3	1
Antler with pedicle	*4*	2	Humerus shaft	-		Femur shaft	-		Phalanx 3	-	
Maxilla fr.	-		Humerus dist.	-		Femur distal	1	1			
Mandibula fr.	*2*		Radius prox.	1	1	Tibia prox.	-				
Deciduous dentition	-		Radius shaft	-		Tibia shaft	-				
Premolars	-		Radius dist.	-		Tibia dist.	3	2			
Molars	4	1	Ulna fragm.	-		Astragalus	14	7			
Cervical vertebrae	*11*	2	Carpalia	1	1	Other tarsalia	4	2			
Thoracic vertebrae	*6*	1	Metacarpus prox.	2	1	Metatarsus prox.	-				
Lumbar vertebrae	*12*	2	Metacarpus shaft	1	1	Metatarsus shaft	-				
Caudal vertebrae	-		Metacarpus dist.	2	1	Metatarsus dist.	-				

Table 4
Bovini specimen counts per skeletal element, Madura Strait assemblage.

Horn core, skull, dentition, vertebrae	*NISP*	*MAU*	*Forelimb*	*NISP*	*MAU*	*Hindlimb*	*NISP*	*MAU*	*Phalanx*	*NISP*	*MAU*
Horn core fr.	*25*		Scapula distal	5	3				Phalanx 1	10	2
Cranium fr.	*1*		Humerus prox.	-		Femur prox.	1	1	Phalanx 2	12	2
Maxilla fr.	*1*		Humerus shaft	-		Femur shaft	2	1	Phalanx 3	1	1
Mandibula fr.	*4*		Humerus dist.	12	6	Femur dist.	1	1			
Deciduous teeth	*4*		Radius prox.	6	3	Tibia prox.	1	1			
Premolar	23	4	Radius shaft	3	2	Tibia shaft	-				
Molar	82	6*	Radius dist.	7	4	Tibia dist.	10	5			
Cervical vertebra	*11*	2	Ulna fragm.	1	1	Astragalus	16	8			
Thoracic vertebra	*12*	1	Carpalia	16	4	Other tarsalia	9	3			
Lumbar vertebra	*12*	2	Metacarpus prox.	5	3	Metatarsus prox.	2	1			
Caudal vertebra	*1*	1	Metacarpus shaft	1	1	Metatarsus shaft	1	1			
			Metacarpus dist.	4	2	Metatarsus dist.	3	2			

* : Based on all 6 molar positions combined. Looking at individual molars, MAU = 10, based on 20 M_2 specimens.

$$\mathrm{Age}_{\mathrm{death}} = \mathrm{Age}_{\max} - 2(\mathrm{Age}_{\max} - \mathrm{Age}_{\mathrm{e}})(\mathrm{CH}/\mathrm{CH}_0) + (\mathrm{Age}_{\max} - \mathrm{Age}_{\mathrm{e}})(\mathrm{CH}^2/\mathrm{CH}_0{}^2)$$

in which,

- $\mathrm{Age}_{\max}$ is the potential ecological longevity or maximum ecological age;
- $\mathrm{Age}_{\mathrm{e}}$ is the eruption age of the measured molar;
- CH is the measured crown height;
- CH_0 is the unworn crown height.

The eruption ages and maximum ecological age have been estimated based on observations in domestic cattle (Silver, 1963), extant wild American buffaloes (Frison and Reher, 1970) and captive and wild *Bos javanicus* (Chaiyarat et al., 2023).

Estimated eruption ages:

M_1:	6 months
M_2:	18 months
M_3:	30 months
Maximum ecological age:	15 years

The unworn crown height has been set at 40 mm for the DP_4 and 70 mm for the three permanent lower molars, which is the average height of the available unworn crowns within the assemblage.

Fig. 9C plots the calculated ages at death for the individual dental elements. For the few DP_4 specimens in the assemblage, the converted ages are straightforward and similar to the age-estimating practice in extant domestic cattle. The unworn DP_4 (Fig. 9A) derives from a calf of less than 6 months. Mandible fragment SBY7149 (Fig. 9A), with a moderately worn DP_4 and an upcoming M_1, represents an age of ~ 6 months. The sample of M_2 and M_3 specimens, dominated by unworn or slightly worn specimens, reflects an age of death shortly after their eruption. Among the sample of lower molars, only a few specimens are strongly worn, which reflects a scarcity of mature individuals among the death assemblage. SBY157D, a strongly worn M_3 from which the posterior lobe has broken off (Fig. 9A), represents the oldest age-at-death of all analyzed teeth, with an estimated age of over 10 years.

The ages-at-death have been subdivided into three age groups, following the criteria of Stiner (1990). In this framework, juveniles are defined by the presence of deciduous dentition. Prime adults have fully developed permanent cheekteeth and are at the height of their reproductive stage. The old adults are characterized by a reproductive decline. The transition to old individuals has been set at 61 % of the estimated maximum ecological age, which is ~ 9 years (for an average maximum ecological age of 15 years). The individual ages-at-death for each of these age groups have been converted into percentages, which for the Bovini of the Madura Strait gives 30 % juveniles, 65 % prime adults and 5 % old adults. These values have been plotted on a triangular graph (Fig. 9D), again based on the methods of Stiner (1990) and with revisions by Bunn and Pickering (2010) and Discamps and Costamagno (2015). The corners of this graph correspond to strong biases toward each of the three age groups. The yellow zones in the central lower part of the graph demarcate the expected ranges of 'U-shaped' and 'living-structure' domains. The U-shaped domain represents attritional or natural mortality due to disease, malnutrition, accidents or predation focusing on the most vulnerable prey. The living-structure domain represents mass or catastrophic mortality. The Madura Strait Bovini form a prime-dominated death assemblage, plotting along the margin toward the living-structure mortality domain.

5. Discussion

5.1. Vertebrate communities, stratigraphic distribution, and taphonomy

The subdivision of the fossil assemblage into three vertebrate communities (Table 2) not only provides insight into past ecosystems, but is also relevant from a stratigraphic and taphonomic point of view. Skeletal remains from the three communities may have had a different distribution in their original stratigraphic context and may have been through different taphonomic pathways.

With respect to the stratigraphic distribution, it may be expected that the remains of terrestrial and fluvial species derive from the fluvial base of the valley fill, whereas the remains of estuarine species derive from the marine or estuarine sediment forming the top of the valley fill (Fig. 2). Ecological mixing would then have been caused by the dredging process. This, however, is clearly not the case. Fossils found as isolated specimens on the surface of the reclamation site often carry adhered sediment or have cavities filled with sediment, providing insight into their original sedimentary context. For most of the fossils of terrestrial or fluvial species, this adhered cemented sand contains shell debris, indicating that the specimens derive from marine or estuarine sediment. Relatively few fossils of terrestrial or fluvial species have adhered cemented sand made up entirely of volcanic grains, indicating that these derive from the fluvial lower part of the valley fill.

A better insight into the original stratigraphic distribution of the fossils is offered by the blocks of uncrushed sediment on the reclamation site. These show that vertebrate fossils are associated with fluvial sandstones, fluvial conglomerates and marine conglomerates (Facies 1–3, Fig. 3). Each of these three fossil-bearing facies contains disarticulated and mostly fragmented remains of terrestrial and fluvial species. The marine conglomerate clearly forms the richest fossil-bearing facies. Almost all observed blocks of this material contain fragmented vertebrate skeletal elements, which are randomly dispersed through the sediment, with no preferred orientation.

There is, however, an obvious but highly relevant taphonomic difference between the vertebrate remains embedded in the different facies: most bone remains in the marine conglomerate are affected by marine bioerosion, whereas this is never the case for material embedded in the fluvial sandstone or conglomerate. This makes marine bioerosion an important and easy-to-observe taphonomic signature of material deriving from the marine conglomerates. Around 80 % of the larger

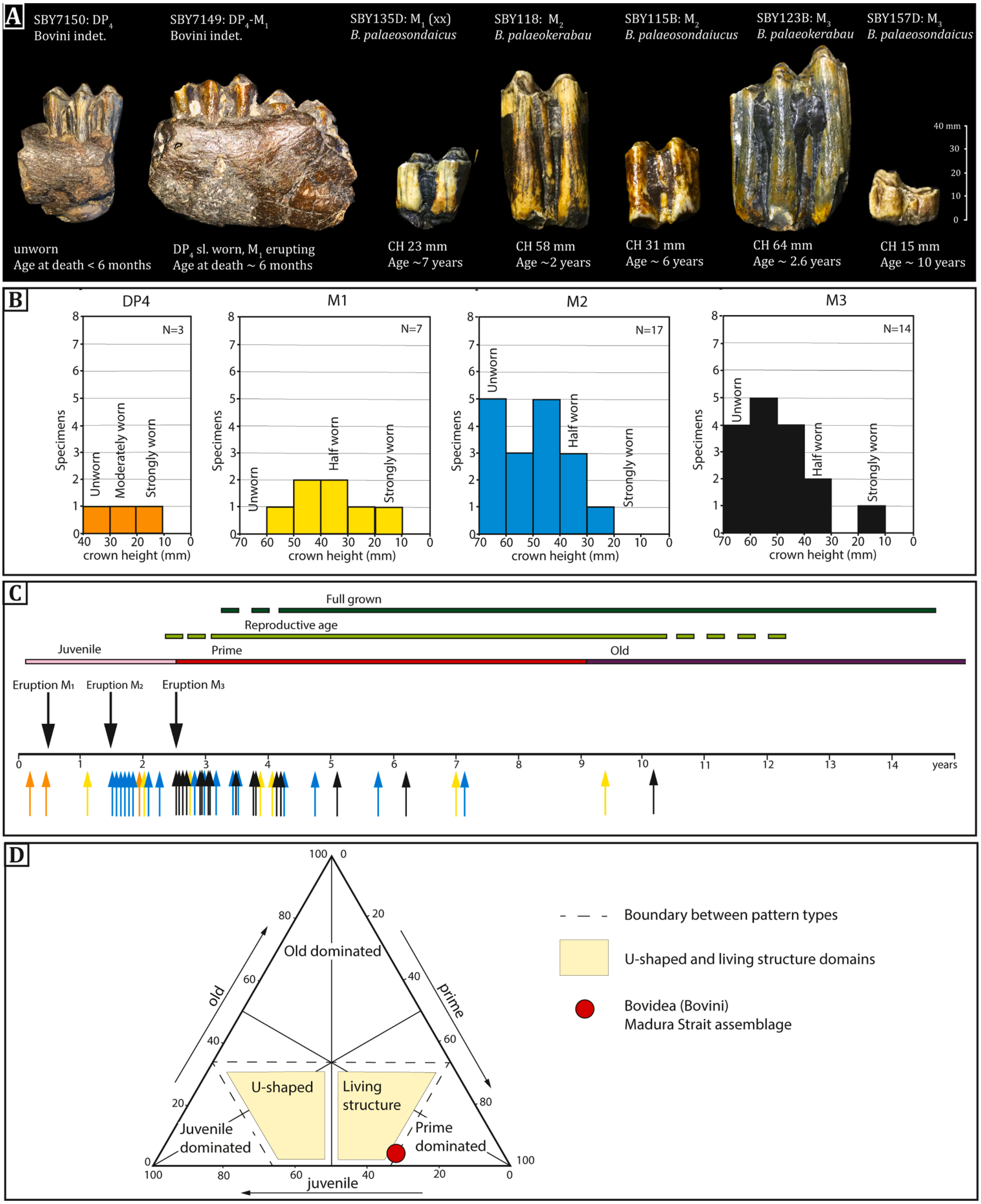


Fig. 9. Mortality profile of Bovini. Madura Strait assemblage. **A:** Selected mandibular dental elements in various wear stages, with age estimates. **B:** Crown height plots for the four investigated tooth positions. **C:** Plotted calculated ages for the individual mandibular dental elements. Colors of the arrows refer to the colors used for the individual dental positions as used in the crown height plots (B). **D:** Triangular graph of Bovini mortality.
Graph based on Stiner (1990).

bone remains that were found as loose specimens on the reclamation site bear traces of marine bioerosion, indicating that this material derives from the marine conglomerate. Dental elements and smaller bone fragments are mostly free of marine bioerosion, but this relates to their unsuitability as a substrate for bivalve boring or encrusting. It may therefore be assumed that around 80 % of all fossils from terrestrial and fluvial species derives from the marine conglomerate and only 20 % from the underlying fluvial sandstones and conglomerates.

It is obvious to assume that the fossil remains of estuarine species derive from the estuarine deposits that form the top of the valley fill. However, this could not be confirmed at the reclamation site, as no fossil remains were observed in blocks of estuarine sandstones and clays

(Facies 4 and 5, Fig. 3). This sediment is, on average, less cemented than the marine conglomerate and the underlying fluvial sandstones and conglomerates, and consequently was more thoroughly crushed during dredging. Unexpectedly, the fossil remains of estuarine species are free of marine bioerosion, which at least partly may be explained by the teeth-dominated composition of this material.

5.2. *Transport, accumulation and concentration*

5.2.1. *Terrestrial and fluvial species*

Based on the observations mentioned above, we infer that the collected fossils of terrestrial and fluvial species derive from the top of the fluvial valley fill, just below the transition to estuarine deposits, and from the overlying marine conglomerate bed, which marks the transition between fluvial and estuarine deposits (Fig. 2). We estimated that ca. 80 % of the specimens derive from the marine conglomerate bed. In both stratigraphic levels, fossils are disarticulated, fragmented and polished. Break patterns point to a dominance of green-state fragmentation.

Fresh bones do not easily break during hydraulic transport (Behrensmeyer et al., 1979), which indicates that green-state fragmentation predates hydraulic transport. The skeletal material must, therefore, have already been fragmented and disarticulated, when it was taken up by the river. The material was probably washed into the river from the floodplain. During subsequent hydraulic transport, the material must have become subject to size sorting, explaining the modest size of the available fossil material, dominated by specimens with linear diameters < 100 mm (Fig. 3) (Pante and Blumenschine, 2010).

The skeletal remains probably stranded on river banks or bars, or became trapped in channel lags, and were subsequently buried by fluvial sediment under conditions of late Middle Pleistocene base-level rise. The skeletal remains in the marine conglomerate may have a similar background of fluvial transport into the estuary and accumulation in tidal channels. However, effective transport of gravel and bones is unlikely in a lowland river, in its slow-moving transitional reach toward the estuary. Transport of skeletal remains in this river reach may have occurred during a catastrophic high-discharge event. But under such conditions, we would expect floating carcasses to be swept to the estuary (Mallon et al., 2018; Brongersma-Sanders, 1957), which contrasts with the fragmented state of the skeletal remains in the marine conglomerate. There is, however, a more likely mechanism for the concentration of vertebrate fossils in the marine conglomerate. In Berghuis et al. (2025a) we identified the bed as a lag deposit, mantling a transgressive surface. Transgression surfaces are often associated with scour by waves and tidal currents, leaving a transgressive surface mantled with a coarse lag of fragmented shells and locally eroded material. In case of a transgression into an incompletely filled incised channel, such transgression-related scour is mainly caused by tidal currents, which are amplified as they become compressed in the drowned valley. Estuarine scour during this initial stage of valley drowning is sometimes amplified by the inability of fluvially supplied sediment to keep pace with the rising sea level: as more sediment is trapped in the lower reaches of the drowning river, sediment input into the estuary is reduced, which may lead to abrasion of previously deposited material (Cattaneo and Steel, 2003; Dalrymple, 1992). Marine abrasion surfaces with fossil-rich lags eroded from the underlying strata have been described from various sites worldwide (Rogers and Kidwell, 2000; Smith and Kitching, 1997; Wells, 1944; Krumbein, 1942). Among such marine fossiliferous lags, tidal scour surfaces over previous fluvial strata have been described as the most productive bone beds (Rogers and Kidwell, 2007).

Our interpretation of the marine conglomerate as a lag deposit covering a tidal scour surface readily explains its high fossil concentration, as well as its exotic facies, as a mixture of fluvial gravel, terrestrial vertebrate fossils and marine shell fragments. It also explains the common occurrence of bivalve borings in the bone remains of the marine conglomerate bed, as this turbulent reworking stage must have been a stage of non-deposition, in which the exhumed skeletal remains were exposed at the sea bed and became colonized by boring and encrusting bivalves.

This taphonomic pathway of temporary burial in fluvial deposits, followed by exhumation and concentration in a tidal lag deposit, also provides an explanation for two other taphonomic features of the Madura Strait assemblage: the polished appearance of the bone remains and the occurrence of straight transverse breaks. Although polishing of bones may relate to fresh-state hydraulic transport, it has often been associated with abrasion of bones in a pre-mineralized state (Rogers et al., 2010; Andrews and Jalvo, 1997; Behrensmeyer, 1988; Morlan, 1980). A similar thing applies to straight transverse breaks. These are highly uncommon in bones fractured in a fresh state. They are sometimes found in bones broken in a weathered state, but are most common in bones broken in a state of incipient fossilization (Lyman, 1994; Johnson, 1985; Morlan, 1980).

5.2.2. *Estuarine species*

The fossil remains of estuarine species must have gone through a different process of accumulation. The fossils, consisting of shark teeth, stingray teeth and batoid vertebral centra, probably occurred as occasional, isolated elements dispersed through the estuarine deposits and may be regarded as an autochtonous, attritional accumulation of fish remains, which Kidwell (1986) referred to as the ‘normal rain of body parts on the seafloor’. This accumulative background also explains the absence of bioerosion, as boring or encrusting bivalves require turbulent bottom conditions, in order to prevent the bored substrate from becoming buried. This attritional accumulation model is supported by two other observations: the fossil remains of estuarine species are mostly unfragmented and unpolished. These relevant taphonomic features are somewhat obscured by the dominance of small, robust and shiny elements as shark teeth, but looking only at batoid vertebral centra, their intact and mostly unpolished state, together with the already mentioned absence of marine bioerosion, forms a relevant contrast with the available bone remains of fluvial and terrestrial species.

Attritional accumulation of fish body parts in the estuary implies that these remains may also occur in the transgressive lag, in which case these are elements that were added to the lag during the reworking stage. Moreover, some species of the estuarine community actually have a mixed estuarine and fluvial habitat. For example, the Ganges shark *Glyphis gangeticus* and the giant stingray *Urugymnus polylepis,* spend most of their life in lowland rivers. Their remains may, therefore, also be expected in the fluvial strata, and may also have been subject to reworking during the transition to estuarine conditions. This potentially long stratigraphic range probably (partly) explains the large numbers of *Glyphis gangeticus* teeth in the assemblage.

5.3. *Age and homogeneity of the assemblage*

A relevant question is, how does this complex taphonomic pathway affect the age and homogeneity of the assemblage? The two OSL-dated sandstone samples were collected on the reclamation site. Referring to the dredging profile, they must derive from the top of the fluvial series, directly below the transgressive lag (Fig. 2). Within the proposed model of fossil accumulation and enrichment, all fossil remains of terrestrial and fluvial species in the assemblage were initially buried in this fluvial sediment, although most of the fossils were subsequently reworked in the marine lag. One of the dated sandstone samples derives from the sandstone fill of the neural canal of a cervid vertebra, directly linking the sampled material to fossil embedding. The obtained OSL-ages, of 162 ± 31 and 119 ± 27 ka, are therefore representative for the age of initial burial, at least for the skeletal remains of terrestrial and fluvial species.

This does not necessarily imply that the OSL-ages are also representative of the ancient environment in which the species lived. In previous papers (Pop et al., 2023; Hilgen et al., 2023; Berghuis et al., 2023, 2022, 2021), we noted that the on-land vertebrate fossil sites of

Java, such as Trinil, bear evidence of multiple cycles of fluvial erosion and sedimentation, resulting in complex and often mixed-age fossil assemblages, either as a result of reworking or uncontrolled fossil collecting. However, these Javanese sites represent upstream fluvial settings, which were characterized by variable and often short-duration fluvial responses, not only to sea-level fluctuations but also to uplift, volcanism, sediment availability and changing local drainage systems. It is reasonable to assume that the Sundaland plains offered more stable conditions, with large lowland rivers that responded primarily to sea-level fluctuations. The OSL-ages link the fluvial sediment in which the fossils were embedded to the lowstand of MIS6 and the subsequent stage of rising sea-level in the run-up to MIS5 (Fig. 10**A**). The preceding

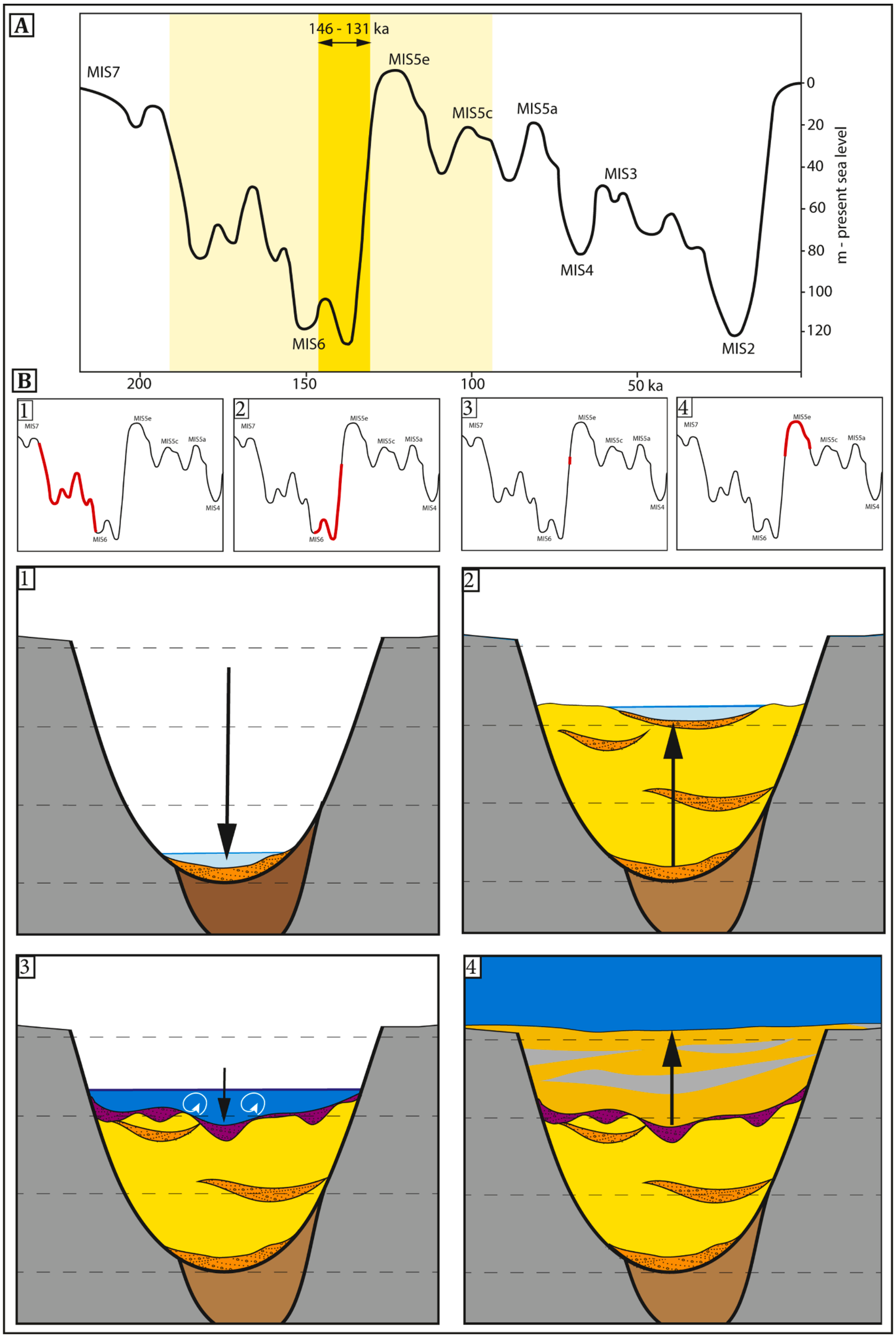


Fig. 10. Development of the Madura Strait paleovalley in relation to the sea-level curve. A: The late Middle Pleistocene and Late Pleistocene sea-level curve (from: Bintanja and Van der Wal, 2008) with projected range of the two available OSL-ages of the fluvial sandstones, including their error margins. OSL-ages are 162 ± 31 and 119 ± 27 ka (Berghuis et al., 2025a). The overlapping age (146 – 131 ka) is the most likely age range of fluvial back-filling. B: Four stages of valley incision and backfilling and their relation to the sea-level curve. For legend: see Fig. 2. 1: Valley incision under conditions of falling valley sea-level preceding MIS6. Note nesting in older valley fill. 2: Fluvial backfilling under conditions of rising sea-level preceding MIS5, accumulation of vertebrate fossils from terrestrial and fluvial species. 3: Drowning of the valley and temporary tidal scour. Fossils embedded in the fluvial sandstones become concentrated in a marine lag. 4: Estuarine deposition during MIS5e highstand conditions. Attritional accumulation of skeletal remains of estuarine fish.

incision of the valley is probably related to the stage of falling sea-level prior to MIS6 (Fig. 10**B, situation 1**). This incision is partly nested in the fill of an older incised valley (Fig. 2). Reworking of fossil material from this older valley fill cannot be excluded, however, such reworked older fossils may be expected in the basal lag of the MIS6 paleovalley, which lies at 50 m -MSL, almost 20 m below the maximum depth reached by the dredging work. It is not very likely that reworked fossils from this older valley fill have become mixed in these higher fluvial layers. Assuming that the stage of rising sea-level offered stable conditions of fluvial backfilling, the skeletal remains in the fluvial sediment may be regarded as a homogeneous fauna, with an age that is contemporary to the age of burial. The OSL-age of the fluvial strata, and thus the age of the environment in which the species lived, may be narrowed to 146 – 131 ka, which is the overlapping interval of the two OSL-ages and their margins (Fig. 10A). This 'most likely age range' fits well with the proposed model of valley-aggradation and valley drowning, as it overlaps with the stage of rising sea-level between MIS6 and MIS5 (Fig. 10B, situation 2).

The fossils occur dispersed through the top of the fluvial series. In theory, it is possible that the fossils derive from a single death event and that stratigraphic dispersal is a result of diffusion during fluvial transport. But it is more likely that the stratigraphic dispersal reflects a steady or intermittent supply of skeletal remains to the river over a longer period, with a most likely age range of 146 – 131 ka. In sections 5.5 and 5.6 we will go deeper into this subject, with a discussion of mortality patterns.

Exhumation and concentration of fossils in the marine lag are associated with subsequent valley drowning, which changed the valley into an estuary. Fluvial aggradation and valley drowning were part of the same transgression, which implies that the period of initial burial, prior to marine reworking, must have been short. In any case, drowning of the valley and the associated stage of marine reworking must have predated peak highstand conditions of MIS5e, which implies that the marine conglomerate is slightly older than 123 ka (Fig. 10B, situation 3). Its vertebrate content of terrestrial and fluvial species, which was reworked from the underlying fluvial strata, may still be regarded as homogeneous, within the most likely age range of 146 – 131 ka.

The fossil remains of estuarine species must be slightly younger. This material derives from the estuarine sand and clay that make up the top of the valley fill and which are associated with peak MIS5e highstand conditions, dating to around 123 ka (Fig. 10B, situation 4). As we regard these fossils as an attritional accumulation of fish remains on the sea bed, their age must be equal to the age of the surrounding estuarine sediment.

5.4. *Bone diagenesis*

The bone remains are evenly mineralized on all sides, without observable colour differences between the bone's cortical surface, break surfaces and the internal walls of marine borings. Bone diagenesis must, therefore, relate to final burial, which for the material from the marine conglomerate implies after the reworking stage.

It is interesting to look in more detail at the strong mineralization of the fossil material. Bone diagenesis involves recrystallization of calcium phosphates into a more stable mineral phase, replacing phosphates by carbonates, fluorides and chlorides. Additionally, Ca^{2+} may be substituted by Fe^{2+}, U^{4+}, Zn^{2+} or Mn^{2} (Keenan, 2016; Pfretzschner, 2004). The good preservation of Pleistocene bones from the Javanese sites probably relates to their embedding granular volcanic material, which provided ion-rich diagenetic fluids.

The embedding in granular sediment of volcanic origin must also have contributed to the strong mineralization of the Madura Strait fossils. Moreover, the sub-marine setting of the site (at least during MIS1 and MIS5) and the embedding of the fossils in or directly below marine sediment may have further increased the availability of dissolved minerals in the circulating porewater. Another relevant difference with most of the on-land sites of Java is that the Madura Strait site has probably been under continuous water-saturated conditions, whereas most of the on-land sites of Java have been under intermittent water-saturated and dry conditions. These intermittent oxidizing conditions frequently left coatings or concretions on the fossils from the Javanese sites, which are absent on the fossils from the Madura Strait.

5.5. *Weathering and fluvial uptake*

The scarcely weathered state of the bone remains of terrestrial species shows that the material was taken up by the river shortly after the animals' death. Most bone remains fall in weathering stages 0 and 1. Behrensmeyer (1978) estimated that weathering stage 0 reflects a surface exposure time of less than one year, whereas weathering stage 1 may represent one to three years of surface exposure. Her estimates were based on African savanna conditions, which may have been similar to the savanna-dominated Middle Pleistocene plains of Sundaland.

Behrensmeyer (1978) also noted that long-term attritional accumulations are usually mixtures of variably weathered material, whereas a dominance of a single weathering stage is indicative of increased or catastrophic mortality. The dominance of unweathered bones in the Madura Strait assemblage may, in that respect, be regarded as an indication of increased or catastrophic mortality. However, as noted in Section 5.3, the dispersal of fossils through the fluvial valley fill rather points to a steady or intermittent supply of skeletal remains to the river during a longer period. This may be explained by a steady supply of skeletal remains in relation to cyclic stages of climate-induced mortality and fluvial uptake. The regional late Middle Pleistocene climate was characterized by a long dry season and a short rainy season, with a high variation in river discharge (Sémah et al., 2010). At the end of a long dry season, animals must have congregated along the river as the last resource for food and water. Under such conditions, we may expect an increased, drought-related mortality, resulting in a high accumulation rate of bones on the floodplain. These could readily be taken up by the river during the subsequent rainy season, supplying a new load of scarcely weathered bones to the river system.

5.6. *Mortality and evidence of selective hunting*

The model of increased, drought-related mortality at the end of dry seasons, followed by fluvial uptake in the rainy season adequately explains the steady accumulation of scarcely weathered bones in the fluvial valley fill. However, this is not in line with the age-at-death frequency distribution of the available bovid molars. Under conditions of drought, a U-shaped age distribution is expected, with an overrepresentation of very young and very old individuals, being the age classes most susceptible to ecological mortality, and an underrepresentation of reproductively active adults. The age-frequency distribution of large bovids from the Madura Strait assemblage is not U-shaped, but prime-dominated (Fig. 9C and D). Prime-dominated mortality patterns are uncommon under natural conditions, because they are in contrast with the structure of a living population and with age-specific vulnerability within such populations. Humans appear to be the only species to regularly produce prime-based mortality in prey (Marin et al., 2017; Driver and Maxwell, 2013; Stiner, 2013, 2009, 1990; Speth and Clark, 2006; Gaudzinski and Roebroeks, 2000; Steele, 2003). As such, prime-dominated mortality is a strong indicator for selective hunting.

However, care must be taken with this interpretation. The mortality signal may for example have been biased by taphonomic factors, such as a low preservation of deciduous dentition (Munson and Garniewicz, 2003) or differential transport of dental elements of different size, shape or weight (Bunn and Pickering, 2010). Indeed, we showed that the Madura Strait assemblage probably represents a period of several thousand years and has been subject to fluvial and dredging-related mixing. Moreover, the bovid dental elements probably do not represent a single kill, but may rather represent a longer period, with repeated hunting and butchery events. Under such conditions of time averaging, the signal of repeated prime-dominated kills is likely to have become overprinted by a normal, ecological mortality signal, which makes the persistence of a prime-dominated signal even more relevant. The Madura Strait age-at-death distribution of bovids, which is prime-dominated, but plotting toward the living structure domain (Fig. 9D), may very well be explained by this overprint of ecological mortality.

There is, however, another strong argument in favor of a hunting-related mortality, and against a drought-related catastrophic mortality, which is the intensely green-state fragmented state of ruminant limb-bone shafts, together with the high representation of intact, ungnawed epiphyses (Section 5.7).

5.7. *Marrow processing*

The fracture patterns in the limb bones of cervids and bovids testify to two fracturing stages: a first stage shortly after death, when the bones were still fresh and rich in collagen, and a second stage during marine reworking, when the bones were in a pre-mineralized state. Referring to the morphology of small shaft fragments, with a dominance of oblique and spiral fracture faces, the extensive fragmentation of ruminant long-bone shafts is linked to the first fracturing stage. As explained in Section 5.2.1, this fresh-state fragmentation must have taken place before fluvial uptake. Potential breaking agents are trampling, predator mastication or hominin battering. With the congregation of herds of large herbivores along the river during the dry season, it is well-imaginable that skeletal remains have become subject to trampling. Trampling is generally associated with randomly oriented scratch marks (Andrews and Jalvo, 1997; Fisher, 1995). These have not been observed. Their absence is not a strong argument against trampling as a breaking agent, as surface marks have been poorly preserved on the polished Madura Strait bones. A more relevant argument that speaks against trampling is that robust bovid limb bones are only vulnerable to trampling in a weathered state (Lyman, 1994). Fresh, collagen-rich bovid bones may occasionally have been broken by trampling, for example by passing herds of proboscideans, but it is unlikely that this caused green-state fragmentation of virtually all limb bone shafts.

Looking at predator mastication, only hyenids are capable of large-scale fragmentation of bovid long bones (Palmqvist et al., 2011; Diedrich, 2012). They feed on the spongy, fat-containing cancellous bone of epiphyses and may crack long-bone shafts to consume marrow. Hyenids were common on the Asian mainland during most of the Pleistocene. Among these was the giant hyena *Pachycrocuta brevirostris* (Dennell, 2008; Boaz et al., 2004; Turner and Antón, 1996). The species went extinct in Asia in the course of the Middle Pleistocene and was gradually replaced by the extant spotted hyena *Crocuta crocuta* (Kurtén, 1956). In the late Middle Pleistocene, this new species also inhabited the southern part of the Asian mainland, with reported fossil finds from southern China (Defen and Chunhua, 2016), Thailand (Suraprasit et al., 2016) and the Taiwan Strait (Tseng and Chang, 2007). However, hyenids are extremely rare in the fossil assemblages from Java. There are few reported finds of *Pachycrocuta brevirostris* (Geraads, 1979; Hooijer, 1964; Brongersma, 1937), which are probably of early Middle Pleistocene age. Its successor *Crocuta crocuta* is unknown from Java. Among the rich late Middle Pleistocene faunal assemblage from Ngandong, hyenid material was not found (Volmer et al., 2016; Von Koenigswald, 1935), which suggests that *C. crocuta* did not disperse this far southwards and may even have been absent on Sundaland (Louys, 2014). Also in the Madura Strait assemblage, which is of similar age as the assemblage from Ngandong, hyenid remains were not found.

Carnivores, however, are elusive species in fossil faunas and it is difficult to be sure that their absence in a fossil record implies a genuine absence in the past ecosystem. It is, therefore, relevant to also look for taphonomic indications of hyenid presence or absence. Typical hyena damages to ruminant long bones are gnawed epiphyses and crushed shafts, associated with scoring and pitting of the cortical surface of the shaft fragments (Lyman, 1994; Johnson, 1985; Binford, 1981). Hyenid bone destruction starts with epiphyseal gnawing, which means that hyenid bone accumulations are characterized by low epiphysis-to-shaft ratios (Marean and Spencer, 1991). This is, however, opposite to what we see in the Madura Strait assemblage, which shows an overrepresentation of epiphyses and an underrepresentation of cylindrical shaft fragments, at least among the ruminant species. Moreover, the abundantly available epiphyseal fragments show no or only modest gnawing damage. Also, the cortical surface of shaft fragments has no convincing hyenid teeth marks. Despite the later polishing, hyena bone-crushing would expectedly have left intense gnawing marks and tooth punctures. Therefore, referring to the absence of hyenas in the Madura Strait assemblage and in similar-aged assemblages from Java, and referring to the absence of convincing evidence of hyena-inflicted bone modification, we may confidently conclude that hyenas were not part of the local ecosystem and cannot have been responsible for the fragmentation of ruminant long bones.

This leaves the hominin population as the main suspect of long-bone fragmentation. The medullar cavities of limb bones are filled with fat- and nutrient-rich marrow, which has been an essential and reliable part of the hominin diet for most of our evolutionary history (Speth, 2010a; Cordain et al., 2001). In eastern Africa, evidence of hominins breaking up limb bones for marrow extraction goes back more than 2 million years (Pobiner, 2007; Pickering and Egeland, 2006; Heinzelin et al., 1999). Intensely fragmented shafts of ruminant limb bones, with green-state fracture patterns, along with a high representation of intact and ungnawed epiphyses, are characteristic of hominin marrow exploitation. Other evidence for hominin-induced breakage of long bone shafts are percussion pits (Blumenschine and Selvaggio, 1988), percussion notches (Capaldo and Blumenschine, 1994) and percussion-induced conchoidal flake scars on the medullary surfaces of shaft fragments (Binford, 1981). Such more direct indications of hammerstone-percussion are scarce among the Madura Strait material, which may relate to the obliterating effect of polishing. However, with trampling as an unlikely breaking agent and an absence of hyenas in the ecosystem, hominin bone-battering appears to be the most plausible explanation for the intense fresh-state fragmentation of the bovid limb bones from the Madura Strait.

5.8. *Hominin foraging strategies*

Discussions on hominin foraging strategies have revolved around the debate over hunting or scavenging (Pobiner, 2020, 2007; Plummer and Bishop, 2016; Egeland et al., 2007; Domínguez-Rodrigo and Pickering, 2003; Domínguez-Rodrigo, 2002; Blumenschine and Cavallo, 1992). Much of this work focused on the analysis of carnivore teeth marks and hominin butchery marks on bones and their order in time. A relevant ecological characteristic of the late Middle Pleistocene Madura Strait fauna, which sets it apart from most Pleistocene ecosystems in Eurasia and Africa, is the absence of hyenas. The Madura Strait hominins must have been the only species in the ecosystem that could gain access to marrow from the medullar cavities of large mammalian limb bones. This may have favored a scavenging strategy, in which the hominins could simply collect limb bones from carcasses left by flesh-specialist predators such as felids, Komodo dragons or crocodiles. However, recent studies of Pleistocene hominin sites in Africa mostly point to early access to carcasses, suggesting active scavenging of felid kills rather than passive scavenging (Domínguez-Rodrigo et al., 2022). Felid carnivores, as well as crocodilians or Komodo dragons, preferentially prey upon the most vulnerable members of the herds, in most cases young individuals. This is not what we see from the age frequency distribution of bovids, with its overrepresentation of prime adults (Fig. 9D). As explained in Section 5.6, we regard this as evidence of selective hunting by the Madura Strait hominins. Selective hunting of prime adult prey was most likely related to their higher fat content. Prime adults accumulate much larger amounts of fat in the medullar cavities of limb bones than juveniles. Juveniles, even when easily accessible in the form of scavengeable carcasses, may, therefore, have been low-ranked resources in comparison to prime adults.

The transition toward selective hunting is regarded as an important evolutionary shift in hominin subsistence strategy (D'Errico, 2003). Selective hunting is associated with modern behavior and requires technological developments such as long-range weapons or cooperative ambush strategies. The timing of the change from non-selective hunting or active scavenging to selective hunting may have varied in different geographical reaches. Prime-dominated patterns are common among Late Pleistocene archaeological faunal assemblages worldwide, but have also been described for Middle Pleistocene assemblages in Europe and the Middle East (Stiner et al., 2009; D'Errico, 2003) and even for Early Pleistocene sites in southern and eastern Africa (Bunn, 2019; Bunn and Gurtov, 2014). In Middle or Late Pleistocene sites of Europe and the Middle East, selective hunting is commonly associated with Neanderthals or other archaic, post-erectus humans (Langdon, 2022; Speth, 2013, 2010b; Stiner, 2009; Domínguez-Rodrigo et al., 2007; Speth and Clark, 2006). In China, a prime-dominated assemblage has been described from the late Middle to early Late Pleistocene site of Xuchang-Lingjing (Wang et al., 2022; Zhang et al., 2009). Here, selective hunting of prime-aged bovids and marrow processing is associated with post-erectus archaic hominins, possibly Denisovans (Li et al., 2017; Trinkaus and Wu, 2017).

Our finding that the late Middle Pleistocene hominins of the Madura Strait were engaged in selective hunting of prime adult prey and marrow processing fits, timing-wise, in a worldwide trend. Of great interest though is that the Madura Strait hominins were probably part of the Ngandong population (Berghuis et al., 2025d), commonly regarded as *Homo erectus* and as the descendants of a long-standing, isolated lineage (Kaifu et al., 2008; Antón, 2003). Relevant question are: did this population develop this modern subsistence strategy autonomously? Or was it introduced by contact with more advanced populations?

Selective hunting and marrow processing by the Madura Strait hominins reflect the important role of animal fat in their diet. Several researchers pointed at the importance of animal fat to our hominin ancestors, who appear to have preferred fatty tissue such as brains, tongue and marrow over lean meat (Ben-Dor et al., 2011; Speth, 2010b; Speth and Clark, 2006; O'Connell et al., 1988). In this respect, it is interesting that the only convincing cutmarks found on the bovid bone remains from the Madura Strait are linear marks on mandible SBY5067 (Fig. 7). Besides their morphological characteristics, their anatomical position and orientation point to butchery. Ruminant mandibles with obliquely oriented cutmarks on the medial face, positioned below the M_2, have been described from various Early to Middle Pleistocene butchery sites, such as Koobi Fora, Kenia (Pobiner et al., 2008) and Combe Grenal, France (Binford, 1981, pp. 99–100) and also from Late Pleistocene or Holocene butchery sites (Bourgeon et al., 2017; Fisher, 1995). The marks are commonly associated with severing the mylohyoid muscle for tongue removal. Apparently, the Madura Strait hominins not only aimed for bone marrow, but also for the fat-rich tongue of their prey.

Our finding that the Madura Strait hominins were engaged in hunting, marrow processing and tongue removal do not necessarily imply that hunting large game was the primary part of the local subsistence strategy. It is well conceivable that the Madura Strait hominins also relied on edible plants, seeds and fruits or insects, and may have turned to animal fat during the dry season, when there was a lower availability of these alternative nutrients (Speth and Clark, 2006). Moreover, cutmarks found on two turtle bones as well as scratch marks and potential percussion notches on turtle shell fragments show that river turtles were also part of the local diet. These marks are the earliest evidence of turtle consumption by hominins in Southeast Asia. Butchery marks on turtle bones have been described for Early Pleistocene assemblages from Kenya (Braun et al., 2010) and Spain (Espigares et al., 2019) and for a Middle Pleistocene assemblage from Israel (Blasco et al., 2016). On Java, butchery marks have been described on turtle bones of Late Pleistocene (ca. 30 ka) age, which must have been associated with anatomical modern humans (Setiyabudi et al., 2021). Earlier, Joordens et al. (2009) already pointed at the likelihood that the ancient hominins of Java foraged on aquatic, river-related species. In a subsequent paper, Joordens et al. (2015) demonstrated that the Javanese *Homo erectus* collected and consumed river mollusks in the Middle Pleistocene, around 500 ka.

5.9. Differential representation of body parts

A disproportional representation of individual body parts was noted among the bovid and cervid remains. Most of these may be related to differences in structural density or differential hydraulic transport. For example, the high representation of small and robust body parts such as molars, carpalia and tarsalia relates both to differential transport of these small elements and to their relatively high structural density, favoring their survival. The importance of structural density for the survivorship of individual skeletal parts is also illustrated by the disproportional representation of individual epiphyseal parts. The dominance of distal humeri, proximal radii and distal tibiae correlates with their relatively high structural density (Kreutzer, 1988), which makes these parts more resistant to destruction, either as a result of hominin battering or post-discard destruction by for example foraging canids or rodents or during hydraulic transport.

Among the skeletal parts of cervids, there is an extreme overrepresentation of antlers and a remarkable scarcity of dental elements and bone remains. In Berghuis et al. (2025b) we related the high representation of antler fragments in the assemblage to antler shedding and to their strong fragmentation, in combination with a well-recognizable morphology. However, there may very well have been other factors involved, such as differential hydraulic transport or ethological factors. The extant cervid species of Indonesia, such as *Rusa timorensis* and *Axis kuhli*, are mostly solitary or live in small groups. They are not dependent on open water, but live from the moisture offered by plants (Ali et al., 2021). They probably did not congregate along the river and may even have avoided these areas, where they may have been subject to intense predator or hunting pressure, which explains the scarcity of cervid skeletal remains in the assemblage. The abundance of shed antlers may relate to shedding behavior. Possibly, solitary bucks left their territory to cast their antlers at sites closer to the river.

An interesting aspect of the frequency distribution of bovid skeletal parts is the low representation of vertebrae compared to long-bone epiphyses. This may very well again relate to differential fluvial transport or differences in susceptibility to post-discard destruction. Within the scheme of Voorhies (1969), vertebrae are more susceptible to hydraulic transport than limb bones. Considering the fact that we regard the assemblage as a downstream accumulation, this would expectedly have resulted in an overrepresentation of these elements and not in an underrepresentation. Note, however, that the Voorhies groups of differential hydraulic transport are based on intact bones. The lower susceptibility to hydraulic transport of long bones relates, within this scheme, to the high structural density of long-bone shafts. Isolated epiphyses and vertebrae have overlapping structural densities (Kreutzer, 1988), both being elements with thin cortical walls and significant grease-rich cancellous portions (Cleghorn and Marean, 2007). This would make these body parts equally susceptible to post-discard destruction and hydraulic transport.

A possibility is that the low representation of vertebrae relates to hominin carcass processing. *Homo erectus* may have crushed limb bones at the kill site, but they may also have transported body parts to a convenient location for processing and consumption, for example to escape competition with other predators (Domínguez-Rodrigo et al., 2007; Oliver, 1994; Potts et al., 1988). Although highly hypothetical, selective transport of bovid limb bones to a riverside camp for marrow processing may provide an explanation for the high representation of long-bone epiphyses compared to vertebrae. And it explains the abundance of long-bone fragments in the assemblage.

6. Conclusions

The fossil remains of terrestrial and fluvial species derive from the fluvial fill of a paleovalley of the Solo, which is associated with the lowstand of MIS6. Part of the fossil material became concentrated in an overlying marine lag deposit, which relates to the subsequent transgression. The fossil remains of the terrestrial species are regarded as homogeneous within a most likely age range of 146–131 ka.

The age-at-death frequency distribution of bovids points to selective hunting by hominins, aiming for fat-rich prime adult prey. Extensive green-state fragmentation of ruminant limb bones points to hominin bone battering and marrow processing. Hunting and marrow processing probably took place on the floodplain, where herds of herbivores gathered during the dry season. Cut marks on a bovid mandible show that the hunters not only aimed for bone marrow, but also for other fat-rich body parts such as the tongue. Cut marks on turtle bones show that the Madura Strait hominins also foraged on turtles.

The skeletal remains, deriving from hunts, but also from natural, ecology-related mortality, were taken up from the floodplain during flooding stages in the rainy season, and accumulated on the valley fill.

Remarkably, there have thus far been no systematic taphonomic studies of the fossil assemblages of Java. As we have shown here, it is expected that such studies will provide essential insights into dietary breadth, prey acquisition and carcass processing by hominins on Java in the Pleistocene.

CRediT authorship contribution statement

Harold Berghuis: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis. **Thijs van Kolfschoten:** Writing – review & editing, Supervision, Formal analysis. **Unggul Prasetyo Wibowo:** Data curation. **Iwan Kurniawan:** Formal analysis, Data curation. **Shinatria Adhityatama:** Resources, Project administration, Funding acquisition. **Indra Sutisna:** Formal analysis, Data curation. **Eduard Pop:** Writing – review & editing, Visualization. **A. Veldkamp:** Writing – review & editing, Supervision. **Josephine C.A. Joordens:** Writing – review & editing, Supervision, Funding acquisition. Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence this work.

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Data availability

The assemblage is curated in the Geological Museum Bandung and available for further research. An open-access data base of the assemblage, with photos and measurements, is not yet available.

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