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

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The Sangiran dome at sunset. View from the southeastern margin of the dome.



Chapter 10

The Pleistocene stratigraphy, biozonation and hominin chronology of eastern Java, a synthesis

CHAPTER 10

From the Solo to the Madura Strait. The Pleistocene stratigraphy, biozonation and hominin chronology of eastern Java; a synthesis

H.W.K. Berghuis, 2026

1. Introduction

This PhD-study aimed for a detailed description of the Madura Strait subsea vertebrate site (**Fig. 1**) and its fossils, and an interpretation against the background of the Pleistocene biogeography of Java and the wider Sunda Shelf. The latter proved to be difficult within the existing framework of the Pleistocene stratigraphy and biozonation of Java. We therefore expanded the research efforts to the onshore vertebrate sites of Java, revising local stratigraphies and re-interpreting available fossil assemblages. The results of these investigations have been presented in **Chapters 2 to 5** of this thesis, focusing on the surroundings of Trinil, Jombang and Mojokerto (**Fig. 1**). These on-land studies provided us with a much-improved understanding of Pleistocene landscapes and vertebrate communities of Java, against the background of tectonism, volcanism, sea-level fluctuations and climate change, and how these are expressed in the complex geological record of Java and the adjacent shelf. This finally made it possible to describe and interpret the geology and fossil fauna of the Madura Strait subsea site, as presented in **Chapters 6 to 9** of this thesis.

The geology and fossil fauna of individual sites have been described in great detail in the previous chapters and will not be repeated here. In this synthesis, I will shift the focus to the bigger scheme of the stratigraphy and vertebrate biostratigraphy for eastern Java. The stratigraphy of Duyfjes (1938a, 1936) and vertebrate biozonation of Sondaar (1984) have become ‘part of the DNA’ of all geologists, palaeontologists and archaeologists working on Java. As I will show, these frameworks require an update or revision. In the next sections, I will briefly describe the existing practice, discuss new insights, and present a revised framework.

The stratigraphy and biozonation of eastern and central Java are extremely complex issues, and the available literature on these subjects is enormous. I can only say that the proposed revisions are ‘work in progress’. Future research will have to fill in the blanks, refine age ranges, and correct my mistakes.

Understanding hominin dispersal and evolution is the holy grail of geological and palaeontological research of Java. The Madura Strait assemblage, with its hominin skull fragments and traces of hominin subsistence strategies, forms an exciting contribution to our knowledge of the Pleistocene hominins of Java and the adjacent shelf. Also, the proposed revisions of the Pleistocene stratigraphy and biozonation of Java have implications for the interpretation of hominin presence in the region. Therefore, I will conclude this synthesis with a reflection on the chronology of hominin presence on Java and the larger Sunda Shelf, and its implications for hominin evolution and dispersal.

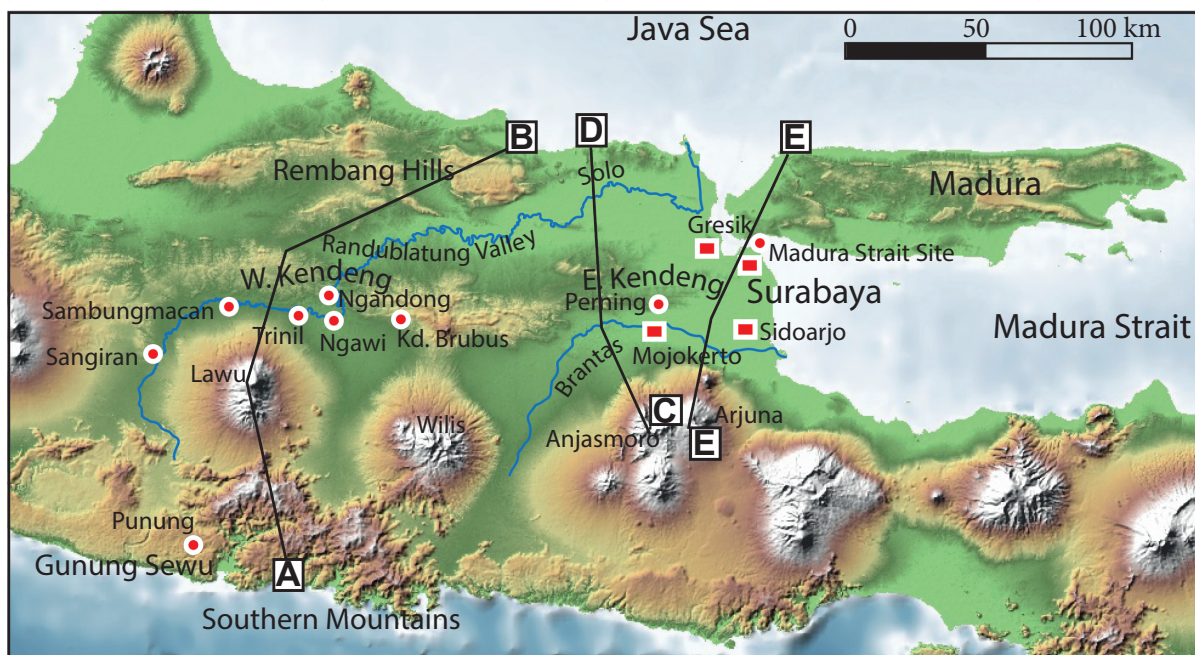


Fig. 1: Eastern Java, the Madura Strait site and other sites mentioned in the text. A-B etc: position of the cross-sections of **Fig. 4**. Map data: GEBCO and ALOS.

2. The shelf and the island

2.1 The shelf

The Sunda Shelf is the world’s largest submerged shelf. The island of Java lies along its southern margin, bordering the Indian Ocean in the south, with the subduction zone, where the Australian Plate subducts under the Sunda Plate (**Fig. 2A**).

Thus far, the Pleistocene stratigraphy of eastern Java has largely ignored its larger landscape context, along the margin of the Sunda Shelf, in a zone of complex subduction-related tectonism. An important question remains un-

answered: how does the Pleistocene stratigraphic record of Java relate to the off-shore stratigraphy of the submerged shelf, and what does this tell us about sea level fluctuations and stages of shelf emergence and submergence? For a shelf island like Java, this must be an essential aspect of its geological history, and one that directly affects our interpretation of the Pleistocene vertebrate communities including the famous *Homo erectus* of Java. Strangely, the Pleistocene vertebrate biozonation of Java is built on a model of such intermittent island stages and land bridges, however, the island stratigraphy does not provide a single clue about this changing landscape.

Since the discovery of ancient drainage systems on the bottom of the Java Sea (Molengraaff and Weber, 1921), it has been known that this wide shelf must have once been exposed. Van Bemmelen (1949) proposed to refer to this Pleistocene landmass as Sundaland. With the recognition of Pleistocene glacio-eustatic cycles, these stages of shelf exposures could be tied to glaciations (Voris, 2000). Sondaar (1984) and Van den Bergh et al. (2001) linked the vertebrate fossil record of Java to this alternation of island stages and land bridges, reflected by either endemism or the arrival of new species.

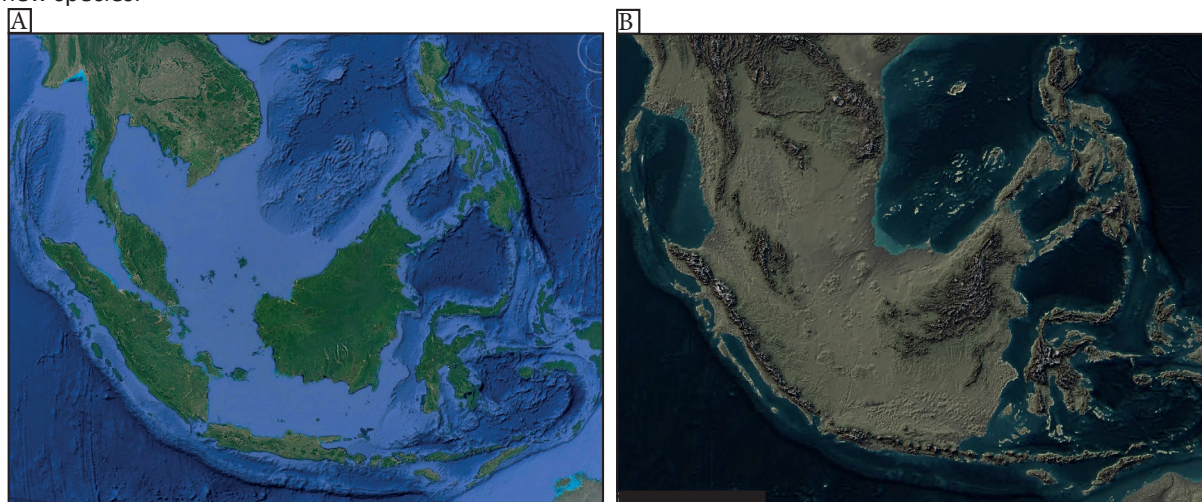


Fig. 2. **A:** The drowned Sunda Shelf, current situation, with the island of Java centrally in the south and the subduction zone south of the island. **B:** The exposed Sunda Shelf or Sundaland. The shelf was probably widely exposed during the Early and Middle Pleistocene, with intermittent stages of surface contraction during highstands from MIS11 onwards. Map data: Google Earth; Vivid maps, coastlines of the ice age.

Recent insights have completely changed our understanding of the Quaternary paleogeography of the Sunda Shelf. Instead of a stable, largely submerged shelf that was subject to intermittent emergence during sea-level lowstands, Sundaland was probably widely exposed throughout the Early Pleistocene (Louys and Kealy, 2024; Louys and Roberts, 2020; Husson et al., 2022, 2020) (**Fig. 2B**). Only in the course of the Middle Pleistocene, regional subsidence, with an estimated rate of 0.2 mm/a, gradually brought the shelf surface within the range of sea-level fluctuations (Sarr et al., 2019). A reconstruction of shelf subsidence and Pleistocene sea-level fluctuations indicates that the first stage of large-scale shelf submergence probably dates back to MIS11 (**Fig. 3A**). On the submerged shelf, this is expressed by a sub-seabed stratigraphy consisting of four to five stacked marine sequences (**Fig. 3B**), overlying a basal unconformity (Susilohadi, 1995). This basal unconformity may be regarded as the subsided Early Pleistocene land surface of Sundaland, whereas the erosive boundaries between the marine sequences represent Middle Pleistocene, post-MIS11 land surfaces.

This new insight has enormous consequences for our interpretation of the stratigraphy and the vertebrate fossil assemblages of eastern Java, and may rightly be regarded as a paradigm shift. Dhani Irwanto (2016) published an on-line reconstruction of the gradually emerging Sundaland surface under the falling sea-level toward peak MIS2 lowstand conditions. This model can also be used for estimating the highstand Sundaland landscape of the last Middle Pleistocene interglacials, referring to the sea-level curve and the projected subsidence graph of **Fig. 3A**.

For example, during peak MIS11 highstand conditions, the sea-level reached a similar level as today, however, the shelf surface lay ca. 70 m higher than today. This implies that the MIS11 landscape may have been similar to the situation of '70 m below present sea level'. Admittedly, these are generalized reconstructions, suggesting a linear subsidence of the entire Sundaland surface. In reality, there were probably differences in tectonic regime across Sundaland. Nevertheless, the reconstructions give an astonishing image of the Middle Pleistocene highstand landscape (**Fig. 3C**). During the highstands of MIS11 and 9, Sundaland contracted but remained a contiguous land surface, connected to the Asian mainland. During MIS7, Borneo became separated from the mainland, but Sumatra and Java appear to have remained connected to the Asian mainland as a peninsula, similar to present-day Malaysia, but longer.

Only during MIS5e, and of course during MIS1, a true island landscape developed, with Borneo, Sumatra and Java as islands in a shelf sea. We will see that this new view of Pleistocene Sundaland has significant consequences for our interpretations of the stratigraphy and vertebrate palaeontology of Java.

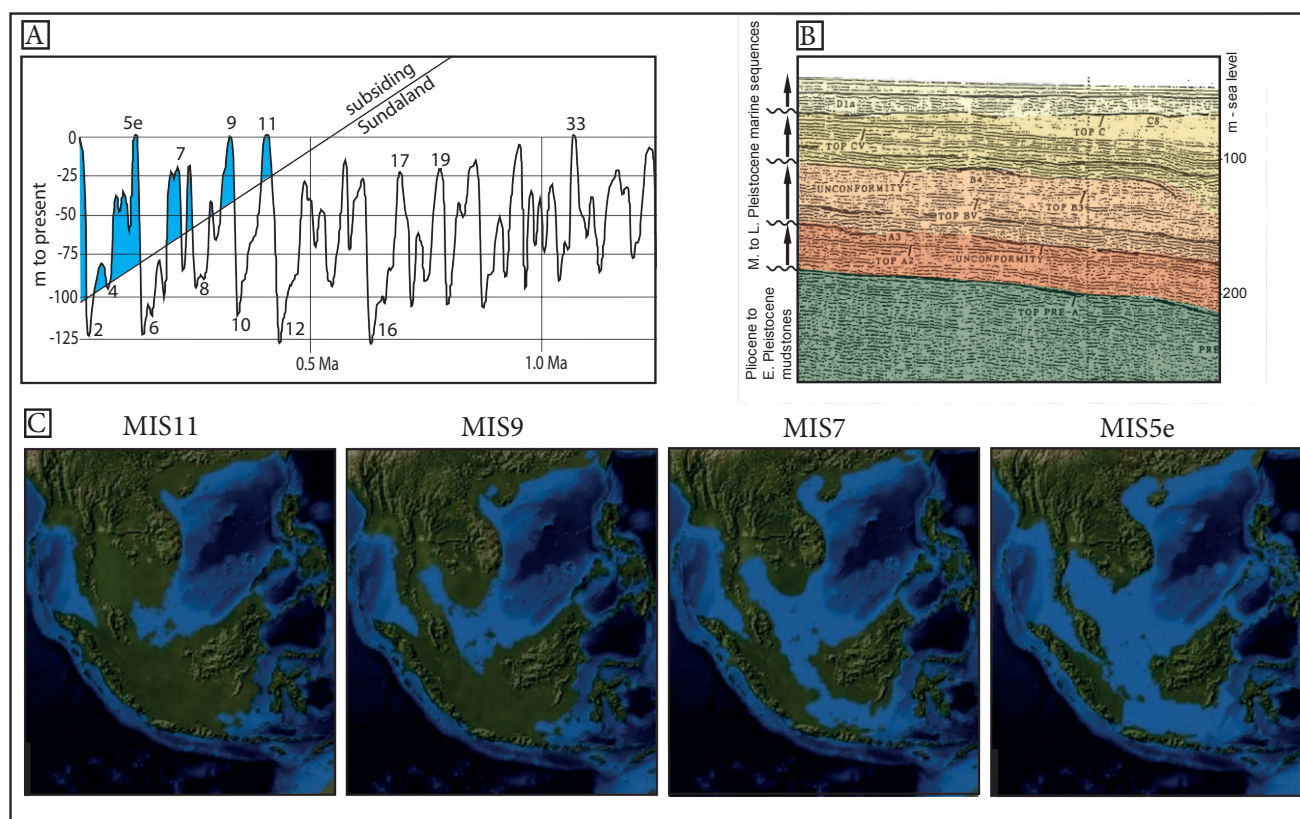


Fig. 3. A: Reconstruction of the subsiding central shelf in relation to sea-level fluctuations and subsidence. Sea-level curve based on Bintanja and van de Wal (2008), regional subsidence of 0.2 mm/a based on Sarr et al. (2019). **B:** Seismic profile over the Madura Strait (Susilohadi, 1995). Basal unconformity represents prolonged Early Pleistocene subaerial exposure. Overlying marine sequences with incised top represent intermittent stages of submergence during Middle Pleistocene highstands, under regional subsidence. First stage of large-scale submergence probably relates to MIS 11. **C:** Reconstructions of the maximum contracted land surface during Middle Pleistocene highstands. Java probably only came under island conditions during MIS5e and MIS1. Map data: Dhani Irwanto (2016).

2.2 The island

Java lies along the dynamic southern margin of the Sunda Shelf, an area shaped by tectonism and volcanism related to the nearby subduction zone. An array of volcanoes forms the core of the island. However, Java is more than just an island arc. Folded Tertiary strata testify to a long and complex geological past. Three north-south cross-sections of eastern Java (**Fig. 4**) illustrate the geological structures of eastern Java down to a depth of 1,000 m. The sections are based on published studies of oil wells, seismic profiles, and outcrops, summarized by Lunt (2013). It is important to note that simplifications were inevitable. The positions of faults and folds are schematic, and strata have been grouped into composite units. Below, I present a brief discussion of the cross-sections, referring to relevant tectonic and volcanic stages in chronological order.

Paleogene rifting

In the Paleocene and Eocene, active subduction temporarily ceased in the area of present-day eastern Java, and the shelf margin came under an extensional regime (Zahirovic et al., 2016b). A rift system formed, consisting of east-west and southwest-northeast oriented grabens and half-grabens (Lunt, 2013). The basement faults are not shown on the cross-sections, but their presence and continued activity are reflected by folds and faults in the overlying strata. The Paleogene graben-fill makes up the core rocks of the Rembang Hills and Southern Mountains. As we shall see, these hill ranges are inversions of ancient grabens.

The Miocene volcanic arc and its back-arc basin

In the Early Miocene, subduction and volcanism returned to this area (Hall, 2013). A volcanic arc developed in the rift valley that is nowadays prominent as the Southern Mountains. To the north, a back-arc basin formed, which covered most of present-day eastern Java. In the cross-sections, this basin is recognizable by its Mio-Pliocene fill. Along its northern margin, the back-arc basin incorporated the older grabens. In the Late Miocene, active subduction again ceased (Hall and Spakman, 2015). The volcanic arc eroded and was covered with coral reefs (Smyth et al., 2008). The back-arc basin became deprived of clastic supply and the sedimentary regime changed to settling of calcareous ooze, which continued throughout the Pliocene.

Pliocene compression, uplift zones, and the development of an intermediate basin

In the course of the Pliocene, the area came under a northward-directed compressive regime (Hall and Smyth, 2008).

The ancient rift valleys inverted, forming the Southern Mountains and the Rembang Hills, which emerged in the Late Pliocene (Husein et al., 2015; Satyana et al., 2004). Several isolated uplifts, such as the Sekarkuring and Ngimbang Hills, are similar inversions. During this same period, the western Kendeng Hills formed in the axial zone of the back-arc basin. Low-angle, northward-verging folds and thrust faults point to compression of the basin-fill, thin-skinned deformation and detachment of the mudstone-dominated basin-fill from underlying more rigid strata (Genevraye and Samuel, 1972).

The emerging uplift zones changed the adjacent area into a sheltered, shallow-marine basin. It had open connections to the Indian Ocean in the south, through tectonic gaps in the Southern Mountains, and probably also to east, over the Madura Strait shelf. In the northeastern part of this basin, a fill of massive marine clays testifies of a high supply of fine detrital material. The sediment was probably supplied from the North Serayu uplift of Central Java. The clays reach a thickness of several hundred meters, pointing to subsidence. This setting, of a narrow, relatively deep, subsiding embayment between emerging hill ranges, points to ongoing inversion, with the subsiding basin as a paleo-high of the Paleogene rift system.

The area around Sidoarjo serves as a striking example of this inversion-related subsidence. This site is well-studied, due to its reservoir rocks and by the disastrous mudflow that was caused by a test drilling. The area was a horst within the old rift system, which changed into a reef-capped shoal in the Miocene back-arc basin. It inverted under Pliocene compression and became a zone of extreme subsidence (Mazzini et al., 2007; Kusumastuti et al., 2002). The local Late Pliocene to Pleistocene fill reaches a thickness of ~ 1,000 m.

In the basinal area in the southwest, south of the western Kendeng, conditions were completely different. A fill of mollusc-rich calcareous mudstones, with burrows and coral fragments, points to the development of a shallow, clear-water lagoon. The lagoon must have been sheltered from mud supply by the western Kendeng. Moreover, the deeper, subsiding embayment in the northeast must have formed an efficient trap for mud, preventing its further transport. The lagoon was connected to the Indian Ocean in the south through a wide gap in the Southern Mountains. This gap is today recognizable as the Gunung Sewu, a low hill range that only became subject to uplift in the course of the Middle Pleistocene (Rizal et al., 2020).

Emergence of the intermediate basin, volcanism, and local subsidence

Paleosols show that the sheltered basinal area eventually emerged. Scarce planktonic markers, as well as estimates of sedimentation rates, suggest that this emergence dates to ~2 Ma. Around this same time, active volcanism returned to eastern Java, reflecting resumed subduction. The Wilis and Old Lawu are the oldest volcanoes in this area. Both developed in the lowland zone between the Southern Mountains and the western Kendeng. In the cross-sections, I assumed collapse structures below the edifices, reflecting emptying of magma chambers and loading by the cones.

The surrounding lowland was occasionally overrun by volcanic mass flows. Stacked volcanic breccia layers with a great lateral continuity illustrate the enormous scale of these mass flows. The breccia layers are separated by ferrallitic paleosols or interbeds of black coastal clays, indicating a setting on a humid, marshy and forested coastal plain that must have been tectonically relatively stable throughout the Early Pleistocene.

The area in the northeast became subject to renewed subsidence and was once again invaded by the sea, forming an embayment that was probably connected to the Indian Ocean in the south. A second unit of marine clays was deposited, with lenticular sandy laminae, pointing to shallow, tide-dominated conditions.

Middle Pleistocene: local uplift, regional subsidence

Around the Early to Middle Pleistocene transition, eastern Java came under renewed or increased compression. The western Kendeng fold zone became re-activated, which also affected the fill of the adjacent basins. In the northeast, the shallow embayment emerged or silted up. This may partly have been triggered by the build-up of the Anjasmoro Volcano, which blocked the connection to the Indian Ocean. With this closing of the southern ocean-connection, the Brantas developed as a large, eastward-directed drainage system. Later, the Solo developed as a second, eastward-directed drainage system.

Around the same time, the wider Sunda Shelf came under a regime of subsidence (Sarr et al., 2019). The lower parts of the shelf became intermittently and progressively submerged during highstands. The Brantas and Solo drainage systems responded to this intermittent drowning of their lower reaches with cycles of incision and deposition, forming incised valleys in their lower reaches that continue below the seabed of the Madura Strait shelf. In the higher reaches, the rivers formed fluvial terraces. The core of eastern Java, however, remained under compression. A series of new anticlines formed, folding the fill of the Plio-Pleistocene, mud-dominated embayment, and shaping the eastern Kendeng Hills.

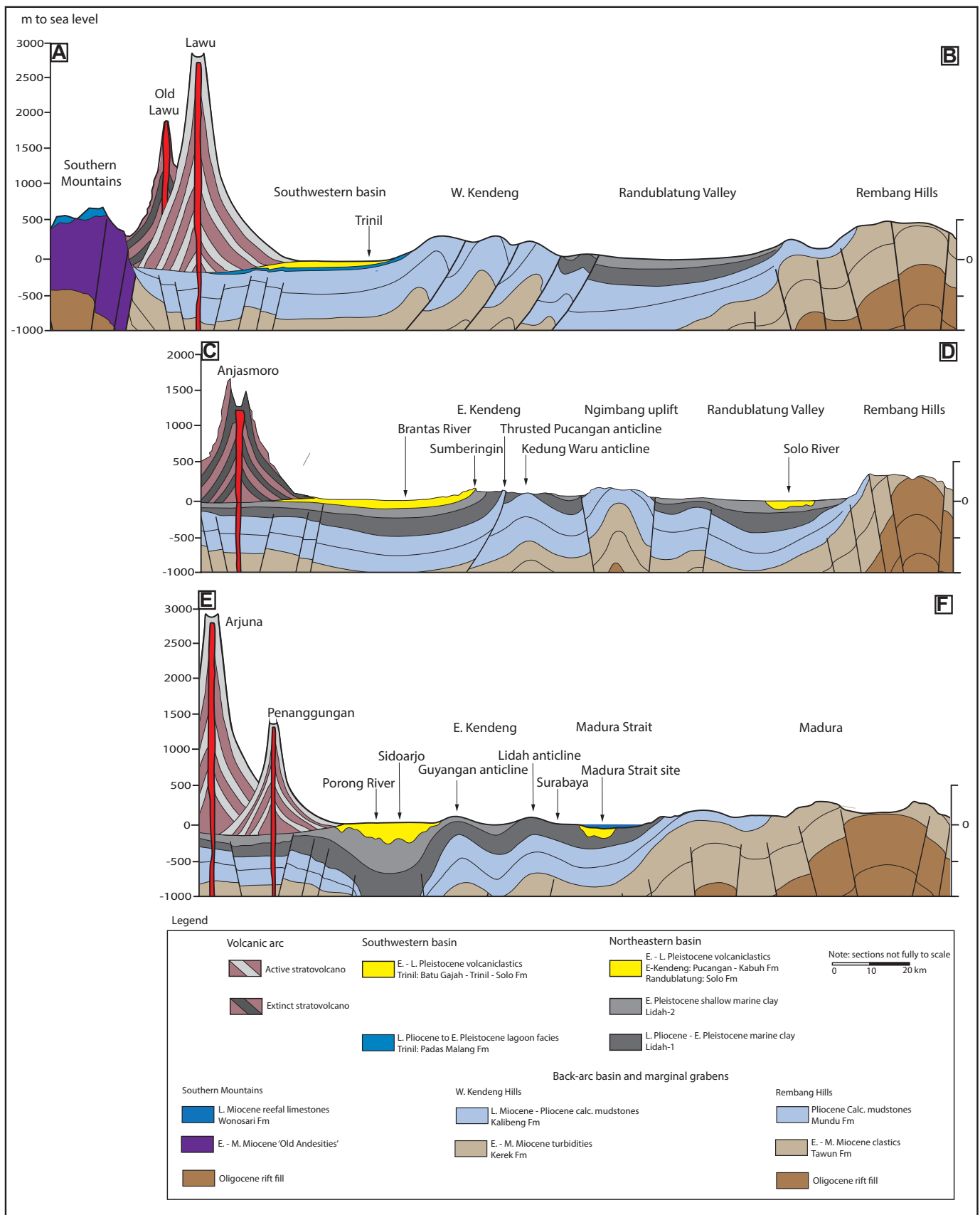


Fig. 4. Schematic cross-sections over eastern Java; structural setting of the relevant depositional basins. Position of the cross-sections indicated on Fig. 1.

3. The late Pliocene and Pleistocene stratigraphy of eastern Java

3.1 The stratigraphy of Duyfjes

For almost a century, researchers have based their interpretations of the Pleistocene geology of eastern Java on the stratigraphy of Duyfjes (Duyfjes, 1938a, 1936). This stratigraphy assumes the existence of an uninterrupted and laterally continuous depositional record of marine, deltaic, fluvial and volcanic strata, reflecting the emergence of eastern Java, as a result of volcanic supply and coastal progradation. This long depositional record was subsequently folded and uplifted, forming the Kendeng Hills. As was normal in these days, Duyfjes' units are chronostratigraphic constructs. His model of uninterrupted sedimentation allowed him to correlate his units across the hill range. Correlations were based on thickness measurements and 'parallelization', which implies that he combined different facies in the same unit, assuming that these strata are of similar age and represent lateral variation of the depositional landscape.

In the introduction to this thesis, I provided a graphic overview of Duyfjes stratigraphy and his correlations.

3.2 New insights

Identifying depositional basins

Duyfjes (1938a) referred to his stratigraphy as the 'Kendeng stratigraphy'. This suggested the existence of a large depositional basin, the fill of which had been folded and uplifted as the Kendeng Hills. However, as explained in **Section 2.2**, the structural setting of eastern Java is more complex. The Kendeng Hills are a composite of two tectonic structures. The western Kendeng is the thrust fill of the Mio-Pliocene back-arc basin. As a result of the uplift of this fold zone, shallow embayments formed in the surrounding area. The eastern Kendeng is younger and is the smoothly folded fill of a Late Pliocene to Pleistocene, mud-dominated embayment. What may have confused Duyfjes is that syntectonic deposition and reactivation of the western and eastern Kendeng affected the fill of the adjacent younger basins. Note the situation along the margins of the western Kendeng thrust zone (cross-section AB, **Fig. 4**), where the deformation of the younger basin fill gives the impression that these strata are part of a folded 'Kendeng stratigraphy'.

In a complex and composite deformation zone as eastern Java, it is helpful to identify relevant depositional basins and define recognizable lithostratigraphic units that describe the fill of these basins. The most obvious basin is the Mio-Pliocene back-arc basin. In **Fig. 4**, it is recognizable by its fill of Early to Middle Miocene volcanoclastic deposits and Late Miocene to Pliocene calcareous deposits. These roughly correspond with Duyfjes' Kerek and Kalibeng Formations, which are valid and useful stratigraphic units.

After the compression of the Mio-Pliocene back-arc basin and the emergence of uplifted ridges such as the Rembang and western Kendeng Hills, a new landscape formed, with an intermediate, shallow marine basin. It is important to distinguish between a subsiding, mud-dominated embayment in the northeast and a tectonically more stable, initially clear-water basin in the southwest. In the latest Pliocene, these two basins may have been partly connected, but the development of the Wilis caused a complete separation. The fill of the subsiding, mud-dominated basin in the east is exposed in the young folds of the eastern Kendeng, around Jombang and Mojokerto. The fill of the southwestern basin is exposed along the southern footslopes of the western Kendeng and in the Sangiran dome.

3.3 A new stratigraphic framework

From local to regional

In **Chapters 2 to 6** of this thesis, I repeatedly emphasised the difficulties of long-distance correlations and the necessity of working with local stratigraphies. Obviously, this may have obscured the context of the eastern Java stratigraphy and the chronological relations between individual sites. With new numerical ages and an improved understanding of the larger Pleistocene landscapes of eastern Java, it is now possible to place these local stratigraphies in a broader context.

The two Pleistocene basins

Fig. 5 presents an overarching stratigraphic summary for the Late Pliocene and Pleistocene of eastern Java, integrating the stratigraphic records of various sites into a chronological framework. The top of the Kalibeng Formation represents the final stages of the Mio-Pliocene back-arc basin. With the uplift and emergence of the Rembang and western Kendeng, two new basins developed.

The northeastern basin, in the figure represented by the Randublatung Valley, Surabaya and Mojokerto, is marked by its mud-dominated fill. Planktonic foraminiferal markers date the transition from calcareous mudstones to marine clays to 3 Ma, which forms a strong indication of the age of emergence of the fold zones and the development of the intermediate embayment. The fill of the embayment has a relatively uniform build-up, consisting of two marine clay

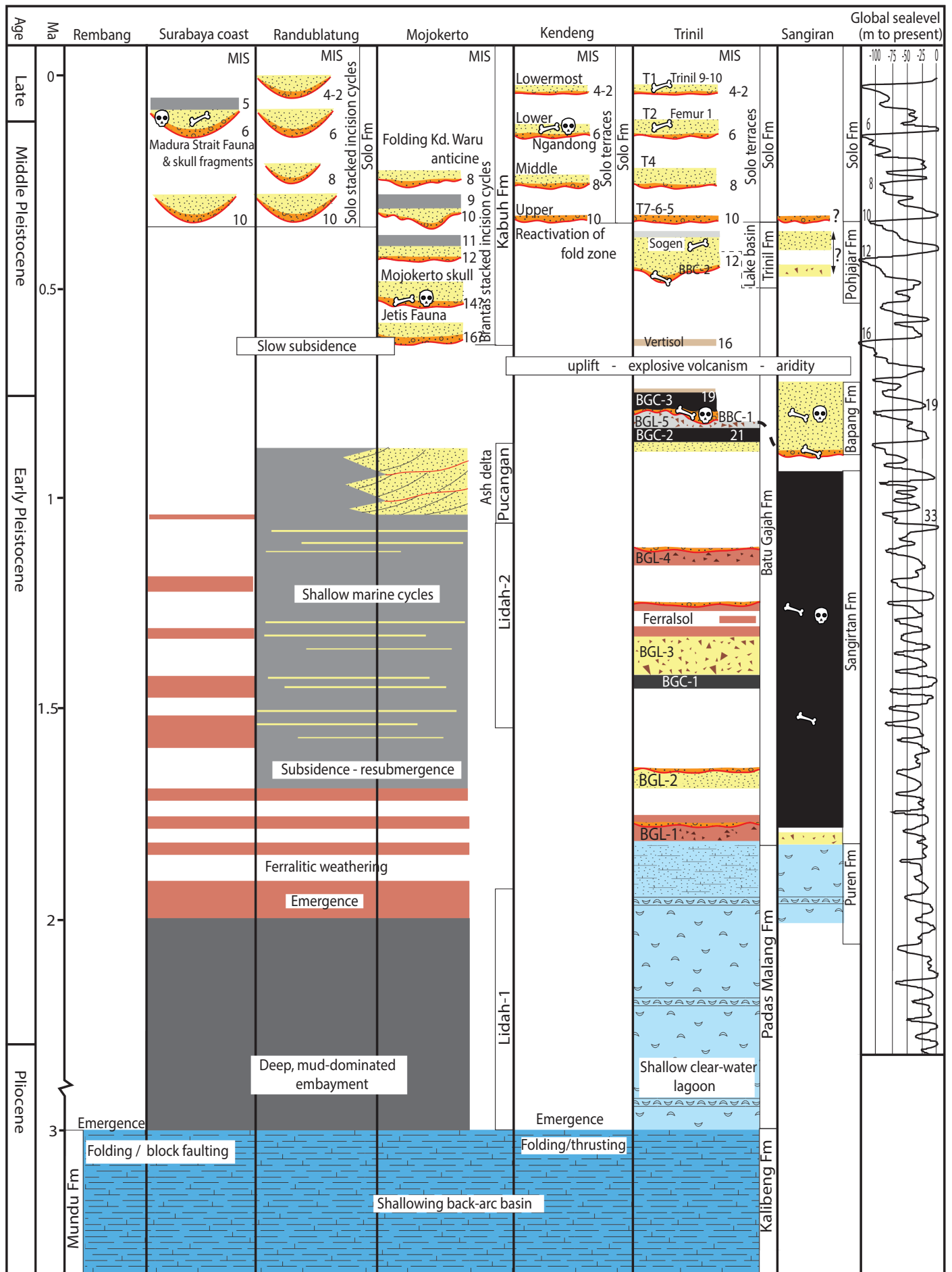


Fig. 5. Stratigraphic summary of eastern Java. Chronological framework of the stratigraphy of various sites and landscape stages. Sea-level curve: Bintanja and Van der Wal (2008). Stratigraphy, ages and correlations based on **Chapters 1-5** of this thesis.

units, referred to as Lidah-1 and 2, representing the early deep-water embayment and the subsequent tide-dominated shallow embayment. The clays are separated by a ferrallitic paleosol.

The southwestern basin, in the figure represented by Trinil and Sangiran, is characterized by a basal fill of calcareous sediment with shells and corals. Planktonic markers again show that the transition from open marine to sheltered conditions occurred during the latest Late Pliocene. The calcareous, shell-bearing strata are overlain by coastal black clays and volcanic breccias, and subsequently by fluvial volcanoclastics.

Stratigraphic units

Duyfjes' defined his Pleistocene units in the eastern Kendeng. In the revised stratigraphy, these units have remained mostly in-tact, though with revised unit boundaries, and with a local significance only, for the eastern Kendeng and the adjacent coastal plains of Surabaya and the Randublatung Valley. All marine clays are referred to as the Lidah Formation, as proposed by Brouwer (1966). This is the most prominent unit of the northeastern basin.

The occurrence of Lidah-1, the oldest massive clays, demarcates the position of the embayment that formed between the emerging hill ranges around 3 Ma. Lidah-2 is the fill of the subsequent, shallower embayment. The Pucangan Formation only refers to the ash-dominated deltaic beds, which locally form the top of the fill of the 'Lidah-2-embayment'. The Kabuh Formation refers to the overlying fluvial sequences of the Brantas, which are only exposed in the eastern Kendeng. Note the erosive contact between the Pucangan and the Kabuh Formations. Instead of a prograding deltaic sequence of foresets and topsets, as previously assumed, both units are unrelated and separated by a depositional hiatus.

The stratigraphic units of the southwestern basin have been defined as a new, local stratigraphy for the Trinil area and replace the former units, which were based on correlations with Duyfjes' reference sections in the eastern Kendeng. Note that the new units cannot be compared one-on-one with the former units of Duyfjes as used in this area. For example, the Kabuh Formation of Trinil appeared to be an amalgamation of fluvial strata of different ages, including terrace-related deposits of the Solo drainage system.

For the Sangiran area, I used the revised unit names by Itahara et al. (1985), which are a renaming of Duyfjes' units, without further justification.

Chronological ordering

The chronological ordering of the deposits that make up the fill of the two Late Pliocene to Pleistocene basins has been based on the detailed stratigraphic studies, as presented in Chapters 1 – 5 of this thesis. Sea-level calibration is most reliable for the Middle to Late Pleistocene fluvial sequences and terraces of the Solo and the Brantas. For the fluvial cycles of the Solo, this sea-level signal is validated by OSL-datings. The cyclic record of the Brantas and the Solo has also been linked to the Middle Pleistocene marine sequences of the submerged shelf, as shown by seismic profiles (**Fig. 3B**).

For older strata, the chronological ordering relies largely on occasionally available radiometric dating studies and paleomagnetic profiles. Rough age indications are also inferred from paleoclimate indicators and volcanic markers. There is ample evidence of a climate shift from a humid tropical to a dry climate with a pronounced rainy season, around 1 Ma. Around the same time, there has been a change of volcanic style, from large andesitic strato-volcanoes that occasionally collapsed, to more explosive ash-rich eruptions. For the oldest marine strata, planktonic foraminiferal markers provide insight into age ranges.

One of the interesting features of this (provisional) chronological ordering is that it highlights the fragmented preservation of the Pleistocene depositional record (**Fig. 5**). The previous, Duyfjes-based stratigraphy of eastern Java has been presented in block-form, suggesting ongoing deposition. This is correct for the marine fill of the Mio-Pliocene back-arc basin, and probably also for the earliest marine stages of the subsequent Plio-Pleistocene basin. However, it certainly does not apply to the overlying coastal and terrestrial strata, which form intricate and laterally variable depositional records, with long hiatuses, that represent either incision or non-deposition.

The bone beds: ages and correlations

Probably the most interesting aspect of the stratigraphic framework is that it places the most important vertebrate-bearing beds of eastern Java in a chronological context. The Sangiran area yields the oldest known vertebrate beds of the eastern part of Java. The fossils are found in a ~ 100 m thick unit of black clays (Sangiran Formation), which was deposited in a coastal marsh. Dated interbeds of volcanic ash and paleomagnetic profiling offer reliable age control over the clay unit (Matsu'ura et al., 2020). The oldest vertebrate fossils are found in its middle part, pre-dating 1.5 Ma. The first hominin fossils are found higher up, at a level that has been dated to ~ 1.1 Ma, or possibly ~1.3 Ma. The black clays of Sangiran form the landscape equivalent of the thinner black-clay interbeds in the brec-

cia-dominated Batu Gajah Formation of Trinil, reflecting a slightly higher topographic setting of Trinil, along the foot of the Old Lawu.

The black clays of Sangiran are sharply overlain by a conglomerate bed (Grenzbank) and subsequently by cross-bedded fluvial sandstones, referred to as the Bapang Formation. Both yielded vertebrate fossils, including hominin remains. The Grenzbank has been dated to ~900 ka. The overlying fluvial sandstones were deposited shortly after. Higher-up in these sandstones, the Brunhes-Matuyama transition (773 ka) forms a reliable age anchor. The hominin fossils of this sandstone unit derive from the stratigraphic range below this polarity reversal.

Since the earliest hominin finds in Sangiran (Von Koenigswald, 1933), the Grenzbank has been correlated with the bonebed of Trinil, traditionally referred to as the Haupt Knochenschicht or HK. Both the Grenzbank and the Haupt Knochenschicht are incisive lags that mark a transition to sandy fluvial deposits. Our re-inventory and dating study of the Trinil excavation site revealed that the Haupt Knochenschicht consists of two superimposed channel lags, which we refer to as Bone Bearing Channel (BBC) 1 and 2 (Hilgen et al., 2023). BBC-1 has an age range of 830 – 773 ka, based on multiple radiometric measurements and its reversed magnetic polarity. BBC-2 is significantly younger and dates to ~450 ka. The correlations between Sangiran and Trinil are of great relevance for our interpretations of fossil faunas and the hominin chronology of eastern Java, which will be further discussed in **Sections 4 and 5**.

Most of the younger bone beds of eastern Java are associated with Middle Pleistocene fluvial sequences of the two large drainage systems. The bone beds of Mojokerto are deposits of the ancient Brantas. In the revised stratigraphy, Duyfjes' Kabuh Formation only refers to these fluvial sequences of the Brantas. This is in line with its vertebrate fossils, forming the Middle Pleistocene Kedung Brubus Fauna. Note that these fossils formed the Early Pleistocene Jetis Fauna of Von Koenigswald (1935), which had made Duyfjes (1938a) decide to regard the material as the Early Pleistocene Pucangan Formation. This inconsistency is resolved in the revised stratigraphy, however note the ongoing discussion on this subject (**Chapter 5**).

The fluvial sequences of the Solo are represented by fluvial terraces in Sangiran, Trinil and the Kendeng traverse valley. The drainage system probably goes back to MIS10. The lower terrace of Ngandong, one of the richest vertebrate sites of eastern Java, was dated to 140 – 92 ka (Rizal et al., 2020) and can probably be correlated to MIS6. OSL-datings and reconstructions of fluvial incision and aggradation cycles indicate that the T2-terrace of Trinil is the equivalent of the Ngandong terrace. Downstream of the Kendeng traverse valley, the fluvial cycles of the Solo proceed as incised channels in the Randublatung Valley and below the seabed of Madura Strait. The Madura Strait subsea vertebrate site is a transgressively filled incision of MIS6, which links this site to the terrace of Ngandong. Note that MIS4 or MIS2 incisions are absent in the Surabaya coastal area. We assumed that during MIS4, a new transverse valley was cut through the Rembang, leading the river towards the Java Sea shelf in the north.

One vertebrate-bearing level has remained unmentioned. This is a ca. 60 m thick unit of fine, parallel-bedded fluvial tuffs, with paleosols and occasional shallow erosion structures, and with interbedded lacustrine clays, exposed in the Trinil area. This material was previously referred to as the local representative of the 'Kabuh Formation', together with unrecognized terrace deposits and the older fossil-bearing lags deposits. The strata, which we referred to as the Trinil Formation, represent an interesting local landscape stage, when the area around Ngawi was isolated from the marine base level, probably by a volcanic barrier between the Lawu and the western Kendeng. The deposits reflect the existence of a lake, surrounded by a fluvial plain. The material overlies BBC-2, and is incised by the terraces of the Solo, which leaves a short time window of ~ 450 to 375 ka as the likely age range of the Trinil Formation. In **Section 5.2** I will present a detailed profile of Trinil, in relation to its hominin fossils, which provides an interesting image of the setting of this unit.

A Mid-Pleistocene hiatus: Uplift, climate change and volcanic ash

The stratigraphic summary (**Fig. 5**) shows the Early to Middle Pleistocene transition as a poorly represented period in the depositional record. The few preserved records from this period, such as the Grenzbank and Bapang Formation of Sangiran, the bone-bearing channels (BBCs) of Trinil, and the ash-rich delta of the Mojokerto area, testify to significant landscape changes. There were probably three factors involved. One, renewed compression and uplift, which pushed the coastal zone around Sangiran and Trinil above the range of coastal sedimentation. Two, a change of volcanic style, toward more explosive, ash-rich eruptions. And three, a regional change from a humid tropical climate to a much drier climate, with a pronounced rainy season. In eastern Java, these three factors caused a severe landscape change, transforming subsiding coastal forests into dry, grass-covered plains subject to local incision and intermittent ash-falls. In Trinil, this landscape is reflected by local occurrences of fossiliferous channel lags, i.e. the BBCs. The lags are rich in reworked carbonate concretions, pointing to erosion of vertisols. The channel lags also contain ash lenses, probably representing contemporary eruptions. The soil erosion reflects intermittent destruction of the vegetation cover, due to periods of extreme drought and/or events of ash-fall. To the east, the increased ash supply is represented by the development of ash-dominated deltas in the shallow 'Lidah-2'-embayment.

Looking in detail at the Trinil stratigraphy of this period, the relatively young age of the two highest clay beds of the Batu Gajah Fm, BGC-2 and BGC-3, appears to be an anomaly, as they fall in the onset of the period with harsher and drier conditions. Their inferred ages have been based on the numerical ages provided by Hilgen et al. (2023) and the observation that the lahar BGL-5 appears to have overrun the coastal marsh of BGC-2, taking up clay balls from the surface. A slightly older age of the BGC-2, which aligns more closely with the age of the clays of Sangiran, seems logical. The significance of the third clay layer, exposed only on the right river bank in Trinil, may also be reconsidered. This is probably not a coastal clay bed with a wide lateral continuity, like the underlying clay beds, but rather the fill of a local pond.

4. The vertebrate biozonation of central and eastern Java,

4.1 The biozonation of De Vos and Sondaar

Since the 1980s, the vertebrate fossils of eastern Java have been interpreted in terms of faunal stages, based on the work of De Vos et al. (1982) and Sondaar (1984), with an update by Van den Bergh et al. (2001). The authors recognized seven faunal units, which are assumed to reflect the vertebrate community of eastern Java during a specific period (see also the introduction to this thesis). The Satir and Ci Saat Faunas refer to the fossil species excavated from a thick series of fluvial sandstones and interbedded black clays exposed near Bumiayu, in the western part of Central-Java. Note that the stratigraphy and palaeontology of this part of Java falls outside the scope of my studies. However, the two faunal units have become relevant for the eastern part of the island by their correlation to the fossil-bearing series of Sangiran (Section 4.2).

The Trinil-HK Fauna contains the fossil species from the basal bone beds of the Dubois excavation site in Trinil, previously known as the Haupt Knochenschicht (HK) and now identified as BBC-1 and BBC-2. The Kedung Brubus Fauna refers to the vertebrate fossils from Kedung Brubus, ca. 35 km east of Trinil. The site, excavated by Dubois in the late 1890s, consists of a fluvial sandstone series with a reported thickness of ~200 m (Duyfjes, 1936; Van Es, 1931). The Ngandong Fauna contains the fossil species from the lower terrace of the Solo in the Kendeng traverse valley. The Punung and Wajak Faunas are cave faunas from the Southern Mountains.

Order		Proboscidea	Primates					Rodent.	Ph	Carnivora			Perisso.	Artiodactyla																							
Species		<i>Sinomastodon bumiliensis</i>	<i>Stegodon trigonocephalus</i>	<i>Elephas sp.</i>	<i>Elephas maximus</i>	<i>Macaca sp.</i>	<i>Trachypithecus sp.</i>	<i>Hylobates sp.</i>	<i>Pongo sp.</i>	<i>Homo erectus</i>	<i>Homo sapiens</i>	<i>Hystrix sp.</i>	<i>Rattus sp.</i>	<i>Manis</i>	<i>Panthera tigris</i>	<i>Panthera pardus</i>	<i>Canis sp. / cuon sp.</i>	<i>Lutrogale sp.</i>	<i>Pachycrocuta brevirostris</i>	<i>Tapirus indicus</i>	<i>Rhinoceros sondaicus</i>	<i>Hexaprotodon sivajavanicus</i>	<i>Sus brachygnathus</i>	<i>Sus macrognathus</i>	<i>Sus sp.</i>	<i>Axis mellekeri</i>	<i>Axis javanicus</i>	<i>Muntiacus muntjak</i>	<i>Rusa sp.</i>	<i>Cervidae indet.</i>	<i>Bubalus palaeokerabau</i>	<i>Bubalus anae</i>	<i>Bos paleojavanicus</i>	<i>Bos javanicus</i>	<i>Bovidae indet.</i>	<i>Duboisia sonlieng</i>	<i>Epileptobos groeneweldti</i>
Unit																																					
Wajak																																					
Punung																																					?
Ngandong																																					
Kd. Brubus																																					
Trinil HK																																					
Ci Saat																																					
Satir																																					

Table 1. Pleistocene vertebrate (mammalian) biozonation of eastern Java, with updated species lists based on De Vos et al. (1982), Sondaar (1984) and Van den Bergh (2001), Badoux (1959), Storm (2001), Storm et al. (2005), Storm and de Vos (2006), Volmer et al. (2015), Van der Geer et al. (2018) Van den Bergh et al. (2019). Punung and Wajak Fauna includes faunal remains from contemporary caves, following the work of the authors mentioned above. See text for clarifications. Note: species list is not complete. See full lists of above-mentioned works.

The faunal units are commonly presented in the form of a species list. **Table 1** is a new update of this list, with revised taxonomic names, an improved taxonomical ordering, additions of new finds and several taxonomic re-interpretations. New species have for example been added based on finds from the Madura Strait site, which falls under the Ngandong Fauna. Taxonomic re-interpretations have been made for the Punung Fauna. Justifications for the changes are provided in the captions and in this text.

The species composition of successive faunal units has commonly been interpreted in terms of alternating island stages and stages with a continental connection, as a result of Pleistocene glacio-eustatic sea-level fluctuations. The Satir Fauna is regarded as an island fauna. It is very poor in species, all of which are renowned for their ability to cross sea barriers and colonize islands. *Sinomastodon*, an archaic proboscidean taxon of Asia, is the marker species of this fauna. The fauna also contains a giant land tortoise, which is highly characteristic of island communities. The Ci Saat Fauna records new arrivals: *Stegodon trigonocephalus* (replacing *Sinomastodon*), bovids, and *Panthera tigris*. In Sangiran, the Ci Saat Fauna also contains a large canid, as a second carnivore species (Volmer et al., 2016). Moreover, it records

the first hominins on Java. These new arrivals, and the extinction of the large tortoise, point to a mainland connection. Nevertheless, the fauna is commonly still described as ‘poor in species’ and ‘unbalanced’, which is explained in terms of marginal isolation, only allowing for corridor dispersal or filter dispersal of vertebrate species (Van der Geer et al., 2018; Van den Bergh et al., 2001).

The subsequent Trinil-HK Fauna again records new species: the small bovid *Duboisia santeng*, *Sus brachygnathus*, several non-hominin primates and a smaller canid. At the same time, the hippo *Hexaprotodon sivalensis*, common in the two previous faunal units, disappears. Yet, the fauna is commonly still regarded as ‘unbalanced’. The subsequent Kedung Brubus Fauna records *Elephas hysudrindicus* and a large-statured cervid of the genus *Rusa* as new arrivals. Moreover, there are scarce records of a new bovid (*Epileptobos groeneveldtii*) and a large suid (*Sus macrognathus*). This fauna is finally regarded as ‘balanced’, reflecting an open mainland connection, which Van den Bergh et al. (2001) linked to the onset of the Middle Pleistocene glacial-interglacial regime, with large-amplitude sea-level cycles and more pronounced lowstands.

The Ngandong Fauna is similar to the Kedung Brubus Fauna. De Vos et al. (1982) noted that it lacks *D. santeng* and *A. lydekkeri*, suggesting that the species may have become extinct. However, in the Madura Strait assemblage, which is of similar age as the Ngandong Fauna, both species are still present. The Punung Fauna is a cave fauna consisting solely of dental elements brought together by porcupines. The fauna is thought to record a major faunal turnover. Most members of the previous community, including characteristic species such as *S. trigonocephalus*, appear to be absent and may have gone extinct. At the same time, it allegedly records the arrival of modern species, which includes herbivores as well as forest-dependent species such as *Pongo* and *Hylobates*.

4.2 New insights

Correlations to Sangiran and updated age ranges

Thus far, most of the available age ranges for the faunal units have been based on the well-dated depositional record of Sangiran, correlating the faunal units from their key sites to the vertebrate-rich profile of Sangiran (Van den Bergh et al., 2001; Leinders, 1985). According to these correlations, the middle part of the black clays yields the fossil species of the Satir Fauna, including its marker species *Sinomastodon bumiajuensis*. The upper part of the black clays contains the Ci Saat Fauna, with, as mentioned above, the first hominin fossils. Moving upwards, the Grenzbank supposedly contains the ‘unbalanced’ Trinil-HK Fauna, and the overlying fluvial sandstones, known as the Kabuh or Bapang Formation, contain the ‘balanced’ Kedung Brubus Fauna.

In the meantime, new numerical ages have become available, for Sangiran, but also for some of the key find sites of the faunal units (Table 2). The new numerical ages contribute greatly to our understanding of the faunal units, but also confront us with an inconsistency between the Sangiran-based age of the Trinil-HK Fauna and the new Trinil chronology of Hilgen et al. (2023). As explained in Section 3.3, the Haupt Knochenschicht of Trinil, key level of the Trinil-HK Fauna, is made up of two superimposed channel lags, referred to as BBC-1 and BBC-2, with a significant age difference. Both channel lags are younger than the Grenzbank of Sangiran and overlap with the age range of the overlying Bapang Formation, which according to the commonly accepted biostratigraphic framework contains the Kedung Brubus Fauna. Especially the age of BBC-2 falls well above the expected age range of the Trinil-HK Fauna.

The double-aged Trinil-HK Fauna

Our finding that the Haupt Knochenschicht consists of two channel lags with a significant age difference questions the significance of the Trinil-HK Fauna as an age-specific vertebrate community. Small-scale test excavations during our 2017–2018 field work did not reveal relevant differences between the fossils from BBC-1 and BBC-2, in terms of species composition or preservation state. Both beds contain fragmented fossil remains, with a dominance of *Stegodon trigonocephalus*, large bovids, *Duboisia santeng* and *Axis lydekkeri*. For a more significant comparison between the fossils of both beds we would need much larger numbers of specimens, which is unrealistic, considering that only small remnants of the original bone beds have remained and that the site is protected.

Unit	Sangiran-based ages	Ages of the key sites
Wajak		> 37.4 – 28.5 ka
Punung		128–118 ka
Ngandong		140 – 92 ka
Kd. Brubus	< 900 ka	
Trinil HK	Grenzbank: 900 ka	BBC-2: ~450 ka BBC-1: 830–773 ka
Ci Saat	1.3 – 0.9 Ma	
Satir	1.9 – 1.5 Ma	

Table 2. Published age ranges of the vertebrate faunal units, based on dating studies in Sangiran and at the key sites of the faunal units. Data from, Sangiran: Matsu'ura et al. (2020). Trinil: Hilgen et al. (2023). Ngandong: Rizal et al. (2020). Punung: Westaway et al. (2007). Wajak: Storm et al. (2013).

Let's assume that the fossil content of BBC-1 and BBC-2 is indeed comparable. An explanation might then be that the fossils in BBC-2 have been reworked from the underlying BBC-1. Both channel lags reflect incision by small rivers. Moderately rounded clasts of locally eroded material point to winnowing rather than significant transport. It is well-imaginable that the BBC-2-river reworked the locally available coarse elements of BBC-1 in its own channel lag. During our 2018 excavations in Trinil, we found a *Stegodon* tusk embedded in BBC-1, but protruding into the overlying BBC-2. This rather strange position can only be explained by active fluvial incision into an older, bone-bearing channel. We can therefore be sure that reworking did take place, but to which extent BBC-2 also contains younger, contemporary fossils is hard to say. There are some reasons to think that such younger fossils are scarce. Van den Bergh (1999) noted that metrically, the *Stegodon* molars from the 'Haupt Knochenschicht' form a homogenous sample, which speaks against a mixed-age. Moreover, BBC-2 appears to lack characteristic Kedung Brubus species such as *Elephas hysudrindicus* and *Rusa* sp., even though its age falls well into the estimated age range of this faunal unit.

If we assume that most fossils of BBC-2 have been reworked from BBC-1, then the Trinil-HK Fauna, as excavated from its key beds, may still be regarded as 'more or less homogenous', with an age range of 830 - 773 ka, and with an unknown admixture of fossils with an age of ~450 ka. Note that it is of course also possible that the BBCs contain fossils older than 830 ka, reworked from strata underlying BBC-1. Fossils may have been reworked from the black clay bed BGC-3 (Fig. 5), which indeed contains occasional skeletal remains. Likely, this clay bed correlates with the top of the Sangiran black clays, suggesting that its fossils are part of the Ci Saat Fauna.

The 830 - 773 ka age range of BBC-1 comes comfortably close to the 900 ka age of the Grenzbank of Sangiran. Yet, it overlaps with the age of the basal sandstones of the Bapang Formation of Sangiran, which is said to contain the Kedung Brubus Fauna. There is no reason to doubt the available numerical ages, which on both sites are based on multiple measurements and supported by paleomagnetic profiles. A more likely explanation of the conflicting age ranges and fossils faunas lies in the definition and interpretation of species lists.

Significance of species lists

Over the past decades, interpretations of the faunal units and their correlations across find sites have relied on a rather strict interpretation of species lists. My work on the Madura Strait assemblage made me aware of the difficulties of such species lists. A major problem is the significance of rare species in fossil assemblages, such as predators, hominins and arboreal primates. For the identification of the Madura Strait assemblage (N=6372 specimens), I listed the numbers of identified specimens per species and added justifications for the identifications. Several species appeared to be quite rare. For example, only one specimen could be attributed to a carnivore (*Panthera pardus*), two to a reptilian predator (*Varanus komodoensis*), two to hominins (*Homo erectus*) and one to an arboreal primate (*Macaca* sp.). The occurrence of rare species may be relevant for the interpretation of a vertebrate community. However, their absence is only meaningful if we have insight into the original sample size and the degree of detail of the faunal analyses. Moreover, we need to have insight into the taphonomic background of an assemblage. For most of the assemblages from Java, specimen counts and systematic taphonomic analyses are not available. This reduces the value of species lists and complicates comparisons.

It is not difficult to see the effects of taphonomy, sample size and analytical detail in the species lists. The Trinil-HK and Kedung Brubus Faunas have been based on enormous sample sizes (tens of thousands of specimens). This tells us something about excellent conditions of bone preservation and accumulation. The assemblages derive from beds that were formed under a rather dry climate, which implies low bone-weathering rates, and with a pronounced rainy season, which forms an effective mechanism for the concentration of skeletal elements in fluvial lag deposits. The resulting bone beds attracted palaeontologists like Dubois and Selenka, who collected several ten-thousands of specimens from the sites. Subsequently, the assemblages were studied and documented in detail, thanks to the work of later taxonomists as Hooijer, Janensch and Stremme. If we now look at the assemblages from Bumiayu, as described by van der Maarel (1932), or the corresponding assemblages from the black clays of Sangiran, as described by Aimi and Aziz (1985), it is clear that the species lists of the Satir and Ci Saat Faunas have been based on much smaller samples and less detailed analyses. This, for example, reflects the different conditions for preservation and accumulation in the humid, marshy setting represented by the black clays, which did not result in rich bone beds, but rather in a scattered occurrence of fossils throughout the profile. The lower numbers of fossils, often collected as occasional finds over a longer period, were not studied to the same level of detail as the assemblages from Trinil and Kedung Brubus.

With these taphonomic and analytical differences in mind, it is no wonder that the Trinil-HK Fauna contains more species than the Ci Saat Fauna. Note in this respect that the species list of the Ci Saat Fauna speaks of 'cervids' and 'bovids', whereas the subsequent Trinil-HK Fauna contains various bovid and cervid species, which clearly reflects the difference in analytical detail. Many of these Pleistocene species were in fact defined based on specimens from the Trinil assemblage. This gives an impression of 'new arrivals' and 'more balanced conditions', but the species may very well have already been present in the Ci Saat Fauna, hidden under the labels 'bovids' and 'cervids'.

Age ranges and stratigraphic ranges

A peculiar aspect of the faunal units is that, with respect to stratigraphic ranges and age ranges, they have much different orders of magnitude (**Fig. 6, left column**). The Trinil-HK Fauna derives from two bone beds, both representing a short accumulation period. The beds may even represent single events of increased mortality, for example caused by an episode of extreme drought, or by an explosive ash-rich eruption. The same may account for the Grenzbank. In contrast, the poorly studied Kedung Brubus site, with a thickness of > 200 m, may very well have a composite build-up, of stacked fluvial sequences of different ages. Theoretically, this unit covers the ~600 ka between the Trinil-HK and Ngandong Faunas. Also in other areas where the fossils of this faunal unit are found, such as in the fluvial series around Mojokerto, Jetis, and Pening, the bone-bearing strata appear to represent a long age range, covering most of the Middle Pleistocene (**Chapter 4 of this thesis**). This places its extensive species list, described as ‘balanced’, in a completely different perspective. The degree of time-averaging in the Kedung Brubus Fauna must be enormous, certainly in comparison to the Trinil-HK Fauna.

A continental perspective

Our new insight of Pleistocene Sundaland as a stably exposed continental area, only subject to progressive submergence in the course of the Middle Pleistocene, requires a thorough re-interpretation of the faunal stages.

The Satir Fauna, consisting of four pioneer taxa, may rightly be regarded as unbalanced and represents convincing island conditions. Apparently, emerging eastern Java, with its uplifted fold zones and the Wilis and Old Lawu as the earliest eruption centers (**Section 2.2**), was not yet connected to continental Sundaland during its earliest stages

The Ci Saat Fauna records a large number of immigrant species, including poor swimmers like bovids, *Rhinoceros sondaicus* and *Panthera tigris*, all of which must have arrived via a full land connection. The vertebrate community holds large and medium-sized herbivores, as well as two carnivores, which shows that there must have been considerable predator pressure. A sustainable tiger population requires a wide territory. All this points to a balanced fauna and continental conditions. The label ‘unbalanced’ was largely based on the relatively low species diversity, but there are important taphonomical and analytical reasons that explain why the Ci Saat Fauna does not contain as many species as subsequent faunal units.

The Trinil-HK Fauna, although commonly still regarded as ‘unbalanced’, contains a wide range of small- to large-bodied herbivores, as well as secondary consumers of all body sizes, including rats, suids, canids and tigers. It is therefore a rich and highly diverse fauna that bears no evidence of isolation. In fact, the difference with the subsequent Kedung Brubus Fauna, commonly regarded as ‘balanced’, is insignificant. Yes, the Kedung Brubus Fauna is slightly richer in species, but this is readily explained by the much longer time range represented by this faunal unit compared to the preceding Trinil-HK-Fauna.

Endemic species or Sundaland species?

In the previous model of Java as an island with intermittent mainland connections, many of the Pleistocene species from Java have been regarded as endemic or dwarfed. The *Hexaprotodon sivalensis* of the Satir Fauna has a reduced body size compared to its relatives in the younger faunal units (de Visser, 2008), which may indeed very well relate to the island conditions of early-emerging eastern Java. However, for the species of the subsequent Trinil-HK Fauna, the occurrence of island dwarfism is doubtful. Rozzi et al. (2013) and Van der Geer et al. (2011) point at the small-statured *Duboisia santeng* as the best example of an endemic, dwarfed species. Indeed, the species is small compared to mainland *Boselaphus*, its closest relative. However, dwarfed island species generally quickly become extinct when exposed to mainland connections. *Duboisia santeng* has remained a common element of the vertebrate community of this part of Sundaland for at least 700 ka, together with larger-bodied herbivores and carnivores. This does not give an impression of island dwarfism. Note also that the species is part of the Madura Strait assemblage and that it was reported from a fossil assemblage in Thailand (Nishioka and Vidthayanon, 2018), which shows that the species must have had a geographic range that extended far beyond present-day Java.

4.3 A revised biostratigraphy

Climate and landscape

Instead of looking at the Javanese fossil assemblages from an island view point, we need to regard them as records of a continental Sundaland fauna. Changes of the vertebrate community may rather reflect climate change and related shifting of vegetation zones over Sundaland. Pollen records (Sémah and Sémah, 2012; Polhaupessy, 1990) as well as ferrallitic weathering profiles (Brasseur et al., 2011) show that present-day eastern Java was under a humid tropical climate throughout most of the Early Pleistocene. The black clays, forming the dominant and characteristic deposits from this period, were deposited in a forested coastal swamp. The first colonizing species of island-stage eastern Java, represented by the Satir Fauna, must have lived in this coastal forest. The same applies for the species of the sub-

sequent Ci Saat Fauna, which I regard as the first continental vertebrate community and which includes the earliest hominins.

The Grenzbank of Sangiran and the BBCs of Trinil represent a drastic landscape change, which, as explained in **Section 3.3**, involved a change from a humid coastal forest to a much drier landscape and a grass-dominated vegetation. In the vertebrate community this is expressed by a shift toward a dominance of grazers such as bovids and the disappearance of *Hexaprotodon*. In essence, it is this climate-related change of the vertebrate community that adequately explains the difference between the Ci Saat and Trinil-HK Faunas.

This new, large-herbivore dominated, grass or open-woodland community, which continues as the rather similar Kedung Brubus Fauna, remained remarkably stable throughout the late Early and Middle Pleistocene. In the course of the Middle Pleistocene, a more pronounced glacio-eustatic cyclicity may have resulted in shifts of climate and vegetation zones over continental Sundaland. Although there is as yet no evidence of significant changes in the vegetation of eastern Java, it is possible that shifting vegetation zones in central Sundaland affected migration patterns of species, possibly explaining the new arrivals of species in the marginal shelf zone of present-day eastern Java. From MIS11 onward, this process may have been amplified by intermittent and progressive contraction of the exposed Sundaland land surface, as shown in **Fig. 3C**. New species recorded by the Kedung Brubus Fauna, such as *Elephas hysudrindicus* and *Rusa* sp., may reflect such migration of species over Sundaland, as a result of shifting vegetation zones and a cyclic contraction of the exposed land surface. However, it is important to note that we have no idea when exactly these species first arrived in this area, within the long time-range covered by the Kedung Brubus Fauna. Note in this respect that a new fossil species is commonly regarded as an 'arrival' on Java, whereas it may very well just represent a brief, possibly climate-related stage, during which the geographic range of a species temporarily covered this part of the Sunda Shelf.

Besides regional climate fluctuations, the gradual development of larger drainage systems, such as the Brantas and the Solo, may have been a relevant factor for the geographic distribution of vertebrate species over Sundaland. The presence of a large river may explain the return of *Hexaprotodon sivalensis* in the Kedung Brubus Fauna. Large drainage systems may also have been of relevance for arboreal primates, migrating along the tree-lined river banks.

MIS6 and MIS5

The Solo terrace of Ngandong was dated to 140 – 92 ka by Rizal et al. (2020). The authors proposed a modelled, most-likely age range for the fossils of 117 – 108 ka. This, however, is not very likely. The fossil fauna is the last representative of the grassland or open-woodland vertebrate community that had existed in this part of Sundaland since ca. 900 ka. As we will see, it definitely pre-dates MIS5e, the first true island stage of Java, represented by the Punung Fauna. Moreover, the fossils derive from the basal conglomerates of the terrace. The fluvial regime must have been determined by various factors, but if we assume that sea-level changes were a decisive factor, then this basal conglomerate may be linked to lowstand-related downcutting rather than highstand-related aggradation. It is plausible to project the Ngandong Fauna in the early part of the age range, for example between 140 and 130 ka, which links the fauna to the penultimate glacial period of MIS6. The fact that the Ngandong Fauna is so similar to the preceding Kedung Brubus Fauna shows that the preceding stages of shelf submergence and Sundaland surface-contraction, linked to the highstands of MIS7, MIS9 and MIS11, left few traces in the local vertebrate community. A new species, only known from the Ngandong Fauna, is *Axis javanicus*. The species is related to *Axis axis* of the Asian mainland and may have reached Java during an MIS6 lowstand dispersal wave.

The Punung Fauna was dated to 128–118 ka (Westaway et al., 2007), which links it to the peak highstand conditions of MIS5e. This makes it a unique faunal record, of what probably was the first island stage of Java. A great faunal difference with the preceding Ngandong Fauna is commonly regarded as a faunal turnover, recording the extinction of the preceding grassland community and the arrival of a modern fauna with rain forest-dependent taxa such as *Pongo*. This faunal turnover has commonly been linked to increasing precipitation rates and a change to forested conditions. Looking at the Sundaland charts of **Fig. 3C**, the decisive factor for the disruption of the former, long-standing vertebrate community may very well have been the MIS5 island-setting of Java.

To get an idea of what MIS5 Java may have looked like, it is interesting to refer to the present (Holocene) island situation. Today, the western part of the island is humid and was, up to recently, fully forested. The eastern part of the island is much drier and has a grass-dominated vegetation, such as preserved in Baluran National Park. However, global sea surface temperatures were ca. 1 degree higher during MIS5e than during MIS1 (Wang and Zong, 2020; Hoffman et al., 2017), and it is reasonable to assume a further eastward expansion of the tropical forest over island-stage Java during MIS5e. This may have reduced the available savanna refuge along the eastern edge of the island.

Although this provides a good explanation for the MIS5 extinction of large herbivore taxa such as *Stegodon*, we need to be careful with the concept of a faunal turnover. The idea that the previous, MIS6 vertebrate community was replaced by a new, modern community is difficult to conceive, within the MIS5e island setting of Java. Van den Bergh et

al. (2001) proposed a temporary land bridge during interstadial MIS5d, at ~115 ka, but this does not fit with the age of the Punung Fauna, which predates MIS5d. To understand potential MIS5e species migration, it is good to make a distinction between arboreal primates and herbivores. Under the upcoming MIS5e interglacial conditions, the forest zone shifted eastward, together with the gradual submergence of the shelf, which ultimately brought island conditions to Java. Large herbivores were pushed eastwards to a relict savanna and may eventually have been 'pushed off the island'. At the same time, arboreal primates moved along with the eastward-shifting forested zone. This readily explains the occurrence of arboreal primates as new MIS5 arrivals recorded by the Punung Fauna. However, under these conditions, it is impossible to explain an arrival of new herbivores. Yet, within the commonly accepted species lists, the Punung Fauna is referred to as a 'fully modern fauna' with new herbivores as *Bos palaeojavanicus*, *Bubalus bubalis*, and *Elephas maximus*. I think this is incorrect. It is interesting that the taxonomy of these species has been subject to different interpretations. Von Koenigswald (Von Koenigswald, 1939, 1940) referred to the bovids and cervids of the Punung Fauna under their Middle Pleistocene species names. Badoux (1959), probably the taxonomist who studied the Punung material in most detail, acknowledged that he could not see the difference between the archaic herbivores of the Middle Pleistocene Javanese sites and their extant relatives. Sondaar (1984) still used the Middle Pleistocene taxonomy, but Van den Bergh (2001) and Storm (2001) changed this to the use of modern species names, without further metric or morphological justification.

Now, it is interesting to zoom in on the fossil remains from the Punung caves. The material has been brought to the cave by porcupines, consuming the bone tissue and leaving only crowns. The Punung Fauna taxonomy is thus based solely on isolated crowns. It is, however, rather complicated to distinguish between individual bovid and cervid species based on dental crowns. My work in the Madura Strait assemblage showed that large samples are needed and that taxonomic decisions can only be tentative. More importantly, there is often no clearly described morphological or metric key to distinguish between archaic species and related modern species. In the Madura Strait assemblage, obviously an MIS6 grassland fauna, I frequently found molar sizes of bovids and cervids that overlap with the extant species. Especially for bovids, the distinction between 'archaic' Middle Pleistocene species and modern species is largely a matter of taxonomical tradition.

To a certain extent, this also accounts for the genus *Elephas*. The Middle Pleistocene *Elephas* of Java is traditionally referred to as *Elephas hysudrindicus* and it certainly differs from the extant *Elephas maximus* by skull morphology (Hooijer, 1955). When it comes to isolated cheek teeth, *Elephas maximus* is characterized by a greater hypsodonty, however with overlapping metric ranges. For the Madura Strait assemblage, it proved to be impossible to distinguish between the two species and we decided to refer to the material as *Elephas* sp. The Punung assemblage contains four tooth fragments, which Sondaar (1984) and later authors referred to as *Elephas maximus*. However, as also acknowledged by Van den Bergh et al. (2001), the material is too fragmented for a sound taxonomical interpretation and its allocation to *Elephas maximus* must therefore be questioned.

It thus seems that the 'modern' taxonomical interpretations of the herbivores from the Punung caves have been coloured by the prevailing model of a faunal turnover. However, the scenario of newly arriving herbivores during peak interglacial conditions is extremely unlikely. It is much more likely that the Punung herbivores are survivors of the previous MIS6 community. In that case, a certain size change of their dental elements could have been a result of a changed diet, or may even be regarded as an effect of island conditions. So, yes, the Punung Fauna records a great change of the vertebrate community, with the extinction of *Stegodon trigonocephalus*, newly arriving arboreal primates and an archaic herbivore community under environmental pressure. But, no, the Punung Fauna does not record a turnover in the sense of a largescale replacement of archaic species by a fully modern fauna.

Modern herbivores, including *Elephas maximus*, probably arrived later on Java, during MIS4 and MIS2, when the Sunda Shelf fully re-emerged, the connection with mainland Asia was restored, and grassy plains once again became the dominant Sundaland landscape.

The faunal units of De Vos and Sondaar

The existing vertebrate faunal units of eastern Java form a valuable basic guideline for interpreting the vertebrate communities of the southeastern part of the Sunda Shelf throughout the Pleistocene. The species lists, however, are not 'cast in concrete' and need to be interpreted with care. Comparisons between the faunal units are complicated by great differences in taphonomy, sample sizes, analytical detail and represented age ranges.

It would be ideal to work with more comparable faunal units, with a similar level of detail, preferably representing the vertebrate community during specific marine isotope stages. This level of detail is available for the Ngandong (MIS6), Punung (MIS5e) and Wajak Faunas (MIS4-2), although differences in taphonomy still complicates comparisons between these assemblages. For the older units, especially the long-duration Kedung Brubus Fauna, this level of detail is not available.

A re-interpretation of the existing faunal units is provided in **Fig. 6**. The previous interpretations of the faunal units as a records of intermittent land bridges are largely incorrect. Only the Satir and Punung Faunas represent island stag-
es, though under completely different conditions. There are no significant differences between the Trinil HK-Fauna, Kedung Brubus and Ngandong Faunas. All three units represent a long period of dry climate conditions, a grass-domi-
nated vegetation and a stable continental vertebrate community. The chronostratigraphic significance of the heterog-
enous Trinil-HK Fauna is unclear, other than that we can say that it probably primarily represents the ‘earlier stages’
of the dry, grass-dominated landscape stage, which started around 900 ka, possibly with admixed older material (re-
worked from underlying strata) and younger material (from BBC-2).

There are records of new species in the subsequent Kedung Brubus Fauna, such as *Elephas hysudrindicus*, but these records are undated and stratigraphically not-specified, which makes it impossible to pinpoint a chronological bound-
ary between the Trinil-HK and Kedung Brubus Fauna. Therefore, at this stage, it is appropriate to assume a gradual
boundary between the Trinil-HK and Kedung Brubus Fauna. This re-interpretation of the Trinil-HK and Kedung Brubus
Faunas makes the apparently contradicting chronologies of Sangiran and Trinil of little significance.

The Ngandong Fauna is very similar to the Kedung Brubus Fauna, but its well-defined age range as an MIS6 lowstand
fauna, shortly before the MIS5e island-stage, makes it of great relevance.

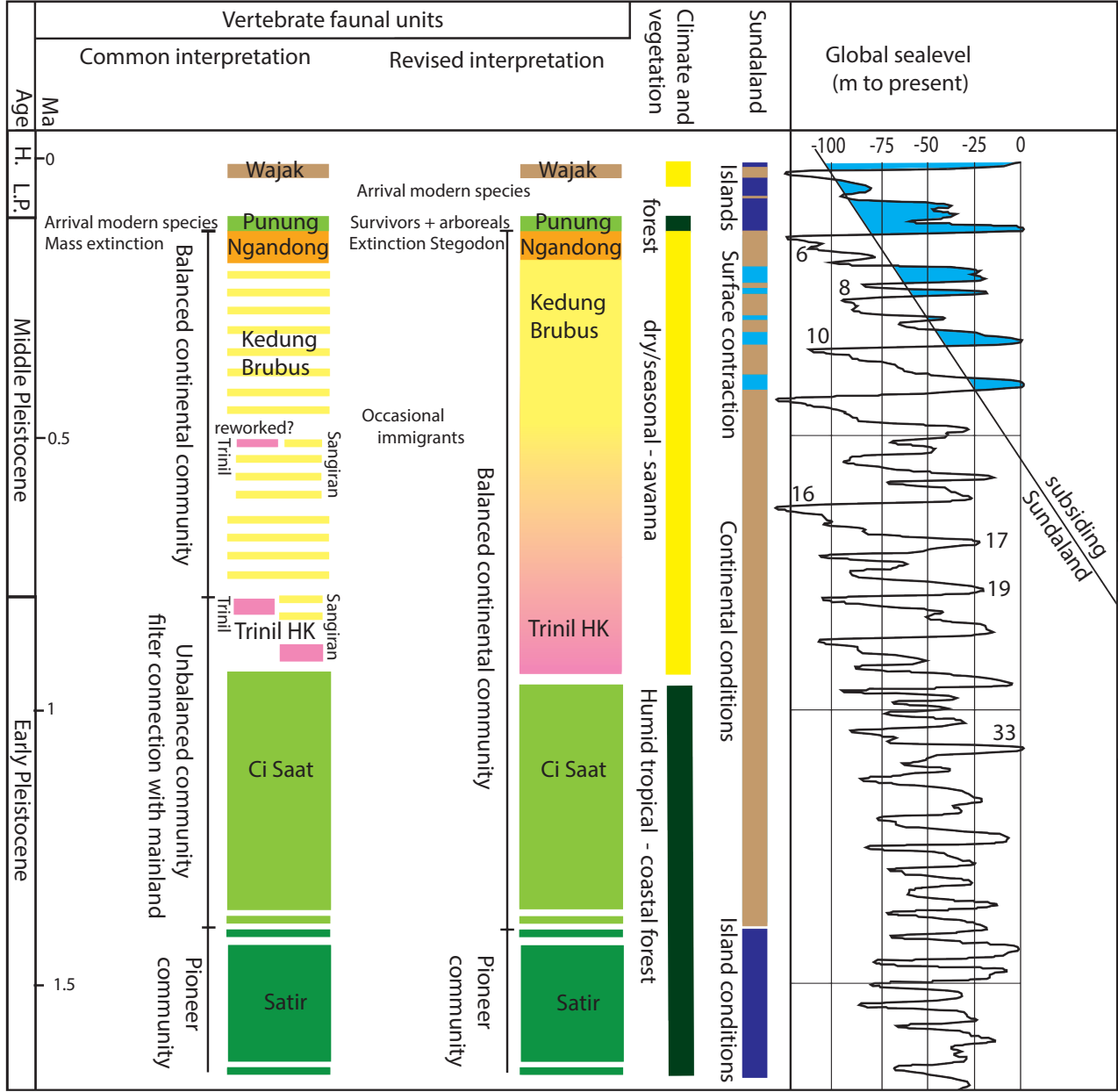


Fig. 6. The Pleistocene vertebrate biozonation of eastern Java: chronology, landscape and climate. Left column: common interpretation, with updated chronology. Right column: revised interpretation. Faunal units based on De Vos et al. (1982) and Sondaar (1984). Sea-level curve: Bintanja and Van der Wal (2008). Subsiding Sundaland: Sarr et al. (2019).

5. The hominin chronology of Java

5.1 The model of the long-standing lineage

From multiple species to a single taxon

The first Pleistocene hominin remains from Java were unearthed in the Wajak cave, in 1888 and 1890. The material, amongst which two partial skulls, was recognized as *Homo sapiens*, though remarkably robust (Storm, 1995; Dubois, 1920). Later in 1890, Dubois found a hominin mandible in Kedung Brubus. In 1891 and 1892, he made his great discoveries in Trinil: two hominin molars, a skullcap and a femur, which he assigned to a new species, *Pithecanthropus erectus* (Dubois, 1895). It took three decades before substantial new hominin fossils were found on the island. Between 1931 and 1933 thousands of vertebrate fossils were excavated from the Solo terrace of Ngandong, including 12 partial hominin crania, with a larger cranial capacity than the *Pithecanthropus* skullcap from Trinil. Oppenoorth (1932) assigned these fossils to a new, younger species, called *Homo soloensis*, which he regarded as a proto-Australian population. In 1936 a skull was found in Perning near Mojokerto. Von Koenigswald recognized it as a *Pithecanthropus* child, but after a dispute with Dubois, he changed this to *Homo mojokertensis* (Von Koenigswald, 1936a; 1936b). In 1937 and 1938, hominin fossils were discovered in the area around Sangiran, including a skullcap with a great morphological and metric similarity to the skullcap from Trinil. Von Koenigswald (1940) assigned all fossils to *Pithecanthropus erectus* and referred to the skullcap as *Pithecanthropus* II (today Sangiran 2). In the same period, Von Koenigswald also excavated fossil remains from the nearby Punung caves, amongst which he recognized a hominin tooth (Von Koenigswald, 1939). He regarded the fossils as contemporary with those from Trinil and assigned the hominin tooth to *Pithecanthropus erectus*.

In 1939, Von Koenigswald discovered a robust partial calvaria in Sangiran (Skull IV), and in 1941, a highly robust mandible fragment (Sangiran 6). Weidenreich (1945) assigned these new specimens to two new species: *Pithecanthropus gigantis* and *Meganthropus palaeojavanicus*, and regarded the hominin species from Sangiran as an evolutionary line, from *Meganthropus palaeojavanicus*, to *Pithecanthropus gigantis*, to *Pithecanthropus erectus*. However, the author acknowledged that the hominin species may also have existed side by side.

Meanwhile, hominin fossils had also been excavated in China, which had been described as *Sinanthropus pekinensis* (Weidenreich, 1943; Black, 1930) and a robust form, described as *Gigantopithecus* (Weidenreich, 1945). Weidenreich (1940) suggested that *Sinanthropus pekinensis* and *Pithecanthropus erectus* may be combined into one new species, *Homo erectus*. This became an accepted taxonomical practice after the publications of Mayr (1950), who also proposed to sink all other Javanese forms, including *Meganthropus*, *Pithecanthropus gigantis* and *Homo soloensis* into this new taxon. Le Gros Clark (1964) expanded the definition of *Homo erectus*, by assigning similar hominin remains from Africa to the species, such as Olduvai 9, previously referred to as *Homo leakeyi*.

Chronological groups

All Early to Middle Pleistocene hominin fossils from Java are nowadays referred to as *Homo erectus*, but the fossil material is subdivided in chronological groups, which echo the former subdivision in species (**Table 3**). Note, however, that the definition of these chronological groups does not align completely parallel among different authors. The most recent subdivision by Kaifu and Athreya (in press) distinguishes between an early and late *Homo erectus* of Java, and subdivide the early *Homo erectus* in two groups: the Sangiran Lower and Upper Group. The Lower Group covers the fossil material from the black clays and the Grenzbank, whereas the Upper Group covers the fossils from the sandstones overlying the Grenzbank, which they refer to as Bapang AG (above Grenzbank). The Sangiran Lower Group has a 'primitive' craniodental morphology, with relatively large molars, hyper-robust cranial bones, and a small cranial capacity. This group includes the specimens formerly regarded as *Meganthropus*. The Sangiran Upper Group includes Sangiran 2 and several well-preserved skulls discovered in Sangiran over the past decades, such as the Sangiran 17 and Skull IX.

The Late *Homo erectus* includes the material from Ngandong, formerly referred to as *Homo soloensis*, as well as four skulls discovered over the past decades: Sambungmacan 1, 3 and 4 and Ngawi 1. These crania are characterized by a widened frontal squama, a lengthened cranial base and a heightened cranial vault, resulting in an increased cranial capacity.

Phylogenetic discontinuity?

The morphological and metric diversity of the hominin fossils from Java has been the subject of a long discussion about their phylogenetic relation.

The oldest chronological group, the Sangiran Lower Group, contains robust mandibles and isolated dental remains that exceed the size range of the known *Homo erectus* sample world-wide, notably mandibles Sangiran 5 and 6, which were formerly regarded as *Pithecanthropus dubius* and *Meganthropus*. The same accounts for the extreme

thickness of cranium Sangiran 31. Robinson (1955, 1953) argued that the specimens are highly similar to *Paranthropus*, whereas Tobias and Von Koenigswald (1965) and Tyler (1995) noted an affinity with *Australopithecus* or *Homo habilis*, suggesting that the fossils represent an older, pre-*erectus* population.

A similar discussion was held over the phylogenetic position of the late *Homo erectus* of Java. Delson et al. (2001), Schwarz (2004), Schwartz and Tattersall (2003), Widiyanto and Zeitoun (2003), Baab (2011) and Baab and Zaim (2017) argued that the voluminous, vaulted brain case of this group points to the arrival of a new, more modern population, unrelated to the older *Homo erectus* of Java.

The single lineage model

Antón (2003, 2002), Baba et al. (2003), and Kaifu et al. (2017; 2008) regard all Pleistocene hominins from Java as a continuous evolutionary lineage, pointing to consistent cranial traits. According to these authors the Javanese *Homo erectus* is single population that lived isolated from other (mainland) populations, such as the Chinese *Homo erectus*. The chronological groups are regarded as time bands of this lineage (Kaifu and Athreya, in press). The robustness of some of the older specimens possibly reflects extreme sexual dimorphism (Kaifu et al., 2011), which may have been a primitive feature of the genus, also recognized in the Dmanisi population (Lordkipanidze et al., 2013).

The single-lineage model has today become commonly accepted. Remarkable is that in Africa and Eurasia, *Homo erectus* was replaced in the course of the Middle Pleistocene, by non-*erectus* hominins with a more voluminous, vaulted braincase, which may collectively be referred to as *Homo heidelbergensis* (Schwartz and Tattersall, 2003; Stringer, 2002). In eastern Asia, this morphologically diverse new population is referred to as archaic *Homo sapiens* (Antón, 2003), late Middle Pleistocene *Homo* (Rightmire et al., 2015), or late archaic *Homo* (Kaifu, 2017). The assumed continuation of the old *Homo erectus* lineage on Java implicates its survival on this remote part of the Sunda Shelf, as a relict population.

Extinction of the lineage and arrival of Homo sapiens

It is generally assumed that the Javanese *Homo erectus* lineage went extinct in the beginning of the Late Pleistocene, together with most other members of the Middle Pleistocene vertebrate community. This ‘faunal turnover’ is commonly linked to climate change, toward more humid conditions and a forested landscape (Rizal et al., 2020; Van den Bergh et al., 2001; Sondaar, 1984). Within this model, the Late Pleistocene Punung Fauna consists of modern species. This brings us back to the hominin tooth from the Punung cave, described by Von Koenigswald (1939) as *Pithecanthropus erectus*. Interestingly, Badoux (1959) recognized five other hominin teeth in the Punung collection, among material that had formerly been labeled as *Pongo*. The author assigned the specimens to *Homo* cf. *Pithecanthropus*. However, in line with the later interpretation of the Punung Fauna as a modern fauna, the hominin teeth were renamed *Homo sapiens* by Sondaar (1984), albeit without further anatomical justification. Storm et al. (2005) tried to trace back the hominin teeth in the Punung Collection of Von Koenigswald in the Senckenberg Museum of Frankfurt, but the specimens appeared to be lost. They did find a single hominin tooth in the collection, from which they assumed that it belongs to the Punung assemblage. The authors assigned this specimen to *H. sapiens* rather than *H. erectus*, referring to its relatively small size.

More reliable records of the arrival of anatomically modern *Homo sapiens* in the Sundaland region date from later in the Late Pleistocene and include the material from Niah Cave, Borneo, dated to ~37 ka (Curnoe et al., 2019) and from Java, such as the Wajak skulls, with a minimum age of 37.4 to 28.5 ka (Storm, 2013), and two femora from the youngest Solo terrace of Trinil, dated to 37–32 ka (Ruff et al., 2022).

The continental perspective

The new insights into the Quaternary paleogeography of Java and the Sunda Shelf urge us to reconsider the model of an isolated hominin lineage. Instead of an island with intermittent land bridges, eastern Java has been an integral part of emerged Sundaland, at least since 1.3 Ma, when a balanced, continental vertebrate community developed. It seems likely that the former island perspective of Java has also coloured our interpretation of the Javanese hominins. Most likely, the geographic range of the Pleistocene hominins was not restricted to present-day Java. The fossil assemblages of Java record the occasional arrival of new species, including herbivore taxa such as *Elephas* and *Rusa*. Apparently, these herbivore taxa could migrate over Sundaland. So, why would the *Homo erectus* population of Sundaland have remained isolated from mainland populations, for a period of time that exceeds one million years?

5.2 New insights

The early Homo erectus and the complex stratigraphy of Trinil and Sangiran

The early *Homo erectus* is mainly represented by fossil remains from Trinil and Sangiran. To understand their chronological relationships and the subdivision of this material into a Lower and Upper Group, it is relevant to dive into the

complex stratigraphy of both sites.

Fig. 7 shows a cross-section over the Solo valley near Trinil, with the Dubois excavation site on the left bank and the museum on the right bank. The right bank features a gravelly strath terrace that truncates a thick unit of parallel-bedded fluvial tuffs. The left river bank presents a lower, younger terrace, with its erosive base reaching almost down to low water level of the Solo. This terrace has a composite build-up. Its basal part reflects downcutting conditions, with gravelly channels and sandy point bars; its top part is a tuffaceous fill, reflecting a change to aggradation, which makes the terrace a fill terrace. The strath terrace of the right bank (T5) is an abrasion level of the oldest Solo, dating to around 375 ka and relates to MIS10. The terrace of the left bank (T2) reflects MIS6 downcutting, followed by aggradation which may relate to the MIS5 base-level rise and/or to increased volcanic supply (**Chapter 2 of this thesis**).

At the Dubois excavation site, older strata are preserved below the erosive base of terrace T2. Among these are fossil-bearing lag deposits of incisive streams that pre-date the Solo drainage system. This level was formerly referred to as Haupt Knochenschicht. It consists of two superimposed channels, which we refer to as BBC-1 and BBC-2, dating to 830 – 773 ka and ~450 ka respectively (Hilgen et al., 2023). During the historic excavations, fossils from both channels have become mixed. Dubois' hominin fossils, the upper third molar (Trinil 1), the skullcap (Trinil 2) and two other teeth (Trinil 4 and 5) derive from either BBC-1 or BBC-2. However, this probably does not account for Trinil 3, also known as Femur I. A reconstruction of its find location indicates that it derives from a T2 channel that cuts through the older fossil-bearing channels (Pop et al., 2023a), which explains its modern, post-*erectus* morphology (Ruff et al., 2015). A prominent T2 channel is also visible east of the Dubois excavation site, at the site of Selenka Grube III. A fill of laminated clay shows that this must have been an abandoned channel. Unknowingly, the excavators missed the bone-bearing lag deposits and worked through the fill of this MIS6 Solo channel.

The Dubois collection also yielded hominin fossils that were only later recognized as such. Femora II-V (Dubois, 1932) have an *erectus*-type morphology and are in a fragmented state of preservation (Ruff et al., 2015), which is quite different from femur I, pointing to a provenance from BBC-1 or BBC-2. Joordens et al. (2015) described fresh water mollusks with opening traces, shell tools and an engraved shell, all deriving from the Dubois collection. The sandy fill of the shells was dated to ~450 ka, which ties the specimens to BBC-2.

Along the right river bank, the BBCs are mostly absent. The facies of the thick unit of bedded fluvial tuff resembles the fill of the T2 terrace of the left bank, however, the unit is tectonically tilted and reaches a much greater height than terrace T2. It is abraded by one of the oldest Solo terraces, indicating that it predates the origin of this river. We referred to this unit as the Trinil Formation. With an age of ~450 ka for BBC2 and a T5 terrace age of ~375 ka, there is only a relatively short time window for this prominent unit. Compared to the incised bone-bearing channels (the BBCs), the stacking of fluvially deposited tuff beds reflects a remarkable base-level rise. We postulated the formation of a volcanic barrier between the Lawu and the Kendeng, forming a lake basin that was quickly filled, by fluvial supply of volcanic ash (**Chapter 3 of this thesis**).

Previously, the fluvial deposits of both river banks had been referred to as the Kabuh Formation. **Fig. 7** shows that it is a composite of deposits of varying ages and different landscape stages: the BBCs are rare traces of an old incisive landscape, the Trinil Formation is the thick tuffaceous fill of a subsequent lake basin, and the Solo terraces are a complex of progressive incision and fill structures.

In 1978, Jacob excavated two hominin femora (Trinil 9 and 10) from the right bank. Recently, the specimens were identified as *Homo sapiens* (Ruff et al., 2022). We were able to relocate their finding spot in a small erosion remnant of terrace T1. This is a poorly preserved fill terrace that correlates with the 31 ka Kendeng terrace (Rizal et al., 2020). Around Trinil, remnants of this terrace are 'glued' to the valley walls, marked by subtle irregularities or small preserved terrace surfaces at ca. 8 m above low water level.

The Sangiran stratigraphy is generally represented as a standard profile (**Fig. 8A**). As explained in **Section 3.3**, the vertebrate-bearing stratigraphic range consists of black organic clays (Sangiran Formation) overlain by fluvial conglomerates and tuffaceous sandstones (Bapang Formation) forming stacked fluvial sequences. **Fig. 8B** shows the standard profile as a chronostratigraphic representation, based on the most recent chronology of Matsu'ura et al. (2020) and with references to other studies. The black clays offer a good age control, established through radiometrically dated tuff laminae, and by a normal polarity zone regarded as the Jaramillo subchron, in the top-range of the clay series. The overlying fluvial sequences also contain ash-dominated laminae that have been dated through multiple single-grain radiometric datings.

In the stratigraphy of (Itihara et al., 1985), the boundary between the black clays and the first conglomerate bed, known as the Grenzbank, is regarded as conformable, an interpretation that still holds strong in recent hominin literature. However, the Grenzbank is a basal lag deposit of an incisive, fluvial (and locally tidal) channel system and the contact with the underlying clays is obviously unconformable. This is confirmed by the available numerical ages: the top of the black clays contains the upper boundary of the Jaramillo subchron of 990 ka (Hyodo et al., 1993),

whereas a few meters higher, the base of the Grenzbank was dated to ~900 ka (Matsu'ura et al., 2020). A clay layer with a thickness of ~10 m is missing, likely due to erosion, resulting in a chronological hiatus of ~80 ka (Hilgen et al., 2022). Also the Bapang Formation is commonly regarded as a record of continuous deposition. In practice, there are probably short hiatuses between the individual fluvial sequences, each consecutive gravel bed being slightly incised into the previous sequence. The basal conglomerate bed, the Grenzbank, probably relates to the lowstand of MIS22. The second fluvial sequence was dated to ~780 ka. Possibly, the basal conglomerate of this sequence correlates with MIS20. The third sequence postdates the Brunhes – Matuyama polarity change and may be tied to MIS18 or MIS16.

Most of the hominin fossils from Sangiran are surface finds, or in-situ finds with a poorly documented provenance. For some of these specimens, the stratigraphic provenance has been reconstructed. Hominin fossils derive from the top of the clays, with a proven first occurrence at ~1.1 Ma (Matsu'ura et al., 2020). This is the oldest reliable record of hominin presence in eastern Java. Likely, the stratigraphic range of hominin remains continues downwards to Tuff 8 (T8 in Fig. 8), dated to ~1.3 Ma (Matsu'ura et al., 2020). Hominin fossils are also reported from the basal two fluvial sequences of the Bapang Formation. However, hominin fossils are unknown from the third sequence, which post-dates the Brunhes – Matuyama polarity reversal.

The subdivision of the hominin material in a Sangiran Lower and Upper Group is stratigraphy-based. The Lower Group derives from the black clays and the Grenzbank. It is dominated by dental or gnathic remains, including the robust specimens formerly regarded as *Meganthropus*. Skull elements from this range are rare, but probably include Sangiran 4 and 31, as well as Bjj 1602, recently discovered in the Grenzbank (Widianto et al., 2023). These skulls are marked by an extremely-thickened cranial bone, as well as an extremely-pronounced nuchal torus, both of which are unknown from any other hominin species. The Upper Group derives from the fluvial sequences overlying the Grenzbank and consists of dentognathic remains as well as skulls, amongst which are the well-preserved crania Sangiran 10, 12, 17, Skull IX and Bukuran.

The question is, how do the hominin fossils from Trinil correlate chronologically to the fossils from Sangiran? Fig. 8A shows the standard stratigraphy of both sites, ordered by their correlation between the Grenzbank of Sangiran and the 'Haupt Knochenschicht' of Trinil. This correlation was proposed by Von Koenigswald (1939) and has survived the later stratigraphic and biostratigraphic revisions. Projected side-by-side, the correlation is certainly not unreasonable. At both sites, this conglomerate bed marks the transition from marshy coastal clays to channelled fluvial deposits. Fig. 8B shows the same profiles, but now with a chronological ordering. This shows that in Sangiran, the black clays offer a more or less continuous record, covering most of the Early Pleistocene. In Trinil, we only have a fragmented record of this period, which consists of volcanic breccias with ferrallitic weathering profiles, levels of slight incision, and inter-bedded beds of organic clays. This marks a slightly higher position of Trinil in the paleo-landscape, closer to the foot of the Old Lawu, and suggests some subsidence of the Sangiran area during this same period. Moving to the overlying fluvial strata, we see again that the Sangiran stratigraphy offers a rather complete record, with a basal conglomerate dating to ~900 ka overlain by several fluvial sequences that appear to correlate with the sea-level curve from MIS22 onward. In Trinil we see this same transition, but the preservation is much less detailed. We only have two incisive conglomerates, BBC-1 and BBC-2, which together make up the former 'Haupt Knochenschicht'. BBC-1, with an age range between 830 and 773 ka, correlates chronologically with the second fluvial sequence of Sangiran. BBC-2 is much younger. If we move further upward in the stratigraphic record, we see that Trinil has a more complete record of the latest Middle Pleistocene than Sangiran, thanks to the occurrence of the lake-basin fill (the Trinil Formation) and the subsequent Solo terraces.

As a result of the former correlation between the Grenzbank of Sangiran and the 'Haupt Knochenschicht' of Trinil, and the practice of adding the Grenzbank specimens to the Lower Group, the 'Haupt Knochenschicht' hominin fossils from Trinil have commonly been regarded as part of the Lower Sangiran Group. This makes Trinil 2 a 'gracile member' of the archaic population. This is incorrect. If we assume that Trinil 2 derives from BBC-1, then it is age-equivalent to the hominin fossils from the second fluvial sequence of Sangiran, which are part of the Upper Sangiran Group. Yet, this correlation of Trinil 2 with the Lower Sangiran Group has confounded evolutionary interpretations. According to the prevalent model, the Lower and Upper Sangiran Groups represent an evolving lineage of *Homo erectus*, an interpretation that is based on the recognition of a shared cranial form. The problem is that reasonably intact crania from the black clays or the Grenzbank are not available, which makes Trinil 2 the best-preserved cranium of the Lower Group. Schwarz and Tattersal (2003) even refer to the Lower Group as the Trinil/Sangiran 2 morph. Nevertheless, Trinil 2 is certainly part of the younger group. Sangiran 2 is a skull of unknown stratigraphic provenance, but with a metric and morphological match with Trinil 2, indicating that it is most likely also a member of the younger group.

From a geological point of view, it is strange that the hominin fossils from the Grenzbank are added to the Lower Group. It is more realistic to regard this stratigraphic level as the base of the overlying fluvial series. However, from a taxonomic point of view, it is understandable. The Grenzbank yielded robust dentognathic remains, which are similar to the fossils from the underlying clays. The level also yielded Sangiran 4, the partial skull previously regarded as *Pithecanthropus robustus*, and the recently discovered robust skull Bjj 1602.

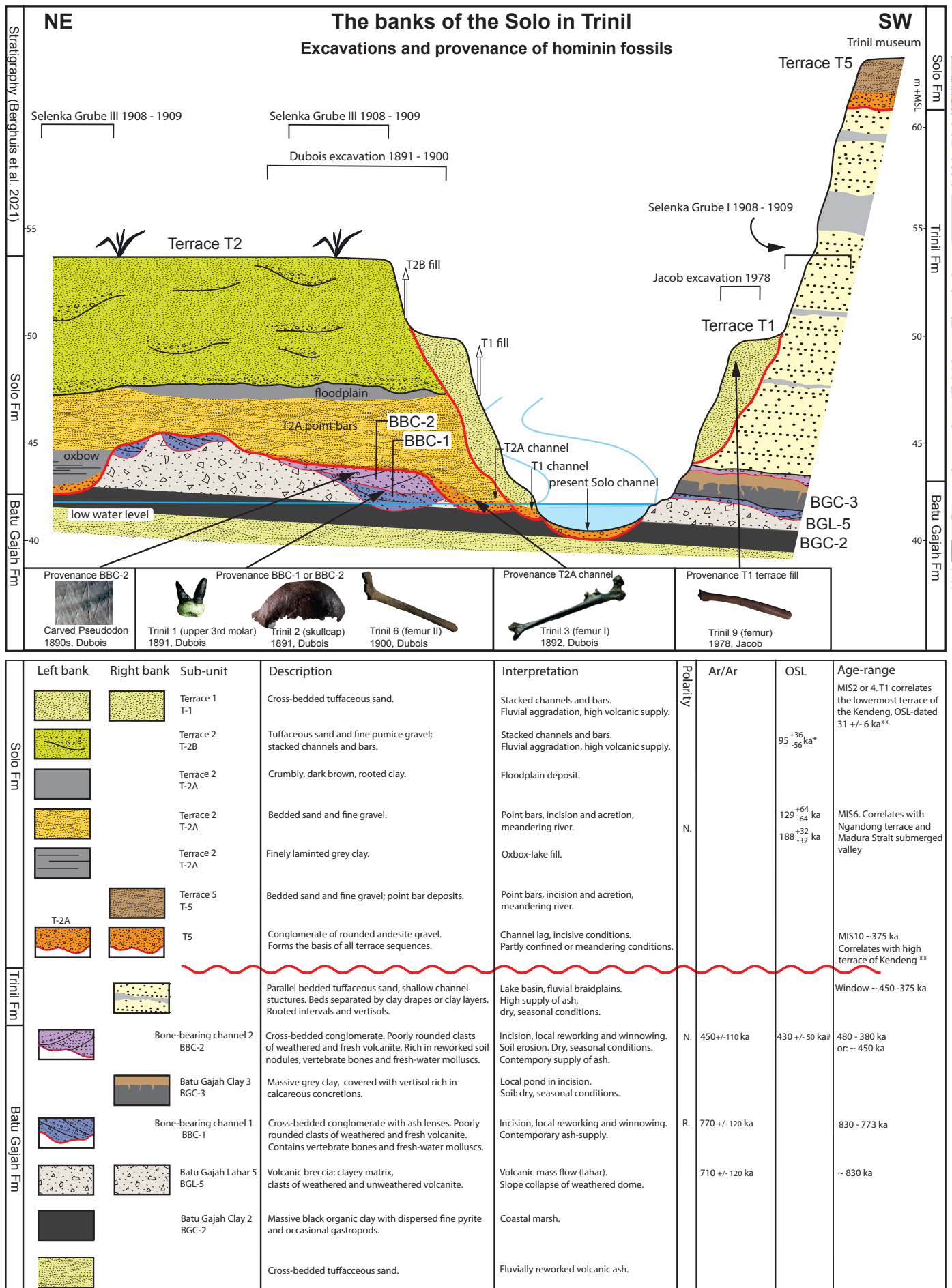


Fig. 7. The banks of the Solo in Trinil: stratigraphy, chronology, and provenance of hominin fossils. All numerical ages and magnetic polarities from Hilgen et al. (2023), except *: Berghuis et al. (2021), **: Rizal et al. (2020). #: Joordens et al. (2015).

In contrast, the hominin remains from the overlying part of the Bapang Formation are more gracile and conform better to the average metrics of *Homo erectus*. In theory, this may imply that the Grenzbank represents a stage of strong evolutionary change. However, the stratigraphy tells a different story. The robust specimens are only found in the basal conglomerate and not in the similarly aged top part of this lowest fluvial sequence. This indicates that the robust fossils may have been reworked from the underlying clays. Also, the incised top of the black clays and the chronological hiatus of ~80 ka points to this direction. This suggests that the Sangiran hominins may be subdivided in two chronological populations, with a clear morphological distinction: an archaic robust population and a subsequent more gracile population. Furthermore, the stratigraphic ranges of the fossils, prior to reworking, suggest that the robust population lived in the humid coastal forest, between ~1.3 Ma (or 1.1 Ma) and ~900 ka. The gracile population lived in the subsequent landscape stage, characterized by dry, grassy plains with local, partly incursive streams, from ~900 ka onward, and possibly disappeared from the area after 773 ka.

This provides a more logical subdivision of the two populations, with respect to morphology, chronology and landscape, but it does not yet answer the question of their phylogenetic relationship. Instead of looking at crania, it is better to compare dentognathic elements, which are available in larger numbers. Compared to the later, more gracile population, the archaic population is characterized by larger post-canine dentition, a thickened mandibular corpus and a relatively narrow dental arcade (Noerwidi et al., 2020; Zanolli et al., 2019; Kaifu et al., 2005). However, authors disagree about the evolutionary implications. Von Koenigswald and Tobias (1965) noted a similarity with the dentition of *Homo habilis*, and postulated an earlier migration wave from Africa. Zanolli et al. (2019) regarded some of the robust dental material as non-hominin and proposed to hold on to the taxon *Meganthropus palaeojavanicus*, as an ape species. Kramer (1994) regarded the dental elements as derived in comparison to *Homo habilis* or australopithecine taxa and proposed a phylogenetic relation with the earliest *Homo erectus* of eastern Africa. Kaifu et al. (2005) came to a similar conclusion, but regarded the robust dentition from the Lower Sangiran Group as ‘equally primitive to or more primitive than’ the earliest *Homo erectus* from eastern Africa.

These interpretations point to an early out-of-Africa dispersal wave, of a population that may perhaps be regarded as ‘earliest *Homo erectus*’. If we regard this early-migration wave of *Homo erectus* as the ancestral lineage of all Javanese *Homo erectus*, then the observed dentognathic reduction and arcade widening must have been a local evolutionary process, which in that case would have been a parallel evolutionary trend, taking place independently on Java and in Africa. The other option is that the earliest population of Java was replaced by a new, more derived *Homo erectus* population, representing a new migration wave.

The late Homo erectus and the time gap

The next question is, how does the typical *Homo erectus* from Sangiran and Trinil relate to the late *Homo erectus* from Ngandong, Sambungmacan, Ngawi and the Madura Strait? Today, the long discussion on phylogenetic continuity or discontinuity between these populations appears to have been settled in favour of the single-lineage model, referring to a common cranial form (Kaifu and Athreya, in press; Kaifu, 2017; Kaifu et al., 2008; Antón, 2002).

There are, however, two problems involved in this model. The first problem is that the single-lineage model is firmly based on the idea of Java as an island, with intermittent land connections during lowstands. However, as explained in **Section 2.1**, Java has probably been part of an exposed Sundaland throughout the Middle Pleistocene. Indeed, the remote setting along the far southeastern margin of Sundaland may have resulted in biogeographic isolation, for example through the occurrence of forest barriers. However, this is not what we see in the vertebrate fossil record, which reflects a stable continental community, lacks evidence of endemism, and records the occasional arrival of new herbivore species such as *Elephas hysudrindicus*, *Rusa* sp., and *Axis javanicus*. The second problem is that there is a huge gap in the fossil record. The *Homo erectus* remains from Sangiran date from the latest Early Pleistocene, between 900 and 773 ka. This also accounts for the material from Trinil, assuming that this derives from BBC-1 or may

have become reworked in BBC-2. With an age range of 140 – 130 ka for the late *Homo erectus* of Ngandong, we have a gap in the fossil record of >600 ka.

The time gap in the fossil record, however, is probably not as large as it seems (**Fig. 9**). We know that hominins were present in Trinil around 450 ka, based on the dated shells with traces of consumption, shell tools and the carved shell (Joordens et al., 2015). Another chronologically intermediate and previously unknown group is known from its core stones and retouched flake tools, which Sander Hilgen found in Sogen, a few km downstream of Trinil, within the newly defined Trinil Formation, with an age range between 450 and 375 ka (Pop et al., 2023b). These are the oldest, unequivocal stone tools, found in an in-situ context on eastern Java. An intermediate-aged cranium may be Mojokerto 1, the child skull from Peking. Published radiometric ages for this bone bed gave very old ages, of 1.5 Ma (Morwood et al., 2003) or even 1.8 Ma (Swisher et al., 1994), which would make the skull the earliest record of *Homo erectus* on Java (Huffman, 2001; Morley et al., 2020). However, all signs point to a much younger age, which we estimated to ~450 ka (**Chapter 4 and 5 of the thesis**).

Although these specimens point to hominin presence on eastern Java around 450 or 400 ka, the tools and the child skull do not give much clarity on evolutionary aspects. Interestingly, we may have adult crania from this period: Sambungmacan 1, 3 and 4 and Ngawi 1 were all found in the Solo Valley not far from Trinil. The field reports mention a provenance from ‘fine-grained volcanoclastic sediment’. Within the revised Trinil stratigraphy, this may either be the bedded tuff of the Trinil Formation or one of the fill terraces of the Solo, likely T4 or T2. Therefore, reconstructing their exact find spots and stratigraphic provenance is essential (see recommendations).

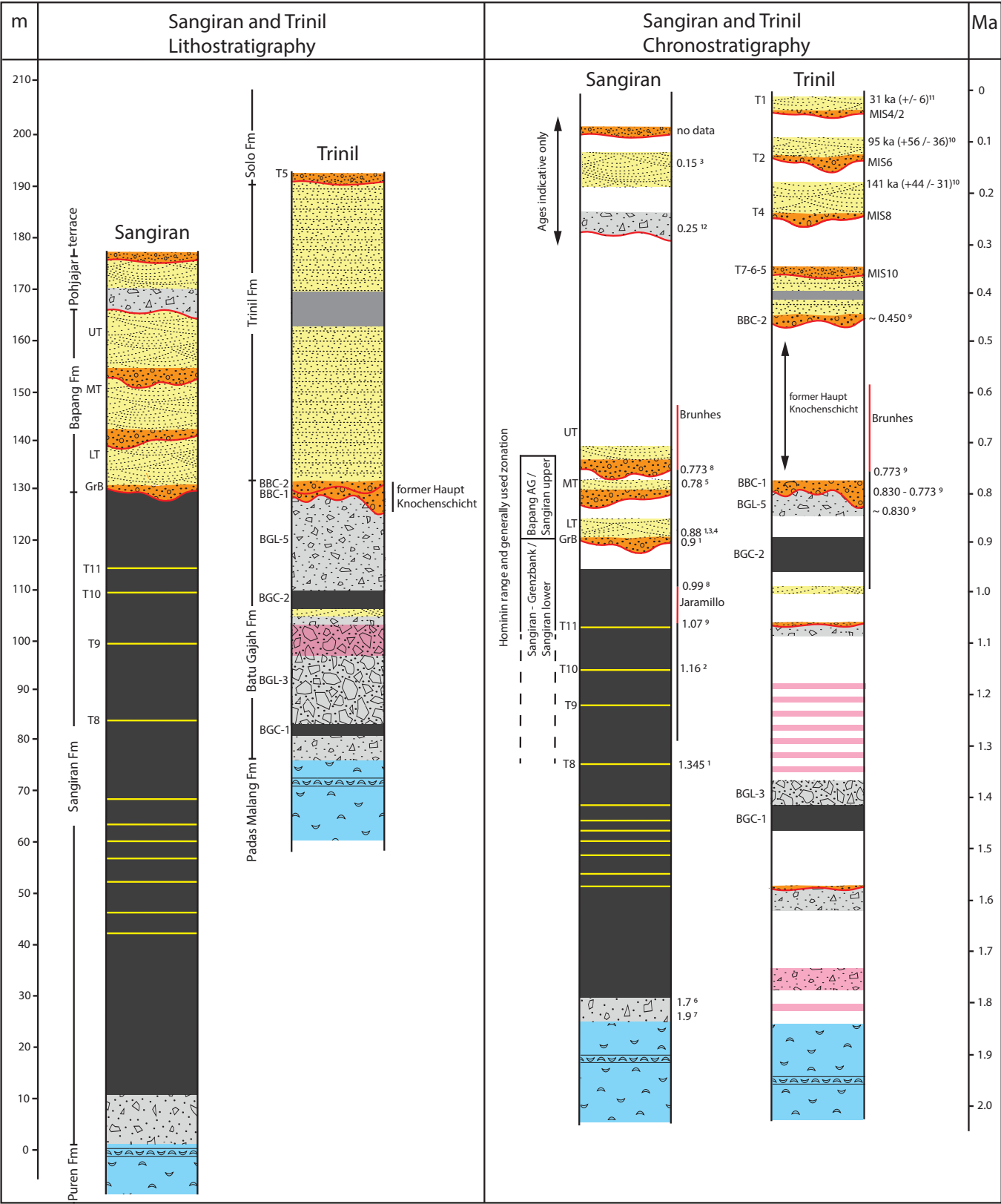


Fig. 8. The stratigraphy of Sangiran and Trinil. **A:** Lithostratigraphy based on Itihara et al. (1985) and Berghuis et al. (2021), with correlation between the Grenzbank and the ‘Haupt Knochenschicht’ as proposed by Von Koenigswald (1939). **B:** Chronostratigraphy based on 1: Matsu’ura et al. (2020). 2: Suzuki (1983). 3: Saleki et al. (1998). 4: Falguères et al. (2015). 5: Shimizu (1985). 6: Sémah et al. (2000). 7: Bettis et al. (2004). 8: Hyodo et al. (2011). 9: Hilgen et al. (2023). 10: Berghuis et al. (2021). 11: Rizal et al. (2020). 12: Suzuki and Wikarno (1982).

Most remarkable is the earliest gap in the hominin record. Why are hominin fossils absent in the third fluvial sequence of the Bapang Formation in Sangiran, post-dating the 773 ka Brunhes-Matuyama polarity change? Is this by chance or due to preservation issues, or does this signal the disappearance or even local extinction of the population?

The Punung hominins as the survivors of the older lineage

According to the prevailing models, the ancient Javanese *Homo erectus* lineage became extinct in MIS5e, together with most other members of the long-standing grass-land vertebrate community, due to the shift toward humid and forested conditions. As explained in **Section 4.3**, this must have been a combination of an island stage, causing strong reduction of the exposed land surface and an eastward shift of the forested zone. However, I also showed that the model of an MIS5e faunal turnover is largely incorrect. Except for *Stegodon*, most of the Middle Pleistocene taxa probably survived this island stage. Most of all, it must have been impossible for savanna-related vertebrate taxa to reach Java during peak MIS5e island conditions. The assignment of the Punung herbivore teeth to modern taxa, as has been common practice for the past 40 years, is a subjective taxonomical decision, apparently made to fit with the model of mass extinction and replacement, which makes this a form of circular reasoning. The same accounts for the hominin teeth from Punung. Their re-interpretation from *Pithecanthropus* to *Homo sapiens*, by Sondaar (1984) and later authors, has not been based on morphological evidence, but rather on an interpretation of the changed conditions.

As explained in **Section 4.3**, the only new arrivals of the MIS5e vertebrate community are arboreal species, which came along with the eastward-shifting forest zone. In theory, these may have included a population of forest-adapted archaic *Homo sapiens*, but this is highly hypothetical and requires strong fossil evidence. An alternative, much more likely explanation, is that the Punung hominins are the survivors of the preceding MIS6 population.

5.3 A new hominin framework for eastern Java

Referring to the morphological variety of the hominin fossil record and their chronostratigraphic ranges, and taking into account the major Pleistocene landscape stages of eastern Java and the larger Sundaland region, I tentatively propose a taxonomical re-interpretation of the Pleistocene populations of eastern Java (**Fig. 9**).

Homo erectus palaeosondaicus, the archaic Sundaland population

Dental comparisons link the archaic hominins of eastern Java to the earliest *Homo erectus* of eastern Africa, which points to an early dispersal wave. They may have left their African territories ~2 Ma, with an oldest record outside Africa in Dmanisi ~1.8 Ma. Recent studies suggest multiple, even older hominin dispersal waves out of Africa to Eurasia, with earliest ages around 2.4 Ma (Curran et al., 2025; Scardia et al., 2021).

Homo erectus' arrival on eastern Java, as indicated by its earliest fossils in Sangiran at 1.1 Ma and likely ~1.3 Ma, has commonly been linked to lowstands and temporary land bridges. However, under the revised regional landscape model, Sundaland was continuously exposed in this period. The first hominin record on eastern Java rather reflects the emergence of this marginal zone of Sundaland, a zone of complex tectonism and volcanism. It coincides with the establishment of a balanced, continental vertebrate community in this area, which shows that emerging eastern Java became a fixed part of the continental ecosystem. The fact that this archaic hominin population was part of this earliest continental vertebrate community of eastern Java suggests that the population was already present on Sundaland prior to 1.3 Ma, suggesting out-of-Africa dispersal along the Indian Ocean rim.

There are two aspects that set this archaic Sundaland population apart from all other known early *Homo* populations. First, its extremely thickened braincase. And second, its remarkable habitat in a humid, coastal forest. Although the first aspect has been drawn to attention by researchers as Tyler (1995) and Westaway et al. (2015), the second aspect has remained largely unnoticed. It completely changes our perception of the geographic ranges and migration routes of this population. These archaic hominins, with robust jaws, large post-canine dentition, and thickened cranial bones, may very well have populated the extensive coastlines of Early Pleistocene Sundaland.

Although its dentognathic characteristics can be linked to an ancestral population of eastern Africa, the thickened cranial vault and the coastal forest habitat are unique features. Possibly, these anatomic features developed in the Sunda region. Alternatively, this ancient Sundaland population may have been related to an ancestral, yet undiscovered, hominin population living in the eastern African coastal forest (see Joordens et al., 2019). In any case, the cranial and dental robustness of this population warrants a taxonomic subdivision. Weidenreich's *Meganthropus palaeojavanicus* is unsuitable, as this classification places the population outside the genus *Homo*. Tyler (2001) therefore proposed *Homo palaeojavanicus*. However, if we agree on a relation with the earliest *Homo* aff. *erectus* of eastern Africa, it is better to distinguish this robust archaic population at subspecies level. Moreover, I think it is relevant to highlight its background as an archaic species of Sundaland. Therefore, I propose to refer to this archaic hominin population as *Homo erectus palaeosondaicus*. A formal description and publication of this new subspecies name is yet to be made.

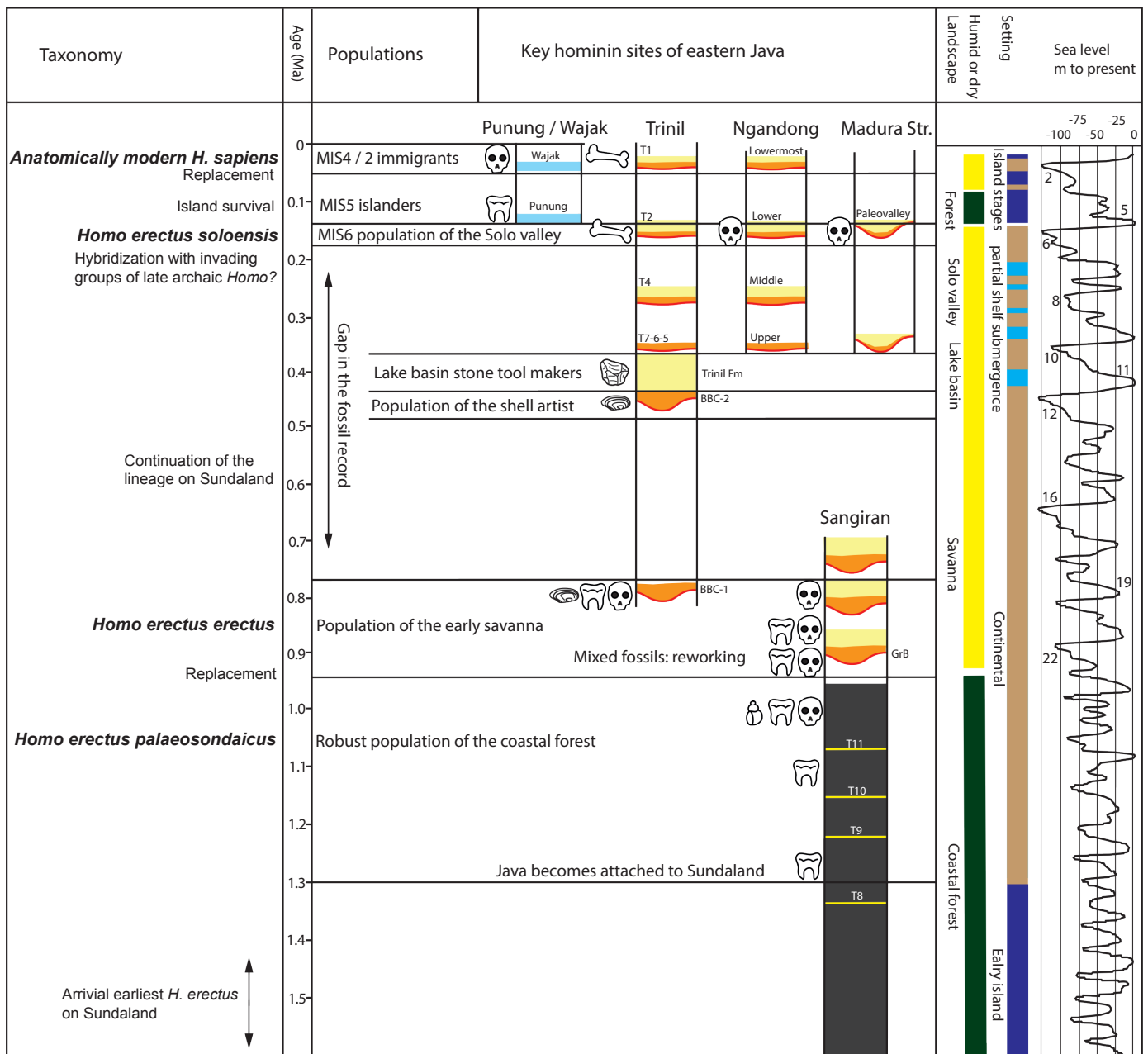


Fig. 9. The Pleistocene hominins of eastern Java: stratigraphy, chronology, populations, and revised taxonomy.

Little is known of the subsistence strategies of this earliest hominin population of Sundaland. Choi and Driwantoro (2007) described bones from the Sangiran black clays bearing cutmarks made by shell tools. Besides such butchering of land animals, I think it is likely that the population exploited aquatic resources, available on tidal flats, in tidal creeks and mangrove swamps, such as mollusks, crustaceans and fish. The coastal forest may also have offered fruit and other plant resources. Aquatic and plant resources are typically eaten by Burmese long-tailed macaques living in a coastal forest, which shows that such exploitation is within the primate repertoire (Haslam et al., 2022; Falótico et al., 2017).

Recently it was demonstrated that Mediterranean Neanderthals exploited aquatic resources and were engaged in diving for molluscan shells (Villa et al., 2020; Zilhão et al., 2020). This raises the question of whether the robust bone anatomy of this archaic Sundaland population relates to their coastal habitat. Verhaegen and Munro (2011), and Amson et al. (2018) suggested that the robust bone anatomy of *Homo erectus* may have been an adaptation for shallow-water breath-hold diving, with the increased bone mass (and thus body density) facilitating a neutral buoyancy with filled lungs at foraging depth (Houssaye and Botton-Divet, 2018). Indeed, *Homo erectus* had heavy cranial and postcranial bones, but evidence of a coastal habitat is scarce. With *Homo erectus palaeosondaicus* we have a population with an extremely robust anatomy, and a coastal habitat. This indeed opens the possibility that its hyper-robustness was a heritable adaptation to a partly aquatic lifestyle and littoral foraging.

Homo erectus erectus, a new dispersal wave over Sundaland

The Mid Pleistocene transition brought a drastic climate and landscape change to the Sundaland region. Forests largely disappeared and wide savannas became dominant. In the stratigraphy of Trinil and Sangiran, we see that the humid coastal forest disappeared around 900 ka. Irregular incisions, eroding soils and occasional events of volcanic ash fall give an impression of a relatively harsh environment. Nevertheless, a rich vertebrate fossil record shows that the local plains must have offered suitable living conditions for a vertebrate community dominated by herbivores such as bovids, cervids and *Stegodon*. Along with this drastic landscape change, there is a marked change in the hominin fossil record, toward a reduced cranial thickness, reduced tooth sizes, a more rounded dental arcade and a reduced thickness of the jaws. As this more gracile population includes cranium Trinil 2, the type specimen of *Homo erectus*, it may rightly be referred to as *Homo erectus erectus* (see Antón, 2003). Whether this is a local evolutionary process, possibly as an adaptation to the changed environmental conditions, or the arrival of a new population is hard to say based on the available fossil record.

Local evolution of a single, isolated Javanese lineage appears to be the convention nowadays. Again, I think this model is largely based on the previous 'island view' of Early Pleistocene Java. However, the new landscape model of a continuous Early Pleistocene mainland connection questions such prolonged isolation of a local hominin lineage. Comparative dental studies show that the post-900 ka hominins of Java have a closer affinity with the contemporary *Homo erectus* from China and eastern Africa than with the pre-900 ka robust population of Java (Zanoli et al., 2019; Kaifu et al., 2005). This may be a result of parallel evolution. However, it is more realistic to assume a second Asian-ward dispersal wave of *Homo erectus*, with a norther route into China as well as a southern route into Sundaland. Recently, Muttoni and Kent (2024) described rapid, climate-driven dispersal of *Homo erectus* into Eurasia during MIS22, around 900 ka, exactly the age of the great change in the hominin record of Java. I therefore postulate a new dispersal wave over Sundaland, of a population that was better adapted to dry, savanna-like conditions than the existing robust population of Sundaland. There may have been a temporary overlap or gene flow between the two populations. But we do see that, after the arrival of *Homo erectus erectus*, the archaic *Homo erectus palaeosondaicus* quickly disappears from the fossil record.

Systematic taphonomic studies to the subsistence strategies of the late Early Pleistocene *Homo erectus erectus* have never been carried out. It would, for example, be interesting to look for indications of hunting or scavenging by this grass-land population. However, during our 2018 and 2019 studies in Trinil, José Joordens noted shells with opening-traces in BBC-1, similar to the shells described from BBC-2 (Joordens et al., 2015). Therefore, we can infer that this population exploited freshwater mollusks from local streams. at least from ~800 ka onwards.

Again, it is relevant to consider *Homo erectus erectus* as a Sundaland species rather than a Javanese species. This also provides a potential answer to the incomplete fossil record of eastern Java. Chronological gaps in the fossil record may represent temporary shifts of the geographic range of the population. The species, or individual communities of the species, may have temporarily left the volcanic foothills of present-day eastern Java, but may very well have persisted on the surrounding Sundaland plains. Such shifting territories may have been related to the availability of food resources, for example by shifts of vegetation zones or migration patterns of herbivores. Later in the Middle Pleistocene, highstands resulted in temporary contraction of the exposed land surface, with a concomitant eastward shift of forested zones, which may also have driven populations to present-day Java. This may explain the presence of the stone tool makers on Java, which coincides with the MIS11 highstand. Whether this Sundaland population of *Homo erectus erectus* indeed remained isolated from the mainland *Homo erectus* is unknown, in the absence of fossil remains from the early Middle Pleistocene.

The MIS6 population of the Solo valley, Homo erectus soloensis, a hybrid hominin?

The MIS6 Solo valley population is regarded as the last recorded *Homo erectus* of Java and the last worldwide representative of this successful hominin species. Looking at the abundance of fossil material, the population appears to have been flourishing. With the discovery of the Madura Strait specimens, we now know that the population lived along the banks of the Solo, not only on the present-day island of Java, but also along its lower reach on the Sunda Shelf, in the area of the present-day Madura Strait. This makes their attribution to *Homo erectus soloensis* (see Antón, 2003) indeed highly appropriate. Most likely, however, similar populations lived along the courses of other Sundaland rivers.

The consensus is that this MIS6 population is the direct descendant of the Early Pleistocene *Homo erectus erectus* of Sangiran and Trinil. However, is it reasonable to assume that this Sundaland population remained isolated for more than 600 ka, despite the continuous land connection? The MIS6 population of the Solo Valley dates from a period in which, on the Asian mainland, the older *Homo erectus* population had been replaced by a morphologically diverse population of larger-brained hominins that may be referred to as archaic *Homo sapiens* (Antón, 2003) or late archaic *Homo* (Kaifu, 2017). Most likely, this was a replacement by invading groups, which included Neanderthals and Deniso-

vans. Others argue for hybridization or even in-situ evolution of the Chinese *Homo erectus* (Wu et al., 2019; Li et al., 2017). With the open land connection, it would be remarkable if these mobile post-*erectus* mainland populations, did *not* disperse over Sundaland. The recent confirmation of the Penghu mandible, dredged up from the sea shelf just off Taiwan, as Denisovan (Tsutaya et al., 2025) shows just how close this coastal Asian mainland population was to Sundaland.

As a population of the submerged lowland plains of Sundaland, the MIS6 hominins from the Madura Strait form an interesting group to search for indications of invading mainland populations. In **Chapter 8** of this thesis we carried out an extensive morphological and metric comparison of Madura Strait 1 (MS1), a frontal fragment with a dextral supra-orbital torus, with Pleistocene crania from the Java, Flores and the Asian mainland. The torus of MS1 is relatively gracile, but basically has a good metric and morphological match with the late *Homo erectus* crania from Java and differs from the late Middle Pleistocene mainland crania in several aspects. The Madura Strait hominins therefore appear to have been part of the larger Javanese or Sundaland population and the cranial fragments do not provide new indications for contact or hybridization with mainland populations.

Interestingly, a taphonomic analysis of the Madura Strait assemblage indicated that the hominin population may have been engaged in selective hunting. This is a modern hunting strategy, commonly associated with Neanderthals (Langdon, 2022; Speth, 2013, 2010b; Stiner, 2009; Domínguez-Rodrigo et al., 2007; Speth and Clark, 2006) or in China with other late Middle Pleistocene hominins, possibly Denisovans (Wang et al., 2022; Trinkaus and Wu, 2017; Li et al., 2017). The use of such hunting methods by the Madura Strait hominins may therefore, carefully, be regarded as indication of contact with post-*erectus* mainland populations.

Suppose that there has indeed been contact between the Sundaland *Homo erectus* and invading late Middle Pleistocene, post-*erectus* mainland hominins, then gene flow into the older, Sundaland *Homo erectus* population may provide an explanation for the increased cranial capacity of the late *H. erectus* (*H. erectus soloensis*) of Java, along with the persistence (and dominance) of an ancient *erectus*-type cranial morphology. There is a fossil that may shed a better light on this matter. For Dubois (1894), Femur I from Trinil was one of his key *Pithecanthropus erectus* finds, and his most convincing argument for an upright posture. As explained in **Section 5.2**, this specimen falls outside the morphological range of *Homo erectus*, and has more affinity with modern humans (Ruff et al., 2015). It derives from terrace T2, which is age-equivalent to the Ngandong terrace and the Madura Strait paleovalley. The modern, non-*erectus* anatomy of Femur I is therefore a strong indication that the MIS6 population was not a full, unmixed descendent of the older Javanese lineage. And, even if there were two separate populations living along the MIS6 Solo valley, then this still implies that there has been contact and possibly gene flow between the Javanese *Homo erectus* and an invading population.

Based on Denisovan introgression into the genome of present-day populations from island Southeast Asia and Oceania, we know that Denisovans must have been present in Southeast Asia before the Late Pleistocene arrival of anatomically modern *Homo sapiens* (Teixeira et al., 2021; Jacobs et al., 2019; Reich et al., 2011). It is interesting to think that Denisovans may have been among invading groups of late archaic *Homo* from the Asian mainland into Sundaland during MIS6, running into the existing population of Sundaland *Homo erectus*. This opens the possibility that *Homo erectus soloensis*, the MIS6 population of the Solo, was a hybrid or introgressed hominin, possibly carrying Denisovan genes.

The MIS5 island population

As explained in **Section 5.2**, I regard the Punung hominins of MIS5e as the survivors of the previous population of *Homo erectus soloensis*. Moreover, they may very well have been the first population that actually became isolated on island-stage Java.

Previously, it was assumed that *Homo erectus* would not have been able to forage under the forested conditions of MIS5e (Storm et al., 2005). It is, however, unsure whether eastern Java was indeed fully forested during MIS5e. More importantly, we have seen that during the preceding MIS6, the Solo population had probably been engaged in deliberate hunting of bovids. Bovid are common in the Punung island fauna, so this food resource remained available. Fruit and other plant-based food resources may even have been available in larger quantities than during the preceding grass-dominated stage. Moreover, the MIS6 population had partly relied on aquatic food resources, such as freshwater turtles, which must also have been available during the subsequent interglacial island-stage.

It is also relevant to note that the Sundaland *Homo erectus* appears to have persisted in this region for more than a million years, which points to a good capability to adapt to ecological changes. I noted that the earliest population of the coastal forest may have relied on littoral foraging. From the later populations, either *H. erectus erectus* from Sangiran and Trinil or *H. erectus soloensis* from Ngandong, Sambungmacan, and the Madura Strait, we only have fossils from fluvial contexts, suggesting that river valleys formed a preferential habitat. However, the Sundaland *H. erectus* may very well also have taken in other ecological niches, which did not yield fossil evidence. A diverse ecological

background would have made the population, as a whole, particularly resistant against climate or landscape changes and may explain its long persistence. It is interesting to think of *H. erectus* groups that continued to live along the Sundaland coast, practicing littoral foraging. Such groups may very well have had the abilities to survive the MIS5e island conditions of Java.

Anatomically modern Homo sapiens

The dispersal of anatomically modern *Homo sapiens* over Sundaland from MIS4 onward is undisputed. They may very well have run into an older population of *Homo erectus soloensis* that had survived MIS5e on island-stage Java, a population that may have carried genes from late archaic *Homo* populations that had arrived in this area during MIS6.

Remarkable is that the Late Pleistocene anatomically modern *Homo sapiens* of Java is represented by the finely-built femora 9 and 10 from Trinil, as well as the robust remains from Wajak, pointing to two contemporary but morphologically different populations (Ruff et al., 2022).

6. Recommendations further studies

The Pleistocene hominins of Java were Sundaland populations. Therefore, it is interesting to search for fossil evidence of these populations on the other Sundaland islands or the Malay peninsula.

The Kedung Brubus site forms a major blank spot in our understanding of the regional chronostratigraphy. Detailed dating studies and controlled fossil excavation from individual stratigraphic levels are urgently required and may provide valuable new insights into Middle Pleistocene vertebrate communities and hominin populations.

The hominin-bearing fluvial series from Mojokerto has a cyclic build-up, which I linked to the Middle Pleistocene Brantas. However, the debate is ongoing. Only a detailed dating study may provide final answers. Instead of looking at the series as a record of continuous deposition, it is better to date individual aggradational sequences. Multiple single-grain radiometric measurements, following the procedures of Hilgen et al. (2023), may be done on samples from the fine-grained tuffaceous beds that make up the top of these sequences. The youngest sequences probably lie within the range of OSL-datings. Again, the series is promising from a palaeontological point of view, as it probably includes parts of the Middle Pleistocene that are not sufficiently covered by available studies of other sites.

The stratigraphic provenance of the Sambungmacan 1, 3 and 4 and Ngawi 1 skulls is to date unknown. Their allocation to the 'Kabuh Formation' is meaningless, as this unit name has been used in this area for a suite of fluvial deposits of various ages. In **Chapter 3** of this thesis, we subdivided these fluvial strata into three units, and provided field criteria to distinguish between these units. If it is possible to relocate the exact find sites of the skulls, it must also be possible to determine their stratigraphic provenance and age.

The hominin assemblage from Ngandong contains two tibiae. Moreover, Sambungmacan 2 is a tibia, possibly of similar age. A comparative morphometric study of these specimens is of great interest. It is possible that they have a post-*erectus* morphology, similar to the contemporary Femur I from Trinil. This would provide strong evidence for introgression by an invading non-*erectus* population.

Finally, it would be very interesting to devote more attention to the relatively understudied *Homo erectus palaeosondaicus*, and, as also suggested by Widiyanto and Noerwidi (2023), to explore for more and possibly even older fossils of this intriguing group.

