

1. The fossil *Pseudodon* shells from Trinil

The assemblage of fossil shells of *Pseudodon vondembuschianus trinilensis* Dubois 1908 derives from excavations executed under the supervision of Eugène Dubois between 1891 and 1900 at Trinil^{1,2} (Indonesia) and is now curated in the Dubois Collection at Naturalis, Leiden, The Netherlands. The site Trinil is located on the banks of the Solo River on Java (7°22'S-111°21'E; Extended Data Fig. 1a). Excavations were conducted during the dry season when water levels were low and the bone-bearing “Lapillischicht,” or Trinil *Hauptknochenschicht* (Trinil HK), was accessible (Extended data Fig. 1b). In total, an area of more than 2000 m² was excavated, with a significant part of the major finds registered within a square meter grid¹. At present, the site cannot be excavated because construction of a dam in 1981 caused permanent high water levels in the Solo River. The deposits of Trinil HK are likely overbank deposits formed under both low energy conditions as well as during periods of high energy fluvial depositional processes, which may in addition to volcanic material also have deposited faunal remains picked up further upstream. However, the excellent preservation of the *Pseudodon* shells as well as the micromorphological study of their infill (see below, Supplementary Information section 2) indicates that these shells were swiftly encapsulated in a fine-grained fluvial matrix.

The stratigraphy of the Trinil site has been documented by Dubois³, and later in more detail by Carthaus⁴ who participated in the Selenka Expedition (1906-1908) at Trinil. Carthaus distinguishes an additional layer, the so-called “Plant Leaf Bed” just above the *Hauptknochenschicht*. He further mentions, as does Oppenoorth⁵, that there is another bone-bearing level at about 5 m above the HK. This also yielded mammal fossils (e.g. of *Stegodon trigonocephalus*, *Hexaprotodon*) but the bones from this level are friable and do not exhibit the heavy mineralisation and chocolate-brown colour typical of bones from the HK⁴. Much later, Bartstra^{6,7} draws attention to the findings of Duyfjes⁸, who recognized the presence of three layers in the upper part of the Trinil stratigraphy, from old to young: 1) a fossiliferous layer (HK) he attributes to the Pleistocene Kabuh Formation, containing heavily mineralised dark-brown bones, 2) a fossiliferous sandy layer, also attributed to the Kabuh Formation, containing much less mineralised, more fragmentary, grey-coloured bones, and 3) Solo river terrace deposits of relatively young age, that may also contain reworked bones of both underlying older layers.

Various workers have stressed that the complexity of the Trinil sequence may have been underestimated by Dubois in 1896⁷, as discussed in an extensive review by Bartstra⁶, and that this could have caused inadvertent mixing of older and younger elements in the Trinil fauna collection (see Supplementary Information section 3). However, it is clear from published sections and from sediment samples Dubois took from the Trinil sections (see below) that he did differentiate several distinct layers above the HK (layer D, Extended Data Fig. 1b): the fossiliferous sandy layer distinguished by Duyfjes likely corresponds to Dubois' layer E (Soft Sandstone), while the river terrace beds may correspond to Dubois' unnamed layer F. Moreover, while Dubois in his published stratigraphy did not specify a layer with fossil plant leaves and wood just above HK, he was certainly aware of this layer as testified by the presence of Trinil sediment sample DUB1704, containing fossil plant leaves and wood, in the Dubois Collection.

Working with historical collections has its drawbacks⁹, and issues such as stratigraphical integrity and inadvertent mixing of fauna have to be taken into consideration when establishing the stratigraphical provenance of the *Pseudodon* assemblage. Though the documentation of the context of the finds in the field was limited in the first stages of the excavation, the recording techniques significantly improved after recovery of the *Homo erectus* skullcap in 1891¹⁰. Unpublished sources (fieldbooks, letters, photographs, maps, etc.) in the Dubois Archive at Naturalis show that Dubois possessed far more information about the locality, the finds and their context than presented in his publications¹¹. We address the issue of stratigraphical integrity in detail here below (Supplementary Information section 3).

For the context of this study, it is relevant that Dubois had a strong interest in fossil shells right from the beginning in 1890 when initial fossil finds were made in nearby Kedungbrubus, as is shown in a letter written by Dubois from Java (Toeloeng-Agung, 25 October 1890) to his wife's cousin F.A. Jentink, then curator at the Rijksmuseum voor Natuurlijke Historie in Leiden (Dubois Archive, Naturalis Leiden). In this letter, he describes the mammalian and reptilian fossils recovered, and adds "*Verder bevat hetzelfde gesteente vaak eene Bulinus en schelpen van de familie Unionidae*" ("Furthermore, the same bed contains often a *Bulinus* (genus of freshwater snail) and shells of the unionid family").

We have various sources of information regarding the stratigraphical provenance of the *Pseudodon* shells from Trinil. Registered information regarding the shells in the Dubois Collection includes the locality (e.g. "Trinil") and in case the locality is not known or uncertain, this is explicitly mentioned on the label, e.g. with the words "geen nadere vindplaats" (no further find locality), "geen vindplaats" (no find locality) or "geen vindplaats, later nagekomen" (no find locality, came later). All the original labels are still present in the Dubois collection. Shell material from Trinil in the Dubois collection derives from two different levels: the "Weicher Sandstein" (soft sandstone) layers situated above Trinil HK, and Trinil HK itself (Extended Data Fig. 1b). The Dubois collection contains 13 bulk shell samples, each consisting of a cigar box full of fossiliferous sediment, collected from the sandstone and andesitic tuff layers at Trinil ("Weicher Sandstein"). These samples are all labeled "Trinil zandsteen" or "Trinil andesiet tuf". Dubois uses the words "zandsteen" (sandstone), "andesiet" (andesite), and "tuf" (tuff) interchangeably. For instance, in one of his notebooks (Box 3 Dubois Archive, p. 245), he mentions "andesietzandsteen bij Trinil" with the word "tuf" written just above "zandsteen". In a previous study⁹, all bulk samples from the soft sandstone layer were inspected, and three of them (with a total weight of 1.5 kg) were analysed in detail by identifying and counting every shell larger than 2 mm. Only one *Pseudodon* fragment was encountered, in bulk sample DUB543.

The *Pseudodon* shells analysed in this study are all labeled "Trinil". All available evidence indicates that they derive from Trinil HK. Based on the careful labelling of the bulk shell samples, we infer that if the *Pseudodon* shells would be derived from the soft sandstone layer above HK, they would have been labelled as such. Dubois discusses shells from Trinil on page 1249 of his 1908 publication¹², starting this particular section with the words "Aus der Knochenschicht von Trinil selbst..." ("From the bonebed of Trinil itself..."). He mentions that two species of freshwater mussel ("*Unio*"), one large and one small, are the most numerous ("allerhäufigsten") mollusc species at Trinil. He assigns the name *Unio trinilensis* to the larger mussel species¹², later renamed as *Pseudodon vondembuschianus trinilensis* by Van Benthem Jutting in her study of the fossil freshwater shells from Java¹³. The smaller unionid mussel that Dubois refers to is *Elongaria orientalis*¹⁴. The caption of Dubois' drawing of the interior of a *Pseudodon* valve (*Unio trinilensis*, plate XXXIXb¹²) reads: Trinil. "Hauptknochenschicht".

This stratigraphical provenance from HK is also evident from the sediments present within articulated shells or adhering to the *Pseudodon* shell valves. During our study, we were able to inspect sediment samples taken by Dubois in the late 19th century from sedimentary layers both over- and underlying the Trinil HK sediments, as well as large amounts of matrix still adhering to many of the large mammalian fossils from Trinil HK in the Dubois Collection. Independent support for the provenance of the *Pseudodon* shells from HK is provided by comparison of the shell infillings and the matrix adhering to the inside of the shells to the sediment of the different layers present at Trinil. The shell sediment infill consists of clay, silt, sand, gravel and volcanic material (see Supplementary Information section 2 for details). The shell infills are very different from the black claystone layer (“Thonstein”) underlying Trinil HK (sediment sample 254 collected by Dubois, curated in the Wichmann Collection, Universiteitsmuseum Utrecht, The Netherlands). They are also very different from the layer just above Trinil HK, named the Plant Leaf Bed⁴ (sediment sample DUB1704, Dubois Collection). The sediments of the “Weicher Sandstein” layer are characterized by their soft, sandy character, and the presence of numerous small shells and shell fragments¹⁴ that are absent in the *Pseudodon* shells infillings and matrix.

In contrast, the infills of and the matrix adhering to many of the *Pseudodon* shells is very similar to the matrix adhering to many of the mammalian bone fossils, e.g. matrix in *Stegodon* cranium DUB4977, from Trinil HK. Moreover, the infill of this particular cranium contains two fossil shells (*Elongaria orientalis*) with the same preservation characteristics as those of the *Pseudodon* assemblage. The skullcap or “calotte” of *Homo erectus* from Trinil was, prior to cleaning, filled with the same type of matrix as is present in the *Stegodon* skull DUB4977 and in the *Pseudodon* shells. Dubois covered the matrix of the skull infill with shellac in order to facilitate production of a cast from the skullcap. After casting, Dubois cleaned out the matrix but kept several small pieces of matrix (with the skullcap in his safe) which we have been able to inspect. Hence, we are confident that the *Pseudodon* shell assemblage described in this study derives from the HK that also yielded the *Homo erectus* skullcap.

The assemblage of *Pseudodon* shells (see separate excel Table S1) consists of 286 paired (connected, articulated) valves, 23 single valves, and 24 valve fragments, of which 19 are with hinge allowing lateralization (determination of right or left valve). Two fragments with hinge could be fitted to form a pair; the other fragments appear to come from single valves. These specimens represent a minimum number of individuals (MNI) of 166 when fragments are excluded, and 184 when the fragments with hinge are included in the count. There is a dominance of paired valves (86% and 78% of the MNI, respectively, depending on the method of (dis)counting fragments) in the assemblage. Of the paired valves, 166 (= 83 individuals) are closed and filled with sediment, 70 (= 35 individuals) are slightly or half open and filled with sediment, and 50 valves (25 individuals) are articulated but loose, not held together by sediment infill.

We found 92 holes in valves of the *Pseudodon* shells, predominantly (73 of 92) located close to the anterodorsal margin (area B1 in Fig. 1b) at the location corresponding to the anterior muscle attachment on the inner side of the shell. In total, 33 % of the MNI (and 32% of MNI when fragments are included in the count) have one or two holes at B1. Fifteen paired individuals contain holes at B1 in both valves, and 35 paired individuals have a hole at B1 in one of the valves only. In the individuals represented by single valves (23 in total), five have a hole at B1. In the individuals represented by fragments with hinge (18 in total), three have a hole at B1. In the paired individuals with a hole at B1 in just one of the valves (total of 35), 14 have a hole in the left valve and 21 in the right valve. The state of preservation of the *Pseudodon* specimens is good, although the outer layers (periostracum and partially also the

prismatic shell layer) have in all cases disappeared. In the assemblage, there is minor shell breakage that can be attributed to sediment compaction; some specimens show pits or holes caused by dissolution of the aragonite (often one valve only, in case of paired valves) because of contact with acidic ground water or due to microbial activity. The umbo is often slightly abraded but does not contain abrasion holes.

2. Micromorphological analysis of two shell infillings

Description of infill DUB9717-b (Extended Data Fig. 1c-f):

The following four layers, featuring sharp and slightly wavy boundaries, were identified:

1. Basal layer of grey clay ranging in thickness from 0.7 mm on the side to 7.7 mm in the middle of the shell. Clay orientation is absent or very weak (undifferentiated to speckled b-fabric) with very few silt and sand grains ($<150\text{ }\mu\text{m}$) and sporadic medium sand grains (200–500 μm). Locally enclosed is a clay-containing sand layer, thickness 0.5–1.3 mm. The layer mainly consists of very fine and fine sand, with very few medium sand grains (200–500 μm) and some brown shell fragments with clear interference colors, thickness 50 μm . Some vertical or diagonal planar voids are developed, diameter $<50\text{ }\mu\text{m}$. Locally, the clay layer is overlain by a clayey sand layer, sometimes with enclosed clay laminae, thickness 0.5–2.3 mm. The sand layer contains sand grains of 50–150 μm in diameter, densely packed with intercalated clay laminae, c. 300 μm thick.
2. Greyish-brown dense clay layer, 2.3–4.6 mm thick. Clay orientation is absent or very weak. Enclosed are some silt and sand grains ($<150\text{ }\mu\text{m}$). Some voids consisting of vertical and diagonal planes (diameter $<300\text{ }\mu\text{m}$).
3. Grey-brown sand layer, thickness 6.7–18 mm, loosely packed, the sand mainly consisting of very fine to medium sand (100–250 μm), few silt grains and few medium sand grains (200–500 μm). The diameter of the packing voids is 50–150 μm . Further present are some pale brown, isotropic aggregates, diameter 0.6–2.5 mm.
4. Locally, a pale-brown to grey-brown clay layer, 0.5–1.0 mm thick lies on top of the infill. Clay orientation is absent or very weak (undifferentiated to speckled b-fabric). Enclosed are some very fine and fine sand grains, diameter 50–100 respectively 100–200 μm . The voids consist of vertical and diagonal planes, diameter $<50\text{ }\mu\text{m}$.

Description of infill DUB9735 (Extended Data Fig. 1g-j)

Three layers, with sharp boundaries, were identified:

1. Locally a grey to grey-brown clay layer, thickness 0.2–2.5 mm; clay orientation is absent or very weak (undifferentiated to speckled b-fabric). Included are some very fine and fine sand grains that are partially opaque-black.
2. A poorly sorted grey-brown clayey sand layer, c. 15 mm thick, consisting mostly of loosely packed very fine and fine sand grains ($<200\text{ }\mu\text{m}$), with grey-brown clay between the grains. Also present are coarser sand grains, some subrounded carbonate nodules, diameter 700–2500 μm and some aggregates especially in the base with more clayey sand, diameter 500–650 μm . Some sporadic long, black opaque fibrous charcoal fragments, diameter c. 550 μm , are present. The sand grains are mainly quartz and feldspars, such as plagioclase and hornblende as well as some additional volcanic minerals. Amongst the sand grains, black unidentified opaque species are common that are of volcanic origin. Packing voids have a diameter of 50–150 μm .
3. An ellipse-shaped grey lens at the upper part of the infilling (11–15 mm thick) consisting of poorly sorted sand grains, 50–1000 μm in diameter (i.e. fine, medium and coarse sand) with locally grey clay between the grains. Also common are subrounded rock fragments, e.g. chalk, with a diameter ranging from 0.5 to 2.5 mm.

Both shell infillings contain an admixture of sand and clay and relatively well-sorted and poorly sorted layers. The generally sharp boundaries between layers point to episodic change in sedimentation regimes. The clay layers in the shells have an undifferentiated to speckled b-fabric that may represent amorphous clay particles such as allophane or kaolinite, often encountered in tropical soils. The well-sorted very fine and fine sand layers and the loose packing indicate a calm sedimentary environment, as do the clay layers. The absence of soil formation and bioturbation within the sediment succession indicates a quick closing of the shell after infilling. Both shells have an initial clayey infill, followed by coarser and less well-sorted sediments implying increasing turbulence. The presence of laminae in shell DUB9717-b may reflect tidal influence.

Combined with the observed dominance of paired valves in the assemblage, the micromorphological analysis of the infilling suggests that a relatively short period of time must have elapsed between death of the mollusc and subsequent burial and infilling of the shell. In case of a long exposure, the organic ligament, instrumental in holding the valves together, would have deteriorated quickly under the tropical conditions of Trinil leading to the separation of the valves. The stratigraphy of sediments inside the shells (as identified by micromorphology) likely reflects a rapid infill that occurred at the onset of the wet season, with initial clay suspension from low-turbulence conditions to sand deposition associated with turbulent flow during high water levels. However, we cannot exclude the possibility that the infilling reflects a number of tidal high-low water cycles. *Pseudodon* individuals were probably living, collected for consumption, and subsequently discarded near the river shore in the shallow upper reaches of the tidal zone dominated by fresh water. In addition to the *Pseudodons* with infillings typical of those described above, the assemblage also includes shells with an infilling or adhering matrix consisting of predominantly of volcanic material, showing that they were deposited in water carrying coarse volcanic material coming from the volcanic uplands. Because of the rapid closure of the shells after deposition, infilling and burial, the quartz and feldspar in the sediment was cut off from sunlight, and the volcanic minerals such as hornblende were protected from weathering. This unique situation is the reason why the infilled *Pseudodon* shells constitute precious “time capsules” that can be used for both $^{40}\text{Ar}/^{39}\text{Ar}$ and luminescence dating (see Supplementary Information sections 10–11).

3. The case of Femur I.

Ever since Dubois' publications on the hominin fossils from Trinil in 1894 and 1896, concerns have been raised about possible intrusions of younger material into the Trinil HK faunal assemblage¹⁵. Most notably, there has been and still is a controversy regarding the potentially composite nature of the type lot of *Homo erectus*, comprising a skullcap (Trinil 2, the lectotype) and the paralectotypes consisting of a femur (Femur I/Trinil 3) and a molar (Trinil 1). For a long time the debate centered on the question whether or not the more “ape-like” skullcap (Trinil 2) really belonged to the same taxon – and perhaps even to the same individual – as the much more “human-like” Femur I (Trinil 3). Nowadays it is unanimously accepted that the skullcap belongs to *H. erectus*. In 2009 the molar (Trinil 1) was demonstrated to be *H. erectus* as well¹⁶. The only real “bone of contention” left is Femur I, one of five hominin femora from Trinil in the Dubois Collection: Femur I (Trinil 3), Femur II (Trinil 6), Femur III (Trinil 7), Femur IV (Trinil 8), and Femur V (Trinil 9)¹⁷. Femur I is a complete but pathological left femur, found at Trinil in August 1892. It is heavily mineralised, with a chocolate-brown colour. The pathology consists of a large exostosis protruding from the medial side of the upper part of the bone (Extended Data Fig. 2a).

Based on morphological data, Bartsiokas and Day¹⁸ suggested Femur I being more similar to *Homo sapiens* than to *H. erectus*; based on chemical and stratigraphical data they also suggested that Femur I might have derived from a more recent stratum above the HK. In 2013 Ruff and colleagues presented computed tomographic (CT-scan) analyses of femoral shaft structure in Femora I-V from Trinil at the Annual Meeting of the American Association of Physical Anthropologists¹⁹. They concluded that Femora II-V exhibit key characteristics shared with other *H. erectus* femora, while Femur I does not, “adding to the evidence that it is not *H. erectus*, but rather derives from a more recent time period”. However, it should be noted that the presence of the exostosis significantly affected the external and internal morphology of the Femur I shaft throughout its length²⁰:

“X-rays show that the medullary cavity at the level of the growth is irregular but not significantly narrowed. The cortex shows irregular opacification and uneven borders throughout the entire posterior and medial shaft beginning at approximately the level of the base of the greater trochanter and extending to a point 165 mm above the horizontal condylar plane. The anterior and lateral cortices do not, however, show these features except at the level of the exostosis. The unevenness involves both the endosteal and periosteal borders of the cortex; the posterior cortex shows irregular thickening throughout the length of the shaft and this thickening continues into the area just superior to the condyles themselves. In non-pathologic fossil and recent specimens, the cortex thins at a considerably more proximal level and it is possible that this particular condition of the cortex in Trinil Femur I is related to the pathologic processes active in the bone. A further interesting aspect of the radiographic appearance of this femur is the presence of linear areas of vertically oriented increased density along the cortico-medullary boundary, extending the entire length of the shaft; this may be due to some post-mortem mineralization phenomenon but was not seen elsewhere in this study”.

Kennedy²⁰ states that because of this severe pathology it would be wise to withhold taxonomic judgement of Femur I based on its morphology. We agree with that view and therefore do not further discuss morphology. Here we assess the chemical and stratigraphical arguments put forward by Bartsiokas and Day on the stratigraphical provenance of Femur I.

In 1993, Bartsiokas and Day¹⁸ conducted Electron Probe Energy Dispersive X-Ray analysis (EDXA) on fossil hominin bones from Java, focusing on Ca and P levels in the bone. The analysis was done for each fossil on one sample (powdered bone drilled from one location in the fossil, e.g. see Extended Data Fig. 2a for the location in Femur I) and consisted of nine or ten measurements on each sample. In the Trinil skullcap and in Femora II-V they found Ca/P values of about 2.2, whereas Femur I appeared to have a much higher Ca/P value of 3.2. They interpreted this difference as significant, and as indication that Femur I derived from a different stratigraphical level.

Our XRF results are presented in the separate excel Table S2, in Table S3 and in Extended Data Figs. 2b-f. The Ca/P ratio in biogenic apatite is 2.16, and expressed as CaO/P₂O₅ this ratio amounts to 1.32²¹. This Ca/P (CaO/P₂O₅) ratio can change drastically through diagenesis of the bone, especially by interaction of bone surface with ground water and by precipitation and illuvation of (secondary) minerals. The ratio can also be affected already during the lifetime of the individual, e.g. being (locally) increased or decreased with age, lifestyle, and/or through pathological (de)calcification of the bone²²⁻²⁴. In order to compare our data with those measured by Bartsiokas and Day, it has to be taken into account that the data were acquired with different methods²⁵. Bartsiokas and Day took one sample per fossil by drilling into the bone, thereby obtaining material from the *interior bone* that consequently could be subjected

to laboratory analysis. Our hand-held (HH) XRF device measures predominantly the composition of *surface bone* material, especially in the case of light elements (including P) since their secondary X-rays are absorbed more easily (cf ²⁶). Hence, any irregularities at the bone surface or minerals formed on the surface due to oxidation of sulphides (e.g. jarosite, gypsum) or to interaction with the burial environment will especially affect the light element readings in the resulting measurement. The heavier elements (including Ca) will be less affected by this phenomenon. Indeed, it is clear that the Ca/P ratios of our HH-XRF study are much higher than those of the EDXA study¹⁸ (Table S3): our Ca values compare well with those of Bartsiokas and Day whereas the P values differ markedly, being lower in our study.

This study	No. of sample locations	Elemental (%)			Weight (%)			
		Ca	P	Ca/P	CaO	P ₂ O ₅	CaO/P ₂ O ₅	CaO+P ₂ O ₅
Bone								
Calotte	5	30.7	8.3	3.7	36.2	14.6	2.5	50.8
Femur I	7	27.9	8.3	3.4	37.7	17.7	2.1	55.4
Femur II	4	28.6	7.4	3.9	37.3	12.6	3.0	49.9
Femur III	5	32.9	9.2	3.6	46.5	21.1	2.2	67.6
Femur IV	5	33.6	8.7	3.9	47.1	20.3	2.3	67.4
Femur V	5	37.9	14.0	2.7	53.0	32.3	1.6	85.3
Average		31.9	9.3	3.5	43.0	19.8	2.3	
Bartsiokas & Day 1993								
	No. of sample locations	Ca	P	Ca/P	CaO	P ₂ O ₅	CaO/P ₂ O ₅	CaO+P ₂ O ₅
Bone								
Calotte	1	26.3	11.5	2.3	36.8	26.4	1.4	63.2
Femur I	1	31.9	10.3	3.1	44.6	23.6	1.9	68.2
Femur II	1	32.1	14.1	2.3	44.9	32.3	1.4	77.2
Femur III	1	35.7	16.3	2.2	50.0	37.4	1.3	87.4
Femur IV	1	34.6	15.8	2.2	48.4	36.2	1.3	84.6
Femur V	1	34.6	16.4	2.1	48.4	37.6	1.3	86.0
Average		32.5	14.1	2.4	45.5	32.2	1.4	

Table S3| The Ca and P data of the Trinil hominin bones. Upper panel: HH-XRF data from this study, where percentages and ratios are averages of the values obtained from several sample locations per bone, and reflect mainly surface bone characteristics. Lower panel: EDXA data from Bartsiokas and Day¹⁸, representing one location per bone, and reflecting mainly interior bone characteristics. Conversion factors from elemental to weight: 1.3992 for Ca, 2.2916 for P.

Extended Data Figure 2b shows that the modern bone sample plots exactly on the theoretical CaO/P₂O₅ line for fresh bone, indicating that the XRF analysis as done in our study reliably captures this ratio. Almost all fossil bones show a deficit in P₂O₅ compared to modern values. The fossil sites Kedung Brubus and Trinil cannot be distinguished based on the CaO/P₂O₅ ratio. Extended Data Figure 2c shows that the CaO/P₂O₅ ratios of the fossil hominin bones span a range of values between ca. 1.5 and 4.5, depending on the location on the bone where the measurement was acquired. The values of skullcap (“calotte”) and Femur I are very similar, and the values of Femur I fall comfortably in the range of values of the other femora. The elevated CaO/P₂O₅ ratios and the considerable range in CaO/P₂O₅ values found in our HH-XRF study show that the surfaces of all fossil hominin bones are affected to a certain degree by weathering/diagenetic processes lowering the relative P content, through influence

of the burial environment. This is evidenced by the relatively high percentage of S and other elements (e.g. Fe), notably at some locations of some of the bones such as Femur II (Extended data Fig. 2c).

The average CaO/P₂O₅ ratio of 1.4 measured with EDXA by Bartsiokas and Day¹⁸ on interior bone material is similar to or only slightly higher than the CaO/P₂O₅ ratio of fresh bone (1.32²¹). Our HH-XRF analysis of the bone surface yielded much higher CaO/P₂O₅ ratios, on average 2.1 (Table S3). This indicates that the interior of the fossil bones, where the EDXA samples were drilled from, is relatively unaffected by diagenetic and weathering processes that may alter this ratio. The surface of the bones appears to be much more affected by those processes, which is logical because that is in direct contact with the soil and groundwater environment. Femur I is the only fossil with a relatively high CaO/P₂O₅ ratio measured in the interior bone compared to the other hominin bones from Trinil: 1.9 versus on average 1.4 (Table S3). However, the measured CaO/P₂O₅ ratio of the Femur I bone surface is 2.1, which is even lower than the average surface CaO/P₂O₅ ratio (2.3) of the skullcap and femora II-V. The latter suggests that Femur I has experienced a similar diagenesis/weathering environment as the other bones.

To further analyse the influence of weathering on the bones and assess the meaning of the high CaO/P₂O₅ ratio in the interior of Femur I, we consider the sum of CaO and P₂O₅ percentages (Table S3). This summary value can be interpreted as a measure of the weathering (loss of mass) of the bone²⁷. High summary values indicate low weathering while low summary values indicate more weathering. In Table S3, two groups can be distinguished: femora II-V (blue) have relatively high summary values, indicating minimal weathering of the interior bone (as also shown by the CaO/P₂O₅ ratio of 1.3) and slightly more weathering of the surface bone. The calotte and femora I-II (orange) have overall lower summary values, indicating that they are in general more weathered than femora III-V. Within this orange group, Femur I is intermediate with respect to surface bone weathering and has the lowest value for interior bone weathering (as also reflected by its relatively low CaO/P₂O₅ ratio). Together, the CaO/P₂O₅ and CaO+P₂O₅ data demonstrate that Femur I does not deviate from the other hominin bones with respect to weathering. Hence, there is no reason to infer it may have derived from another layer, such as the layer several meters above the Trinil HK that has yielded heavily weathered grey-coloured friable bones (see Supplementary Information section 1).

We conclude that the deviating high CaO/P₂O₅ ratio measured with EDXA in the interior of Femur I is not caused by differential weathering and diagenesis after burial, but likely by processes occurring during the lifetime of the individual. Femur I has a pronounced exostosis with pathological effects evident also in internal bone morphology along the length of the shaft²⁰. The bone has a peculiar characteristic: the presence of linear areas of vertically oriented increased density along the cortico-medullary boundary inside the bone, extending the entire length of the shaft²⁰. The sample subjected to EDXA analysis by Bartsiokas and Day¹ was taken dorsomedially, just below mid-shaft, as evidenced by the small filled hole (Extended Data Fig. 2a). It appears likely that the choice of this particular sampling site resulted in the recovery of pathological bone material from inside the bone characterised by an increased density, e.g. due to calcification, which would readily explain the relatively high Ca/P ratio. This is a much more parsimonious explanation for the deviating ratio than the contention that the bone was from a younger stratigraphic layer with a different diagenetic influence. The skullcap (calotte; see Table S3) appears to have suffered the most from weathering, likely due to its shape: the relatively thin bone layer (compared to the femora) is more strongly affected by the two-sided contact with the burial environment. This may also

explain the deviating F/P_2O_5 value of the skullcap (4.1 versus the average of ca. 6.0 for Trinil HK hominin femora and non-hominin bones) that was found by Matsu'ura¹⁷.

Other elements measured in our XRF analysis are: Fe, Mn, Ti, K, Al, S, Cl, Sr, Ba, Y, Zr, Zn, Cu and Pb. None of these elements show significant differences between bones, except sulphur (S), iron (Fe), barium (Ba) and yttrium (Y; separate excel Table S2). The iron content in fossil bone is a function of exchange with pore water and formation of secondary iron oxides or sulphides. Extended Data Fig. 2d shows the S and Fe content of bones from Trinil and Kedung Brubus. Samples situated above the pyrite line contain more S than could be explained by the presence of pyrite, which can be caused by oxygenated conditions causing pyrite oxidation. This explanation is supported by the observation by Dubois¹² that freshly excavated bones from the Trinil Hauptknochenschicht (HK) sometimes have deposits of pyrite (FeS_2) on them due to the high sulphur content of the surrounding tuff. During and after excavation of fossils from HK, the adhering pyrite then oxidised to jarosite. The samples from Trinil are all situated above the pyrite line; samples from Kedung Brubus can be found on both sides of the line. Femur VI is an undiagnosed shaft fragment that derives not from Trinil but from an unknown part of the Kendeng region, possibly Kedung Brubus²⁸. The values measured on Femur VI plot with Kedung Brubus samples, providing support for Dubois' inference.

In fresh bone, the barium (Ba) concentration is generally less than 150 ppm²¹; during bone fossilisation Ba can replace Ca, thus increasing the Ba content of the bone over time. The yttrium (Y) concentration in fresh bone is very low; during fossilisation, yttrium and lanthanide elements are scavenged by the bone surface, hence the content of Y in fossil bones is indicative of the burial environment²⁹. The scatterplot of Ba versus Y (Extended Data Fig. 2e) shows that the hominins and non-hominin fauna from Trinil all cluster together with relatively low Ba and Y values, whereas the fauna from Kedung Brubus exhibits a wide range of Ba and Y values -in line with the spread of Fe and S values in Kedung Brubus samples on both sides of the pyrite line (Extended Data Fig. 2d). This phenomenon could be due to the fact that fossil fauna from Kedung Brubus may derive from a much wider geographic area than the spatially constrained excavation from Trinil. Mostly, the Y values are higher in Kedung Brubus bones than in Trinil bones. With respect to Y, Femur VI clusters with Kedung Brubus fossils, thus confirming the alleged provenance of Femur VI from Kedung Brubus. Extended Data Fig. 2f presents a detail of 2e, showing that Femur I plots right in the middle of the Trinil cluster together with the other femora II-V, and also overlaps with the calotte. The Trinil herbivore bones generally have higher Ba content than the bones of the Trinil hominins and the Trinil tiger (*Panthera tigris*). It is possible that this is a remnant of the original Ba signal, as herbivore bones are known to have a higher in vivo Ba content³⁰.

In conclusion: the deviating relatively high Ca/P value of Femur I found by Bartsiokas and Day likely represents calcified pathological material inside the bone shaft. Our HH-XRF data -that predominantly reflect the chemical (weathering/diagenetic) processes occurring at the bone-environment interface- show that Femur I is chemically very similar to the other hominin fossils from Trinil, indicating a similar burial environment. This was also concluded by Matsu'ura¹⁷ who found that the ratio between fluorine (F) and phosphate of Femur I falls in the typical range of F/P_2O_5 values that characterizes the other hominin femora and non-hominin bones from Trinil HK. Hence, we conclude there is no reason to infer that Femur I may have derived from a younger layer or a different site than Trinil.

Regarding the provenance of Femur I in the Trinil stratigraphy, Bartsiokas and Day¹⁸ state: “Most importantly, Femur I was found before the ‘fossil layer’ (Hauptknochenschicht, HK, in which the Trinil calotte was found) was reached”. The authors base this statement on a short description of the 1892 excavations by De Vos and Aziz¹, which only mentions the beginning and the end of the fieldwork, and does so in an incomplete way. This may have caused Bartsiokas and Day to misinterpret the course of events in 1892. Here we provide a full description of the discovery of the first femur from Trinil, based on the dated correspondence between the excavators Kriele and De Winter at Trinil and Dubois at Tulung-Agung (Dubois Archive, Naturalis, Leiden). We conclude that Femur I was excavated between 15 and 29 August 1892 at the left side of the river, from the HK deposits.

The excavations in 1892 started in May in the beginning of the dry season when the Solo river water level was falling. On 15 August, Kriele and De Winter sent six boxes of bones, with an accompanying letter, to Dubois. On 22 August they wrote to Dubois acknowledging the return of the boxes at Trinil. On 30 August, Kriele and De Winter sent another batch of eight boxes of bones from the left side of the river to Dubois, with a letter in one of the boxes reporting on the progress of the work. Dubois found the femur (Femur I) in one of these boxes, and immediately, by return mail, asked for details of the find spot of the femur. In response to Dubois’ question, Kriele wrote in a letter, on 31 August, that the femur was found at about the same depth as the skullcap (Trinil 2): “approximately at the same depth as the chimp skull [sic] at the level of the previous low water level and approximately 12 meters from each other”. (“...het been is zoo wat ongeveert gevonden op de diepte van de chimpskop [sic] gelijk met de vroegere lagen water spiegel van elkaar zowat 12 meter”). It is clear that the find level they refer to is within the HK. In that same letter they write that they had to stop working because between 29 and 30 August the river water rose one meter. This fickle and unseasonal water level rise made the HK inaccessible. In September 1892 they took up the excavation again. In order to look for more “Pithecanthropus” fossils, Dubois decided to make a trench (with a length of 25 m and a width of 9 m) by removing the layers on top of the HK close to the femur findspot. However, when in mid-November 1892 the HK was finally reached (at a depth of 9 m) excavations had to stop because of the onset of rainy season. Hence, the statement that Femur I was found before the ‘fossil layer’ was reached is irrelevant, as this applies to the excavation area that was opened in September–November, after recovery of the femur from the HK layer earlier that year in August.

As a further argument, Bartsiokas and Day¹⁸ have also commented upon the westward inclination of the Hauptknochenschicht based on a section in Carthaus⁴, and suggested that “...although the calotte and the femur may have been at the same level relative to the water level, they probably came from differing strata owing to the inclined stratigraphy” (1993: 121). However, their reading of the Carthaus section - which steered their interpretation of the Dubois 1896 section (Extended Data Fig. 1b) - is at odds with the results of levelling operations carried out by geologists of the Selenka Expedition at the site, published in the same edited volume as the Carthaus⁴ paper to which they refer. Through extensive augering and through study of exposures on both banks of the Solo River at Trinil, Dozy³¹ was able to accurately map the spatial distribution of the HK. He concluded that the HK is a local sediment, with a slight inclination where it ends, in Grube II (the section discussed in Bartsiokas and Day) and in Grube I, through its deposition on a slightly sloping (c. 12 degrees) surface (see Tafel X, Profil A). Dozy³¹ stresses that everywhere else the layer is horizontal, as shown through leveling in between Grube I and II, a distance of 200 m (“Im übrigen liegt die Schicht horizontal, wie durch Nivellierung festgestellt wurde. Die Entfernung zwischen den beiden Punkten (im Norden der Grube I und im Osten von II), wo

die Schicht sich auskeilt, beträgt 200m". It is worthwhile noting that the find spots of Femur I and the skullcap (calotte) were minimally 50 metres north of the eastern edge of Grube II³¹, i.e. within the more "horizontal area" mapped by Dozy. These data therefore lend no support to the inference¹⁸ that calotte and femur "...probably came from differing strata owing to the inclined stratigraphy".

The large-scale Selenka excavations also underlined, as mentioned above, that faunal remains from sediments above the HK were rare and differed from the ones from HK. Carthaus⁴ (p.30-31) mentions that a few bones were found here and there above the HK layer, and stresses that their state of preservation was significantly different from the HK faunal remains, which were better preserved and more fossilized than the few usually very fragile bones found in higher levels ("*...wenigen Knochenresten, welche sich hier und da auch in den die Hauptknochenschicht überlagernden Schichten fanden, die meisten viel starker verwittert und ausgelaugt erschienen – dabei auch viel mehr Neigung zum Zerfallen an der Luft zeigten – als die in der Hauptschicht gefundenen*"⁴). This is in line with later observations for the Trinil area and beyond⁸ that the unambiguous HK finds are heavily mineralised and of a conspicuous dark-brown colour, in contrast to the less well-preserved (and rarer) faunal finds from the overlaying deposits, which are considerably less mineralized, more fragmentary and grey in colour. Femur 1 has a heavy mineralisation and the dark chocolate-brown colour typical of fossil bones from the HK, and is same as the skullcap.

We conclude that there is no chemical or stratigraphical evidence to support the inferences made by Bartisiokas and Day¹⁸ and Ruff et al¹⁹ on the possible provenance of Femur I from levels above the Trinil HK. The available evidence indicates that Femur I is derived from the HK deposits that also yielded the *Homo erectus* skullcap.

4. *Pseudodon* shell dimensions compared to recent shells

The recent *Pseudodon* populations contain bivalves of all sizes (age classes) with the exception of juveniles < 30 mm (separate excel Table S1, Extended Data Fig. 1k). This is also the case for the *Unio crassus* assemblage from the Seine River (France), but there even smaller specimens of ~ 10 mm are present (Table S1). In contrast, the fossil *Pseudodon* assemblage from Trinil contains only adult shells with a length between 80 and 120 mm, and a single, slightly smaller shell with a length of 65 mm (Table S1). Smaller juvenile shells are absent, even though small fragments of larger shells as well as juvenile individuals of other species were collected during the Trinil fieldwork in the same layer, implying that the large size of Trinil specimens is not the result of an excavator bias. Occurrences of solely large-sized pearly freshwater mussels have been observed in populations where reproduction has ceased, especially as a result of anthropogenic modifications of fluvial biotopes³². However, the presence of a hole in about a quarter of the *Pseudodon* individuals from Trinil renders it unlikely that this assemblage represents burial of a living population where reproduction had ceased.

In freshwater bivalve shells, length to height ratios can be influenced by local environmental conditions such as current velocity^{33,34}. This environmental control yields a linear strong L/H correlation for shells deriving from the same location, as shown by the recent *P. vondembuschianus* populations on Java (on average $R^2 = 0.98$). In the *Unio crassus* population from the Seine, L/H correlation is equally strong ($R^2 = 0.98$). The Trinil assemblage features instead a weaker L/H correlation ($R^2 = 0.59$). In the light of what is known about the influence of local environment on L/H ratio, the lower L/H co-variance observed in the Trinil population probably reflects collection of shells from different

subpopulations³⁵. For example, high current velocities in river channels correspond in some Unionids to elongate forms, and low current velocities in ponded parts of the same river to more ovate shells³⁴. Alternatively, pathological malformation appears to occur on the posterodorsal margin of some of the more ovate specimens, suggesting pathology may have caused some shape variation.

Articulated shells dominate the *Pseudodon* assemblage (at least 78 % of the MNI). Articulated shells are rare in shell middens³⁶, although dominance of articulated valves has been reported from Holocene sites, indicating processing of shells without heating, and/or shell discard in water-side environments with high rates of sedimentation causing rapid shell burial after consumption^{37,38}. Dead bivalves articulated by the ligament tend to gape, as their adductor muscles are no longer able to pull the valves together^{36,39}. However, the presence of articulated closed valves in midden sites suggests that there is a process whereby at least some shells remain forced together, indicating that closing of ligament-articulated valves occurred during or after discard³⁷. Micromorphological study of the infillings of two *Pseudodon* shells (see above) suggests that the shells must have been (partially) open during the initial stages of the infilling process, but became partially or completely closed during subsequent burial, likely as a result of sub-horizontal orientation after discard.

5. Holes in the *Pseudodon* shells and potential predators

The holes in the fossil *Pseudodon* shells generally have a diameter of ~ 5-10 mm, although post-depositional breakage has widened holes in some specimens (Extended Data Fig. 3a-f). Some edges are slightly smoothed due to weathering. The holes in the fossil *Pseudodon* shells are unlike the perfectly circular, small holes made by marine carnivorous snail species (e.g. muricids and naticids) that predate on bivalves and brachiopods^{40,41}. Holes produced by these carnivorous snails have a smaller diameter (typically 1-3 mm) and have polished surfaces caused by the predator's radula. Moreover, such holes are randomly distributed on the studied bivalve and brachiopod shells^{40,41} in contrast to the non-random predominance of holes at the location of the anterior adductor muscle in the Trinil *Pseudodon* shells (Fig. 1b). The ragged, irregular-shaped holes made by marine ranellid gastropods are also not confined to a specific area of the shell as seen in the Trinil *Pseudodon*⁴⁰. Other predators can produce holes in shells (e.g. mantis shrimps, octopuses⁴²), but these holes have more irregular shapes and likewise lack a preferred location on the shells. Abiotic abrasion processes can produce holes in unionid shells, but these holes are situated at the location of the umbo^{34,43} and not at the location of the anterior adductor muscle. Dissolution can also produce holes, but these are very variable in size and randomly distributed on the shell surface, in contrast to the non-random distribution of the characteristic similar-sized holes at the location of the anterior adductor muscle in the *Pseudodon* shells from Trinil.

Possible shellfish-consuming agents identified in the Trinil fauna are the otter *Lutrogale* sp., the rat *Rattus trinilensis*, and the primates *Macaca* sp. and *Homo erectus*⁹. Several bird species in the region are also known to consume large freshwater bivalves⁴⁴. The White Ibis *Treskikornis molucca* is known to hold freshwater mussels with its foot on a wooden or stone 'anvil' and then uses its bill to hammer open the shell, leaving shell fragments around the anvil stone⁴⁵. Birds such as gulls and crows drop bivalves from heights on a hard surface in order to break and open them^{44,45}. The European otter *Lutra lutra* is known, when preying on freshwater molluscs, to bite the weakest part of the shell just above the underlying adductor muscle in order to get access to the meat. Similarly, muskrats (*Ondatra zibeticus*) prey on freshwater mussels using their teeth to bite one valve in order to open the shell, damaging one

valve and leaving one valve intact^{46,47}. To our knowledge, no report exists in the literature mentioning shells from otter or muskrat middens have holes such as those seen in the fossil *Pseudodon* shells from Trinil. The Australian water-rat (*Chrysomys hydrogaster*) has been observed to place freshwater mussels in the hot sun to open them; the mussels start to gape when the temperature rises, which allows the rats to pry open the shells without causing any damage to them. This procedure leaves shells largely unbroken and still articulated⁴⁴. Long-tailed macaques open mangrove and marine bivalves using hammer stones, axing stones, and hand-sized pointed gastropod shells (*Turitella attenuata*) as picks to axe oysters attached to rocks. Food debris left by these monkeys consists of smashed shells⁴⁸. The White-shouldered capuchin monkey (*Cebus capucinus*) collects mangrove bivalves and opens them by hitting and rolling the shell (without breaking it) over a tree trunk in order to tire the adductor muscle. As soon as the muscle tires, the shell cannot be kept shut and starts to gape, whereupon the monkey can open the shell and eat its content⁴⁹. When the mollusc is consumed, the two valves are still connected. Pre-Hispanic inhabitants of the Caribbean region made more or less circular holes (10–20 mm) in the shell spire near the apex of the conch “*Strombus*” (= *Lobatus gigas*) with the purpose of detaching the adductor ligament (Extended Data Fig. 3g–i). These holes, made with a pointed tool, often the central columella of a *Strombus* shell, give access to the columellar muscle attachment, which is cut to allow extraction of the animal from the shell⁵⁰.

None of the shell remains left by the above-mentioned non-human animals, after opening of bivalve shells with a wide range of methods, including with tools, contain holes such as those observed in fossil *Pseudodon* shells. In contrast, the holes in conchs made by Pre-Hispanic humans are comparable to the holes in the *Pseudodon* shells. They have a similar shape and are always present at the exact same location of the shell: in the case of *Strombus*, just below the apex where the muscle needs to be cut so that the operculum can be opened and the meat extracted from the shell.

6. CT scans and experimental opening of living unionid mussels

Indirect percussion, using a pointed fossil shark tooth struck with a hammer stone, with the purpose to puncture a hole at the location of the adductor muscle in the left valve of *Unio mancus* resulted in the breakage of the tooth and the shell. However, “drilling” by applying a shark tooth to the shell at the location of the anterior adductor muscle with a rotating motion, produced a hole in the (still intact) right valve of *Unio mancus* similar in size and morphology to the holes from Trinil. Since the left valve of this specimen was already broken, we could not study the reaction of the bivalve to damaging the adductor muscle. Hence, the same drilling technique was applied to the *Potomida littoralis* specimen. A hole drilled in its left valve away from the adductor muscle left the specimen firmly closed. However, a successive hole drilled in the right valve that hit the anterior muscle (Extended Data Fig. 3j–m) resulted in a sudden loss of control on shell closure: the valves slightly gaped and could be opened easily with the fingers, giving access to the mollusc meat without any breakage of the shell. Based on this experimental drilling procedure, the Video S1 was made using the CT scan of *Unio mancus turtonii*.

To penetrate the periostracum, the prismatic outer shell layer and the nacreous inner shell layer of unionid shells⁵¹, a drilling motion is required that leaves circular striations on the edge of experimental holes. However, as soon as the nacre layer is reached, the pointed tooth can be directly pushed inward to penetrate the nacre, leaving more ragged, “chipped” traces of breakage in this layer. In the fossil *Pseudodon* shells, we could not find any circular striations

on the edge of the holes. All holes in these fossil specimens are slightly weathered, which makes it problematic to assess whether striations may have been present originally. However, a ragged, chipped widening of the perforation is found in a substantial number of the Trinil specimens. We have found further breakage along the chips in some specimens, possibly as a result of compaction after burial.

7. The availability of shark teeth at Trinil

The Dubois Collection from Trinil contains fossil teeth of two shark species: 16 teeth attributed to a freshwater shark of the genus *Glyphis* (probably the Ganges shark *Glyphis gangeticus* Müller & Henle 1839) and two teeth of the sand tiger shark *Carcharius taurus* Rafinesque 1810⁵². Sharks of the genus *Glyphis* inhabit tropical freshwater systems⁵³, while *Carcharius taurus* is a marine shark that occurs in the surf zone and in shallow bays, and on the outer continental shelves at depths of up to 191 m⁵⁴. Sharks continuously shed teeth during their lifetime so loose shark teeth can be collected in shallow water and on beaches. Fresh teeth of the freshwater shark *Glyphis* would have been available for hominins to collect in the riverine ecosystem at Trinil. Teeth of *Carcharius taurus* could probably be found only in shallow water and on beaches of estuaries and coastal areas near Trinil. In addition, due to the presence of older marine layers on Central Java (belonging to the Kalibeng Formation), it is probable that hominins could find fossil shark teeth as well, e.g. of the species *Isurus hastalis* and *Carcharius megalodon*⁵².

Based on our experimental experience with shark teeth (Supplementary Information sections 6 and 9) we consider the pointed teeth of *Glyphis* sp. and *Carcharius taurus* (without any modification such as knapping or hafting) to be suitable for drilling holes in shells as well as for engraving of a shell surface. Shark tooth enamel, especially the tip of the tooth, is known for its hardness⁵⁵. The use of shark teeth (fresh and fossil) as tools by humans is described in the archaeological and anthropological literature. For instance, the earliest evidence in North America indicating that Native Americans gathered and used fossil shark teeth originates from Holocene burials in Florida: shark teeth found in the graves show that many were hafted and used as cutting, scraping, incising, and drilling implements^{56,57}. More recent Native Americans also used fossil teeth of *Carcharius* sp., *Isurus hastalis* and *Hemipristis serra* as tools⁵⁷. The teeth of *H. serra* are of similar size and shape (pointed, with serrated edges) as teeth of *Glyphis* from Trinil. Pacific islanders used shark teeth to engrave wood; for example the artifact collection made by Captain Cook in the 18th century contains a hafted shark tooth from Tonga (No. 174, Cook-Voyage Collections, Pitts Rivers Museum of the University of Oxford). The tooth, probably of *Carcharius taurus*, is tightly bound to a wooden handle with plaited coconut fibre, and was used to carve fine designs in clubs⁵⁸⁻⁶⁰. The Rongorongo tablets of Easter Island provide another example of shark tooth use: obsidian and shark teeth were used to engrave glyphs of a (as yet undeciphered) script in wooden tablets⁶¹. In Papua New Guinea, shark teeth were used to carve turtle shell into intricate elements for so-called “Kap kap” ornamental headdress ornaments.

Detailed inspection of the *Glyphis* teeth of Trinil revealed that of the 16 teeth in total (15 upper teeth and one lower tooth), four are undamaged (Extended Data Fig. 3n) and 12 are damaged. Two teeth have damage on the side (Extended Data Fig. 3o), seven on the tip (Extended Data Fig. 3p) and three on tip and side (Extended Data Fig. 3q). The teeth of *Carcharius taurus* also show minor damage on tip and sides (Extended Data Fig 3r-s) but less pronounced in comparison with the *Glyphis* teeth. Sharks incur damage on their teeth as a result of biting prey during their lifetime. For example, recent shark dentitions of

Carchariunus have about 10-50 % damaged teeth in the functional tooth row, consisting of tip and side damage broadly similar to the damage in the Trinil shark teeth (Taco Bor, pers. com). Therefore, without further research including use wear experiments, it is not possible to distinguish between hominin tool use and shark bite use as causal agents of the observed damage in the fossil shark teeth from Trinil. We can only conclude that shark teeth suitable for tool use were available to hominins at Trinil.

8. Shell tool analysis

The single shell valve DUB5234-dL shows signs of modification by retouch (Extended Data Fig. 4). The ventral margin features contiguous flake scars, which have removed the nacreous layer between the ventral margin and the pallial line (Extended Data Fig. 4a-b). At a microscopic scale, this area reveals invasive, at places bifacial, step fractures associated with rounding and smoothing of the edge (Extended Data Fig. 4c-e). Indurate sediment and micro-concretions adhering to concavities testify to the antiquity of the micro-flake scars. Shallow striations run parallel to the retouched edge (Extended Data Fig. 4f). At the center of the ventral margin, close to the retouched edge, the area between the ventral margin and the pallial line is damaged by numerous micropits produced by contact with different sharp agents (Extended Data Fig. 4g). These features may have been produced when pecking the shell surface to weaken its structure before retouching it or during the use of the tool. Traces of damage by roots or fungi are present inside and across these striations, demonstrating that they pre-date weathering of the shell before or after burial (Extended Data Fig. 4h). The striations most likely result from contact of the inner shell surface with hard material while using the tool.

Anthropogenic shell modification is further suggested by the presence of an impact pit with an associated scoring mark, produced by the percussor sliding across the surface of a shell with a characteristic hole at the location of the anterior adductor muscle (DUB7923-bL; Fig. 1a, arrow 2). To our knowledge, we do not know of any non-human animal producing such a mark on bivalve shells. The elongated triangular shape of the pit indicates that the percussor may have been a pointed tooth, possibly the same tool that was used to make the hole. The weathering of the scoring mark reveals the aragonitic structure of the shell, resulting in a succession of short lines. The location of the pit shows that the percussion was not aimed at damaging the adductor muscles. The pit and scoring may result from an attempt to break the shell to produce a tool (after opening of the shell for consumption purposes).

9. Engraved pattern analysis

All the lines in specimen DUB1006-f share the same morphology: a groove without any side striations, indicating that the lines were produced with a pointed tool making a unique contact with the shell surface (Extended Data Fig. 5-6). We have considered the possibility of the shell having been used as a cutting board, with the engraved lines as result of cutting action. However, shells do not make suitable cutting boards, as they are very prone to breakage due to compression forces. In addition, our experiments to manufacture similar lines in a fresh shell taught us that making these lines, and especially the angles (points), requires a very sharp, pointed object, as well as considerable manual strength and precision such that it can only have been achieved in a deliberate manner.

The smooth, rounded appearance of the interior of the grooves in DUB1006-f, showing weathering and smoothing of individual aragonite crystals (Extended Data Fig. 6a, e, i, m), contrasts with the more jagged and sharp-edged appearance of the interior of the

experimentally made grooves in fossil *Pseudodon* (Extended Data Fig. 6b-d, f-h, j-l). This indicates that the engraved lines are ancient and pre-date burial and weathering of DUB1006-f. Comparison with experimentally made grooves reveals that the Trinil grooves (Extended Data Fig. 6a, c, m) are most similar to the experimental grooves made with a shark tooth; the latter feature an asymmetrical cross section with a ridge on one side, and no striations inside the groove (Extended Data Fig. 6b, f, j). The groove experimentally made with a flint point also has an asymmetrical cross section, but has conspicuous internal striations (Extended Data Fig. 6c, g, k). The groove made with the steel scalpel is symmetrical, without internal striations (Extended Data Fig. 6d, h, l).

The SEM and Infinite Focus imaging, as well as measurements of 3D roughness parameters made on different areas of the shell surface, demonstrate that the archaeological grooves are highly abraded in the protruding areas (ridges) of the shell, less so in the concavities, and that their differential preservation is function of the degree of abrasion affecting neighbouring surfaces crossed by the engraved lines (Extended Data Figs. 5-6, Table S4). The wear pattern suggests a gentle long lasting taphonomic mechanical abrasion affecting to the same degree the engravings and the shell surface. This further supports the antiquity of the engraved pattern. Artificially rubbing or polishing of the shell to forge “ancient” engravings, or storage during a century in a museum collection, are unlikely to produce such consistent smoothing inside and outside the grooves. This can only be achieved through slow weathering processes taking place after burial of the shell.

	Area 1 (µm)	Area 2 (µm)	Area 3 (µm)
Sk	8.16	7.68	8.35
Spk	3.36	2.96	3.03
Sa	2.85	3.08	2.84
Sq	3.75	3.81	3.54
Sp	12.55	17.41	18.45
Sv	21.37	31.68	14.33
Sz	33.92	49.09	32.78
Ssk	-0.3	1.03	0.38
Sku	4.09	2.76	3.28

Table S4| Roughness parameters determined with Infinite Focus. These parameters are measured, with cut-off filter for long waviness 800 µm, in selected areas (surface 1.4 mm²) just above (Area x), on (Area y) and just below (Area z) the abraded ridge of DUB1006-f (see Extended Data Figs. 5b, c, g for location of the areas). Sk: core roughness depth, height of core material. Spk: reduced peak height, mean height of peaks above the core material. Sa: average height of selected area. Sq: Root-Mean-Square height of selected area. Sp: maximum peak height of selected area. Sv: maximum valley depth of selected area. Sz: maximum height of selected area. Ssk: skewness of selected area. Sku: kurtosis selected area.

The geometric pattern is most deeply engraved at the posterior end of the shell where the zigzag is pronounced, which suggests that the engraver started engraving at the position marked as number 1 (Extended Data Fig. 5a), holding the shell with the ventral side upwards in the left hand, and moving the tool in downward direction towards position no. 2. For a right-handed engraver, this location is the most logical place to start, since the shell surface is relatively flat. Progressing in anterior direction, engraving would become increasingly difficult as the shell surface becomes more convex, making it harder to maintain steady

pressure of the tool on the shell. Similarity in length, internal morphology and orientation of lines no. 6-7 and no. 8-9 compared to lines no. 4-5 and 2-3 suggests that the zigzag between positions 1 and 5 (Extended Data Fig. 5a) originally continued at least up to position 9. Absence of joining lines is certainly due to the fact that the zigzag was made on a fresh shell specimen still retaining the brown outer layer (periostracum) typical of freshwater mussels. Surviving lines correspond to parts of the engraving in which the tool tip has cut the periostracum and marked the underlying prismatic shell layer.

10. $^{40}\text{Ar}/^{39}\text{Ar}$ dating

Feldspars, glass shards and hornblendes were obtained from *Pseudodon* shell infills. Analysis of the $^{39}\text{Ar}/^{37}\text{Ar}$ ratios of the feldspars reveals that all feldspars were plagioclase and due to the low K content the analytical uncertainties were relatively high. The glass shards were enriched in potassium with respect to the feldspars, but still fairly calcic. Both the glass shards and the feldspars yielded ages in the range from c. 3-30 Ma (separate excel Table S5), revealing the geological complexity of the hinterland of the Solo River.

In contrast, all hornblende multi-grain single fusion experiments younger than 2.0 Ma can be understood in terms of three main populations (Table S5, Extended Data Figs. 7-8), excluding three outliers at 2.2 Ma, 3.8 Ma and 4.8 Ma. These three groups define weighted mean ages of 1.65 ± 0.04 Ma ($n = 10$), 1.12 ± 0.04 Ma ($n = 9$), and 0.64 ± 0.06 Ma ($n = 11$), which represent age groups that are not easily reconciled with the provenance from the hinterland, as revealed by the plagioclase and glass shard data. We identified the age groups by including data, until MSWD values were higher than the students T-distribution at the 95% significance level (Extended Data Fig. 7c). Inverse isochron representation of all three data sets shows overlap of the respective non-radiogenic intercepts with atmospheric $^{40}\text{Ar}/^{36}\text{Ar}$ ratios and the isochron regression of each of the three subsets (Extended Data Fig. 8). For the youngest population hornblendes (with a weighted mean age of 0.64 ± 0.06 Ma), that is crucial for defining the upper age bracket for the window for deposition of the sediment, we propose that the corresponding isochron age ($^{39}\text{Ar}/^{40}\text{Ar}$ vs. ^{36}Ar vs. ^{40}Ar) of **0.54 ± 0.10 Ma** is the best representation of the true age of this population.

Our data are consistent with what can be expected from a river deposit: the detritus reflects multiple phases of volcanic activity in the uplands of the Solo drainage basin; the plagioclase and glass shards point to episodic Oligocene to Pliocene volcanic activity. The hornblende data reveal that at least three discrete volcanic events have dispersed hornblende in the Solo drainage basin. One of such events has been documented before by Swisher and colleagues⁶² who in addition to the event at 1.6 Ma also described a 1.8 Ma component in the hornblende population. In our data set, there is no compelling evidence for the older 1.8 Ma component. However, in our data we do find discrete populations at 1.12 ± 0.04 Ma and 0.64 ± 0.06 Ma in addition to the older components. A similar Middle Pleistocene volcanic component, with an isochron age of 0.557 ± 0.003 Ma, was found by Indriati and colleagues at Ngandong⁶³. Given that all populations are detrital, and the data are based on multi-grain sample splits, the interpretation must be that the Trinil HK sediments were deposited at 0.54 ± 0.10 Ma or later. We cannot exclude that some of the mammal and hominin fossil remains in the HK are older, washed in with either of the older hornblende rich volcanic detritus. Reworking for the Trinil *Pseudodon* shells appears impossible given their preservation state. Our results provide a maximum age of **0.54 ± 0.10 Ma** for the *Pseudodon* shells from Trinil.

11. Luminescence dating

Dose rate - Neutron activation analysis does not allow checking for secular disequilibrium in the Uranium decay chain⁶⁴. However, for one of the samples from the *Stegodon* skull infill, we had sufficient material to prepare a sample for gamma-ray spectrometry. Results for this sample yielded no evidence for secular disequilibrium in the Uranium decay chain, with activity concentrations for ²³⁴Th, ²¹⁴Pb and ²¹⁴Bi comfortably in agreement within uncertainties. Based on these results we assumed that the Uranium decay chain was in equilibrium for all samples. Results of gamma-ray spectrometry also indicated that the assumption of 20 % Radon escape for the ²³⁸U decay chain was reasonable (with ²¹⁰Pb activity concentration 20 % lower than the other radionuclides). Results of the dose rate analysis are given in the separate excel Table S6. Dose rates are similar for all samples, and range from 1.05 ± 0.09 to 1.21 ± 0.12 Gy/ka for the K-feldspar separates. Calculated uncertainties are about 10%, and adequately reflect the uncertainties in the assumptions that had to be made (explained in the Methods section).

Palaeodose - Results of a dose-recovery experiment showed that a given laboratory dose could be accurately recovered (ratio 1.04 ± 0.06 , $n = 6$). Laboratory fading tests on a subset of the investigated samples indicated that the pIRIR signal used was stable (fading rate -0.4 ± 2.5 % per decade, $n = 3$). This result is in line with published information on laboratory fading rates for pIRIR signals (e.g.⁶⁵) and with other evidence that pIRIR signals are stable over geological time scales⁶⁶. The sample average onset of saturation (D_0) of the exponential component ranged from 246 ± 22 to 291 ± 42 Gy for the five samples, yielding minimum palaeodoses of 462 ± 44 to 552 ± 84 Gy after subtraction of the estimated residual dose at the time of deposition (see methods section for details).

Ages - The pIRIR minimum ages for the five samples obtained from the cemented sediment infill of four shells from the HK are all very similar, and range from 394 ± 61 to 465 ± 86 ka. The average minimum age of the five samples is **429 ± 46 ka** (Table 1), at one sigma confidence level. Including the one sigma error, this provides the minimum age of 383 ka (0.38 Ma) for the burial age of the sediments that fill the Trinil shells.

12. The Trinil engraving in broader archaeological context

In Extended Data Figure 10 we present the engraved shell DUB1006-f from Trinil in broader archaeological context, against the backdrop of the marine isotope record⁷⁰. With a minimum age of 0.43 ± 0.05 Ma, the engraved shell is considerably older than other geometric engravings documented thus far (Extended Data Fig. 10). An enigmatic series of grooves on a bone is known from the hominin site Bilzingsleben⁷¹ in Germany, but the intentionality of that c. 350 ky old object is debated⁷². The oldest (c. 100 ka) undisputed engravings were made on pieces of ochre and derive from Klasies River Cave 1⁷³ (Extended Data Fig. 10c) and from Blombos Cave⁷⁴ (Extended Data Fig. 10d) in South Africa. Of about the same age is the engraving on a core from Qafzeh⁷⁵ in Israel (Extended Data Fig. 10e). The famous – and more elaborate – Blombos engraving⁷⁶ (Extended Data Fig. 10f) is dated to c. 75 ka. In addition, well-known are the at least 60 ky old engravings on ostrich egg shell from Diepkloof⁷⁷ in South Africa (Extended Data Fig. 10g), and the engraving on cortex from Quneitra⁷⁵ (Syria) attributed to *Homo neanderthalensis* (Extended Data Fig. 10b).

Our results allow for a comparative technical evaluation of the complexity of the engraving process. The Trinil engraving consists of a series of joined lines forming a zig-zag pattern created in a single session with the same tool (Supplementary Information section 9). Thus, it

is evident that the Trinil engraving is less complex than the well-known Blombos engraving on ochre dated to c. 75 ka (Extended Data Fig. 10f), which consists of a design made by superimposing three sets of differently oriented lines, thereby creating closed triangular spaces^{74,76}. The Blombos engraving implies a more complex mental template in its construction, but previous technical analyses⁷¹ and results presented here suggest that both the Blombos and Trinil engravings are the result of deliberate actions. The Trinil engraving is comparable in its technical complexity to a number of other engraved pieces from Blombos Cave, Klasies River Cave 1 and Qafzeh, all of which are slightly older than the above-described 75 ka Blombos artifact. We conclude that the Trinil artifact demonstrates that at least as early as 0.43 ± 0.05 Ma, *Homo erectus* in Asia was capable of producing a geometric engraving on shell substrate.

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