Geology and Discovery Record of the Trinil *Pithecanthropus erectus* Site, Java

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ABSTRACT

Firsthand accounts and contemporaneous field photographs, presented here, document the discovery history and geology of Eugène Dubois' *Pithecanthropus erectus* (*P.e.*) Skullcap (Trinil 1), Femur I (Trinil 3) and associated paleontological specimens, and lead to insights about *Homo erectus* paleogeography. The Trinil finds were unearthed in 1891–1893 from small excavations dug into a flat-lying bonebed exposed near the seasonal low-water level of the Solo River at the foot of an incised embankment. Dubois' on-site supervisors specified that the two *P.e.* fossils came from a bonebed subunit traced at a single elevation for ~12m from the 1891 Skullcap pit (~30m^2) to the 1892 Femur-discovery excavation and across its expansion in 1892–1893 (25-m and 40-m trenches of ~170m^2). These excavations and those of 1895–1908 removed the embankment and a great majority of the bonebed from near the discovery. The depositional co-occurrence of the finds nevertheless is supported by numerous archival records: The supervisors' letters to Dubois about the Femur I discovery, his relevant memoranda to government sponsors, numerous 1892–1893 field accounts about removing more of the *P.e.*-bearing stratum, Dubois' concurrent government submissions, his 1894–1896 publications, Dubois' annotations on unpublished 1894 site photographs, and a letter he wrote the year he died (1940). Additionally, the Selenka Expedition in 1907–1908 and geological field studies from the 1920s to 1970s confirmed essential aspects of the site geology and paleontology. Four more *P.e.* femora were recognized in 1932 from Dubois' 1900 excavation.

The *Pithecanthropus erectus* discovery bonebed contained fossils referable to the extinct Trinil-fauna species such as *Axis lydekkeri*, *Duboisia santeng* and *Stegodon trigonocephalus*. The Selenka Expedition excavations, ~25m away, had a similar assemblage in the same stratigraphic position (named the Hauptknochenschicht, the main bone-bearing layer). The fossils ranged from proboscidean craniums and logs to rat teeth, freshwater mollusc shells and leaves. The terrestrial-vertebrate elements are overwhelmingly disarticulated and frequently broken and have bony surfaces with little indication of fluvial abrasion. The fossil density varied from place-to-place and vertically within the bonebed. Large bioclasts were matrix supported. No substantial internal depositional hiatus was reported. The bone fossilization is quite uniform. More than one hundred ungulates evidently perished in forming the bonebed. No indication of hominin- or terrestrial-carnivore involvement in the deaths was reported. Given Trinil's paleogeographic context, these features implicate a catastrophic mortality of ungulates in a population aggregating along the floodplain of a perennial paleo-river, followed by lahar-flood deposition of gravel-size lithic and biotic materials.

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Trinil provides evidence favoring a broad archaic hominin presence in southern Sundaland. The Trinil fauna is a lynchpin in a long-lasting paleobiogeographic association between *Homo erectus* and certain lineages of large bovids, cervids, proboscideans, rhinoceros, suids and tiger. The Trinil paleogeographic setting exemplifies the stratovolcanic drainages that *H. ere*ctus occupied for >0.8 million years in Java, including the watersheds of a marine delta ~150km east of Trinil, a volcanic island ~100km north of Trinil, and plausibly areas for 500km to the west where the Trinil fauna occurs. In the Java Sea (Sunda Shelf), seismic data image immense Pleistocene river and coastal terranes, which archaic hominins and other large mammals like those at Trini potentially inhabited when sea level was lower than today.

INTRODUCTION

September 23, 1892, was a seminal day in paleoanthropology. Eugène Dubois wrote to the Indies Government that he had unearthed a skullcap, femur, and tooth at Trinil. The discovery *"brings humans in closer relation"* to *"the most advanced extant anthropoids;"* he hoped to *"get us started along the road to resolving the great mystery of human descent via paleontology,"* having already concluded that *"the evolution of the femur … predated that of the skull"* (Dubois 1896b: 260, 270, translated; also, Dubois 1896f).

The advances Dubois sought have been realized. The Trinil Skullcap, known as *Pithecanthropus erectus* after 1894, became the first fossil to be widely accepted as representing humanity's deep evolutionary past. His research in Sumatra and Java, which was guided by geological mapping, spurred science towards the purposeful discovery and metric analysis of primate and hominin fossils (de Vos 2002, 2008, 2014; Henke 2007; Leakey and Slikkerveer 1993; Morwood et al. 2004; Shipman and Storm 2002; Theunissen 1985, 1989; van Gorsel 2022a; Wood 2020). His discoveries started anthropology towards establishing low-profile craniums, erect-bipedal posture, limited arboreal capabilities, modest brain expansion, hands-freed-for-tool use, and wide geographic dispersal as benchmarks in early human evolution. The limestone caves and volcaniclastic contexts that Dubois explored over 128 years ago are today the prime targets for archaic-hominin discovery in South-East Asia.

For decades, scientists accepted the *Pithecanthropus erectus* Skullcap, Femur I and most other Trinil fossils as sourced from one stratum (e.g., Aziz et al. 1995; Bartstra 1982b; Bartstra et al. 1976; Boule 1923; De Terra 1943; de Vos 2008; Huffman et al. 2005; Joordens et al. 2015; Matthew 1928; Osborn 1915, 1924; Reader 1981; Shipman 2001; Soeradi et al. 1985; Sollas 1908; van Es 1931). However, the utility the finds has had for further scientific study was impaired by uncertainties in provenience information that Dubois provided during the 1890s and deficiencies in his underlying documentation (Bartstra 1982; Brodrick 1948, 1964; Brongersma 1941 in de Vos 2014: 78; de Vos 1982; de Vos and Aziz 1989; de Vos and Sondaar 1982; Theunissen 1989; also, Alink et al. 2016).

Among the uncertainties has been the geological *"contemporaneity"* of the 1891 *Pithecanthropus erectus* (*P.e.*) Skullcap and 1892 Femur I (Rightmire 1990: 16), a controversy stemming from the *Homo sapiens*-like anatomy of the long bone. More than a hundred fossils from Java have been attributed to *H. erectus*, seeming to make Trinil's *P.e.* finds less relevant, even though the Java fossils might well represent several hominin species (Antón 2013; Antón et al. 2007, 2014; Baab and Zaim 2017; Indriati 2004; Kaifu 2017; Kaifu et al. 2008, 2015; Mayr 1950; Noerwidi et al. 2016; Santa Luca 1980; Schwartz 2016; Tyler 2003; Washburn 1951; Weidenreich 1946; Zanolli et al. 2019). Trinil has seemed at risk of becoming tangential to the hominin record in Java (e.g., Sémah et al. 2016).

Here we use firsthand observations and century-old photographs to detail the geology and fossil discovery record of *Pithecanthropus erectus*. We define the discovery bed using Dubois' only geological display of the site, a partially schematic geological cross section published in 1895 and 1896 (see Figure 2a below). Dubois (1896d: 241, Figure 1) specified that the *P.e.* finds, *"amidst hundreds of other skeletal remains,"* occurred in about a meter-thin *"Bed of lapilli-rock,"* which we name the Lapilli Bed (**LB**).

The year before, Dubois (1894a: 1) had specified in his monograph on *Pithecanthropus erectus* that *"the left femur was excavated … at the same level* [a subunit of the **LB**; Figure 2a] *… about 15 meters* [from the Skullcap] *upstream in the direction of the current that during Pleistocene time …."* had been opposite to the flow of the modern Solo River (Supplementary Information [SI] II-199; also, SI II-183). Besides providing provenience information, he had offered a cryptic expression about the paleogeography of the ancient river valley in which the **LB** accumulated. Later fluvial incision exposed the **LB** and an overlying embankment of layered *"Sand rock"* (see Figure 2a below; SI II-230; SI II-230 in the form generally cited here).

Today, the *Pithecanthropus erectus* (*P.e.*) discovery spots are in the middle of the Solo River, making verification of the provenience circumstances difficult to ascertain (Figure 1c). However, when the river drops towards dry-season low levels, the discovery area begins to appear as baulks, spoil piles and a scarred bedrock platform. At lowest river levels, outcrops become visible in the immediate vicinity of the *P.e.* discovery point (SI I-2). The platform and riverbank lie next to former excavation trenches (see Figure 6d below).

The bonebed seen in the platform is flat-lying, well-lithified gravelly volcaniclastic sandstone that is notable for its cross bedding, very poor granulometric sorting and large Trinil fauna fossils (SI I-2b; also, Aimi and Aziz 1985;

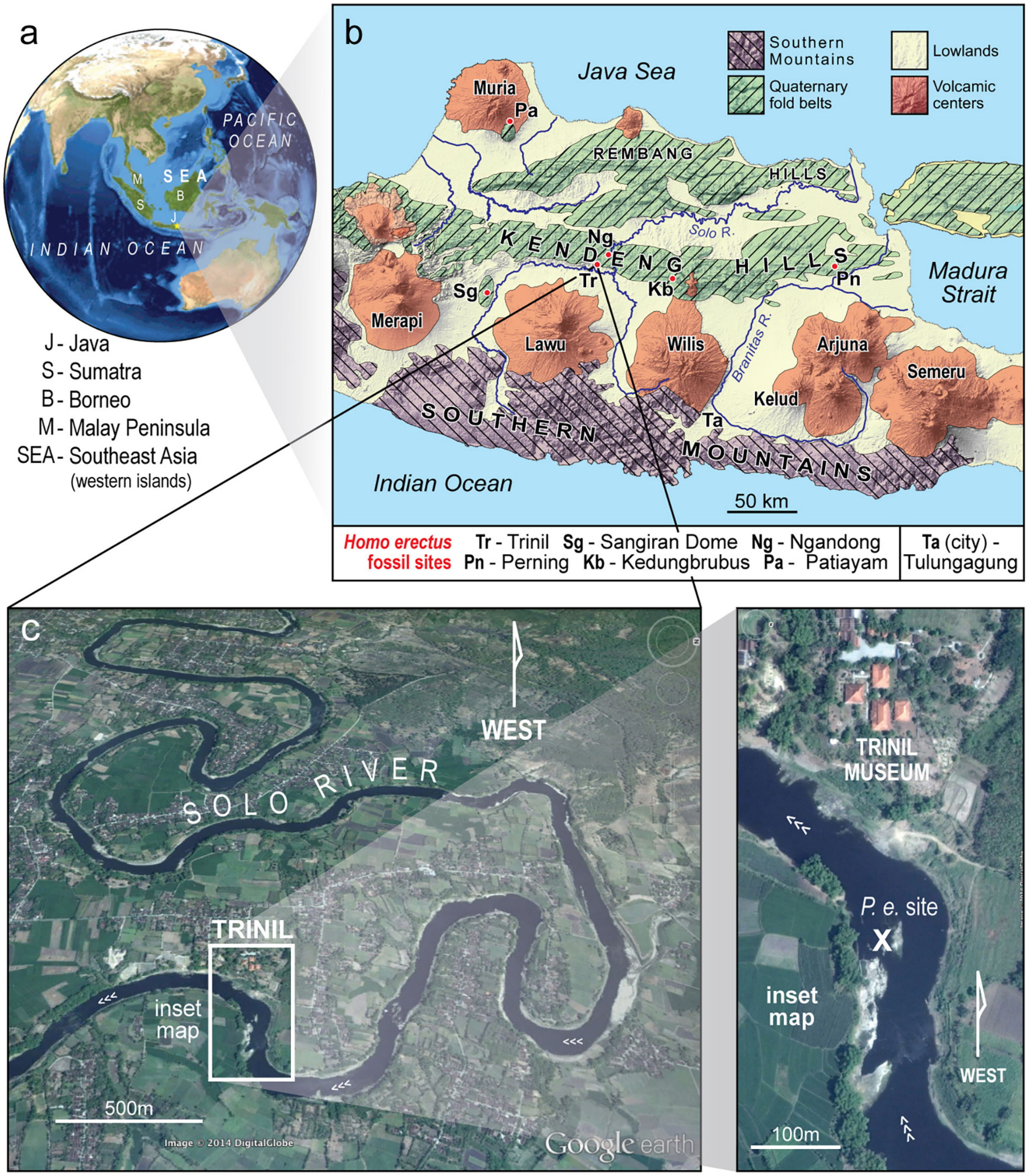


*Figure 1. Trinil's location. (***a***) In Southeast Asia. (***b***) In eastern Java with key* Homo erectus *fossil sites (see Table 5, see Figure 13; SI I-38) on a generalized geological map (also, Huffman et al. 2010a: Figure 1). (***c***) The spot (***X*** in the inset map) is where the* Pithecanthropus erectus *(*P.e.*) fossils and other large vertebrate bioclasts were excavated during seasonal low-water level of the Solo River in 1891–1892 (e.g., see Table 1, see Figures 2 and 3; de Vos and Sondaar 1982; Huffman et al. 2015, 2018). Since the 1920s, geologists have been able to see scars of the original excavations in the riverbed during times of particularly low water (see Figure 9). The Solo River in the vicinity is largely bounded by high-standing incised banks (see Figure 6). The embankment near the* P.e. *site and nearly all the* P.e.*-bearing stratum itself were excavated away in 1892–1908 (see Figures 3 to 5). The white* **>>>***'s indicate the direction of river flow.*

Huffman 2016). The sandstone qualifies as a bonebed by virtue of its high density of vertebrate bioclasts (Table 1). The paleontological concentration stood in marked contrast to the generally low fossil content that Dubois and Selenka reported encountering in superjacent strata of the former embankment (Table 2). Orientation of cross bedding is the type of information that Dubois used to infer the current direction when the Skullcap and Femur I were embedded in the ancient river valley.

For decades, the Selenka publications stood as confirmation of Dubois' general stratigraphic portrayal of the *Pithecanthropus erectus* discovery context (e.g., Boule 1923; de Terra 1943; Osborn 1915). Selenka Expedition member Emil Carthaus coined the term Hauptknochenschicht (**HK**), the main bone-bearing layer (Branca 1908; Carthaus 1911b: 14; Dubois 1908: 1242; also, Alink et al. 2016). In the late 1970s, the bone-rich stratum was mapped in fine detail along the left bank and given the name 'KBG 1' connoting Duyfjes' (1936) placement of the bonebed in his Kabuh Formation (SI I-17 and -18; Soeradi et al. 1985; also, van Gorsel 2022c).

The coarse gravel, large bioclasts and cross bedding in KBG 1 apparently reflect bed-load deposition of an ancient flood (Huffman et al. 2010a, b, 2012b). A map unit underlying the KBG 1 includes laminated siltstone and matrix-supported sandy pebble-cobble conglomerate, which potentially represent the same set of depositional events as the bonebed (Huffman 2016). The units wedge out to the east against a boulder-diamicton (SI I-18) which corresponds to a 'breccia' that Dubois placed at the base of his geological cross section of the site (Figure 2a). He appears to have recognized the stratigraphic relationship of the breccia to the overlying beds in 1890 before excavation at Trinil started (SI II-205). In Indonesia, the term 'breccia' often denotes an indurated boulder-bearing, matrix-supported conglomerate of volcanic materials (a volcanic diamicton).

The Selenka geologists were confident that the **HK** they had encountered in excavation was the same sedimentary deposit as Dubois' **LB** (Oppenoorth 1907; Selenka and Blanckenhorn 1911; also, van Gorsel 2022d). Nonetheless, the term Hauptknochenschicht is not a satisfactory stratigraphic substitute for the **LB** because the **LB** was the reported source of the *P.e.* fossils, not Selenka's **HK** (see Figure 2a). Moreover, between 1895 and 1900, after Dubois left Java and before the Selenka Expedition arrived, Dubois' crews undertook the largest excavation ever done at Trinil (Figure 3a) and discovered the great majority of the fossils from the site (see Table 1). When Selenka was at Trinil, Dubois' 1900 spoils buried the 1891–1893 *P.e.* discovery pit and trenches that were the basis for Dubois' attribution of the Skullcap and Femur I to a single sedimentary deposit.

To maintain precision in reporting on the discoveries, we refer to the fossil-rich stratum encountered in 1895–1900 as the **LB-HK** (see Table 1). We employ the term 'main bonebed' as a general referent. In the early 1930s, Dubois (1932, 1934, 1935) recognized four more *Pithecanthropus erectus* femora among fossils from his 1900 collection (Femur II to Femur V; Ruff et al. 2015; SI II-136, -137). We attribute these hominin finds, which fit taphonomically with other fossils attributable to the main bonebed, to the **LB-HK**.

Although the remnants of Dubois' **LB** are today no more than low-lying baulks, and his overlying 'Sand Rock' was entirely excavated away, photographs dating from 1894 to 1907 provide a reliable means of visualizing the eight-to-nine meters of strata removed and lead to an independent stratigraphic framework for fossil discoveries at the site (see Figures 2 to 5 below; Huffman et al. 2015, 2018). The images reveal that the beds were nearly horizontal, which turns out to be consistent with firsthand excavation accounts (SI I-4 to -14, translated accounts in SI II-1 to -195). Therefore, when Dubois' field supervisors used elevation to specify the provenience of the Skullcap, Femur I, and other finds, the descriptions were equivalent to stratigraphic designations.

Firsthand reporting allows the progress of the field operations to be followed closely, often week by week. While there are many gaps in field documentation, eyewitness accounts compensate substantially for the maps, profiles, and other geological displays that in later decades normally accompanied site reports. Furthermore, the firsthand narrations on Trinil commonly include the field taxonomic identity of prominent finds (see Tables 1 to 3 below). This validates previous characterizations of the fauna in the main bonebed, and places well-known elements of Trinil fauna into the very excavations where the *Pithecanthropus erectus* Skullcap and Femur I were found (de Vos and Sondaar 1982).

The primary purposes of this paper are, first, to introduce site photographs into geological analysis of the left-bank (see Figures 3 to 7 below; SI I-4 to -15), and then given these results, to document the stratigraphic attribution of the fossil discoveries recovered from excavation (see Tables 1 to 3 below and SI II). In the latter case, we address Dubois' central provenience conclusion: The 1891–1893 *Pithecanthropus erectus* *"remains … were found at exactly the same level ….* [and thus were] *deposited at the same time"* together with many hundreds of other finds of broad biotic composition (Dubois 1896e: 4; SI II-231; de Vos and Aziz 1989).

We evaluate the geology and paleontology of Trinil in the Site Geology and Fossil Discovery Record sections below. Both depend on the same collection of old photographs, maps, and firsthand accounts (see Figures 2 to 7 below; SI I-4 to S I-15 and SI II). We endeavor to interweave detail, much unpublished hitherto, into an approximation of an excavation report that Dubois never prepared. Despite the many shortcomings in the record, it justifies a robust presumptive acceptance of Dubois' geological and provenience conclusions about Trinil. The archival materials, given the site geology, lead us to consider the discovery of the Skullcap, Femur I, and thousands of associated fossils to be products of the rational actions of individuals who were skillful in excavating a well-understood stratigraphy under difficult operational circumstances.

Besides site-specific issues, the century-old records form a basis for developing attractive hypotheses about both the formation of the main bonebed in a Pleistocene

TABLE 1. PROMINENT TAXA EXCAVATED AT TRINIL IN 1891 TO 1907.[1]

	A. Finds noted in Dubois' field supervisors' letters and other records and publications of Dubois and Selenka[1]							B.[2] Percentages of non-hominin specimens in the Dubois Collection	
Location of the find >	Left bank (south side) of the Solo River (see Figure 1c)[3]				Right bank of the river		Bank unspecified		
Years of discovery [3] >	'91 '92 '93	'95 '96 '97	'99 '00	'07	'91, '92, '95 '96	'07	'91 '92 '95		
Source bed [3] >	**LB**	**LB-HK**	**LB-HK**	**HK**	**LB-HK**	**HK**	**LB, LB-HK**		
TAXA v v v v v v v	● = At least one fossil of this taxon was reported . ☐ = This species was not mentioned.								
CERVIDAE (Cervini) *Axis lydekkeri* [2]	● ● ●	☐ ● ●	● ●	●	● ● ● ●	●	● ● ●	28%	68%
BOVIDAE (Bovini)[2]								40%	
Bibos palaesondaicus	☐ ● ☐	☐ ☐ ●	● ●	●	● ☐ ● ☐	●	● ☐ ●		
Bubalus palaeokerabau	● ☐ ●	☐ ☐ ●	● ●	●	☐ ● ☐ ☐		● ☐ ●		
PROBOSCIDEA *Stegodon trigonocephalus*	● ● ●	● ☐ ●	● ●	●	☐ ☐ ● ●	●	● ☐ ●	13%	19%
BOVIDAE (small) *Duboisia santeng*	● ● ●	● ☐ ☐	☐ ☐	●	☐ ● ☐ ●	●	● ☐ ●	6%	
CROCODYLIA								2%	7%
Crocodylus siamensis	☐ ☐ ●	☐ ● ☐	☐ ●	●	☐ ☐ ● ☐	●	● ☐ ●		
Gavialis bengawanicus	☐ ● ☐	☐ ☐ ☐	☐ ☐	☐	☐ ☐ ☐ ☐	☐	● ☐ ☐		
TESTUDINES (Geoemydidae; Trionychidae)	☐ ☐ ●	☐ ● ☐	☐ ●	●	☐ ☐ ☐ ●	●	● ☐ ●	5%	
HOMINID *Pithecanthropus erectus* [4]	● ● ☐	☐ ☐ ●	☐ ●	☐	☐ ☐ ☐ ☐	☐	☐ ☐ ☐		

[1] Taxonomic identifications as originally reported have been changed to current taxonomic nomenclature on the basis of the Trinil species that are currently recognized in the Dubois Collection (Naturalis Biodiversity Center, Leiden; see Table 3). The entries for the Selenka Expedition are from Selenka and Blanckenhorn (1911) and an unpublished listing of finds, the 1907 Listing ('PM_S_II_Selenka_FB_1-78.pdf' at the Museum für Naturkunde Berlin; MNB), in part based on input from a specimen-by-specimen examination of the fossils at the MNB by Lawrence Todd (personal communication, 2015; see also, Hill et al. 2015).

[2] Based on Storm's (2012) tabulations of 3857 identified non-hominin specimens from Trinil, as recorded in the 2002 electronic catalogue of the Dubois Collection.

[3] Dubois' left-bank excavations of 1891–1900 are denoted as follows: 1891 Skullcap Pit is '91; 1892 25-m Trench is '92; 1893 40-m Trench is '93; 1895 Ledge is '95; 1896 Left-bank Pit is '96; 1897 Downstream and Upstream Pits are '97; 1899 Trench is '99; and 1900 Trench '00. There were no Trinil excavations in 1898. Selenka Expedition right-bank and left-bank Pits I and II are '07. The source bed in 1891–1893 is the **LB** (see Figures 2 and 10); in 1895–1900, the source bed is the **LB-HK**; and in 1907, the bed is the **HK** (see Figure 7).

[4] Dubois (1894a) attributed three fossils from Trinil to the new species *Pithecanthropus erectus* (Trinil 1 to 3) without designating a single holotype specimen, so that three equally ranking syntypes form the holotype. No lectotype that conforms to the standards of the International Code of Zoological Nomenclature has been assigned. The Dubois Collection at Naturalis retains the Skullcap but it does not have an accession number. Jacob (1975a) referred to the 1891 Molar (see Figure 2) as Trinil 1, the Skullcap as Trinil 2, and Femur I as Trinil 3. Dubois (1932, 1934) attributed four additional femora to *Pithecanthropus erectus* (Femur II to Femur IV; Trinil 6 to Trinil 9) from among materials collected in 1900 (SI I-137, -138), leading to a Minimum Number of Individuals of 3 from Trinil (Storm 2012). Ruff et al. (2015) reviews the literature concerning the femora.

TABLE 2. VERTEBRATE FINDS OF THE SELENKA TRINIL EXPEDITION PITS I AND II OF 1907.

A. The number of finds listed by excavation area and layer (field designations) shows the concentration of fossils in the **HK**[1]

Excavation name	PIT I (right bank of the Solo River)					PIT II (left bank of the Solo River)				
Stratigraphic position	above HK	Hauptknochenschicht (**HK**)			below HK	Units 2-4, see Figure 4a		Hauptknochenschicht (**HK**)		below HK (?)
Layer #s in 1907 Listing	10-14	15	16	17	18–20	1 [2]	2	3 [2]	4	5–9
# of finds in the layer(s)	50	545	86	429	26	17	67	299	106	17
# of identifiable finds[3]	42	449	68	305	17	13	38	191	52	11
% identified finds	84%	82%	79%	71%	65%	76%	57%	64%	49%	65%
Number of identified finds by taxon										
CERVIDAE (Cervini)	16	285	50	190	7	0	19	116	21	5
BOVIDAE (Bovini)	11	73	10	79	7	0	1	35	22	4
Stegodon trigonocephalus	10	47	3	13	0	9	0	9	2	0
Duboisia santeng	1	4	1	7	1	0	3	6	2	0
CROCODYLIA	1	6	2	6	0	2	2	3	0	1
TESTUDINES	3	18	0	4	1	0	0	0	1	1
Sus brachygnathus	0	1	0	2	0	0	4	8	2	0
Rhinoceros sondaicus	0	8	1	0	1	0	0	1	1	0
Hexaprotodon	0	0	0	0	0	**1**	0	0	0	0
Fish	0	0	0	1	0	1	5	9	1	0
[Antlers [3]]	[9]	[243]	[41]	[140]	[3]	[0]	[2]	[11]	[3]	[1]

B. Paleontological similarities and differences in the Hauptknochenschicht (**HK**) finds of Pits I and II

Name (location) of the excavation	PIT I (right bank)	PIT II (left bank)	PIT I and PIT II	
Stratigraphic terminology	Hauptknochenschicht (**HK**)			
Layer #s in the 1907 Listing	15–17	3–4[4]	3–4 and 15–17	
HK finds identified taxonomically	78%	59%	72%	
Number of finds (and % of total finds) by taxon				
CERVIDAE (Cervini) [3]	525 (64%)	133 (56%)	658 (62%)	(83%)
BOVIDAE (Bovini)	162 (20%)	57 (23%)	219 (21%)	
Stegodon trigonocephalus	63 (8%)	11(4%)	74 (7%)	(9%)
Duboisia santeng	12 (1%)	8 (3%)	20 (2%)	
CROCODYLIA	14 (1%)	3 (2%)	17 (2%)	(4%)
TESTUDINES	22 (3%)	1(-%)	23 (2%)	
Sus brachygnathus	3 (-%)	10 (4%)	13 (1%)	(2%)
Rhinoceros sondaicus	9 (1%)	2 (1%)	11 (1%)	
Fish	1 (-%)	10 (4%)	11 (1%)	(2%)
Other	11 (1%)	4 (2%)	15 (1%)	
Total identified entries	822 (100%)	239 (100%)	1061 (100%)	(100%)

[1] From the 1907 Listing; the Museum für Naturkunde Berlin, MNB, document 'PM_S_II_Selenka_FB_1-78.pdf' and in part L. C. Todd (personal. communication, 2015) and Selenka and Blanckenhorn (1911, translated in Berkhout and Huffman 2021). The number of finds with layer attributions is 96% for Pit I and 75% for Pit II. Oppenoorth (1908a, b, 1911) reported 2000 finds in 1908 but gave no details on source layers.

[2] Layer 1 is the "*Stegodon* bed" (SB; see Figure 8).

[3] 'Layer 3' includes 7 "Pithe[can]thropus" bed entries; excluded here are eighteen June 5–6 entries that are ambiguous as to source Pit and bed. Taxonomic identification based on various sources. Stremme (1911) examined ~375 bony cervid fossils and 527 *Axis* antler beams (230 of which were shed).

[4] The Selenka Expedition unearthed ~2,200m^3 of rock in 1907, exposed ~260m^2 of **HK**, and collected ~700 fossils; in 1908, the Expedition removed ~950 m^3 of material, dug ~110 m^2 of **HK**, and should have made ~300 finds (Berkhout and Huffman 2021: 53; Dozy 1911a: xlii; Oppenoorth 1908b: 145, 1911: xxxviii). The average vertebrate-fossil density in the **HK** was ~2.7m^{-2} based on ~1000 specimens from ~370 m^2.

DUBOIS' GEOLOGICAL DOCUMENATION OF THE *PITHECANTHROPUS ERECTUS* DISCOVERIES

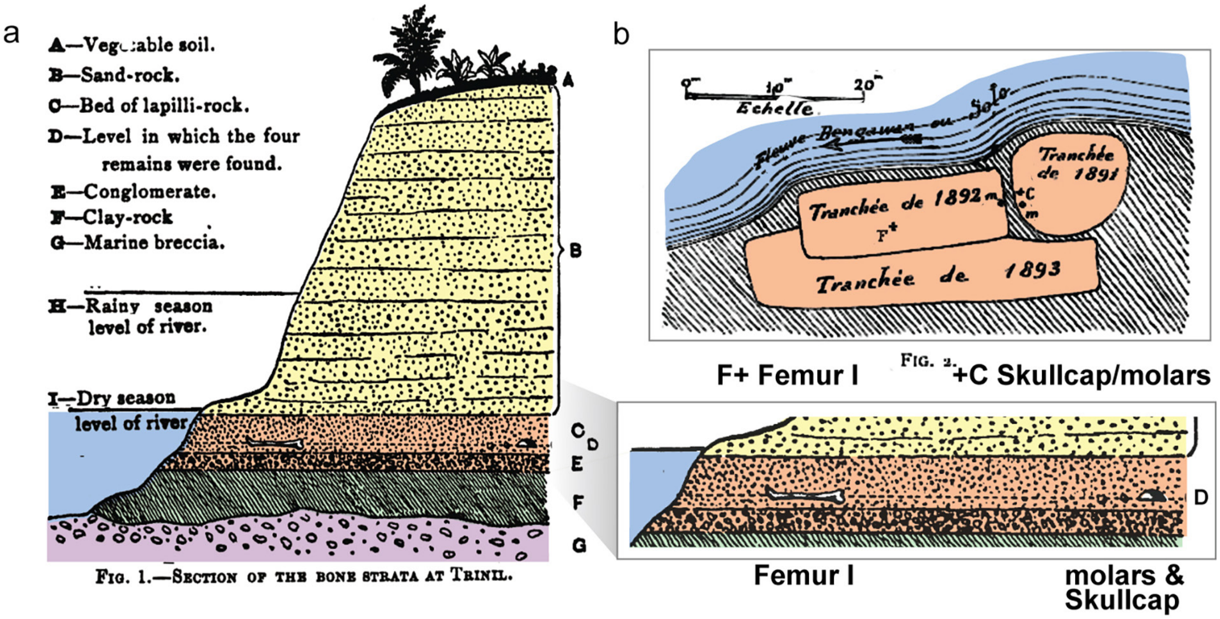


Figure 2. (**a**) *Dubois' principal geological display of the* Pithecanthropus erectus *discoveries was a partially schematic cross section (SI II-226, -230; rearranged and colorized after Huffman et al. 2015, 2018). Dubois' discovery stratum (C), which is the Lapilli Bed (***LB***) herein, contained the* "Level in which the four [hominin] remains were found," *which is a stratigraphic subunit that we term the Principal Fossil Zone (***PFZ***). Dubois (1896b: 251) characterized the* "Sand-rock" *(B) above the* **LB** *as* "tight and hardened volcanic tuffs consisting of clay, sand and lapilli" *(SI II-227). His conglomerate (E) and claystone (F), which underlies the* **LB**, *were encountered in the 1893 excavation, and the breccia (G) was known to him from outcrops in the vicinity (SI II-47, -51, -53, -160, -179; also, SI II-194, -195, -210 and SI I-18).* (**b**) *Dubois (1895a: 158) published only one map of the excavations (SI II-228). His* "Tranchée de 1891" *is our Skullcap Pit, where the 1891 Molar ('*m*' in the map) and 1891 P.e. Skullcap ('*c*') were discovered (see Table 1, footnote 4). His* "Tranchée de 1892" *is our 25-m Trench, where Femur I ('*F*') and the 1892 Molar ("*m*") were found (see Figure 3a).* "Tranchée de 1893" *is our 40-m Trench. We adopt this terminology to conform better to unpublished firsthand reporting (e.g., SI II-183, -191).*

valley, as mentioned by Dubois in 1894, and some broader paleogeographic implications of Trinil. These issues, which were of a type that was integral to his understanding of the fossils he collected in Java and have been of interest to us for decades, are discussed in the sections on the Formation of the Main Bonebed and Paleogeographic Implications (with support in SI I-16 to -52).

MATERIALS AND METHODS

This article contains a fine-grained analysis of primary documentary sources, which are largely unpublished, and 130 years of literature on the discovery, stratigraphic framework, and paleontology of Trinil. The literature is anchored by Dubois' own publications (1892–1908), as well as Selenka and Blanckenhorn (1911), and includes numerous useful analytical and summary works (Albers and de Vos 2010; de Vos 1985b, 1989, 2004, 2014; de Vos and Aziz 1989; Hooijer 1946a-1974; Joordens et al. 2015; Shipman 2001; Storm 2012; Theunissen 1985, 1990; also, van Gorsel 2022e).

We incorporate all unpublished materials recognized as relevant to fossil finds from the left-bank discovery area at Trinil and greatly expand resources available for evaluation over previous compilations (e.g., de Vos and Aziz 1989; de Vos and Sondaar 1892; Shipman 2001). The fossils from Trinil that Dubois attributed to *Pithecanthropus erectus* (*P.e.*) continue to be referred to as such to help maintain a focus on his records.

Central to our evaluation is the premise that contemporaneous firsthand accounts of field observations are potentially interpretable in terms of the stratigraphic units (see Figure 3c; Figure 4a) and fossil species (see Table 1). Individual source documents often include information that is simultaneously relevant to the stratigraphy and fossil recovery. Crucial to making full use of these resources has been compiling site photographs and translated Dubois materials in forms that can be closely interrelated.

This type of analysis is feasible because the Naturalis Biodiversity Center, Netherlands, preserves Dubois' notebooks, diaries, fossil inventories, maps, reports to superiors or drafts thereof, academic papers, photographs, correspondence received, and drafts or handwritten copies of letters Dubois sent (collectively known as the Dubois

DUBOIS' GEOLOGICAL DOCUMENATION OF THE *PITHECANTHROPUS ERECTUS* DISCOVERIES

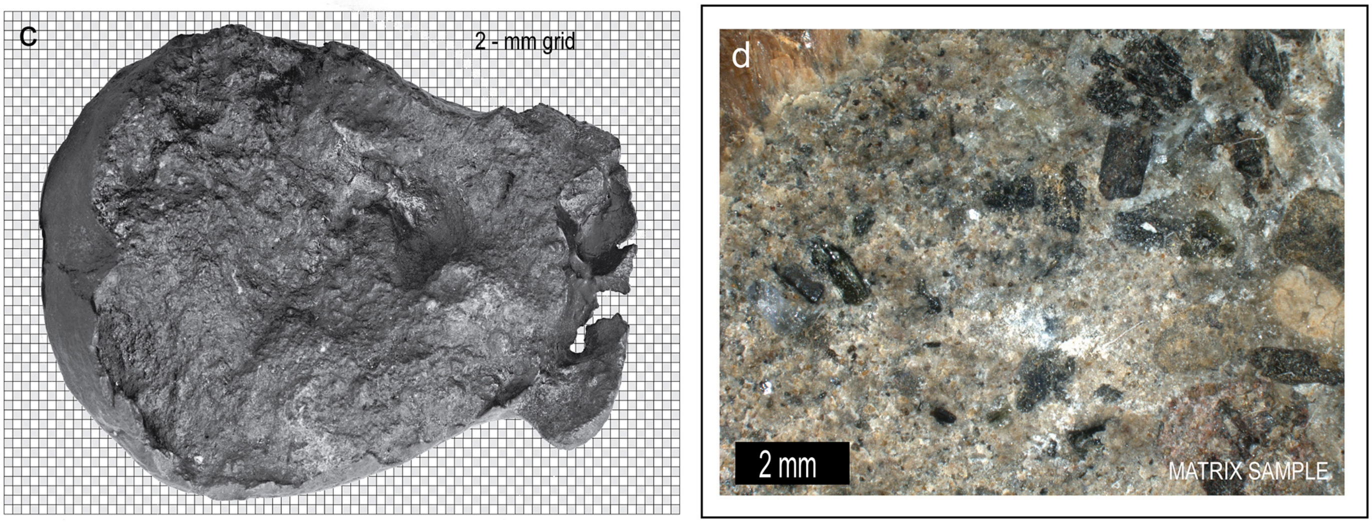


*Figure 2 continued. Vast unpublished materials lie behind Dubois' provenience reporting. (***c***) This photograph is one of many taken of the Skullcap filled with coarse-grained sandstone or fine conglomerate (scan DUBO1303, Naturalis Biodiversity Center; the grid highlights granule-sized gravel clasts, 2–4mm in diameter). (***d***) Dubois kept this sandstone sample in a safe with the Skullcap specimen (photograph by F.P. Wesselingh).*

Archive). Overall ~30,000 pages of paper, and >2,500 photographic glass negatives, film negatives, and prints have been scanned by the Naturalis Biodiversity Center, and each has a unique identifier, which we include where pertinent to our account in Supplementary Information. The scans of Dubois photographs generally have reference code in the form DUBO#### (Albers and de Vos 2010). Most other individual documents have Naturalis scan codes with the form MM774-0000##-### (e.g., MM774-000058-538), abbreviated here as M…###-### (e.g., M…058-538).

The geological evaluation of the 1894–1932 photographs of the left bank expands on our preliminary site evaluations (de Vos and Aziz 1989; Huffman et al. 2015, 2018), and includes extensive presentation of interpreted images in Supplementary Information I (individual page numbers are cited in the abbreviated form 'SI I-##'). Primary narrative sources and much of the literature are written in Dutch and German. English translation of these materials is provided in the Supplementary Information II (citations to individual page have the form 'SI II-##;' e.g., SI II-1 with M…058-538).

The principal record on the provenience of fossils consists of the letters Dubois field supervisors wrote to him about their excavations and his routine reporting on them to governmental sponsors. Dubois' complimentary letters to his field supervisors are not part of the known record (see also, SI II-220). Dubois compiled drafts of his governmental memoranda into one volume, which facilitates following his growing understanding of Trinil (SI II-157, -183).

Vital additional information on the stratigraphy and paleontology of Trinil comes from the 1906–1908 Selenka Trinil Expedition (e.g., Selenka and Blanckenhorn 1911). Most of their published material, originally written in German, is now available in English translation (Berkhout and Huffman 2021; also, Huffman 2020). Expedition geologist W.F.F. Oppenoorth took many valuable photographs in 1907, and most of them were never published (see Huffman et al. 2010a and van Gorsel 2022d for biographic information on Oppenoorth). His family saved negatives and prints and provided many to the Naturalis Biodiversity Center for our use (J.M. Oppenoorth, personal communications, 2010 and 2015; also, Huffman et al. 2010a for background). Naturalis made high-resolution scans of key images for our stratigraphic and provenience analysis (e.g., Figures 8 and 9 below; SI I-8 to -15).

Our research also brought to light unpublished Selenka Expedition documentation in the Museum für Naturkunde, Berlin (MNB). Among the records is a 1907 enumeration of field identifications of fossils, and the entries often specify the stratigraphic origin of the finds. We refer to this document (MNB PM_S_II_Selenka_FB_1-78.pdf) as the '1907 Listing.' Most of the identifiable finds are attributed to **HK** layers (see Table 2). Moreover, field numbers can still be read on many fossils retained by the MNB (Lawrence C. Todd, personal communication, 2016). This has expanded paleontological study of the **HK** (e.g., Hill et al. 2015; Janssen 2017; Janssen et al. 2016). For definition of the Pleistocene, we follow the International Union of Geological Sciences time scale wherein the base of the Pleistocene is 2.58 Ma (Gibbard et al. 2010; SI I-50a).

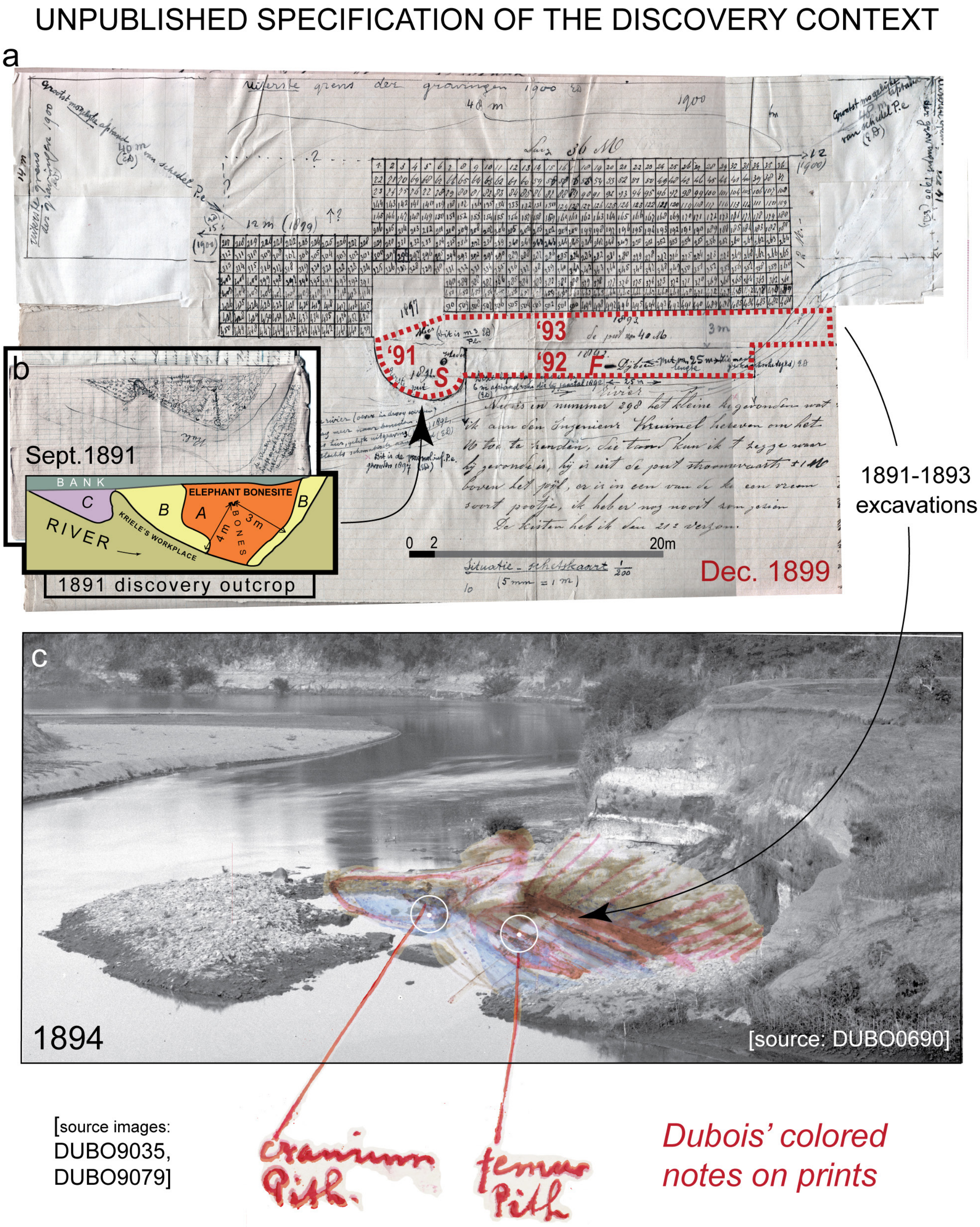


Figure 3. (**a**) *In 1899, Dubois' field supervisor G. Kriele prepared the most detailed known representation of the 1891–1900 excavations (compare to Figure 2b). Dubois annotated it in apparent approval (SI II-135). Represented are the discovery points of the Skullcap* (**S**), *Femur I* (**F**), *and 1891 Molar* ("this is m3/P.e."; *the 1892 Molar is not shown). The 1899 Trench is gridded and the 1900 Trench is as proposed. The 1891–1893 pit and trenches (~200m²) are small compared to 1895–1900 excavations of ~1650m² (SI II-155). They extended for ~24m south of the Femur I discovery point, according to Kriele's plat (SI II-155).* (**b**) *Kriele's September 18, 1891, map of the Trinil fossil site with a colorized redisplay of the left bank portion (south is up; SI II-2).* (**c**) *A photograph of the 1891–1893 left-bank excavation area taken during low-water level on September 5, 1894. The embankment on the south (right) was removed in 1896–1900 (SI I-3c). Dubois annotated prints of the 1894 image to specify the hominin-discovery spots relative to the nearby outcrops (Huffman et al. 2015, 2018; SI I-3). The DUBO0690 image is a 4800-dpi scan of a glass negative produced courtesy of the Naturalis Biodiversity Center, Leiden, as also is the case for the images used in Figures 4b and 5 (Huffman et al. 2015).*

SITE GEOLOGY

Visitors typically view the *Pithecanthropus erectus* (*P.e.*) discovery site from a high bluff at the Trinil Museum, looking eastward up a broad loop of the Solo River (see Figure 1c). When the river drops towards dry-season low levels, former excavation baulks and spoil piles begin to appear near the waterline (see Figure 6d below). At lowest water level, Dubois' Lapilli bed (**LB)** is exposed close to the *Pithecanthropus erectus* discovery spots towards the middle of river (SI I-2a, -18). To visualize the eight-to-nine-meter stratigraphic sequence that once held up the high excavation backwalls and place **LB** outcrops into stratigraphic context, we employ unpublished photographs, maps, and eyewitness accounts dating from 1891 to the 1970s.

STRATIGRAPHY, 1891–1894 EXCAVATIONS

Dubois was in Java from 1890 to 1895 and saw the 1891–1893 *Pithecanthropus erectus* discovery excavations firsthand. His 1895–1896 published accounts on the stratigraphic context of the finds (e.g., see Figure 2a, b) were based on his own observatons in the Trinil area (for at least 67 days; SI I-52) and the reporting of field supervisors G. Kriele and A. de Winter (KdW), as well a photograph Dubois had taken of the left bank discovery area in 1894 (see Figure 3c; Figure 4a). This photograph is an independent resource for assessing the site geology reported in firsthand and published accounts (Huffman et al. 2015, 2018). KdW worked in the discovery excavations from 1891–1897 and Kriele continued alone until completion of Dubois' excavations in 1900 (SI II-1 to -156).

1891 Skullcap Pit

The 1891 Skullcap Pit was dug into an ~40m^2 natural outcrop that seasonal low-water levels (LWL) of the Solo had exposed on the left bank (see Figure 3b; SI II-2). Fossils were *"chiseled out of the flat rocky ledge that reaches out … from the foot of the steep bank"* (Dubois 1896b: 251; SI II-227; also SI II-4). When operations got underway in early September 1891, the bonebed outcrop contained a *Stegodon* tusk and cranium (Kriele's "Elephant bonesite" in Figure 3b; SI II-2). A particular concentration of fossils was encountered when the pit was deepened below the seasonal low-water level (LWL) to expose a subunit of the **LB** that we name the Principal Fossil Zone (**PFZ**; SI II-2). This became the *"level in which the four* [hominin] *remains were found"* of Dubois' 1895 site cross section (see Figure 2a). The Skullcap was found *"among hundreds of other skeleton remains, in the lapilli bed on the left bank"* (Dubois 1896c: 2; SI II-229). The endocranial space of the Skullcap unearthed in October 1891 was filled with indurated volcaniclastic material (see Figure 2c and 2d). **LB** in the Skullcap Pit included many other large-sized bioclasts (described in the Fossil Discovery Record section). Molluscan and aquatic reptile fossils indicated that the **LB** was a freshwater deposit (SI II-168).

Mid-1892 25-m Trench

By the end of 1891, the Dubois field team established a stratigraphically controlled excavation protocol that all later operations followed—remove the flat-lying fossil-poor strata making up the precipitously incised embankment of the Solo to mine the fossil-rich **LB** near river level. To do this during the low-water season of 1892, KdW had to move westward from the Skullcap Pit along the shoreline (see Figures 2b, 3a, and 3c) and dig through a substantial thickness of overlying beds (SI II-183; also SI II-10). As they did, the local stratigraphy and paleontology of the **LB** became even clearer than it had been in 1891. The left-bank pit and trenches of 1891–1893 ultimately formed a narrow band ~50m long. Annual excavations in those years were ~30m^2, 50m^2, and 120m^2 (see Figure 3a).

When the river fell enough to expose the **LB** in late June 1892, the crew unearthed a *"harvest of bones …* [as] *plentiful as last year's"* (SI II-180; also, SI II-179). The finds noted then included key Trinil fauna species (see Table 1; Table 3). In later publication, Dubois (1896c: 4) recounted, a *"new cutting was now made in the left rocky bank ….* [and] *bones were again found in great numbers, especially … in the same level of the lapilli bed, which had contained the skull-cap and the molar tooth, the left femur was found"* (S II-229). He was referring to KdW's conclusion that Femur I (Trinil 3) was found at the same **PFZ** level that produced the 1891 Molar (Trinil 1) and Skullcap (Trinil 2) the year before. KdW were able to track the bonebed westward from the Skullcap Pit into the 1892 excavation (see Figure 3). They regarded the **PFZ** as a subunit of the **LB**, as their later reporting manifests. The Femur I context is assessed further in the Fossil Discovery Record section.

Mid-1892 Field Studies

The archival record reveals how Dubois and KdW informed themselves scientifically about the sedimentary features being excavated at Trinil. Dubois spent 14 full and 8 partial field days in the Trinil area during 1892 before Femur I was discovered (SI I-52). He closely observed the fluvial bedding expressed in the modern sand- and gravel-bars of the meandering Solo River and inferred corresponding paleocurrent patterns from cross bedding in the ancient sandy and gravelly formations exposed in its banks, including those excavated at Trinil (SI II-179, -206, -207, -208).

Dubois' June 1892 submission to the government addressed the sedimentology: *"at about 1 meter below the lowest water level of the river near Trinil, a blue-gray clay*[stone] *variety was found, immediately below the sandstone-like tuff,"* which might refer to the **LB** itself; the claystone *"indicates a time of stagnant or very slowly flowing water,"* while the tuffaceous facies *"must have been deposited in faster flowing water"* (SI II-179; also, SI II-207). Dubois noted elsewhere, *"at Trinil bonebeds on both sides of the river (separated by a distance of 70m) have truncated thin* [cross] *beds dipping 30 degrees from west"* (SI II-206; also, SI II-179). Dubois concluded that the paleo-river flowed in a direction opposite to that of the modern Solo River; the Skullcap, Femur I, and associated skeletal remains were not deposited by the present day river but in an ancient valley (SI II-183; also 1894a, b; SI II-199)

Records from 1892 indicate that G. Kriele understood Dubois' innovative field methods for measuring paleocur-

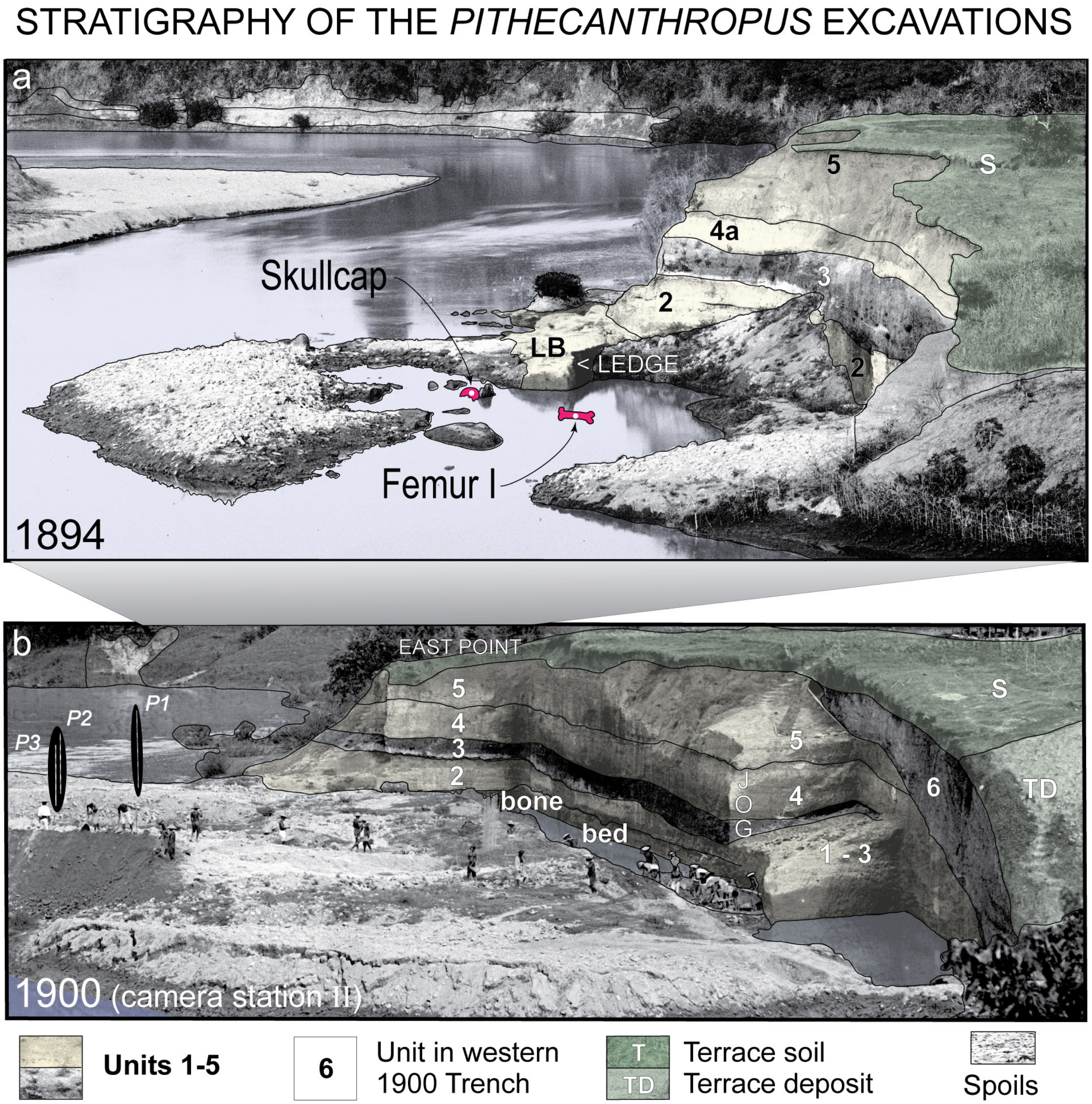


Figure 4. *Site photographs from 1894, 1900, and 1907 permit geological analysis of the rock removed by excavation (after Huffman et al. 2015, 2018). (***a***) The 1894 image shows remnants of the 1893 40-m Trench where the hominin discovery stratum* **LB** *(see Figure 2a) is overlain by a stratigraphic sequence that we subdivide photographically into units* **2**–**5** *(also, SI I-4). Only soil mantled the terrace surface (***S***) that capped these units (the Skullcap and Femur I locations are from Figure 3c). The geological circumstances seen in 1894 generally match those shown in Dubois' schematic 1895–1896 site cross sections (see Figure 2a). (***b***) The same stratigraphic units are recognized tens of meters away at about the same elevations in the high-standing backwalls of Dubois' 1900 Trench. This November 1900 photograph looks eastward and was taken from camera station II on the Site Map (in Figure 6a; also, SI I-7). Workers were still excavating the bonebed. We highlight three scale poles staked into the spoil (P1 to P3) to mark buried discovery locations for the Skullcap, 1891 Molar, and Femur I (SI II-149). Other interpreted 1900 photographs are in Figure 5 and SI I-6. The 1894 and 1900 photographs, as well as the 1900 Site Map (see Figure 6a; SI II-222), have been published widely without geological analysis (e.g., Albers and de Vos 2010; Alink et al. 2016; de Vos and Sondaar 1982; de Vos and Aziz 1989; Leakey and Slikkerveer 1993; Reader 1981; Shipman 2001; Theunissen 1989).*

TABLE 3. TAXA IDENTIFIED FROM TRINIL.

TAXA	NOTES		RELATED MODERN TAXA
C's = confirmed as a main bonebed species. T's = Trinil fauna taxa.[1, 2]			
TERRESTRIAL SPECIES			
Axis lydekkeri (Martin 1886)	C	T	*Axis kuhlii*, Bawean deer
Bibos palaesondaicus Dubois 1908	C	T	*Bos javanicus*, Banteng (cattle)
Bubalus palaeokerabau Dubois 1908	C	T	*Bubalus arnee*, Asian Wild buffalo
Duboisia santeng (Dubois 1891)	C	T	[Extinct Boselaphin genus]
Hexaprotodon sivajavanicus (Hooijer, 1950)	C	T	[Extinct *Hippopotamus* genus]
Homo erectus (*Pithecanthropus erectus*) Dubois 1894	C	T	*Homo sapiens*
Hylobates sp. Illiger 1811[3]	--	--	*Hylobates* ssp., subssp.
Hystrix cf. *refossa* Gervais, 1852	C	T	*Hystrix* ssp., Old World porcupine
Macaca (Raffles, 1758)	C	T	*M. fascicularis* subssp., Crab-eating macaque
Muntiacus muntjak (Zimmerman 1780)	C	T	*Muntiacus* ssp., Southern Red Muntjac (Barking deer)
Panthera tigris trinilensis (Dubois 1908)	C	T	*Panthera tigris* subssp., Tiger
Prionailurus bengalensis trinilensis Dubois 1908	--	T	*Prionailurus bengalensis*, *P. javanensis*, Leopard cat
Python sp. Daudin 1803[3]	--	--	*Python* ssp., Python
Rattus trinilensis Musser 1982	--	T	*Rattus* ssp., rat.
Rhinoceros sondaicus Desmarest 1822	C	T	*Rhinoceros sondaicus,* Javan Rhinoceros
Stegodon trigonocephalus Martin 1887	C	T	[Extinct proboscidean family]
Sus brachygnathus Dubois 1908	C	T	*Sus verrucosus* and *S. blouchi*, Javan and Bawean Warty Pigs
Trachypithecus cristatus robustus Hooijer 1962	--	T	*Trachypithecus* ssp., subssp., Langur/Lutung
Varanus sp. Merrem 1820[3]	--	--	*Varanus salvator*, Monitor lizard
Xenocyon trinilensis (Stremme, 1911)[3]	--	--	*Canis aureus*, Golden Jackal
BIRD SPECIES[3]			
Branta cf. ruficollis (Pallas 1769)	--	--	Red-breasted Goose
Ephippiorhynchus cf. asiaticus (Latham 1790)	--	--	Black-necked Stork
Leptoptilos cf. *dubius* (Gmelin 1789)	--	--	Greater Adjutant
Tadorna tadornoides (Jardin and Selby 1828)	--	--	Australian Shelduck
AQUATIC REPTILE SPECIES			
Amyda cartilaginea (Boddaert 1770)	--	--	Asian Softshell Turtle
Batagur affinis (Cantor 1847)	C	--	Southern River Terrapin
Crocodylus siamensis Schneider 1801	C	--	Siamese Crocodile
Gavialis bengawanicus Dubois 1908	C	--	Gharial
Orlitia borneensis Gray 1873	--	--	Malaysian Giant Turtle

TABLE 3. TAXA IDENTIFIED FROM TRINIL (continued).

TAXA	NOTES		RELATED MODERN TAXA
C's = confirmed as a main bonebed species. T's = Trinil fauna taxa.[1, 2]			
FISH SPECIES[4]			
Anabas testudineus (Bloch 1792)	--	--	Climbing Perch
Carcharias taurus (Rafinesque 1810)	--	--	Sand tiger shark
Channa cf. *striata* (Bloch 1793)	--	--	Snakehead (Murrel)
Clarias batrachus (Linnaeus 1758)	--	--	Walking Catfish
Clarias leiacanthus (Bleeker 1851)	--	--	Forest Walking Catfish
Glyphis gangeticus (Muller & Henle 1839)	--	--	Ganges shark
Hemibagrus nemurus (Valenciennes 1840)	--	--	Asian Yellow Catfish
Urogymnus polylepis (Bleeker 1852)	--	--	Giant Freshwater Whipray
MOLLUSC SPECIES			
Ameria duboisi (v. Benthem Jutting, 1937)	C	--	Pond snail (Lymnaeidae)
Bellamya javanica (von dem Busch 1844)	C	--	Freshwater snail (Viviparidae)
Corbicula sp.	C	--	Freshwater and brackish water clam (Corbiculidae)
Elongaria orientalis (Lea 1840)	C	--	Freshwater mussel (Unionidae)
Lymnaea javanica (Mousson 1849)	C	--	Pond snail (Lymnaeidae)
Mieniplotia scabra (Müller 1774)	C	--	Freshwater snail (Thiaridae)
Pila conica (Gray 1828)	C	--	Freshwater (Apple) snail (Ampullariidae)
Pseudodon vondembuschianus trinilensis (Dubois 1908)	C	--	Freshwater mussel (Unionidae)
Rectidens sumatrensis (Dunker 1852)	C	--	Freshwater mussel (Unionidae)
Sulcospira testudinaria (von dem Busch 1842)	C	--	Freshwater snail (Pachychilidae)
Tarebia granifera (Lamarck 1822)	C	--	Freshwater snail (Thiaridae)
Thiara zollingeri fennemai (Martin 1905)	C	--	Freshwater snail (Thiaridae)
PLANT REMAINS			
Reedy stems	C	--	Sedges and grasses
Tree- and shrub-woods, fruit, and leaves	C	--	Ever-green and deciduous-trees and -shrubs

[1] The C's indicate those Trinil species in the Dubois Collection (DC) that have firsthand reporting or labels confirming their origin from the **LB**, **LB-HK**, and **HK** (main bonebed). Other taxa are listed when fossils in the DC and Selenka and Blanckenhorn (1911) have paleontological features matching known main bonebed specimens (examples are shown in SI II-243).

[2] The Trinil (biostratigraphic) fauna (T's) was largely established from specimens attributable to the main bonebed based by written records with the fossils in the Dubois Collection and Selenka and Blanckenhorn (1911; de Vos 1982, 1989; de Vos and Sondaar 1982; also, van den Bergh 1999 regarding the *Stegodon*). No fossil of the cervid *Rusa* has been identified at Trinil; the species occur with *Axis lydekkeri* elsewhere in the *Stegodon-Homo erectus* faunal association (see Table 5). Dubois (1908) indicated that no hippopotamus fossils had been found at Trinil, yet a lower jaw with molars was reported from the Skullcap Pit (SI II-6) and a lower jaw is in the Dubois Collection from Trinil (Hooijer 1950; see Table 5, footnote 4). *Hexaprotodon sivajavanicus* occurs in the *Stegodon* bed (SB) ~5m stratigraphically above the **HK** in Selenka Pit II (see Figures 7 and 8; also, de Visser 2008).

[3] The *Hylobates* sp. is from a single well-preserved specimen (Ingicco et al. 2014). The *Xenocyon trinilensis* was formerly *Mececyon trinilensis* Stremme 1911 (van der Geer et al. 2018; also, Volmer et al. 2016). The fish are updated from Joordens et al. 2009. The Trinil *Varanus* material is not significantly different from the modern *V. salvator*, according to Hocknull et al. (2009; also, Hooijer 1972). Bird fauna here is after Weesie (1982; also, H. Meijer 2014, and personal communication 2017). See Groves (1997) for *Prionailurus bengalensis*, and Groves and Leslie (2011) for *Rhinoceros sondaicus* (also, Hoogerwerf 1970; Nardelli 2016).

[4] Information on the aquatic reptiles and fish species is from Allen (2013,) Asian Turtle Trade Working Group [ATTWG] (2000a, b), Auliya (2006), Auliya et al. (2002, 2016), Berra(2007), Bogan (2011), Bonin et al. (2006), Budha et al. (2016), Chaudhry (2010), Chowdhury et al. (2017), Das (2008a, b), Delfino and de Vos (2010), Fritz et al. (2014), Jackel (1911), Janensch (1911a), Rigby et al. (2021), and van Benthem Jutting (1937).

rents. Dubois had to return to his home at Tulungagung in East Java on July 20, 1892, ending his field session around Trinil. He had a relapse of malaria contracted in Sumatra before the Java field project began. Dubois asked Kriele to go upstream of Trinil to record crossbedding in strata that Dubois had not analyzed (SI II-18). To have success in this field assignment, Kriele must have been instructed on how to recognize lithostratigraphic formations, lithofacies differences within them, and bed sets and planar structures from never-before-seen outcrops of prehistoric strata which matched the lithofacies under excavation at Trinil.

Once Kriele located appropriate upstream outcrops, he needed to measure the direction of inclination of foreset laminations, having comprehended Dubois' use of crossbedding as proxies for paleocurrent directions. Kriele's synoptic presentation of the results to Dubois on August 15 shows that the two men shared essential understandings about these sedimentological matters and associated geological field skills. Kriele presented small, annotated cross sections of the three localities. Each one showed the directions of internal cross-laminations within bed sets bounded by horizontal stratigraphic layers (SI II-19).

Crossbed analysis seems to have been a core field practice for Dubois and his field supervisors, and as such, reporting crossbed measurements serves to suggest that a high level of sedimentary knowledge was being applied to the Trinil excavation. Dubois' first crossbedding observations were made as soon as he started working the Kendeng Hills in 1890 (e.g., SI II-163, -204, -212). In 1893, he had de Winter take notes about crossbedding at Sangiran Dome, when *"very nice 'oblique lamination' … within horizontally bedded structure ….* [allowed] *the direction of* [the paleo] *current"* to be deduced (SI II-194; also, SI II-195). The orientation of cross-laminations continued to be on Dubois' mind (SI II-63) and among Kriele's competencies until near the end of excavation in 1900, when Kriele wrote: *"The thin slanted beds* [cross lamination sets] *about which you … asked me have been observed in 4 different places. They all dip approximately in this indicated direction S.W. ////////// N.E. but also N.N.E. …"* (SI II-145).

Dubois' novel strategy for the use of fluvial paleocurrents to reconstruct river valley paleogeography was more than a half-century in advance of sedimentologists' development of this approach (Potter and Pettijohn 1963/1977). KdW had sufficient geological training to put this strategy into practice, fostering confidence in their reporting about the sedimentary co-occurrence of the Skullcap and Femur I.

Late-1892 Excavation

Following the femur discovery, KdW expanded the excavation to the south, digging downward from the top of the embankment toward their target layer. Dubois was sure about the expected stratigraphy and the hard rock and anticipated:

> *This stretch of embankment* [destined to be the 25-m Trench] *… will have to be continued* [downward from the surface of the embankment] *to what we now estimate* [to be] *a depth of 9 meters, since … other remains* [of hominin] *are expected* [to occur in the **PFZ**] *below the water level during the East Monsoon* [low-water dry season]*. The sedimentary material to be removed is only soft enough for actual digging near the surface* [e.g., the soil of the terrace upland atop the embankment]*, but for the most part we have a fairly hard sandstone-like andesitic tuff which* [is so well indurated that the material] *can only be removed with pickaxes and crow bars. …* [and] *very few other finds were made* [in the strata higher than ~2.75m above the **LB**]. (SI II-183).

Soon, KdW wrote to Dubois that they had removed the upper 6.25m of the embankment and *"not a lot of bones have been found"* (SI II-28). Approximately 70% of the eight-or-nine-meter-thick section overlying the **LB** had few vertebrate fossils and the strata were so lithified that they were tough to dig.

No more *"Chimpanzee"* remains had been seen by November 9 when KdW reported that *"the corners of the pit* [25-m Trench] … *are about 20 cm into the target bone layer* [**PFZ**]*"* (SI II-31). The Femur I subunit could be traced from near the Skullcap Pit through and beyond the discovery point (see Figure 3a). The men also would have stood before a tall, excavated face ~25m long. One point at the base of the scarp was just a meter or so away from the Femur I find spot (see Figure 3a).

This was the field situation when Dubois paid his last visit for 1892 on November 10–11. A week later, the river inundated the **PFZ**, ending the excavation season (SI II-33). Dubois reported, *"no other parts of the* Anthropopithecus *…* [were found before] *rising water … forced us to finally abandon the work … after having only excavated about 1/5th of the level of interest* [the **PFZ**]*"* (SI II-185). While the **PFZ** was exposed across the ~50m^2 25-m trench, much of the **PFZ** volume was still in place (see Figure 3a). KdW's November 9 reference to the Trench having 'corners' was among the few mentions that their letters made to the shape of the excavation (SI II-29, -30, -31; also, SI II-35, -36, -37, -42, -44, -52).

1893 40-m Trench

Kriele's crew began a 40-m-long, 5-m-wide excavation (SI II-191), located immediately to the south and southwest of the 25-m Trench by removing the soil on the terrace upland at the top of the embankment and anticipating that the **LB** would be accessible during June and July when river levels subsided. Dug downward in horizontal increments, the penetration *"progressed extremely slowly because of the severe hardness of the rocks,"* a condition Dubois witnessed himself on June 6–8 and 26–28, 1893 (SI II-42 to SI II-51 and SI II-192; Huffman et al. 2015). The **LB** was just as rich with large vertebrate bioclasts in the 1893 40-m Trench as the unit had been in Skullcap Pit of 1891 and the two excavations had much of same fossil biota (addressed in the Fossil Discovery Record section).

KdW also gathered new stratigraphic information from the 40-m Trench. Below the **LB** *"a different layer emerges;"* its top contact *"slopes downstream"* to the west (SI II-47). Elsewhere in the Trench, the **LB** was *"becoming a little coarser downward"* with *"almost nothing in it"* by way of fossils (SI

II-51). Soon, most of the dig was deep enough to expose *"almost entirely coarse gravel"* with *"very little* [in it by way of vertebrate fossils]*"* (SI II-53, -54). KdW had encountered the conglomerate that Dubois would illustrate as underlying the **LB** two years later (see Figure 2a; also, SI II-194, -195).

Dubois' notes for October 21, 1893, described the stratigraphic changes he observed during an on-site examination of the near-finished 25-m and 40-m Trenches (SI II-210). Above a claystone at the base of the excavation sequence, the crew apparently had exposed as much as 3.7m of sandstone, lapilli-rich sandstone, and conglomerate. The **LB** described later in publications was the upper portion of this coarse-clastic interval (see Figure 2a). Dubois' notes do not address the distribution of fossils within the lapilli-bearing sandstone, other than the position of the Skullcap.

Close to the Skullcap Pit, as Dubois' notes recount, the *"top of black claystone* [was] *about 1 meter deeper than the Chimp skull"* had been found and this discovery was in the stratigraphic middle of a *"lapilli bed about 2 meters thick"* (SI II-210). Along the backwall of the 40-m Trench, near the Femur I discovery spot and 18m to the west of the first place he described, the crew had *"excavated 1.30m deeper into conglomerate after* [penetrating the] *alternating lapilli and sand."* The *"deepest spots* [in the Trench] *are about 3 meters below the current river level."* The conglomerate above the *"black clay*[stone] *layer"* was 0.5m thick. Dubois' descriptions notably employ standard geological terminology that KdW were not using.

The apparent dip at the top of the claystone was ~6º westward, not the near-horizontal attitude of the upper **LB** and **PFZ** described by KdW (SI II-210). There is nothing in Dubois' October 1893 reporting to suggest that the **LB** and conglomeratic unit had an internal stratigraphic boundary denoting a substantial cessation of accumulation, only subtle internal changes of lithofacies. When Dubois made the inspection, a high excavated wall 40-m long loomed over the Femur I find spot (see Figure 3b), but his remarks have essentially nothing about strata above the **LB**.

Dubois' notes about the trench on October 21, 1893, are consistent with KdW's previous stratigraphic reporting on the **LB** but partially inconsistent with Dubois' 1895–1896 published descriptions (SI II-226). For example, he (1896b: 251; SI II-227) glossed over complexities observed in the field when he published that the lapilli *"predominate in the …* [**LB**] *about 1-meter thick, which in turn transitions downward into a 1/2-meter-thick* conglomerate *bed that primarily consists of about walnut-sized rock fragments."* Dubois (1896e: 4; SI II-231) also wrote that *"the rocky slopes on the banks of … Solo. … consist here primarily of … not very consolidated sandstone,"* rather than the hard rock described vividly during excavation in 1892 and 1893. Moreover, his cross sections showed the low-water well above the top of the **PFZ**, despite field reporting to the contrary (e.g., see Figures 3b, and SI II-2, -5, -10, -11, -22, -23, -27, -31, -44, -45). Most of his versions portray strata dipping slightly (e.g., SI II-226 to SI II-232), in conflict with other evidence.

By year's end in 1893, Kriele had shipped 25 crates of fossils and 6 crates of wood to Dubois (SI I-45, -56). The area of **PFZ** excavated in 1893 had been ~170m^2 (adding the unfinished 80% of the 25-m Trench to the 40-m Trench of Figure 3a). Twice as much of the **PFZ** had been unearthed in 1893 as had been taken in 1891–1892, and evidently, most of the fossils Dubois recovered from the left bank over the three years came from the 1893 effort. The continuity of the fossil bone concentration across the three years of excavations signaled that the **LB** was widely present below strata of the unexcavated embankment to the south, setting the geological predicate for the work that was conducted during 1895–1908 (see Figure 2a).

1894 Photograph

Dubois documented the *Pithecanthropus erectus* discovery area photographically in 1894 (see Figure 3c) during a seven-day boat journey down the Solo (SI I-52). The September 5 image and Dubois' annotations on prints of it depict the 1891–1892 *P.e.* Skullcap Pit and the 25-m Trench in relation to the stratigraphic sequence visible in a degraded 1893 backwall (see Figures 4a and 10 [below], SI I-3; Huffman et al. 2015, 2018). Dubois never published the 1894 photograph or a description of it. But his unpublished annotations depict the Skullcap Pit next to a sandstone 'Ledge' that lay just above river level (see Figures 3c and 4a; SI I-3). The Ledge (an ~6m area) produced vertebrate fossils in 1895 (SI II-75; also, SI II-32, -69, -101). The 1894 backwall was ~35m north of the present-day shoreline, according to G. Kriele's later mapping of trenches (see Figure 3a; also, SI I-7).

To help track the stratigraphy of the left bank, we divide the beds identifiable in the 1894 photograph into informal lithostratigraphic units: Lapilli Bed (**LB**; unit **1**) is at the base of the scarp (e.g., at the Ledge); **2** through **5** make up the embankment with **5** just below the terrace upland on which a soil **S** is developed. Units **2** to **5** correspond to the *'B-sand rock'* in the version of the Dubois cross section that we present; **S** is his *'vegetable soil'* (see Figure 2a; SI II-227, -228, -229, -230, -231, -232).

The embankment contains no noticeable inset fluvial-terrace deposit in either the 1894 photograph or Dubois' cross section (Huffman et al. 2015, 2018). The soil-covered upland, which extended away from the lip of the embankment, rose gently southward (see Figure 4a; Figures 6c and 7a below; SI I-2a). When Dubois (1896b) was asked at an 1895 public lecture about the presence of geologically younger deposits at the *Pithecanthropus erectus* discovery site, he described the Solo River valley as *"more of an eroding one than of alluvial deposits* [filling it]*"* (SI II-228). He apparently thought that the local geomorphology originated when the Solo River cut downward through the nine meters of bedrock strata lying between the terrace soil **S** and the **LB**.

The 1894 photograph provides independent evidence about the structural attitude of the strata excavation during 1891–1893. The **1-5** sequence in the 1894 embankment exhibits little- or no-apparent dip in the photograph (Huffman et al. 2015). Any inclination having an east-west component of more than ~3° would have appeared strongly accentuated in the photograph because it was taken at a shallow oblique angle to the excavation face (the camera station in 1894 was west of the 1891–1893 pits and trenches on the right bank near the Dubois monument; see Figure 2b; Figures, 6 and 9 [below]). The photographic indication of apparent horizontality matches Kriele's September 1891 sketch showing **LB** outcrops lining both shorelines of the river (see Figure 3b) and KdW's explicit eyewitness accounts about the **LB** being flat-lying in the 25-m and 40-m Trenches (SI II-1, -2, -5, -11, -22, -23).

The annotated 1894 photograph and Dubois' and KdW's written records of 1891–1893 confirm that the geological circumstances at the *P.e.* sites were largely as straightforward as Dubois showed schematically in published representations (see Figure 2a, b).

STRATIGRAPHY, 1895–1900 EXCAVATIONS

After Dubois returned to the Netherlands in mid-1895, he sponsored an expansion of the left-bank excavations. It began modestly in 1895 and ended in 1900 with the largest annual program ever at Trinil (Figure 3a; SI II-114, -121, -135, -144, -153). Dubois relied upon G. Kriele's correspondence and sketch maps for information on the characteristics and provenience of the paleontological finds (addressed in Fossil Discovery Record below; SI II-139 to -154).

As the excavations were coming to an end in November 1900, Dubois had three high-quality, large-format images taken of the left-bank excavation area (see Figures 4b; Figure 5; SI I-5 to -7; SI II-149); de Vos and Aziz 1989). Surveyors spotted the camera stations on mapping that was subsequently used to prepare Dubois' 1900 Site Map (Figure 6a). Because the locations of the camera stations are spotted on the Map and key landscape features are visible in multiple photographs, the photographic fields of view for the three images have been determined, as have the locations of three scaled poles staked into the spoil pile (P1-P3), positioned to indicate where the buried *Pithecanthropus erectus* find spots occurred beneath spoils. However, the poles were one of several errant attempts made to relocate the find spots within the 1891–1900 area of Dubois' excavations (SI I-7). In 1932, fossils of three more fragmentary femurs were recognized in material Dubois attributed to the 1900 Trench, as is addressed in the Fossil Discovery Record below.

Dubois apparently did not write down the insights he gained from the 1900 photographs, but they are eminently interpretable geologically (Huffman et al. 2015, 2018). The sequence evident in 1900 had the same stratigraphic order and horizontal attitude as is visible in the 1894 image, even though nearly two-thousand square meters of the former embankment had been excavated away between the 1893 40-m Trench and 1900 Trench backwalls (see Figures 3a and 4; SI I-7; SI II-153, -155). The lithofacies exposed appear to range from mudstone to conglomerate and diamicton, and seemingly reflect varied depositional conditions, even within individual stratal units (SI I-4 to -6).

The eastern end of the 1900 Trench (de Vos and Aziz 1989) produced an excavated prominence that we refer to as 'East Point.' The locale was ~40m east-southeast of the Skullcap Pit, according to Dubois' notes on an 1899 map (see Figure 3a; SI II-135). The beds exposed at East Point provide the best stratigraphic tie between the 1894 and 1900 photographs (Huffman et al. 2015, 2018). Units **1-5** lie at approximately the same elevation relative to low water level seen in the images.

Unit **3** is clearest in revealing this site-wide stratigraphic continuity and structural attitude. Unit **3** at East Point is seen to have had little- or no-dip on approximately orthogonal excavation faces (see Figure 4b; SI I-5). Horizontality is also clear in another 1900 photograph taken looking south from across the Solo River (see Figure 5; SI I-7a camera station III). That the strata stood in near-vertical walls across ~100m of the excavation is a testament to the cohesion of the sedimentary deposits, if not their lithification. The contact between unit **5** and terrace soil **S** occurs at lower elevation at East Point than this boundary does in the western 1900 Trench (see Figure 4b), apparently due to a shallower depth of erosion on the west during the formation of the terrace surface.

In the western 1900 Trench (and in Selenka Pit II), a stratigraphic unit **6** overlays an erosional surface cut into **2–5** (see Figures 4b and 5; Figure 7). Unit **6** has prominent large-scale internal bed sets that backfill and overstep its erosional base. The upper portion of **6** is truncated at the soil **S** along the terrace upland, seeming to reflect an origin for the terrace surface by erosion rather than substantial fluvial accumulation. The upland rose in elevation southeastward to >12.5m above the river at low level and reached a height of ~20m above low water farther from the 1900 Trench (e.g., higher terrace in SI I-3b). A bar-form feature, apparently a terrace deposit (**TD**), is visible above **6** in the 1900 images (see Figures 4 and 5).

In toto, the 1894 and 1900 photographs show that the embankment removed by excavation in 1895–1900 contained a uniform, indurated, essentially flat-lying stratigraphic sequence (units **1–5**) that included a younger unit **6** in the western 1900 Trench (see Figures 4 and 5).

STRATIGRAPHY, 1907–1908 SELENKA EXCAVATIONS

The Selenka Trinil Expedition photographs and firsthand accounts confirm the persistence of a vertebrate-fossil concentration in a stratigraphic position that lies near the seasonal low-river level of the Solo (see Tables 1 and 2) and extends underneath the same eight-to-nine-meter-thick sequence that Dubois' 1900 Trench had penetrated (see Figure 7; Figure 8).

W.F.F. Oppenoorth, the Expedition's supervising field geologist in 1907, reported that *"the bonebed … washed free"* at the end of April (SI II-247). The top of the stratum was visible above low-river level in late May near East Point, where the fossil concentration was collected and documented photographically (SI I-8a and 9; SI II-251; Oppenoorth 1911: xxxi, xxxiii and Figure 20, xxxiv; Berkhout and Huffman 2021: 31–38). Oppenoorth (1908a, b, 1911)

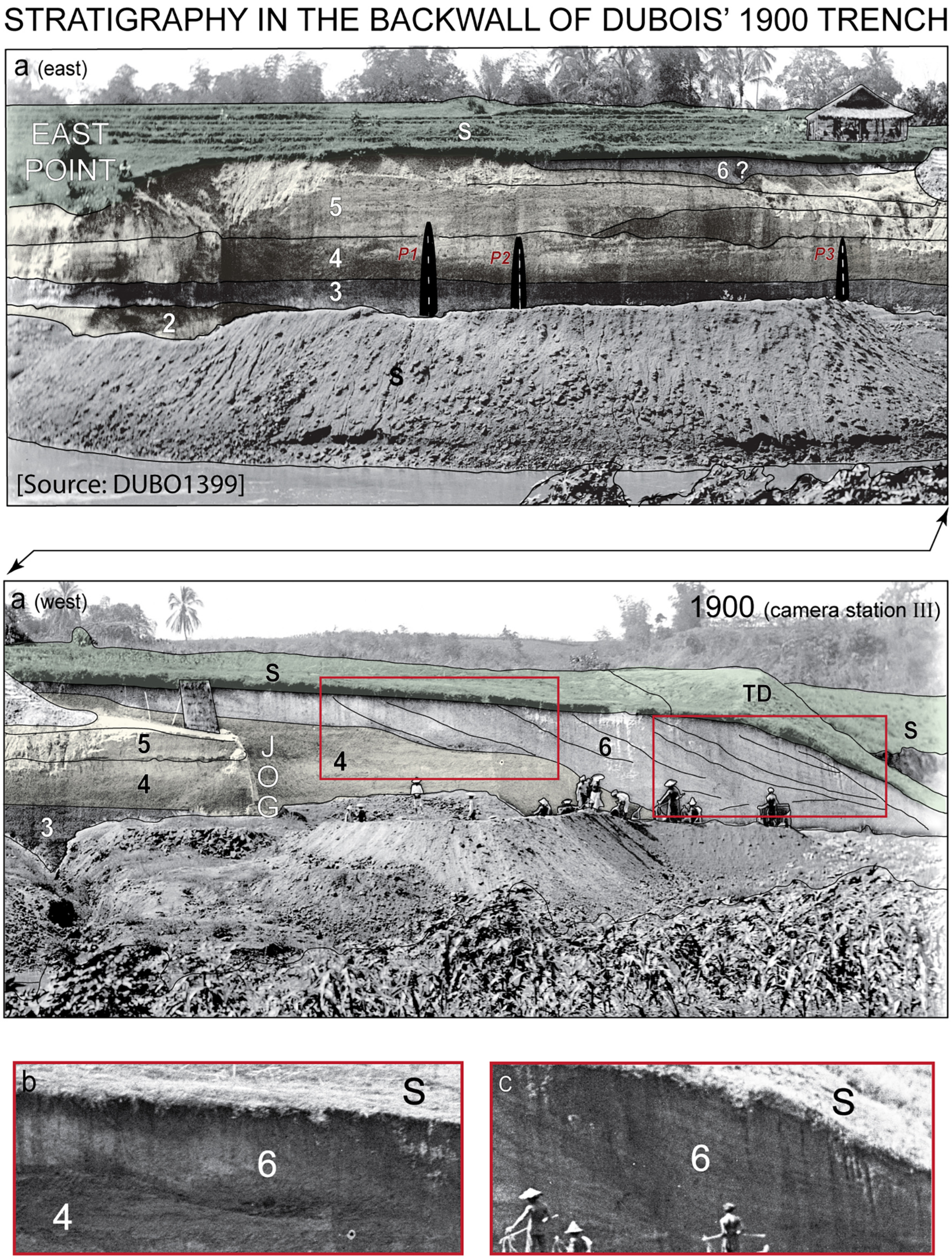


*Figure 5. (**a**) A second November 1900 image of Dubois' 1900 Trench confirms the lateral continuity and approximate flat-lying structural attitude of units **2**–**5**, as well as their stratal relationship to the terrace surface on which the soil **S** developed (after Huffman et al. 2015). Portions of unit **5** had collapsed during excavation near East Point and the JOG. In the western parts of the Trench, a stratigraphic unit exhibiting foreset bedforms (our unit **6**) is seen to overlie an erosional surface cut into **2**–**5** (highlighted in Figure sections **b** and **c**). The Selenka Pit II also encountered unit **6** (see Figure 7a), and a remnant of it was still present in 1926 (see Figure 9). An apparent young bar-form feature, seemingly a terrace deposit (**TD**), is visible above unit **6** in the westernmost part of the 1900 image. The photograph looks South and was taken along a sight line perpendicular to the ~100m long dimension of the 1900 Trench from camera station III in Figure 6a (SI I-7a shows the full field of view of the image).*

took many other useful images of the left-bank from boats and the opposite shore, and geologically significant photographs have not been published before now (Berkhout and Huffman 2021: 30, 31, 32, 37).

By July, Selenka's crew was digging southward into the 1900 backwall, which was as much as eight-to-nine meters high (SI I-9; Oppenoorth 1911: xiii, xv, xxxii, xxxiv; Berkhout and Huffman 2021: 5, 12, 15, 32, 37). The workmen used *"pickaxes"* to remove the hardened flat-lying strata, just as Dubois' excavators had done in cutting downwards the 25-m and 40-m trenches (see Figure 8b; SI I-9). Units **2–5** are securely recognizable in the 1907 images because they show 1900 backwalls as well as those from 1907.

Emil Carthaus, who assumed Oppenoorth geological duties in August 1907, termed the bone-rich stratum 'Hauptknochenschicht' (**HK**) because it had a much higher concentration of vertebrate fossils than other widespread beds (see Table 2; SI II-248, -249; also SI II-252). In 1908, C.M. Dozy (1911a: xli) located the northern termination of the **HK** in Pit I and another depositional boundary ~200m away at the eastern end of Pit II, where the *"main bone bed had completely pinched out"* against a local paleotopographic prominence formed on the breccia (Berkhout and Huffman 2021: 47). This was the diamicton that Dubois had identified (see Figure 2a). Dozy made important corrections to 1907 drafts of the Expedition's widely known cross-section of the left bank, the *"Idealized Profile … after Carthaus"* (Selenka and Blanckenhorn 1911: 7; also, Branca 1908; Berkhout and Huffman 2021: 63).

Little information is available on the 1908 Pit II. Dozy (1911a: xli) did explain that in 1908 the Expedition *"could not work further to the east …* [or] *towards the south* [into the embankment there because] *the land was privately owned ….* [so that 1908 work largely] *"focused on the right-bank"* Pit I (Berkhout and Huffman 2021: 47). Thus, the **HK** was never seen to pinch out southward by the Selenka geologists and doubtless continues beneath the modern left bank. Dozy's emphasis on Pit I helps account for why only one 1908 photograph of the left bank is known (SI I-8b).

With two seasons of excavations done, Dozy (1911a: xli) reported that survey instruments had *"proven by leveling"* that the **HK** in Pits I and II was at about the same elevation (Berkhout and Huffman 2021: 47), which confirms the horizontality of the **LB** that Kriele had shown to crop out on the right- and left-banks in 1891 (see Figure 3b). Dozy concluded that the **HK** was a thin sedimentary lens that filled a paleotopographic low at the top of a sequence of diamictons (later included in the Pucangan Formation by Duyfjes 1936, translated in Huffman 2020).

The **HK** in Pits I and II were also closely comparable in (i) stratigraphic thickness (<1m), (ii) lithofacies (sandy and conglomeratic), (iii) degree of consolidation (lithified and indurated), and (iv) abundance of large-sized vertebrate bioclasts, according to Selenka Expedition accounts (Selenka and Blanckenhorn 1911; Berkhout and Huffman 2021). The similarities support the inference that the **HK** across the Trinil site was a single bioclast-rich depositional unit. None of the fossils Selenka found at Trinil were attributable to *Pithecanthropus erectus*.

The **HK** finds from Pits I and II represent much the same set of species but their numbers in the two excavations differ in taxonomic proportions and vertebrate-bioclasts density (see Table 2). The Selenka assemblages in the Museum für Naturkunde, Berlin, exhibit the same uniform stony fossilization and taphonomic parameters as is seen in the Dubois Collection at Naturalis (L. C. Todd, personal communication, 2015; also, Hill et al. 2015). The collections together represent the vertebrate fossil recovery from the entire span of left- and right-bank excavations from 1891 to 1908 (see Table 1).

The Selenka Expedition documented vertebrate-fossil concentrations above the **HK** at two stratigraphic positions (see Table 2). The upper one was unearthed soon after excavation of left-bank Pit II began in 1907 and the field crew encountered a cluster of vertebrate fossils ~5m above the **HK**. This deposit, the *Stegodon* bed (SB), is in the lower part of our photographic unit **5** (see Figure 8; SI I-9 to -10; Oppenoorth 1911: xxxii; Berkhout and Huffman 2021: 34).

The SB overwhelmingly consisted of the disarticulated and dispersed elements of a *Stegodon trigonocephalus* individual embedded in a clayey conglomerate with some crocodile and 'fish?' remains indicative of aqueous deposition (see Table 2; S I-10). The SB apparently formed when *Stegodon* bones accumulated locally in an erosional swale cut into an unconsolidated unit **4**. No fossil concentrations are known to have occurred in the ~4m of deposits and soil above the SB.

The 1894–1907 photographs of the left bank reveal other sedimentary features suggesting that deposition of units **2**-**5** was dominated by fluvial processes. For example, unit **4** contained inclined bedding and had a truncated top, features which are reminiscent of migrating river bars; and the **4–5** contact exhibited soft-sediment deformation (as did other **2–5** stratigraphic levels), which is consistent with accumulation on uncompacted substrates in a river valley (SI I-3 to -6).

Similar features were evident in the excavated walls of Selenka right-bank Pit I (SI I-11b). To the south of Pit I, the bluff reaches ~16m above low water level and the terraced upland stands significantly higher than did the terrace south of Pit II (see Figures 6b, 6c; SI I 7a). Dubois and the Selenka field teams could see prominent natural outcrops in the bluff (SI I-14) but did not describe the portion of the right-bank stratigraphic section that was higher in elevation than the terrace surface on the left bank (Selenka and Blanckenhorn 1911; also, Huffman 2016, and Widiasmoro and Boedhisampurno 2001).

The Selenka Expedition evidently could not settle on a stratigraphic correlation for the post-**HK** sequences in the two excavations. In 1907, the Expedition chose separate numbering schemes for stratigraphic units in Pits I and II (see Table 2; Selenka and Blanckenhorn 1911). Moreover, a *"blue-grey ash with … intercalated clay …* [and] *thin beds* [lenses] *… formed of leaf remnants"* (the Main leaf bed) occurred between ~0.35m and ~4.10m above the **HK** in Pit I, but this facies was rarely identified in Pit II (Berkhout and

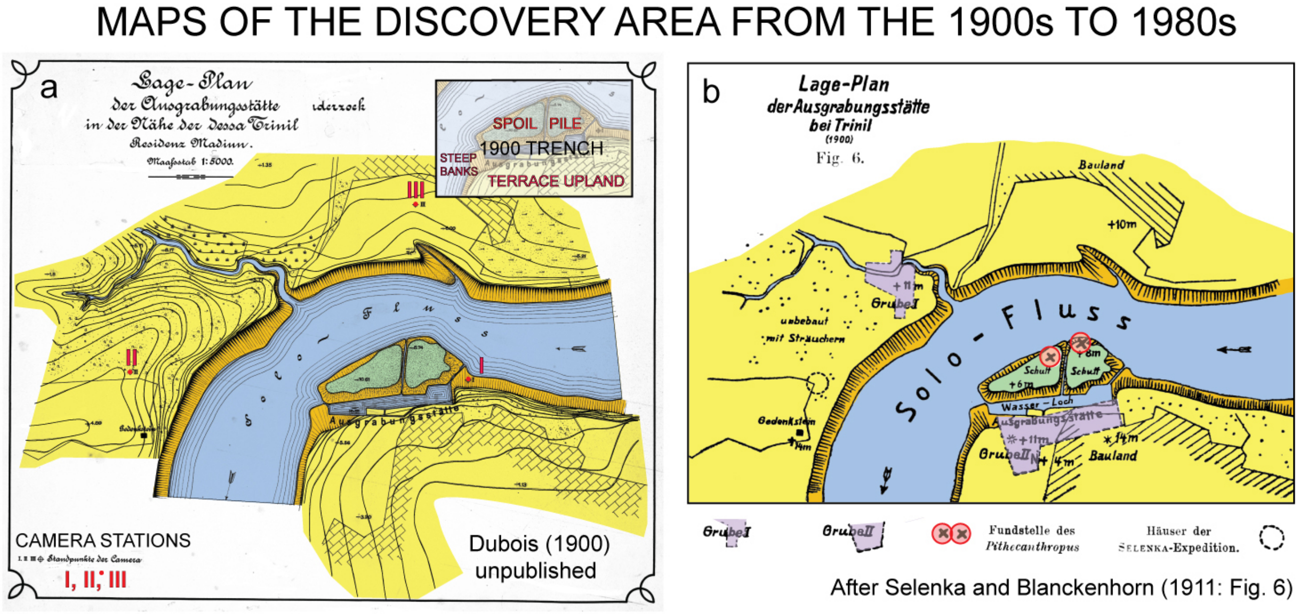


Figure 6. Maps and a satellite imagery of the Pithecanthropus erectus *discovery area (north is up; after Huffman et al. 2015, 2018). (**a**) Dubois' 1900 Site Map shows a partially inundated 1900 Trench lying between a spoil pile and terrace upland (highlighted in the inset; the map is colorized and annotated from SI II-222). The piles buried the **LB** in the vicinity of the 1891–1893 pits and trenches under more than four meters of excavation spoils (SI II-143). The upland south of the Trench is defined by 1m contours. They show the terrace surface rising to an elevation of >12.5m above the river at low-water level and reaching ~20m farther away (e.g., the higher terrace in SI I-3c; also, SI I-16).). The camera stations for three 1900 photographs are indicated (see Figures 4b and 5; SI I-7a shows the field of views of the images). Dubois Collection prints of the map have scale indications that reflect their intended sizes in reproduction, not the scale of the original mapping. (**b**) The Selenka Trinil Expedition re-use of Dubois' map includes failed attempts to relocate the Skullcap and Femur I findspots (Selenka and Blanckenhorn 1911: xiii, Plate I, Fig. 1 and 2; Berkhout and Huffman 2021). The postulated findspots are separated by a distance that is greater than Dubois reported (SI I-7b). The Selenka map greatly exaggerates the size of their left-bank excavations (Pit II) at the level of the main bone-bearing layer (Hauptknochenschicht, **HK**, see Figure 7b). Unannotated versions of Dubois' 1900 Site Map are in de Vos and Sondaar (1982), Leakey and Slikkerveer (1993), Shipman (2001), and others.*

Huffman 2021: 193; Schuster 1911b: 235; also, Branca 1908; Carthaus 1911a; Dozy 1909, 1911b).

STRATIGRAPHIC WORK, 1920S AND 1930S

1926 Photograph

The Dubois collection has a 1926 image that shows the left-bank *Pithecanthropus erectus* site at a critical point after excavation ended in 1908. The spoils which had covered the discovery site in 1907–1908 were largely gone by 1926, giving geologists exposures of the main bonebed, surrounding the former excavations. The photograph also helps to relate units **1–6** to the rocks cropping out along the south shore today (Figure 9; SI I-18).

Dubois attributed the image to L.J.C. van Es, an Oppenoorth colleague at the Geological Survey of the Netherland Indies (Huffman et al. 2005; 2001b; van Gorsel 2022d). Van Es (1927, 1929, 1931) was making the first proper geological map of the Trinil area (Berkhout and Huffman 2020).

The 1926 photograph makes at least four key contributions to understanding the geology of the left-bank site. First, in annotating a print of the 1926 image, Dubois added an ink dot at the gravelly bank north of the left-bank baulks and trenches (SI I-3d). The 1894 and 1926 images can be overlain precisely because numerous landscape features have the same spatial relationships in the two photographs (see Figure 9a, inset). In combination the images allow the location of the camera stations to be contextualized relative to the topographic features of the Trinil area (see Figure 6). The 1926 photographer stood at nearly the same high point on the right-bank that the camera stood in 1894, this being at or near the Dubois monument and the present-day Trinil museum (SI I-7a; SI II-42).

Once the two images are superimposed, Dubois' ink dot coincides with the Skullcap discovery point that he marked on the 1894 image (see Figure 9b). The ink dot apparently records Dubois' successful effort to situate the *Pithecanthropus erectus* discovery into the landscape visible on the left bank 35 years after he last visited Trinil.

Second, the 1926 photograph shows that van Es had extraordinarily good outcrops on which to map the left bank geologically. As he understood the stratigraphy, a vertebrate-bearing sandstone unit rested on a black-clay map unit, which in turn overlay a boulder-tuff (volcanic

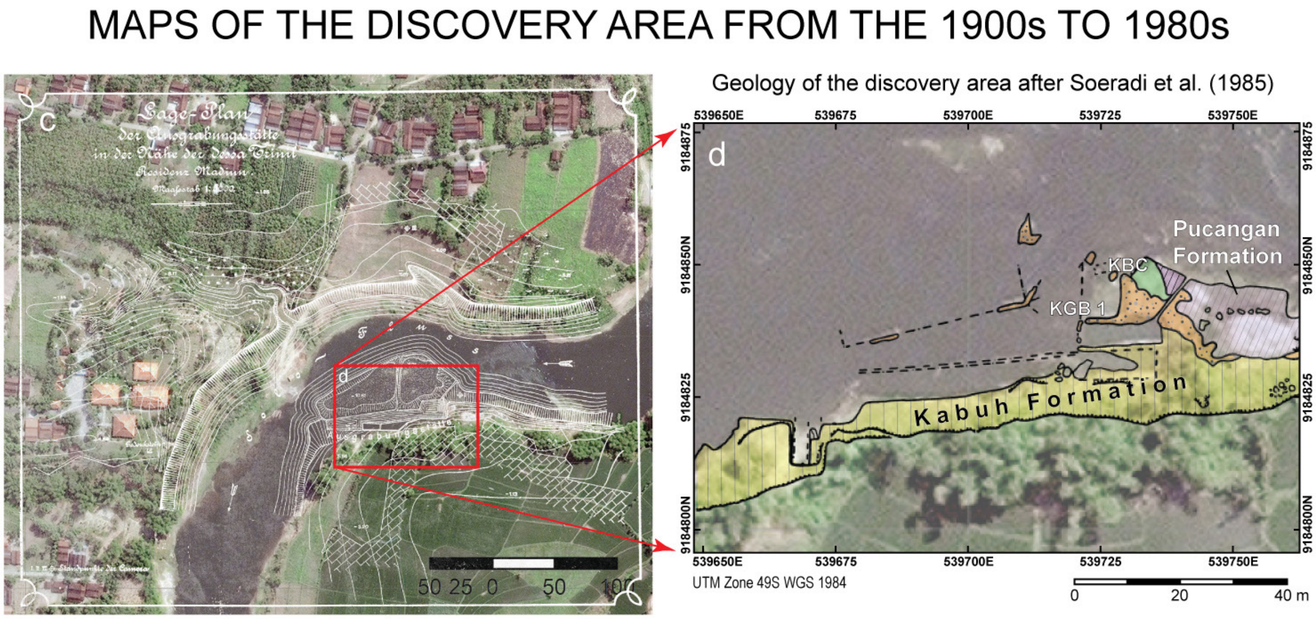


Figure 6 continued. (**c**) *The 1900 Site Map (white lines) is superimposed approximately on an ortho-rectified satellite image (after Huffman 2016; Huffman et al. 2018, using WGS_1984_UTM_zone_49S purchased in 2013).* (**d**) *1:250 geological mapping of Soeradi et al. (1985) is adjusted to fit onto the image (SI I-18). The Soeradi team mapped outcrops of the main bonebed (KBG 1) near the 1891–1908 excavations and recognized that the strata thereabouts were the Kabuh and Pucangan Formations of Duyfjes (1936; also, Datun et al. 1992; Huffman 2016, 2020; I.J.J.S.T. 1992; SI I-19). The KBG 1 and KBC pinch out eastward against the Pucangan (SI I-18b). The large outcrop of KBG 1 and KBC comprises the low-water bedrock platform mentioned in the Introduction.*

diamicton) unit, much like Dubois reported (see Figure 2a). Van Es saw the sequence as dipping southward. He did not recognize a terrace-deposit unit atop the dipping strata.

Van Es was widely experienced as a geologist in the late 1920s (van Gorsel 2022f). By the time he published his final map of Trinil, he (1931) had mapped much of the Kendeng Hills geologically, improving on the work of Verbeek and Fennema (1896) who were preparing a comprehensive geological map of Java during Dubois' time there (van Gorsel 2022g, h). Dubois had exchanged geological ideas with Verbeek, and in doing so, showed a perceptive understanding of the stratigraphy of the Kendeng Hills and related sedimentary processes (S II-212 to -215).

Third, the 1926 photograph permits additional geological interpretation of Trinil. Erosion-resistant **LB**-**HK** was exposed then just above low water, and blocky outcrops of indurated rock underlay the riverbank where we project units **2**–**5** to occur (see Figure 9b). The rocky nature of the baulks and outcrops visible in 1926 convincingly support the inference, drawn from older site photographs and first-hand accounts, that the strata removed by excavation along the left bank were well lithified. Units **2**–**5** cannot be identified individually from the image, since by 1926, the former high-standing excavation faces of 1900–1907 had been reduced to irregular river-bank outcrops.

Fourth, unit **6** is seen in 1926 to form a prominent remnant near low-water level in the far southwest of the former excavation area. By contrast, cross-bedded strata attributable to unit **6** are not discernible near low-water river elevations where the 1899 Trench was dug (see Figure 9b). This is consistent with the Dubois' archival records wherein the **LB**-**HK** was encountered west of Femur I discovery point in the 25-m Trench, 40-m Trench, 1896 Left-bank Pit, and 1897 Downstream Pit (for 1896 and 1897, see, SI II-84, -91 to -93, -101, -107, -109 to -114). There is no reason to suspect that unit **6** occurred close to the **LB** level in the 1892–1893 pits and trenches.

1930s Excavation and Mapping

In 1931–1932, the Survey conducted excavations at Trinil (von Koenigswald 1934/1935, 1956; also, van Gorsel 2022i). An Oppenoorth photograph shows a Survey dig on the right bank (SI I-15). Large-scale trenching was evidently not re-initiated on the left bank then, so that the Dubois' 1900 Trench and Selenka Pit II has bordered the left shore of the Solo since 1908 (see Figure 9; SI I-2, -18). In May and June 1933, the Survey charged geologist J. Duyfjes (1933, 1936) with the task of tying the geology of the greater Trinil area into a regional lithostratigraphic framework that he and Survey colleagues, such as van Es, had developed for the Kendeng Hills (SI I-16, -17; also, Huffman 2020).

Duyfjes (1936: 147) attributed the strata on the left bank near the *Pithecanthropus erectus* site to his self-defined, widely mapped Kabuh Formation. The main bonebed was placed near the base of the Formation, and the Kabuh section there was capped by soil (SI I-17b). Duyfjes' mapping is consistent with Dubois cross section in this regard (see Figure 2a). Over a broader area around Trinil, Duyfjes

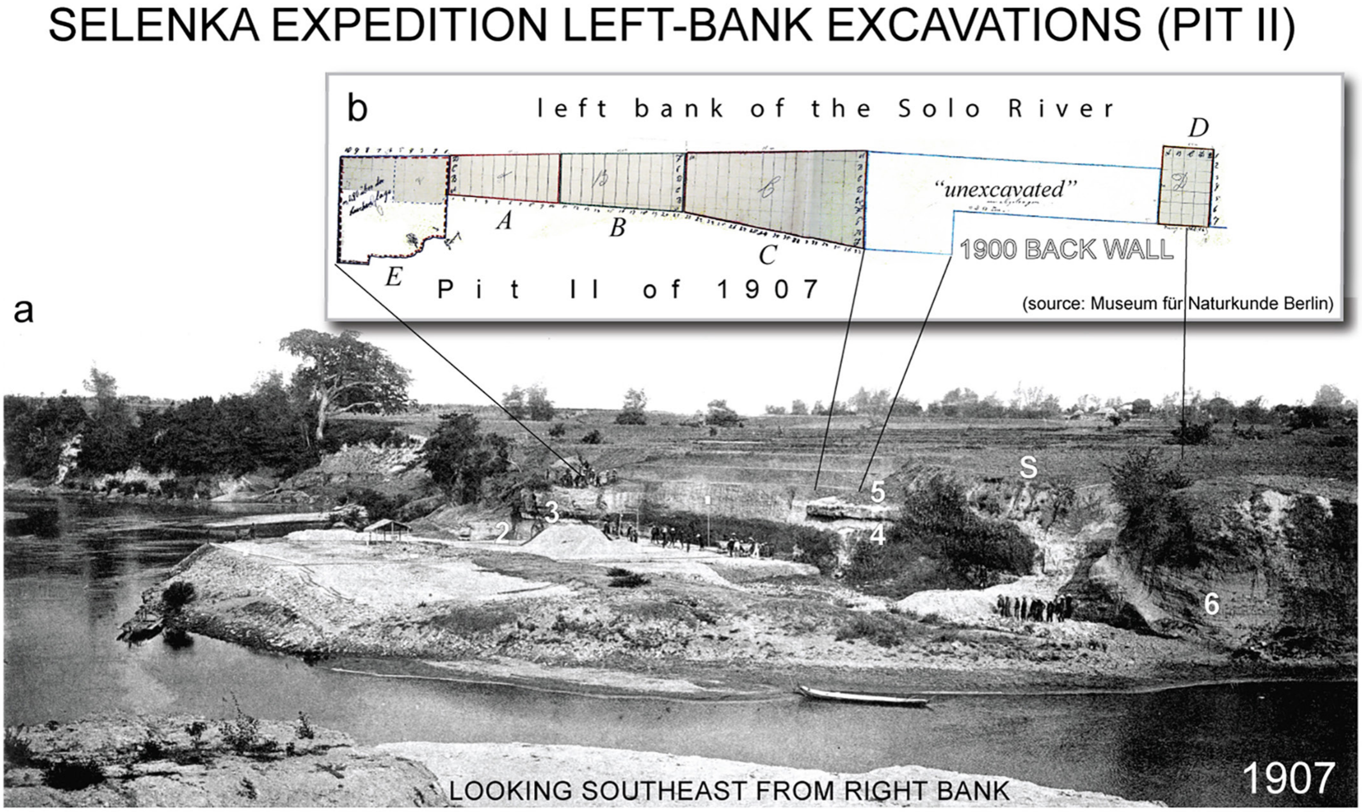


*Figure 7. (**a**) An August 1907 photograph and (**b**) excavation plat of the Selenka Expedition 1907 Pit II. It was started near the "East Point," then dug into the 1900 Trench backwalls, and was expanded in 1908. Today, Pit II and Dubois' 1900 Trench lie adjacent to the bank of the Solo River at seasonal low-water levels (see Figure 9b; SI I-2). Selenka's team encountered the Hauptknochenschicht (**HK**) near low-water beneath our units **2–5** (the **HK** is not seen in this photograph). The plat shows the 1m excavation units used when unearthing the **HK** (Oppenoorth 1908a; SI II-245). The erosional base of our unit **6** reached river level at the west end of the Pit (also, SI I-11a). The Selenka team could not see the **LB** around 1891–1893* Pithecanthropus erectus *discovery site because spoils deeply covered it (see Figure 6a). The photograph was taken from a station on the high bank near Selenka Pit I (see Figure 6b; SI I-7a). The 'a' image includes most of the photograph published by Selenka and Blanckenhorn (1911: Fig. 2; also, Selenka and Blanckenhorn 1911: Fig. 1, 8; and Oppenoorth 1911: Fig. 17, 18 and 19; Berkhout and Huffman 2021). The 'b' map is an image (PM_B_IX_148.tif) of an original drawing provided courtesy of the Museum für Naturkunde, Berlin (MNB).*

mapped substantial thicknesses of both flat-lying terrace deposits and tilted bedrock formations, the latter of which included the Kabuh Formation (SI I-16).

Duyfjes (1933: 13) characterized the Kabuh in the area as *"primarily … andesitic sandstones and tuff sandstones…* [which] *mostly contain clearly rounded grains and often show some crossbedding. …* [The sandstones] *sometimes alternate with conglomeratic beds …* [and] *ash tuff….* [and] *often contain fossil bones and fresh water mollusks,"* reflecting fluvial transport and deposition and subsequent lithification of the deposits (Berkhout and Huffman 2020: 9). Duyfjes attributed diamictons underlying the Kabuh to his Pucangan Formation (this evidently included Dubois' "breccia" unit, see Figure 2a, and van Es' "boulder tuff" of 1931). The larger clasts in the Pucangan were embedded in very poorly sorted sedimentary matrix typical of lahar deposits originating on volcanoes in eastern Java (see Figure 1b).

By the time of Duyfjes' mapping at Trinil in 1933, he had observed and mapped outcrops of the structurally folded Kabuh and Pucangan Formations, as well as older carbonate-bearing and younger volcaniclastic formations, along the southern Kendeng Hills for an east-west distance of ~175km (see Figures 1b and 13 [below]). His mapping extended from a point ~7km west of Trinil through the Kedungbrubus *P.e.* site where Dubois' first *Homo erectus* originated in 1890 (SI I-36, -39, -41 to -42) and Perning site where the fossilized Mojokerto child's skull was unearthed in 1936, and continued to the shores of Madura Strait (see Figure 13 below; SI I-43; Duyfjes 1933, 1934, 1935, 1936, 1938a-d; also, van Es 1931; Huffman 2001b, 2016, 2020, and Huffman et al. 2005; also, van Gorsel 2022c, d, e, and f).

Based largely on Duyfjes' field results, the acknowledged stratigraphic sequence in the greater Trinil area became (from older to younger) the Kalibeng Formation, Pucangan Formation, Kabuh Formation and Notopuro Formation, all of which are unconformably overlain by terrace materials along the Solo River valley (SI I-19, -35).

1977 MAPPING

A detailed geological re-study of the left bank was conduct-

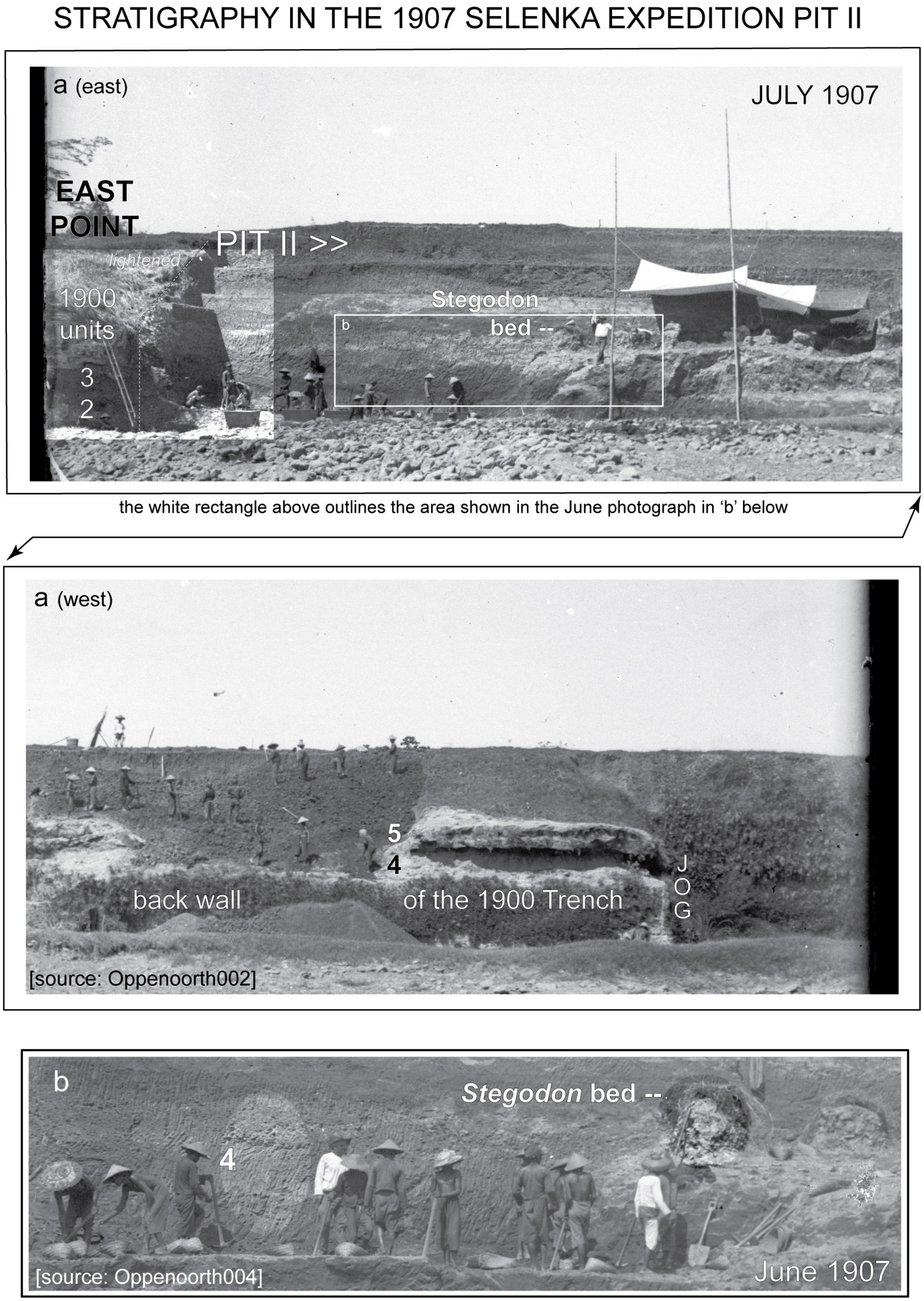


*Figure 8. Selenka Expedition geologist W.F.F. Oppenoorth photographed the left bank multiple times (this view is looking south, like the one in Figure 5). The fossils dug from Pit II originated from points just a few meters away from the modern south shore of the river (see Figure 7b). (***a**, **east***) Later in July, the Selenka crew exposed the Hauptknochenschicht (***HK***) in the easternmost Pit II (left in the image). Farther west, the dig was still at a stratigraphic level ~5m higher (our basal unit* **5***) where the elements of a* Stegodon trigonocephalus *skeleton lie covered in straw on pedestals (Stegodon bed,* **SB***; SI I-9, -10). (***a**, **west***) West of the* **SB***, units* **4** *and basal* **5** *were still visible in the 1900 backwall. (***b***) An enlarged portion of a June photograph of eastern Pit II shows the excavators using pickaxes to penetrate units* **4** *and* **5** *where the backwall also has pick scars (highlighted by the lighter oval; also, SI I-9).*

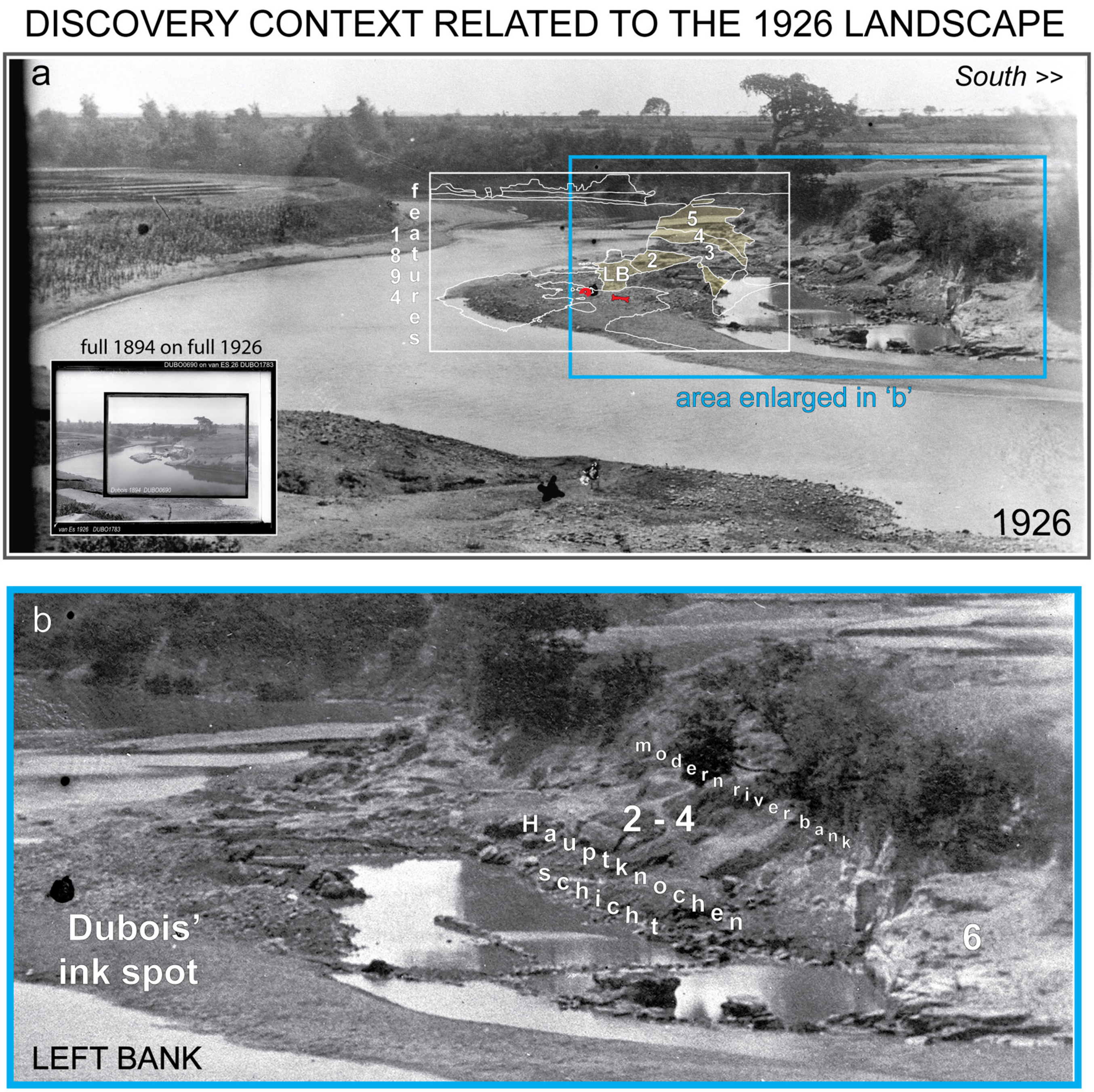


*Figure 9. (**a**) The stratigraphic features of the* Pithecanthropus erectus *(*P.e.*) site as we interpret them from the 1894 photograph (see Figure 4a) are superimposed as white outlines on a 1926 site photograph, which was taken from near the 1894 camera station high on the right-bank, which was at or near the Dubois monument (the two images are superimposed as the inset illustrates). The archive's print of the 1926 image is annotated in Dubois' handwriting and includes an ink dot. Once the 1894 is superimposed, the dot is found to coincide with the Skullcap discovery point from the 1894 image (see Figure 3c; SI I-3d). (**b**) An enlarged portion of 'a' highlights indurated baulks and river-margin outcrops of the flat-lying main bonebed and units **2** to **4**. A cross-bedded remnant of our unit **6** is still visible on the far west, but no **6** is seen at low-river level closer to the* P.e. *discovery area. The 1926 photograph indicates that the spoils that covered the discovery area in 1900–1907 (see Figure 7) were gone by 1926, giving geologists a better opportunity to examine the main bonebed in the baulks of former excavations. When the left bank was analyzed geologically in 1977, the main bonebed unit was mapped as unit KBG 1 (see Figure 6d; SI I-18). The source for the 1926 image is a 2014 Naturalis scan (DUBO1783).*

ed in 1976–1977 as part of the comprehensive Indonesian-Japanese project "Quaternary Geology of the Hominid Fossil Bearing Formations in Java…." (Watanabe and Kadar 1985). The 1976–1977 project personnel had the benefit of investigating *Homo erectus*-bearing formations from Sangiran Dome to Perning. The fieldwork at Trinil was done when the level of the Solo River was low enough to expose a platform-like outcrop lying east of the Dubois excavations and baulks and outcrops situated as much as ~30m north of the left bank (see Figure 6d; SI I-2, -7, -18). The mapping team stated, *"the* Pithecanthropus erectus *I of Dubois (1894) was confirmed to have been unearthed from the gravel bed located at the base of the Kabuh Formation* [of Duyfjes 1936]*."* The Kabuh overlies the Pucangan Formation in the platform (I.J.R.C.P. 1979; Soeradi et al. 1985: 50). The gravel bed is the KBG 1 mapping unit mentioned in our Introduction. The strata in the vicinity are horizontal. No terrace deposits were recognized. A narrow notch that cut into the embankment of Kabuh Formation to the far west is the westernmost Selenka Expedition Pit II (portion 'D,' see Figure 7b). A trench adjacent to the riverbank farther east contained displaced blocks like those seen in the 1926 photograph. Experienced field teams after the 1976–1977 effort concurred with placing the post-**HK** beds in Duyfjes' Kabuh Formation, presumably having given weight to how the lithification of strata on the left bank corresponds to the induration of folded Kabuh and Pucangan sandstones and mudstones elsewhere in the Kendeng Hills (e.g., SI I-19).

TERRACE DEPOSITS AT TRINIL

Terrace deposits complicate mapping the stratigraphy along the Solo River valley near Trinil, leading to proposals that a substantial thickness of terrace deposits occurred in Dubois' left-bank excavations. G.-J. Bartstra (1982, 1983) postulated that the excavations penetrated both the Kabuh Formation and terrace deposits, and hence the Dubois Collection from Trinil contained a mixture of older and later Quaternary specimens. Bartstra provided neither field observations near the *Pithecanthropus erectus* discovery site nor paleontological data supporting his proposals (SI I-35). Since Duyfjes' day, as Bartstra correctly stressed, terrace deposits have been known to overlie the Kabuh and other bedrock formations in the greater Trinil area (Duyfjes 1933, 1936; Lehmann 1936; Oppenoorth 1936; also, Huffman 2016; Berkhout and Huffman 2020). Berghuis et al. (2021) revived Bartstra's idea that strata in the left-bank near the discovery site include Late Pleistocene terrace deposits. Field evidence at the site was not presented by Berghuis et al. (SI I-35), and their inferred geological age conflicts with paleontological data from museum collections of Trinil fossils (described below).

GEOLOGICAL SUMMARY

Roughly two-thousand square meters of the left bank were removed in 1891–1908 for the purpose of extracting fossils from the *Pithecanthropus erectus* (*P.e.*) bonebed near the seasonal low-water level of the Solo River. Photographs (1894–1926), eyewitness excavation accounts, and later geological investigations generally establish that eight-to-nine meters of strata formed in a single, essentially flat-lying and mostly well-indurated (bedrock) sequence lying between the bonebed and soil near the surface of the terraced embankment.

In 1891–1893, Dubois and his field supervisors recorded the placement of vertebrate fossils in the Lapilli bed (**LB**) excavated over ~200m^2 on the left-bank (a tenth of the estimated total left-bank excavated area). The **LB** had an internal bioclast concentration, our Principal Fossil Zone (**PFZ**), which was the reported source of the *Pithecanthropus erectus* finds (see Figures 2 and 3). The Selenka Expedition applied the name Hauptknochenschicht (**HK**) to the fossil-rich bed in their ~370m^2 1907–1908 left-bank Pit II, which was situated several-tens of meters away from Dubois' hominin discovery points and lies beneath the modern south bank of the Solo River in the vicinity.

Only sparse geological information is available on the lithology of the **LB-HK** bonebed where it was encountered in the large intervening 1895–1900 excavation area. These excavations were conducted by Dubois' field supervisor G. Kriele who could relate the stratigraphy then to that from 1891–1893. In addition to Kriele's letters and maps, Dubois had access to information on the **LB-HK** from the nature of the fossils received and sedimentary rock encasing them.

Today, site photographs dating to 1894, 1900, and 1907 allow for the recognition of stratal units within the sedimentary sequence overlying the main bonebed. Our units **2–5** occur at about the same elevation across two-thousand square meter 1895–1907 excavation area and doubtless underlie the present-day left bank (see Figures 3 to 5, 7, and 8; SI I-3 to -6, -8, -9, -12). A soil is seen to have developed on unit **5** at the terrace surface atop the incised river embankment (e.g., see Figure 4; SI I-4, -5), much as Dubois' site cross sections portray (see Figure 2a). Units **2–5** had relatively few vertebrate fossils but the basal part of unit **5**, ~5m above the **HK**, contained the localized *Stegodon* bed (**SB**). The *Stegodon* individual at this level had a larger body size than those specimens attributable to the main bonebed (van den Bergh 1999, personal communication, 2022).

The upper portion of the photographically defined sequence contains a unit **6** in the western parts of the Dubois 1900 Trench and Selenka Pit II, where **6** rests on units **2** through **5** across an erosional surface (see Figures 4, 5, and 7; SI I-11a). Unit **6** is not known to have been fossiliferous. It is not seen near the **LB** level in the 1891–1893 excavation area, judging from the 1926 photograph (see Figure 9) and firsthand accounts that place the **LB** in the 40-m Trench and the **LB-HK** in the 1896–1900 excavations between this Trench and the known occurrences of unit **6**.

From 1936 onwards, geologists have attributed the left-bank excavation remnants to the bedrock Kabuh and Pucangan Formations, and this was the case in 1977 when a detailed geological map of the left bank was produced (see Figure 6d; SI I-16 to -19). The alternate suggestion in the literature that Solo River valley fill makes up some or all of the rock volume excavated along the left bank in 1891–1908 lacks critical supporting evidence, such as field observations of terrace deposits at or adjacent to Dubois' 1891–1893 *Pithecanthropus erectus* discovery excavations and paleontological evidence of mixed taphonomic assemblages in museum collections from Trinil.

FOSSIL DISCOVERY RECORD

Dubois' and Selenka's photographs, maps, and firsthand accounts, which prove useful in elucidating the site geology also record the nature of the large vertebrate fossils found in the main bonebed (**LB**, **LB-HK**, and **HK**). Many of the finds can be identified as particular species by making use of information in Dubois (1908), Selenka and Blanckenhorn (1911), and later paleontological works. Tables 1 to 3 present summaries.

1891–1894 FINDS

When Dubois saw Trinil on September 6–7, 1891, he considered the site to be his *"best find of all"* (SI II-171; also, SI II-160, -168, -227). He was an experienced fossil hunter by then. He had mapped the central Sumatra highlands geologically during 1888 to locate fossiliferous caves, one of which now is significant for being the source of 63–73 ka Anatomically Modern Human remains (Albers et al. in review; de Vos 1983; Dubois 1888, 1892a; Duval et al. 2021; Louys et al 2022, in review; Westaway et al. 2017). Starting in May 1890, Dubois conducted a pioneering geological and paleontological reconnaissance of the vertebrate-bearing deposits of eastern Java, investigating both cave deposits near the southern coast of Java and fossiliferous volcaniclastic bedrock formations in Kendeng Hills (see Figure 1b; e.g., Dubois 1892a; SI II-166; also, SI II-158 to -162, -211, and Aziz and de Vos 1989). His efforts in the Kendeng Hills produced a partial *Homo erectus* mandible in November 1890 (SI I-36; S II-164, -165). Dubois could reasonably express high praise for Trinil because the site offered the opportunity to excavate a single well-lithified deposit containing large fossils representing multiple extinct vertebrate species that he already had recognized in the geological formations cropping out in the Hills (Dubois 1892a; SI II-166).

September 1891 (Skullcap Pit)

G. Kriele began excavating the **LB** along the left bank about September 1, 1891 (see Figure 3b; SI II-1). He was a military corporal assigned by the government to assist Dubois. He described the work that month at the Trinil site as follows: The *"exposed dry shallow sandstone ledges in the riverbed were excavated below water level on both sides"* of the Solo River; the *"bone remains* [were] *about 0.20 meters below"* the outcrop surface (SI II-170, -171). Dubois summoned A. de Winter, his second military assistant, to come from Patiayam (see Figure 1b; SI I-47) and collect from the **LB** cropping out along the right shoreline at Trinil (see Figure 3b; SI II-170).

On September 3, before Dubois returned to Trinil himself on September 6–7, the left-bank **LB** produced specimens now attributable to *Bubalus palaeokerabau*, *Duboisia santeng*, and *Stegodon trigonocephalus* (see Table 1, see Figures 2b and 3a; SI II-1). The fossils were *"found all together"* stratigraphically in *"andesitic sandstone,"* and included deer (*Axis lydekkeri*), turtle and mussel, and *"tree trunks"* and *"leaf imprints;"* the bony elements were *"often fractured"* and disclosed no evidence of human or carnivore activity (SI II-168, -170; also, SI II-171).

On September 18, Kriele sent a sketch map of the ledges showing a *Stegodon* mandible and tusk *in situ* at the Skullcap Pit outcrop on the left bank (see Figure 3b). The fossils transmitted then were *"all either from a depth of around 0.20 m below the water level or even with it"* (SI II-2), as Dubois duly notified the government (SI II-168). The lower parts of the exposed proboscidean mandible in the Skullcap Pit appear to have been at this elevation (see Figure 3b, inset). The hemimandible of a *"fossil cat … about the size of an average royal tiger* [*Panthera tigris*]*"* and specimens of crocodile (*Crocodylus siamensis*) and gharial (*Gavialis bengawanicus*) were in 28 crates of fossils collected in 1891 from both riverside ledges (SI II-171, -175; also, SI II-10, -12).

The **LB** material included in a September shipment with *"a considerable number of* fossils *…* [from] *the two sand*[stone] *ledges"* and contained *"the upper-right third molar … of a chimpanzee"* (1891 Molar), according to the third-quarter report Dubois provided to the government Director of the Department of Education, Religion and Trade, Netherland Indies (SI II-171; also, SI II-170). Dubois is not known to have visited the Molar discovery spot before the surrounding rock was removed.

Skullcap Discovery (October 1891)

Dubois' October 1891 government memorandum reported that *"close to the place where the molar was found in volcanic tuff on the left bank … a magnificent skullcap was excavated* [in Skullcap Pit]*"* (see Figures 2 and 3b; SI II-172; also, SI II-157, -199). The cranial find must have been contained in the one October shipment, transmitted on the eleventh. The Skullcap discovery came about 16 months after Dubois started in Java and six weeks after digging began into the **LB**.

Dubois visited Trinil on October 21–24, but his October memorandum did not describe what he saw in the Skullcap Pit. No extant record contains the date of the Skullcap finding, names of the discoverer(s) and his (their) discovery-day experiences, or other fossil remains or lithologies observed nearby. However, M. Selenka, who interviewed Kriele in 1902 about Trinil (SI II-156) and took de Winter to Java as a field consultant in 1907, understood that both supervisors were *"present during the excavation of the skull"* (Berkhout and Huffman 2021: 5, 13; Selenka and Blanckenhorn 1911: i, xiii).

In 1891, Dubois is not known to have made a map of the Pit or illustrated the context of the Skullcap in profile form. He (1894: 1) did stipulate in his monograph that the 1891 Molar and Skullcap had been found a meter apart (SI II-199; also, see Figure 3a). In 1895, he (1896d: 241) elaborated that the Skullcap and 1891 Molar were discovered *"in the lapilli bed on the left bank* [the **LB** in the Skullcap Pit] *… amidst among hundreds of other skeleton remains"* (SI II-230).

The first public announcement of the Skullcap and molar discoveries appeared in Dubois' Fourth Quarter report, which was drafted January 20, 1892, and published anonymously, as was the government's practice (SI II-176). His unpublished memorandum to government officials concerning October 1891 had stated *"of all known living and fossil anthropoids … the new Java chimpanzee undoubtedly ranks the highest"* in an evolutionary scale (SI II-172; also, SI II-218). He soon wrote to an official that the fossil was *"truly a new and closer link in the largely buried chain connecting us to the 'lower' mammals"* (SI II-174).

Dubois asserted to government sponsors that Trinil *"has become so important to science"* and transformational in anthropology that continued excavation was *"essential;"* he concluded that even though the *"major part"* of the original low-water exposures of *"sandstone-like tuff in the riverbed … had already been excavated,"* the bonebed and its *"well preserved fossils … extends much farther than the* [original] *ledges"* beneath the adjacent embankment (SI II-174 to -176).

Besides *Homo erectus*, the mammalian assemblage of the Skullcap Pit is known from contemporaneous reporting to have included vertebrate fossils attributable to *Axis lydekkeri*, *Bubalus palaeokerabau*, *Duboisia santeng*, *Stegodon trigonocephalus*, and *Hexaprotodon sivajavanicus,* as well as fresh-water Mollusca shells and wood (see Table 1; see Figure 3b; SI II-1 to -4, -168, -227, -230). Recovered were at least two *Stegodon* craniums, one *Duboisia* skull with horns, and one *Axis* skull with antlers (SI II-3; also, SI II-171). Among the recognizable species excavated on the two banks in 1891 (thus potentially present in the Skullcap Pit) were *Bibos palaesondaicus, Crocodylus siamensis, Gavialis bengawanicus, Panthera tigris, Rhinoceros sondaicus, Sus brachygnathus*, and Testudines, as well as the *"fossil wood and imprints of leaves"* (SI II-12, -170, -171, -227, -230).

Femur I Discovery (August 1892)

While uncertainty surrounds the date in August when Femur I was discovered, the archival record contains critical information on its provenience and the actions of the discoverers. In June, Kriele and de Winter (KdW) started *"excavations … into the river bank done from above,"* so that when the dig was deepened and the river dropped *"a large surface area of the fossil-bearing layer"* (**LB**) could be removed in its entirety at about the same time (SI II-178; de Vos and Sondaar 1982). Indeed, the *"harvest of bones"* unearthed from the upper portion of the **LB** during the last days of June included *Axis lydekkeri* remains *"buried here in large numbers"* (SI II-180; also, SI II-178). The excavation was the first segment of the 25-m Trench (see Figure 3a). It also already had produced fossils referable to *Bibos palaesondaicus*, *Duboisia santeng*, and *Stegodon trigonocephalus*, and possibly *Gavialis bengawanicus* and *Sus brachygnathus* (see Table 1; SI II-180, -181).

On September 7, 1892, KdW explained by letter: *"the bone of the chimpanzee* [Femur I] *…. was found on the same side* [of the river] *as the skull*[cap] *and also at approximately the same depth* [elevation as the cranium] *and even with the previous low-water level* [LWL within the **PFZ**], [the Skullcap and Femur I] *separated from each other by about 12 meters"* in the excavations (SI II-23 has a full unannotated translation). The letter was written by Kriele on behalf of the two supervisors, per protocol for their Trinil letters to Dubois (SI II-1 to -43).

KdW's first letter about the find, written on August 31 but delayed in the mail, had been even clearer: *"The bone in question was found on the same side of the river where earlier the chimpanzee was, and if de Winter remembers it correctly the following bones were found nearby: a mandible and tusk of an elephant. The bone was found at approximately the same depth as the chimpanzee skull even with the previous low-water level and separated from it by about 12 meters"* (SI II-22 has the entire letter; also, SI II-182). When the full contents of the two letters are considered together and in context (SI II-22, -23), they reveal the situation within the excavation on the day of discovery and the actions Dubois took after receiving Femur I. We highlight five implications.

First, KdW's August 31 letter states that de Winter recalled *"a mandible and tusk of an elephant* (*Stegodon*)*"* nearby Femur I (SI II-22). The specification that de Winter was the one who remembered the *Stegodon* reflects the fact that he discovered Femur I. In November, KdW affirmed this (SI II-31). Moreover, M. Selenka (1911: xiii, xiv) learned from him that he *"personally dug up the* Pithecanthropus *femur"* (Berkhout and Huffman 2021: 13).

Second, the reporting about the mandible and tusk underscored the paleontological match between the Skullcap Pit and the stratigraphic level of the 25-m Trench where Femur I was found. All three men would have known that the large *Stegodon* fossils fit a **PFZ** provenience. Most plausibly, the tusk lay parallel to the horizontal stratification and the mandible took up nearly the full thickness of the **PFZ**, making these fossils prominent in the field and de Winter's memory. Dubois presumably had identified the mandible and tusk in the shipment of finds he received in August. He would have had a large collection of specimens of known **LB** provenience to compare to the new *Stegodon* material and Femur I. Dubois must have seen Femur I as taphonomically compatible with previous **LB** finds.

Third, the August 31 letter reflects other actions Dubois and KdW took. After examining Femur I, Dubois sought explanation from the men on how certain chips of bone had been lost off the end of the specimen. KdW responded on the 31st: *"About the bone* [Femur I] *de Winter tells me that the pieces that are missing* [from it] *were blown away while on a djati* [teak] *leaf by heavy winds during the process of gluing and we cannot find them again* [right now]*"* (SI II-22). De Winter's recollection about the small missing chips, like the nearby *Stegodon* mandible and tusk, stems from the events he experienced on the day of discovery.

Fourth, high-water prevented access to the discovery excavation so that KdW could not recover the pieces immediately (SI II-22). De Winter must have distinctly remembered the location of the loss and condition of the trench because KdW promised on August 31, *"as soon as the water level subsides* [such] *that we can work on the opposite* [left] *side where the bone* [Femur I] *was found….* [we will be] *searching carefully for the pieces that had been knocked from the bones."* Hence, De Winter's preparation of the specimen must have taken place below an elevation subject to the flooding, most plausibly within or next to the Femur I excavation on the day of discovery.

Finally, by asking KdW about the lost fragments, Dubois divulged that he had examined Femur I closely. The losses were from a hole in the popliteal surface and *foss intercondyloidea* (intercondylar notch) of the posterior epiphysis, losses still notable on the specimen (SI II-241, -242). He (1926a) eventually stated that holes had been *"caused by excavation"* (SI II-241; also, Dubois 1926b; SI II-242). Perhaps he drew this conclusion before writing KdW in August 1892. Dubois also might have had observed by then, as he reported three years after the discovery, that *"the marrow canal has been partly filled with a stony mass,"* which helped make the specimen *"more than twice as heavy as a recent human femur of the same size"* (Dubois 1896e: 3; SI II-231; also, SI II-227 to -229, -241) and substantiated a **LB** provenience.

There is no written record about the nature of the lithic matrix surrounding Femur I when it was *in situ*, or even about the matrix when the fossil was in de Winter's or Dubois' hands, only evidence that preparation of the specimen was essentially completed by the end of 1893 (Dubois 1894, 1895a; SI II-199). The greatest challenge of preparation presumably was cleaning rock around the exostosis, a task which also was complete by then (SI I-1; SI II-242).

Late September to November 1892 (25-m Trench)

As KdW's letters and Dubois' memoranda explained in late 1892, the Femur I discovery excavation was expanded into the embankment south of the find spot, efforts which ultimately created the full 25-m Trench (see Figure 3a). After digging downward from the top of the bank and passing through for eight-to-nine meters of largely hardened volcaniclastic sandstone and other lithofacies with few fossils, the crew again reached the fossil-rich **LB**.

On September 23, 1892, before he is known to have gone to Trinil that month, Dubois reported to the government that the three fossils of the future *Pithecanthropus erectus* originated from one *"level of the sediments"* (**PFZ**; SI II-182; also, SI II-229). He inexplicably started saying that Femur I was 10m from the Skullcap, not KdW's 12m. The day after composing the memorandum, Dubois went to Trinil. He did not report the results of his field checking then, just as he had failed to do after his field examination of the Skullcap discovery place.

Before September 23, Dubois had asked KdW how they might find more parts of the recently discovered Femur I individual. Their response reflects a sharp awareness of the site stratigraphy, and Dubois' approval of their plan and his confidence in their knowledge of the situation on the ground. First, they proposed deepening the pit near the discovery spot, since the **PFZ** had not been fully penetrated and the lower **LB** might be fossiliferous; second, they proposed cutting down the high embankment immediately south of the find spot to expose more **PFZ** (SI II-23).

KdW letters and Dubois government reporting thereafter in 1892 are explicit about the stratigraphy encountered while enlarging the 25-m Trench (also described in Site Geology above). They reported that the upper two-thirds of the eight-to-nine meters above the **LB** was *"a fairly hard sandstone-like andesitic tuff which can only be removed with pickaxes and crow bars"* (SI II-183). By October 28, 1892, KdW wrote, *"the corners* [of the full 25-m Trench] *… progressed to about the depth* [elevation] *at which the leg bone* [Femur I] *and skull* [Skullcap] *were found"* (SI II-29). On November 9, they reported that *"the corners of the trench* [25-m Trench were] *… about 20cm into the target bone layer* [**PFZ**]*"* (SI II-31).

By then, KdW had stopped mentioning the prominent fossils encountered, plausibly because Dubois already knew the paleontology of the upper **LB** well. Importantly, KdW reported being able to follow the Skullcap and Femur I **PFZ** stratigraphic level from a corner near the Skullcap Pit through and beyond the spot in the 25-m Trench where the femur was found (SI II-185). This confirmed the continuity of the **PFZ** across ~50m^2 of excavation (see Figure 3a) and the presence of about nine meters of indurated, generally fossil-poor strata overlying the **LB** (see Figure 3c).

At the end of the season, Dubois had to report to the government that *"rising water … forced us to finally abandon the work on November 16th, after having only excavated about 1/5th of the level of interest* [the **PFZ**]*"* (SI II-185). While the top of the **LB** was exposed along the full length of the 25-m Trench, only 20% of the full **PFZ** and basal **LB** had been removed. Thus, in August 1892 when Femur I was found, the area in which the **PFZ** had been fully excavated appears to have been no more than ten square meters of the final ~50m^2 trench. KdW must have gained confidence in their identification of the **PFZ** at the discovery point from the exposure of the upper **LB** across the twelve meters between the Femur I discovery location and the Skullcap find point, together with the large-sized bioclasts of known species that the modest-sized discovery trench had produced.

Records about three particular 1892 finds support our provenience conclusions about fossil provenience in the 25-m Trench: (i) A macaque tooth which is present in the Dubois Collection has a label, most likely written by Dubois, that reads, *"trench of 25 m of 1892, lowest level, ½ m below pe"* (DC no. 3789; de Vos 1989: 227). The "pe" surely refers to the *Pithecanthropus erectus* stratigraphic level so that the macaque tooth came from below the **PFZ** in the lower **LB**. (ii) A molar of the Asian porcupine *Hystrix lagrelli* was recovered *"at the lowest level"* of the river, according to a label (DC no. 1482a; de Vos and Sondaar 1982: 47, 49; also, SI II-185). (iii) A fourth *Pithecanthropus erectus* (*P.e.*) specimen, the 1892 Molar, was found during October close to the east end of the 25-m Trench (see Figure 2b) *"in exactly the same* [stratigraphic] *plane"* as other *P.e.* remains (**PFZ**; Dubois 1896b, d, e: 3; SI II-186, -227, -230, -231).

1893 (40-m Trench)

The firsthand reporting about the 1893 40-m Trench recounts events that are closely comparable to those of late 1892. Most pertinent here, the accounts again document large fossils in the **LB** (see Table 1) and the indurated poorly fossiliferous nature of the overlying strata.

The 1893 field crew once more proceeded from the terrace tread downward in horizontal increments to an excavation depth of about eleven meters below the terrace upland surface. Dubois' experiences in 1892 motivated him to have the crew remove this *"fossil-poor rock mass as quickly as possible"* to reach *"the deeper … rich bonebed"* (SI II-190). His desire for speed notwithstanding, after removing a soft soil near the top of the 40-m Trench, the excavators encountered strata of *"severe hardness"* (SI II-190). Dubois saw the situation personally.

The laborious removal of beds continued for six-to-eight weeks. KdW wrote that the rock was *"so terribly hard that it is almost impossible to get through,"* and repeated the complaint when digging the *"lower part"* of the sequence (July 7 and 14; SI II-42; also, SI II-40), referring to our units **1** and **2** in the 1894 photograph (see Figures 3c and 4a). Dubois' government memorandum concerning this period stressed the *"relative paucity of fossils"* above the **LB** (SI II-192).

When Dubois visited Trinil on August 17–19, 1893, the crew was poised to greatly expand the horizontal exposure of the **LB**. Part of the 40-m Trench was only a few meters away from the Femur I discovery point (see Figure 3a). Near the end of August, Kriele detailed finding *"1 nice elephant tusk* [*Stegodon trigonocephalus*]*, 1 crocodile skull* [*Crocodylus siamensis*]*, 1 antelope skull* [*Duboisia santeng*]*, 1 turtle* [Testudines]*, a few leg bones, deer antlers* [*Axis lydekkeri*]*, some ribs and vertebrae"* (SI II-44). By September 1, 1893, while excavating the *"target layer"* (**PFZ**), *"rather many bones"* and a lot of *"wood"* and *"shells"* were recovered (SI II-45). The crew found the cranium of *Stegodon* with *"the molars still in it"* (SI II-46). The abundance of **LB** fossils continued through most of September (SI II-48).

Soon, however, coarser, conglomeratic fossil-poor sandstone was evident in the lower **LB** (SI II-51; also, SI II-49). Despite the different lithology in the lower levels, they produced a buffalo cranium (*Bubalus palaesondaicus*) and two craniums of antelope (*Duboisia santeng*; SI II-52). Kriele recommended halting work in this *"the hard coarse* [conglomeratic] *layer ….* [which had] *nothing* [in important fossils]*,"* only a few antlers and isolated finds (SI II-53). Compared to the **PFZ** and upper **LB**, the lower **LB** clearly had fewer large fossils and more large gravel.

In November, Dubois summarized: A *"black coaly clay bed …. 11 to 12 meters below ground level …. proves to be the underlying formation to the bone-bearing volcanic tuffs ….* [, the **LB**, which produced] *"many antlers of the small* Axis*-like deer species* [*A. lydekkeri*] *and also remains of* Stegodon [*trigonocephalus*]*,* [*Duboisia santeng*]*,* Bubalus [*palaesondaicus*]*, ….* [together with] *the first almost complete skull of a crocodile* [*C. siamensis*]*"* (SI II-195).

Finally, he reported that *"last year's excavation* [of the 25-m Trench which was] *…, only partially worked …"* had been combined with the 1893 40-m Trench (SI II-194), so that the crews *"were able to essentially dig away the entire bone-bearing bed* [**LB**] *… before the 26th* [of November] *when the work* [site] *became hopelessly inundated"* (SI II-197).

The richness of bioclasts in the **LB** was evident in the 25 crates of fossils and six crates of wood that Kriele shipped from Trinil. Dubois admitted that *"none were the hoped-for additional parts of the curious* Anthropopithecus *….* [, whose remains must have] *washed away during the formation of the* [incised modern Solo] *river bed, together with a large portion of the bone-rich tuff* [**LB**]*"* (SI II-198). With this disappointment facing him, Dubois ended the Trinil operations, and had KdW install the *"P.e."* monument which still stands at the Trinil Museum (SI II-58; also, SI II-41, -42, -197, -198).

1894, Dubois' Last Visit

Early the next year, Dubois (1894, 1895a) turned attention to completing his *Pithecanthropus erectus* monograph (SI II-199). It arrived at the publishers on February 8 and was published on August 25, 1894, three years after vertebrate-fossil collecting had commenced in the sandstone ledges on the shores of the Solo River. Neither the monograph nor Dubois' final 1893 periodic submissions to the Indies government enumerated the taxa he identified while scrutinizing the Trinil fossils. On September 5, Dubois had a photograph made of the left-bank excavation site (see Figure 3c, addressed above in Site Geology). In November, he wrote to a colleague about the toll success had cost him. *"I have sacrificed my whole career, my health and my good humor"* and even the well-being of *"my wife and children"* (SI II-219; also SI II-217). He spent much of 1894 following up his earlier study of the geology and paleontology near Kedungbrubus, Butak, and elsewhere in the Kendeng Hills (SI I-36; SI II-200 to -202; also, Albers and de Vos 2010). The fossils his field crews found near Kedungbrubus are the basis for the biostratigraphic Kedung Brubus fauna, while those from Butak contribute to our recognizing the Butak bonebed (see Table 5 below; SI II-200; also, SI I-41).

1895–1900 FINDS

Kriele's letters to Dubois about the 1895–1900 excavations (see Figure 3a) describe finding other large bioclasts of Trinil fauna species near the seasonal low-water level of the Solo River (see Table 1; SI II-63 to -154). Kriele also sometimes refers specifically to the bonebed and the rarity of vertebrate remains stratigraphically above it (in our units **2–5**). The fossils he noted can only rarely be linked to individual Dubois Collection (DC) specimens, but the assemblage Kriele reported matches the taxonomic and taphonomic characteristics of Trinil fossils in the DC. Highlights from Kriele's accounts follow.

1895–1897

When the level of the Solo in 1895 dropped *"as low as it was in the first years"* of 1891–1893, the **LB-HK** Ledge next to the Skullcap Pit (see Figure 4a) yielded *"an incomplete antelope skull* [*Duboisia santeng*] *… with one horn, an elephant molar* [*Stegodon trigonocephalus*]*, as well as several other pieces of bone"* (see Table 1; SI II-64, -76; de Vos and Sondaar 1982). Wood and molluscs were found there in 1896 (SI II-93) before new pits and trenches were dug south of the 1891–1893 Skullcap Pit, 25-m Trench, and 40-m Trench (see Figure 3a).

Kriele's provenience descriptions and sketch maps on the post-1894 work seems to have been specific enough for

Dubois to be confident that the fossils returned to the Netherlands still originated from the same fossil-rich stratum that he had seen in 1891–1893 and described in 1895–1896 publications. The 1896 Left-bank Pit was dug far to the west of the 40-m Trench (SI II-121, -155) and *"as deep as the bone bed …. more than 2 meters below the water level,"* where Kriele reported an *Axis lydekkeri* skull, *Sus brachygnathus* mandible and *"1 complete turtle"* (see Table 1; SI II-92, -93).

Kriele's October 1897 illustration of the left bank shows that the 1897 Upstream Pit was south of the Skullcap Pit (SI I-114; also, SI I-101). By annotating the sketch, Dubois is seen to approve Kriele's representation of the 1892–1893 left-bank excavations, which differed from his own 1895 published mapping (see Figure 2b; also, SI II-121, -131, -132, -133, -135). Kriele's drawing shows the 1897 Premolar in the 1897 Upstream Pit. This left lower premolar (P_2 sin.; Trinil 5) was attributed to *Pithecanthropus erectus* by Dubois (1899) at the 1898 Fourth International Congress of Zoology in Cambridge (de Vos and Sondaar 1982; Smith et al. 2009; Theunissen 1989). The 1897 Upstream Pit was *"brought to the depth on which no more bones are to be expected"* and *one complete deer skull with antlers* [*Axis lydekkeri*]*"* was found, apparently while digging the **LB-HK** (see Table 1; SI II-107, -108).

The 1897 Downstream Pit, which was situated between the 40-m Trench and the 1896 Left-bank Pit (SI II-121), encountered *"nothing special"* when the penetration was *"8 meters down"* (units **2–5** appear to have been poorly fossiliferous). But according to Kriele's reporting, upon reaching twelve meters in depth, after passing through the **LB-HK**, large bioclasts referable to the Trinil fauna species were excavated: a complete *Stegodon trigonocephalus* tusk 1.55m long, an incomplete *Bibos palaesondaicus* cranium with complete horn cores, and an incomplete *Bubalus palaeokerabau* cranium with one full horn core (SI II-109, -110). Additionally, a *Sus brachygnathus* mandible in the Dubois Collection (no. 502) has an original label indicating *"that the specimen has been found … 1.25 m below the lowest water level"* in the 1897 Downstream Pit where also occurred *"a right upper first molar (M^1 dext., Coll. Dubois no. 317)"* of *Rhinoceros sondaicus* from *"0.75 m below the lowest level of the river"* (de Vos and Sondaar 1982: 48; SI II-101, -112; entries for the 1897 Upstream and Downstream Pits are combined in Table 1).

The 1897 Downstream Pit and the 1896 Left-bank Pit confirmed a westward continuation of the large Trinil faunal bioclasts in **LB-HK** that was beyond the terminus of the 40-m Trench (SI II-121, -155). There was no excavation at Trinil in 1898.

1899

In December 1899, Kriele submitted his most detailed illustration of the left-bank excavations (see Figure 3a). By Dubois' annotations on this map, he is again seen agreeing with Kriele on the relative locations of the Skullcap Pit, 25-m Trench, and 40-m Trench, as well as the siting of the 1896 Left-bank Pit, 1897 Upstream Pit, 1897 Downstream Pit, and 1899 Trench, together with plans for the 1900 Trench (de Vos and Aziz 1989: Fig. 5: 414; SI II-135). The 1899 Trench lay directly south of the 1893 40-m Trench, so that strata removed in 1899 held up the embankment visible in the 1894 photograph (see Figures 3c and 4a). The 1899 Trench was divided into 450 one-meter squares, making it more than ten times the size of the 40-m Trench.

Once Kriele *"reached the bone bed"* (**LB-HK**), he highlighted the recovery of massive fossils that are now attributable to the Trinil fauna—a *Stegodon trigonocephalus* tusk two meters long; a partial *Bubalus palaeokerabau* cranium; a complete upper *Rhinoceros sondaicus* cranium; an incomplete *Panthera tigris* mandible; some complete *Axis* antlers; and what *"turned out to be an ape's tooth"* that was *"found about 0.5 meters above the lowest water level"* (a non-hominin catarrhine; SI II-133). By December 21, 1899, Kriele had seven crates with 1069 finds, apparently all from the 1899 Trench (SI II-134). The average frequency appears to have been 2.4 fossils per m^2 including 850 teeth, molars, and a diversity of other specimens.

Among the large-sized bioclasts reasonably attributable to the **LB-HK** from the 1895–1899 excavations and identifiable taxonomically are two complete *Axis* craniums with antlers, three partial *Axis* craniums, multiple *Axis* antlers, one *Bibos palaesondaicus* cranium with complete horns, a *Bubalus* cranium with horn core, one *Stegodon* cranium with tusks and molars, another *Stegodon* tusk ~2m long, a third tusk, ~1.10m long, a fourth tusk, ~1.55m long, one smaller tusk and molar of *Stegodon*, the partial cranium with horn core of *Duboisia*, one *Rhinoceros* calotte and a molar, one partial *Sus brachygnathus* mandible, complete Testudines remains, partial *Crocodylus* craniums, wood, and Mollusca (see Table 1; SI II-132 to -134).

1900

Dubois (1899) launched an even-larger left-bank excavation in 1900 (see Figure 3a), having been encouraged to do so by the 1898 Fourth International Zoological Congress (SI II-138; Shipman 2001). As diagrammed by Kriele in advance (and generally confirmed during excavation), the 1900 Trench comprised some 900 one-meter squares (see Figures 3a and 4b; SI II-135, -153; also, SI II-155). It extended ~100m east to west and was 6-to-19m north to south.

The crew had encountered no bones in the top two meters of the river embankment, and when about half of the 1900 Trench was dug to *"an average depth of around 4 meters,"* only *"some insignificant specimens"* were in hand (SI II-140 to -142). Judging from this, our unit **5** was nearly devoid of sizeable vertebrate fossils. Once at a greater depth late in 1900, Kriele reported large-sized finds, evidently from the **LB-HK**—a *Stegodon trigonocephalus* cranium with complete tusks and molars, a *S. trigonocephalus* mandible with complete molars, a complete *Bubalus palaeokerabau* cranium with horn cores and molars, a partial *Bibos palaesondaicus* cranium, two partial *Axis* craniums with antlers, and the incomplete remains of several turtles (see Table 1; SI II-145 to -154, which summarizes the finds).

One DC specimen has labeling of a type that Kriele might have prepared for many of the finds he delivered to Dubois (e.g., SI II-81). As de Vos and Sondaar (1982: 43) reported, *"no. 536, a lower jaw of* Bubalus palaeokerabau *Dubois, on which a label was stuck with* [the detail that the fossil was found in] *… fine sand, 1.25 m above the lowest level of the river"* in the western part of the 1900 Trench (also, SI II-135). When considered with fossils reported from elevations below river level, the buffalo mandible might indicate that discovery depths spanned 2.75m (SI II-145 to -154).

While Kriele thought he had *"not been able to get anything of the ape-human"* (SI II-145), he had failed to identify four *Pithecanthropus erectus* femoral shaft fragments that Dubois (1932, 1934; also, 1935) concluded came from the 1900 workings. At least 850 Trinil fossils are recorded from 16 crates shipped to Leiden in 1900 (SI II-150 to -155). Considering the size of the 1900 Trench, Kriele seems to have been instructed to leave many finds in Java.

Kriele's letters in 1900 have essentially no information on **LB**-**HK** lithofacies, except the cross-lamination patterns that he once reported (mentioned in Site Geology above). Dubois nonetheless would have had an abundance of information on the discovery bed lithology from the sandstone and conglomerate adhering to museum fossils. Lithic matrix is still visible on the DC specimens, even after extensive cleaning over the course of a century (SI I-20 to -24).

As mentioned previously, Dubois belatedly recognized additional hominin femora in his 1900 assemblage, *Pithecanthropus erectus* Femur II to V (also known as Trinil 6 to 9). They have the same dark color and stony fossilization characteristic of other Trinil specimens in the DC. Kriele had written *"Trinil"* on Femur II and Femur V, suggesting that while not identified as anthropoid, Kriele knew they were more consequential than the most post-cranial fossils that he transmitted to Dubois; additionally, when Dubois first saw Femur II, it was partially encased in hard pyrite-bearing rock, a lithology he knew was common in the **LB** and **HK** (SI II-136, -234, -235, -236, -241, -251; also, Berkhout and Huffman 2021: 73; Carthaus 1911; SI II-249). Very coarse-grained sandstone is still present in the medullary space of Femur II, as it is in Femur I (Dubois 1896e; SI II-231; also, Ruff et al. 2013, 2015, 2021).

Although Dubois (1907, 1908) published little on the geology of the 1895–1900 excavations, his unpublished archival materials reveal a geological continuation of the fossil-rich concentration lying near the low-water levels (see Table 1) and the poorly fossiliferous eight-to-nine-meters superjacent strata (our units **2–5**, see Figures 4 to 5; SI I-3 to -6, -8, -9). Dubois made a reconstruction of a full body standing *Pithecanthropus erectus* for the 1900 Paris International Exposition (Shipman 2001; a recent rendering uses Femur II, rather than Femur I, as the principal post-cranial Trinil *Homo erectus* element https://www.kenniskennis.com/homo-erectus/).

1907–1908 FINDS

Information available from the Selenka Expedition's left-bank Pit II offers far more detail on the fossils from the main bonebed than Dubois' records do. This permits an estimate of the spatial density of bioclasts. Together moreover, the Dubois and Selenka records document the unusually diverse paleobiota in the main bonebed (see Table 3) compared to other *Homo erectus* discovery beds in Java (see Table 5 below). The Selenka Expedition encountered one prominent local fossil concentration, the *Stegodon* bed (**SB**), above their Hauptknochenschicht (main bone-bearing layer; see Figure 8).

Hauptknochenschicht (HK)

Oppenoorth readily identified the *Pithecanthropus erectus* discovery deposit on the left bank in 1907 (SI I-8, -9; SI II-247, -249). The final Pit II of 1907 expanded modestly upon Dubois' 1900 Trench and was ~37m east-to-west and ~4m to ~9m north-south (see Figure 7b; SI I-7). Oppenoorth (1908a: 181) mentions that *"about 700"* fossils originated from Pit II in 1907 (SI II-245), and the bonebed was soon named the Hauptknochenschicht (**HK**) by Carthaus (SI II-248, -249); also, Berkhout and Huffman 2021: 61–64). The 1907 Listing, the unpublished Selenka tabulation of 1907 fossils from excavation, enumerates 506 **HK** finds from Pit II (field layers 3 and 4; see Table 2; e.g., SI II-251). Sixty percent have been attributed to taxa (243 of 405; 36% of total Pit II entries). Terrestrial species comprise ~93% of the taxonomically recognized finds (225 of 243). Cervid and large-bovid specimens make up ~86% (61% cervid plus 24% large bovids). Fossils attributable to *Stegodon trigonocephalus*, *Sus brachygnathus*, and *Duboisia santeng* account for 1%–5% each of the 243 identified specimens (see Table 2). *Rhinoceros*, hippopotamus, and primate occur as one or two entries each. The remaining finds are fish, Crocodylia, and bird fossils. The identified species are substantially the same as those from Dubois excavations (de Vos and Sondaar 1982), although the combined frequency of cervid and large bovid specimens listed from the **HK** is somewhat greater than the 68% sum of these taxa in the Dubois Collection (see Tables 1 and 2).

Bioclast Variations in the HK

Although the average content of vertebrate fossils in the **HK** was about three bioclasts per cubic meter, the density differed between Pits I and II and varied vertically within the **HK** of Pit I.

Just a month after leaving the field during 1907, Oppenoorth wrote that in *"the actual bone bed…. fossils are distributed rather randomly"* (SI II-244). He (1908a) soon specified that the **HK** of 1907 Pit II had *"produced about 700 fossils over a surface area of 250 square meters … mostly smaller bones, teeth, vertebrae, hand* [fore-] *and foot* [hind-limb] *bones, etc.,"* making the Pit II average ~2.7 fossils per square meter (SI II-245). Given the **HK** was generally not more than about one-meter thick, the average volumetric density in the bonebed exceeded ~2.7m^{-3}. Oppenoorth was nonetheless clear that spatial distribution of vertebrate fossils varied. *"Many times, the number of specimens found per square meter was larger (or smaller)* [than the average]*,"* and *"sometimes more than 100 specimens had been deposited within a few square meters"* (SI II-245).

The 1907 Pit II contained fewer large bioclasts, judging from Oppenoorth's reporting, than the 1891–1893 pit and trenches from which the Skullcap and Femur I came. The **HK** assemblage from Pit II also differed in several ways from the fossils in 1907 Pit I on the other side of the Solo River (see Figure 6b). In Pit I, *"about 1224 pieces …. were spread over a surface area of about 350 square meters"* in the **HK**, giving *"an average* [fossil density] *of 3.5 pieces per square meter …. mainly* [comprised of] *the large bones like skulls, pelvis, vertebrate, ribs, etc.,"* as opposed to the conditions in Pit II (SI II-245).

The Pit I fossils were concentrated in the upper and lower levels of three **HK** stratigraphic subunits (see Table 2b; S II-246). This vertical bioclast distribution was essentially the opposite of that in the 1891–1893 left bank excavations, where **PFZ** fossil concentration was in the middle of the **LB** (see Figure 2a). In Pit I, the number of finds (per subunit) ranges spatially from zero to ten in individual meter-sized squares (SI I-11c). Despite the variations of bioclast-density in the Pit I **HK**, the fossil assemblages in the three subunits were consistent in taxonomic composition. Cervids, large bovids, and *Stegodon* fossils comprised 90%, 93%, and 92% of the finds in subunits 15, 16, and 17, respectively; cervids were 63%, 74%, and 62% of the finds in the three subunits (see Table 2b). This consistency is strong evidence that the subunits derive from the same precursor taphonomic events, and the differences in spatial density were sedimentological consequences.

Antlers were especially common in the **HK** of 1907 Selenka Pit I (see Table 2b) but infrequent in the 1907 Pit II, where most of the deer were in the western portion. There are other indications that the density of *Axis* fossils varied. KdW had noted the large number of antlers in the right-bank **LB** in 1891 (SI II-2; also, SI II-4) and the 1892 25-m Trench apparently produced more antlers from the **LB** than did the Skullcap Pit. In his 1891–1893 excavations, Dubois (1896e: 725) recalled seeing *"hundreds of complete antler beams and fragments"* (SI II-231; also, SI II-193).

Vertebrate Fossils Above the HK

The 1907 Listing enumerates just two fossil concentrations above the **HK** in Pit II but gives information on their faunal composition (see Table 2).

Seventeen finds are listed as layer 1, the *Stegodon* bed, **SB** (see Figure 8), mentioned previously. The **SB** fossils principally were the disarticulated remains of a *Stegodon trigonocephalus* individual, including a partial maxilla with dentition and tusks and a largely complete mandible (SI I-9, -10). Other **SB** fossils were crocodile, hippopotamus, fish, and mollusc. No cervid- and bovid-remains, which were common in the **HK**, were reported being in the **SB**. Pit II layer 2, situated at an unspecified stratigraphic level between the **HK** and the SB, had only 67 finds, compared to the 405 from the **HK** layers, and the taxonomic composition of layer 2 differed from the **HK** (see Table 2a).

This is consistent with conditions across the whole site, where vertebrate fossils occurred *"sporadically"* above the **HK** (SI II-246), and comprised only *"incidental bone remains … here and there"* (SI II-249; these finds were mostly large bovid and *Stegodon*, rather than the deer common in the **HK** (see Table 2). Pit I occasionally encountered shallow bone-beds in 1908. A thin *"red bone-bearing"* lens was 4–5 meters above the **HK**; *"2 thin lapilli beds (2 and 5 meters above the main bonebed)* [were] *on average 0.20 m thick"* and *"in appearance are identical to the main bonebed …* [notably being as] *rich in skeletal remains"* and molluscs; the shells were *"primarily* Unio [a fresh-water mussel] *and* Melania [an aquatic gastropod]," which also were well-known in the **HK** (Dozy 1909: 609; Berkhout and Huffman 2021: 49; Selenka and Blanckenhorn 1911 Plate X ["Tafel" in original German]). One of the Selenka's shallow bone-bearing lenses also might have been the *"richest fresh-water mollusc bed"* recognized in the 1907 Pit I (Berkhout and Huffman 2021: 62; Selenka and Blanckenhorn 1911, Plate VI, Profil 2).

In Dozy's (1909: 611) judgement, the shallow *"thinner bonebeds … originated from … heavy eruptions"* of volcanoes in addition to having fluvial deposition like the **HK** (also, Berkhout and Huffman 2021: 88; Dozy 1911b: 35). The Selenka reporting about fossil beds above the **HK** matches Kriele's encounter of *"a complete thigh bone, a complete tibia and a tusk, all of an elephant* [*Stegodon trigonocephalus*]*, in addition to a few vertebrae and ribs"* in the top 6m of the 1895 Dubois excavation, which probably was dug on the right-bank (SI II-69).

Overall, the lithofacies *"overlying the main bone bed is highly variable"* at the site (Dozy 1909: 608). Indicative of this, plant-rich layers (without reported vertebrate fossils) were prominent above the **HK** in Pit I but rare in Pit II, and no plant beds were described at all for the large left-bank excavations of Dubois, except to the extent that wood and leaves were noted in the **LB** and **LB**-**HK**.

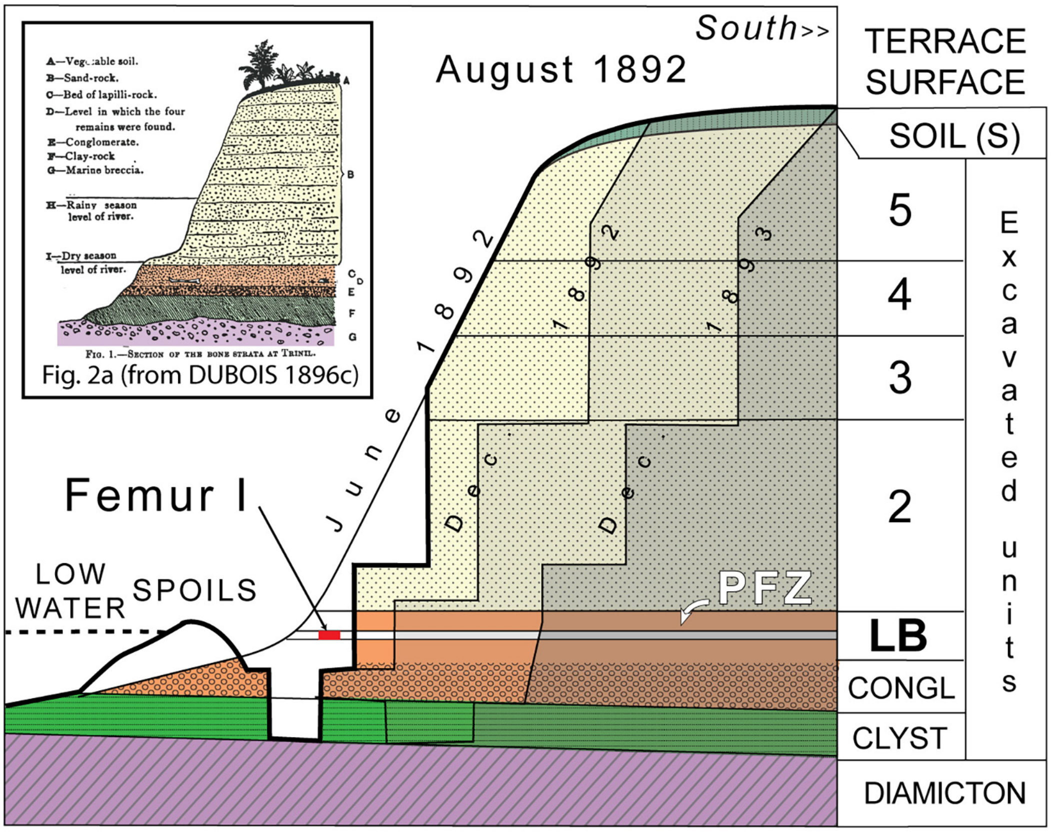
PROVENIENCE OF FEMUR I

The foregoing analysis puts us in unique position to reassess the provenience of Femur I and this leads us to endorse KdW's and Dubois' stratigraphic placement of Femur I in the **LB**/ **PFZ** (Figure 10) over conjectural possibilities that do not take the archival records into full account (SI I-35). Our reasoning is as follows.

The on-the-ground circumstances along the left bank in 1891–1893 were straightforward geologically, particularly regarding the flat-lying attitude of erosion-resistant strata and the high concentration of large-sized vertebrate fossils in one prominent stratum. At the end of June 1892, a month before Femur I was found, excavation of the embankment on the left bank neared the seasonal low-water level, and *"a large surface area of the fossil-bearing layer"* (**LB**) produced a *"harvest of bones"* (SI II-180) including large bioclasts of a species known from the Skullcap Pit (SI II-1 to -4, -168, -180). No fossil concentration was reported above the **LB**.

Dubois already had acquired particularly valuable expertise important for analyzing the paleontology and stratigraphy of the Femur I excavation. First, he evaluated the paleontological characteristics of the **LB** fossils, and second, he studied the fluvial sedimentary processes visible along the modern Solo River and evident from deposits exposed in its banks (e.g., SI II-180, -181, -206 to -208). When Dubois received Femur I, he had other **PFZ** and **LB** fossils in hand

DISCOVERY CONTEXT OF FEMUR I



LB = Lapilli Bed (Dubois 1896c unit C) **PFZ** = principle fossil zone (his D)
Units 2 to 5 (Dubois' unit B) Conglomerate (his E) Claystone (his F)

Figure 10. This diagrammatic cross section illustrates our reconstruction of the Femur I discovery context based on Dubois' records, including his published cross sections (inset) and unpublished materials (after Huffman et al. 2015, 2018). The excavation is depicted during the month that Femur I was discovered, August 1892. Shading shows the progression of excavations from June 1892 through December 1893 (the shape of the excavation profiles over time and thicknesses of individual stratal units are schematic). When the embankment was excavated to the south of the August Femur I discovery point, the **LB** *was unearthed beneath hardened rock, confirming the Femur I discovery stratigraphic context (as described in the text). The 1894 photograph depicts a stratigraphic sequence like that shown here. Excavations in 1895 to 1907 that dug farther southward into the embankment encountered the same strata (see Figures 4b to 8; SI I-4 to -6). The right edge of this cross section is still several tens of meters north of the present-day riverbank, judging from the 1899 map (see Figure 3a) and 1926 photograph (see Figure 9).*

with which to compare the taphonomic condition and adhering sediment of the new find.

Kriele's sharp geological awareness at the time is evident in his early August 1892 field evaluation of cross-bedded strata, which Dubois had not seen (SI II-19), and the accurate September 7 assessment about how to encounter more **LB** near the Femur I discovery spot (SI II-23).

KdW's description placing Femur I in the **PFZ** portion of the **LB** was unambiguous, given this background (SI II-22, -23). Dubois promptly reported the provenience specification to the Indies government (SI II-182 to -184). His confidence in the attribution did not alter after visiting Trinil in September 1892. His 1895–1896 published accounts unequivocally attributed the *Pithecanthropus erectus* fossils to the same stratigraphic level (**PFZ**) in one fluvial deposit, the **LB** (see Figure 2a).

During September 1892 Dubois had firsthand information on both the stratigraphic co-occurrence of Femur I and the Skullcap and the startingly anatomical similarity of Femur I to the femora of *Homo sapiens*. Dubois (1926a, b, 1932, 1934, 1935) continued to be interested in the anatomical comparison, especially after the recognition in 1932 of additional femora from among his 1900 collection of finds from Trinil (e.g., SI II-136), but he is not known to have developed doubts that Femur I and the Skullcap came from one deposit. Indeed, he expressed this view near the end of his life in 1940 (SI II-220).

Later in 1892 and again in 1893, KdW and Dubois gained confirmatory evidence on the stratigraphic context of the **LB**. The crew twice dug the embankment downward from its top by horizontal increments through sparsely fossiliferous indurated beds toward the **LB** situated near the seasonal low water level. The **PFZ** and **LB** were traceable from the edge of the Skullcap Pit to points near the Femur I discovery spot and beyond across the 25-m and 40-m Trenches.

No stratigraphically higher fossil concentration or stratigraphic disturbance was reported. As the 1892 and 1893 excavations approached completion, eight-to-nine meters of strata were newly exposed across 25-m and 40-m-long excavations. Dubois documented the stratigraphy with a high-quality photograph in 1894, which shows the strata that the 1892–1893 excavations had penetrated nearby (see Figure 3c; SI I-4).

Dubois' cross sections published in 1895–1896 indicate that this same stratigraphic sequence was projected to extended widely under the south embankment of the Solo River (see Figure 2a). The sequence indeed is traceable photographically across several thousand square meters of former excavation area from the outcrops visible in 1894 to backwalls evident in 1900–1907 (units **1–5** indicated on Figures 4 and 5). The 1900–1907 trenches encountered a channel-form unit (our **6**) near river level in the far west of the area excavated, but in the 1926 photograph, the unit is not seen anywhere close to the pits and trenches from which the *Pithecanthropus erectus* came (see Figures 7a and 9b).

Firsthand reporting contradicts various alternative provenience speculations about Femur I. The fossil could not have come from below the **LB** because KdW's September 7, 1892, letter indicates more **LB** remained under the discovery level at the spot where the Femur I was found (SI II-23). No stratigraphically higher fossil concentration was reported as having occurred in the 1892 and 1893 excavations, nor in adjacent ones dug during the late 1890s. No terrace deposits or slumped beds were recognized by KdW or Dubois in 1891–1893; rather, their contemporaneous accounts report excavating well-indurated strata arrayed in regular depositional order.

No large-sized, well-preserved fossil, such as Femur I, was reported as having been introduced into the excavations by flooding of the Solo River during the years of Dubois' work at Trinil, leaving no support for the proposition that Femur I was an extraneous clast carried into the 25-m Trench by high water (the trenches did fill with sediment in the 1893 wet season; SI II-36).

If Femur I was found close to large *Stegodon* fossils, as de Winter remembered, the context seemingly would have been difficult to mistake because, in part, large proboscidean bioclasts were known by then to characterize the **LB**. He might have recalled the *Stegodon* specimen because it was first encountered before digging reached the Femur I stratigraphic level or because the proboscidean fossil was below Femur I and had to be dug out later in August.

The *Stegodon* mandible unearthed in the **SB** ~5m above the **HK** from Selenka Pit II (see Figure 8), which was well south of the *Pithecanthropus erectus* discovery point, but KdW and Dubois never reported a comparable shallow fossil horizon in the 1891–1893 trenches and a provenience error off stratigraphically by five meters is not credible for the Femur I discovery. Additionally, the Trinil *Stegodon* mandibles that are reasonably attributable to the main bonebed are smaller anatomically than the one from the SB (van den Bergh 1999, personal communication, 2022). The specimen de Winter remembered from the Femur I discovery excavation presumably was among this smaller-bodied cohort that characterizes the main bonebed fauna.

It is implausible to suppose de Winter lost track of who was working in what stratum during August 1892, in view of the straightforward stratigraphy under excavation, ~10m^2 size of the Femur I discovery dig (at the **PFZ** level), and consistent operational procedures KdW followed, such as excavating downward by horizontal increments. If Femur I was collected before de Winter saw it *in situ*, he surely would have noticed that a crew member had been excavating at a large, well-preserved fossil significantly above the well-known **PFZ** context in which de Winter and the rest of the men were working.

If de Winter had been handed a well-preserved fossil that he did not see *in situ*, but thought might originate from above the **LB**, KdW surely would have searched in stratigraphically higher beds with the hope of finding more high-quality specimens. If KdW or Dubois subsequently suspected that important fossils might occur above the **LB**, they would have paid close attention to this potential while re-excavating the embankment in late 1892 and 1893. KdW letters about work during these times would have prominently reported that more fossils had been found in a higher level. The letters do not mention that any were.

The narrative and photographic records, considered as a whole, provide uncontroverted evidence that the Skullcap and Femur I, together with other Trinil fauna species, originated from one fluvial accumulation, as the discoverers asserted. It is thus probable that the Skullcap and Femur I were embedded contemporaneously and are of the same geological age.

No alternative case has been published that has substantial provenience, sedimentary, and paleontological support (SI I-35). Presumably, such an alternative would include evidence from the Trinil museum collections that two prevalent taphonomic suites or biostratigraphic faunas occur, and from fieldwork in the immediate vicinity of the Skullcap Pit and 25-m Trench, that two deposits with large, well-preserved, vertebrate fossils exist and possess taphonomic, sedimentary, and geochronological indications of meaningfully different geological ages. As it stands, the records from both 1891–1893 and later excavations support Dubois.

FORMATION OF THE MAIN BONEBED

The same Dubois and Selenka records used to analyze the geology and paleontology of left-bank strata also provide a foundation for developing proposals for taphonomic and depositional origin of the main bonebed and considering its implications for *Homo erectus* paleogeography.

BIOCLASTIC FEATURES

Firsthand reporting and fossils in museums indicate that the terrestrial-vertebrate skeletal material from the main bonebed consisted overwhelmingly of broken elements that are not articulated. They have uniform fossilization, bony surfaces with fine surface preservation, low levels of weathering and abrasion attributable to fluvial transport, and an absence of evidence of hominin- or terrestrial-carnivore involvement in the ungulate deaths. Both vertebrate and vegetal bioclasts occurred in a great size range (as large and long as proboscidean craniums and tusks and tree trunks). They were dispersed and apparently matrix-supported *in situ* with both horizontal and vertical changes of density. The longest bioclasts had bed-parallel orientations (that is, horizontal), and the largest fossils would have taken up most of or all the thickness of the bonebed. It contained a greater biotic diversity than any other *Homo erectus* discovery deposit known in Java (e.g., see Table 5 below). Key observations from firsthand observers follow.

The **LB** fossils that Dubois saw were *"generally isolated and widely distributed and usually broken"* but included the ribs and vertebrae of *"large ox in their natural relative"* positions (SI II-168, -178, -180; also SI II-3). Oppenoorth (1911: xxxiv) observed in 1907 that *"the bones were mostly embedded in broken condition … and in a few* [instances, the breakage clearly occurred] *before fossilization* [resulting in] … *many bone fractures … filled with tuff"* (SI II-247).

After examining his 1891–1900 collection, Dubois (1908: 1242–1243) thought that the bones *"were deposited in fresh condition"* (SI II-234). Carthaus (1911b: 26, 28) claimed the **HK** *"is characterized by undamaged animal bones"* lacking signs of *"long distance transportation"* (Berkhout and Huffman 2021: 87). He remarked that *"articulated whole skeletons are absent,"* the remains having been *"transported more or less already decomposed animal corpses* [only] *a number of days, weeks or even months"* after death (Berkhout and Huffman 2021: 87–88).

Dubois (1908: 1242–1243) thought that the occurrence of *"hundreds of antlers of the same deer species …* [was] *explained by the simultaneous extermination of the entire herd of these Axis-like deer"* (SI II-234). Carthaus (1911b: 28–29) surmised that the *"animals had been killed during the initial explosive eruption"* at a distant volcano (Berkhout and Huffman 2021: 87). Site geologist in 1908 C.M. Dozy proposed a similar scenario (1911b: 36; Berkhout and Huffman 2021: 95).

The large size range, broken shapes, and good surface preservations of the vertebrate fossils from the main bonebed are evident in the Dubois Collection (DC) and paleontological illustrations of Trinil specimens (e.g., Hooijer 1958a; Selenka and Blanckenhorn 1911; also, SI I-20 to -22, SI II-243). Hill et al. (2015) tested the impressions of Dubois and the Selenka scientists quantitatively analyzing 3736 Trinil vertebrate fossils from the DC and Selenka material at the Museum für Naturkunde, Berlin (MNB; the study sample was 68% of the combined assemblages). The study material consisted dominantly of cervid and large-bovid specimens. No other such study has been done.

Overall, a *"limited amount of pre-burial weathering and transportation damage"* is evident (Hill et al. 2015). Comprehensive taphonomic evaluation of 234 humeri, representing 4.4% of the total Trinil assemblage, found ~95% of the specimens lacked notable signs of abrasion rounding (codes 2 and 3 of Fiorillo 1988) and weathering (stages 0 and 1 of Behrensmeyer 1978; M. Hill and L. Todd, personal communication, 2015). Fractures are often sediment-coated or -filled (Hill et al. 2015; M. Hill and L. Todd, personal communication, 2015, personal observation). The common occurrence of nearly complete finely preserved long bones is notable in the DC.

Dubois further observed that *"in no case were the usually recognizable signs of the teeth of land predators undoubtedly observed"* on the ungulate fossils of the **LB** (SI II-180). Hill et al. (2015) verified this 125-year-old conclusion based on examining 1891–1907 finds in the museum collections (also, Choi 2003).

Dubois had had a particular anthropological reason for interest in the crocodiles. He (1926a; SI II-241) reported that Femur I was one of the remains that had crocodile damage: The *"caput femoris, preserved for the most part, presents however extensive defects on the margin of the globular articular surface, which were probably caused by crocodiles."* He had surmised that the reptiles served to *"break …. and distribute"* the bones after carcasses of terrestrial animals arrived at Trinil, their *"soft tissue"* theretofore having *"protected* [the bones] *against wear at the bottom of the current"* (SI II-180; also, -178).

On the other hand, H. Stremme (1911) noted that only one well-preserved **HK** specimen in the Selenka materials had punctures that were probably referable to crocodile predation (MNB MB.R.1959; in Selenka and Blanckenhorn 1911: 146). Hill et al. (2015) confirmed that circular compression fractures are present on certain Trinil specimens (e.g., DC 1860 and MNB MB.Ma22309; MB.Ho.476.1), but a Crocodylian origin for the marks on the proximal end of Femur I is less conclusive (M. Hill and L. Todd, personal communication, 2015).

No porcupine gnawing marks have been reported from the bony remains or teeth in the main bonebed, although porcupine fossils are present in the DC materials from Trinil (*Hystrix lagrelli*, NISP=2, SI I-33; SI II-34, -129, -243). Gnaw-marked teeth are prominent in geologically younger fossils in eastern Java cave deposits (e.g., at the Punung and Gunung Dawung sites; Storm 2012; Storm and de Vos 2006; Storm et al. 2005). If skeletal remains had been on the surface of the Trinil paleo-river valley for substantial time, porcupine gnawing presumably would be evident on the main bonebed fossils.

Two additional features of the embedded condition of bioclasts are of special interest. First, elongate skeletal fossils, particularly tusks one-or-two meters long, must have lain parallel to the boundaries of the main bonebed, which was often less than a meter thick. In 1891, *"the tree trunks and leaves are always found horizontally"* (SI II-171; also, SI II-170). Segments of trees 1–3m long had a *"random"* attitude within the **HK** (Berkhout and Huffman 2021: 72; Carthaus 1911b: 14). The long-bones and ribs of large ungulates, complete deer antlers, and cattle-buffalo horn cores presumably also tended to have bed-parallel attitudes in the main bonebed (that is, horizontal). Second, crania of *Stegodon*, *Bibos*, *Bubalus*, and *Rhinoceros* (when the remains were largely complete) presumably took up the full thickness of the main bonebed. For instance, large cranial fossils attributed to the 0.20 m thick **PFZ** would have extended into or through the upper **LB**. This also would be the case for the *Stegodon* *"tusk and skull"* visible in the initial left-bank **LB** outcrop (SI II-2, -3) and the *"mandible and tusk"* of *Stegodon* that de Winter noted as in the **PFZ** *"nearby"* Femur I (also, SI II-1, -9, -22, -44, -46, -76, -92, etc.).

DEATH OF HUNDREDS

Museum collections of Trinil fossils provide evidence that hundreds of individuals lived as a single paleofaunal community and died penecontemporaneously, much as Dubois and Carthaus envisioned (Dubois 1892a; SI II-166; Dubois 1908: 1242–1243; SI II-234; and, Berkhout and Huffman 2021: 87–88; Carthaus 1911b: 28–29). The taxonomic makeup of the assemblage confirms that it represents a single paleofauna (see Tables 1 to 3) and the numbers and taphonomy of the ungulate fossils evince the death of hundreds (Table 4). Among 3478 specimens in the Dubois Collection, the Minimum Number of Individuals (MNI) for *Axis*, *Bibos*, *Bubalus*, *Duboisia*, *Stegodon*, *Sus*, and *Rhinoceros* totaled 164 (94% of all non-hominin taxa in terms of MNI). No taphonomic distinction has yet been recognized that would indicate that any large number of specimens is inconsistent with a single mortality event. Rather, Hill et al. (2015) saw isotaphonomy among large-bodied vertebrate bioclasts in the Trinil collections of Dubois and Selenka (Museum für Naturkunde, Berlin). Prime-age individuals greatly outnumbered those of pre- and post-prime ages, based on preliminary assessments of dentition in deer and *Duboisia*, and the deaths involved appear to have been catastrophic rather than attritional (Hill et al. 2015; M. Hill and L. Todd, personal communication, 2020). Van den Bergh (1999: 362) concluded that the *Stegodon* population of the main bonebed appears to have been healthy and mostly juvenile when struck by *"catastrophic death"* (see Table 4, footnote 4). The Trinil fossil assemblage also had low but considerable frequencies of several forest ungulates, such as rhinoceros and pig (NISP of 122, see Table 3; SI I-30, -31). The five hominin femora that Dubois (1894, 1926a, b, 1932, 1934, 1935) attributed to *Pithecanthropus erectus* comprise a MNI of 3 (Storm 2012; also, Ruff et al. 2015).

PALEOBIOTA

During the months or few years before the catastrophic death, the paleo-river floodplain upstream of Trinil must have had herd-sized populations of cervids, bovids, and proboscideans, and sufficient herbaceous open-terrain or forest-understory to sustain them. *"The high number of large bovids means a drier biotope"* and *"a more open woodland"* in the Trinil paleo-river floodplain than existed when orangutan lived in a *"humid forest"* in the Southern Mountains of Java and highlands of Sumatra during the Late Pleistocene and Holocene (Punung fauna; de Vos 1985a: 216, de Vos 1989; de Vos et al. 1994: 131; also, Aziz et al. 1995). As the biotope was envisioned, the paleo-lowland that predated the accumulation of the main bonebed was like the modern grassland-forest mosaic in northeast India's Brahmaputra River lowland, an area with high annual levels of strongly monsoonal rainfall. That lowland supports large populations of *Axis*, cattle, water buffalo, and elephants; the deer inhabit tall- and short-grasslands, wetlands, and mixed-deciduous forests, and hundreds of the deer are periodically carried away by floods (SI I-26, -27).

Key Trinil fauna species were not necessarily restricted to biotopes like those that were in the Trinil paleo-river floodplain. *Axis*, large bovids, *Panthera,* and *Stegodon* fossils are widespread and long-lasting in *Stegodon-Homo erectus* faunas (*S.-H.e.*) of Pleistocene Java (Table 5). The *S.-H.e.* taxa appear to have been sufficiently flexible ecologically to inhabit varying biotopes over the course of hundreds of thousands of years during which strongly contrasting climates would have affected Java (SI I-26 to -30; also, SI I-49). Such flexibility is consistent with the wide distributions of the historical cattle, deer, and tiger in South and Southeast Asia (see Table 3).

The inferred paleogeographic conditions surrounding the assemblages from individual fossil sites and collection areas in Java indicate that *S.-H.e.* faunas were adaptable paleoenvironmentally. For example, populations of *S.-H.e.* mammals found suitable habitats in the Mojokerto paleodelta lowland (represented by the Perning *Homo erectus* bonebed), Ngandong paleo-drainage (Ngandong *Homo erectus* bonebed), Solo paleo-watershed (multiple bonebeds and fossil deposits at Sangiran Dome), Trinil paleo-river valley (*Pithecanthropus erectus* main bonebed), and valleys near stratovolcanoes (Butak bonebed, Kedungbrubus collection area, and Patiayam), as summarized Tables 5 and Figure 13 [below] (also, SI I-39 to -46).

The conditions in the Trinil paleo-river can be inferred reliably from the present-day ecologies of the Trinil aquatic species because nearly all the species are extant (see Table 3). On this basis, the main bonebed accumulated along a distal lowland segment of a large perennial river that was linked to long-standing lakes and ponds, and had crocodiles, turtles, and certain air-breathing fish along its banks during the monsoonal dry seasons. *Crocodylus siamensis* (Siamese Crocodile), a key main-bonebed species, was historically widespread from Java, Borneo (Mahakam River), and Indochina (see Table 3; SI I-32). Modern analogs of the Trinil Testudines also indicate that the Trinil paleo-river floodplain had extensive perennial water bodies.

Fish closely related to those found at Trinil are distributed widely in Indomalaya rivers. The most-numerous Trinil fish have adaptations favoring dry-season survival (see Table 3, footnote 4). Mussels and gastropods in the main bonebed further establish the biotic diversity of the Trinil paleo-river (see Table 3). The molluscs include species that today inhabit both sizeable perennial rivers and

TABLE 4. MINIMUM NUMBER OF UNGULATE INDIVIDUALS (MNI) IN THE DUBOIS COLLECTION FROM TRINIL (AFTER STORM 2012).

Taxa	NISP	MNI
Axis lydekkeri[1]	1075	63
Bibos palaesondaicus[2]	51	30
Bubalus palaeokerabau[2]	94	24
Unidentified large bovidae[2]	1406	-
Duboisia santeng	231	18
Rhinoceros sondaicus[3]	44	4
Stegodon trigonocephalus[4]	499	16
Sus brachygnathus[3]	78	9
Ungulate subtotal (% of all specimens)	3478 (90%)	164 (94%)
All non-hominin taxa	3857	174
Axis, *Bibos*, and *Bubalus* MNI (117) is 2.5 times that for other ungulates. *Rhinoceros* and *Sus* are 8% of the total.		
The large-bodied predator *Panthera tigris* has an NISP=10 and MNI=1 (*Panthera* sp., an NISP=10 and MNI=1)		

[1] The cervid NISP is 1075 in the Dubois Collection (DC) but this includes only 101 antlers and antler fragments (9.4% of cervid total). Firsthand accounts indicate that antlers were far more frequent in the main bonebed (SI II; also, records of deer in Selenka and Blanckenhorn 1911, Berkhout and Huffman 2021). *A. lydekkeri* skullcaps, mandibles, and tibias analyzed by Stremme (1911) from the Selenka collection increases the MNI; each analyzed element gives an MNI of 11–12, hence a total known MNI of ~75 for the site. Stremme (1911) reported seeing 527 antler beams (230 were shed). Hill et al. (2015) found MNIs of 69–75 for several post-cranial elements from cervid- and large-bovid specimens in the Trinil material at the Dubois Collection and Museum für Naturkunde, Berlin, Germany (MNB), indicating >140 large-bovid and deer-individuals are represented. The MNI for cervids rose to 102 when frontal/pedicle fragments were tallied (Hill et al. 2015; M. Hill and L. Todd, personal communication, 2015). Since antler pedicles are male developments, the 102 represents a larger number of the deer. Prime-age large bovid, deer, and *Duboisia* individuals greatly outnumbered those of pre- and post-prime ages, based on first assessments of dentition (Hill et al. 2015; M. Hill and L. Todd, personal communication, 2015; also, Stremme 1911). Storm (2012) does not calculate MNIs for aquatic and non-ungulate terrestrial remains; the NISPs show frequent occurrences: Testudine (185), Crocodylia (95), fish (50), Cercopithecoidea (13), Squamata (5), birds (5), and Rodentia (5).

[2] The large-bovid NISP in the DC contain only 145 specimens identified to species level. This is largely due to the unresolved difficulty in distinguishing most anatomical elements of the two species from isolated fossils (Hooijer 1958a).

[3] Forest-prone taxa. Other forest taxa are missing in the assemblage, potentially including flying foxes, moon rats and shrews, bats of multiple genera, marten, forest badger, stink badger and weasel, banded linsang, Indian civet, Palm civet, Binturong, mongoose, squirrels, ground squirrels, pygmy squirrel, flying squirrel and giant flying squirrel, mice and rats of various genera, bandicoot rat and tree mouse; and hare and Fishing cat (based on Corbet and Hill 1992).

[4] Van den Bergh (1999: 353/Table 77D, personal communication 2022) reported a *Stegodon* MNI of 32 based on DC dental elements that are reasonably attributable to the main bonebed based on labels, historic register of DC specimens, fossilization/matrix, and degree of preservation (both isolated teeth and those embedded in bone were counted).

still-water settings, including lakes or freshwater swamps. Some specimens of one prominent mussel species, including its type specimen (Dubois 1908), are known to have originated from the main bonebed, although none of the shells of this species that have patterns of breakage potentially attributable to hominin action are clearly attributable to the bonebed (Joordens et al. 2009, 2015).

Plant macrofossils and palynological data indicate that the Trinil paleo-river lowland was largely open arboreally and dominated by reeds and grasses but also had wet forests (e.g., swamp forest and riparian forest) and montane forests higher in the drainage. The main bonebed commonly contained bioclasts of wood, leaves, and reedy grasses (Cyperaceae), according to firsthand reports (SI I-34). The main leaf bed, which had its lowest expression just above the **HK** in the Selenka right-bank Pit I, had leaves from lowland (evergreen) rainforests (as discussed extensively in Berkhout and Huffman 2021; Schuster 1911a, b; Selenka and Blanckenhorn 1911; also, Flenley 1979; Matthew 1928).

Palynological analyses of the Pucangan and Kabuh Formations at Trinil strongly suggest that while the paleolowland had herbaceous vegetation with forested portions,

TABLE 5. *STEGODON-HOMO ERECTUS* FAUNA ASSOCIATION.

Homo erectus-bearing faunas	*STEGODON-HOMO ERECTUS* FAUNA ASSOCIATION (*S.-H.E.*)[1]			
Biostratigraphic order	Older (<<<) to younger (>>>) biostratigraphic units in Java			
Faunal relation to mainland	Derived from South Asia via faunal filtering along the Siva-Malayan route[2]			
Faunal components[1]	**Ci Saat**	**Trinil**	**Kedung Brubus**	**Ngandong**
Linkage to mainland Asia[2]	Isolated	Limited	Extensive	Diminished ?
Key occurrences (Figs. 1b and 13)	Sangiran Dome	Trinil, Sangiran Dome	Kedungbrubus-Butak	Ngandong
Formation(s) with the fauna[3]	Pucangan	Kabuh	Kabuh, Pucangan	Ngandong
Key hominin-fossil beds at the Sangiran Dome, Trinil, Butak, Perning, Ngandong	Bukuran (Sg)	Grenzbank *H.e.* bonebed (Gb)[3] Main (*P.e.*) bonebed (Tr)	Butak bonebed (Bk)[3] Perning *H.e.* bonebed (Pn)[3] Ngebung hominin bed (Nb)[3]	Ngandong *H.e.* bonebed (Ng)[3]
Site- and bonebed-summary in Supplementary Information	SI I-44 (Sg)	SI I-39 (Tr) and -45 (Gb)	SI I-41 (Bk), -42 (Pn), and -46 (Nb)	SI I-40
🔴 🔵 ● = a known constituent in a fauna or reasonably attributed to it (criteria specified in Table 3). The taxa shown in a bold font are in the Trinil fauna (see Table 3). 🔴 and 🔵 = a taxon that is present in four- and three-faunas, respectively[4, 5] ☐ = not known from a particular fauna. -- = a taxonomic group that is not known from a particular fauna. ? = potentially present as an unidentified species.				
CERVIDAE				
Axis lydekkeri (and *Axis* sp.)	🔴	🔴	🔴	🔴
Muntiacus muntjak	🔵	🔵	🔵	☐
***Rusa* sp.**	☐	☐	●	●
BOVIDAE				
(large Bovidae)	●	--	--	--
Bibos palaesondaicus	?	🔵[5]	🔵	🔵
Bubalus palaeokerabau	?	🔵[5]	🔵	🔵
Epileptobos groeneveldtii	?	☐	●	--
(small Bovidae)	☐	--	☐	☐
Duboisia santeng	☐	●	●	☐

TABLE 5. *STEGODON-HOMO ERECTUS* FAUNA ASSOCIATION (continued).

Homo erectus-bearing faunas	*STEGODON-HOMO ERECTUS* FAUNA ASSOCIATION (*S.-H.E.*)[1]			
PROBOSCIDEA				
Elephas hysudrindicus	☐	☐	●	🔴
Stegodon trigonocephalus	🔴	🔴	🔴	🔴
SUIDAE				
Sus brachygnathus	☐	●	☐	?[4]
Sus macrognathus	☐	☐	●	●
[OTHER UNGULATES]				
Hexaprotodon sivajavanicus [4]	🔴	🔴	🔴	🔴
Rhinoceros sondaicus [5]	☐	●	●	☐[4]
Rhinoceros unicornis kendengindicus	☐	☐	●	☐
Tapirus indicus [6]	☐	☐	●	●[4]
CARNIVORA				
(large-bodied carnivores)				
Hyaena brevirostris	☐	☐	●	☐
Panthera sp.	🔴	--	--	--
***Panthera tigris* ssp.** [6]	?	🔴	🔴	🔴
(small-bodied carnivores)				
Lutrogale palaeoleptonyx	☐	☐	●	☐
Prionailurus bengalensis	☐	●	☐	☐
Xenocyon trinilensis	☐	●	☐	☐
PRIMATES				
Homo erectus	🔴 [4]	🔴	🔴	🔴
***Hylobates* sp.** [6]	☐	●	☐	☐
***Macaca* sp.**	☐	🔵	🔵	🔵
Trachypithecus cristatus	☐	●	☐	☐
[OTHER]				
Hystrix lagrelli [6]	☐	●	☐	☐
Manis palaeojavanica	☐	☐	●	☐
Rattus trinilensis	☐	●	☐	☐

TABLE 5. *STEGODON-HOMO ERECTUS* FAUNA ASSOCIATION (continued).

[1] The Pleistocene biostratigraphic units were proposed by de Vos et al. (1982) and Sondaar (1994), who ordered them in a logical geochronological sequence (Aziz et al. 1995: 352). The *Stegodon-Homo erectus* fauna association (*S.-H.e.*) consists of four faunal units that contain *Homo erectus* and the extinct proboscidean *Stegodon* (de Vos 2004, 2007; de Vos and Long 2001; Hertler et al. 2007; van der Geer et al. 2010; also, de Vos 1996a, b, 2006; de Vos et al. 1892, 1993, 1994, 1999; Sondaar et al. 1983). The component faunal units are based on the presence of newly arrived species[2] and advanced forms in the assemblages from different fossil-rich locales. Van den Bergh et al. (2001) have a late version of the lists, which is partially undated here. The placement of the Trinil fauna in a younger biostratigraphic position, the Kedung Brubus fauna (Puspaningrum et al. 2020), is not accepted here.

[2] The Java mammalian fauna was derived from ancient Indian lineages (Dubois 1908; Martin 1884). Pleistocene low sea level has contributed to mammalian dispersal across the Sunda Shelf from Myanmar and Indochina (Colbert 1943; de Terra 1943; Molengraaf 1921; Rensch 1936), a dispersal movement that has come to be termed the Siva-Malayan route with paleogeographic implications over geological time (Aziz 2000; Aziz et al. 1989, 1995, 1999; de Vos 1988, 1993, 1995a, b; de Vos and Long 2001; de Vos et al. 2007a; van den Bergh 1999). See maps of the Sunda Shelf in SI I-50. The Trinil main bonebed has the first definitive occurrences of two large-bovid species *Bibos palaesondaicus* and *Bubalus palaeokerabau*. *Elephas hysudrindicus*, which is absent in the Trinil fauna, co-occurs with *Stegodon* in the Kedung Brubus and Ngandong faunas, and is related to *Elephas hysudricus* of South Asia and Myanmar; *E. hysudrindicus* was replaced during the Late Pleistocene by *Elephas maximus*, the Indian Elephant (Hooijer 1955; van den Bergh 1999). See Puspaningrum et al. (2020) for additional information on fossil proboscideans from Java.

[3] In some publications, the Pucangan Formation at Sangiran Dome is termed the Sangiran Formation and the Kabuh Formation at the Dome is the Bapang Formation. Aimi and Aziz (1985) report a *Tapirus* sp. in the Grenzbank bonebed at the Brangkal excavation site, and the upper canine of the saber-toothed *Megantereon* sp. *in situ* in the Grenzbank at the 1976–1979 Brangkal excavation site (Aimi and Aziz 1985; de Vos and Aziz 1989). Moigne et al. (2004b; also, Sémah et al. 2016) attribute the Ngebung bonebed (their stratal units "Ngb A" and "Ngb B") to a "Late Trinil" fauna, based on species that often occur in the Kedung Brubus fauna (*Rusa* sp., *Epileptobos groeneveldtii*, *Hyaena brevirostris*, and *Hystrix lagrelli*) along with *Axis lydekkeri* and *Hexaprotodon sivajavanicus*. The taxa found by excavation of the Butak bonebed (in the Pucangan Formation north of Kedungbrubus, SI I-36 and -42) is based on a list of von Koenigswald (1934: 191, Tafel II) and the "Boetak" material in the Dubois Collection. Combined, the taxa are: *Stegodon trigonocephalus*, *Hexaprotodon sivajavanicus*, *Leptobos cosijini*, *Axis lydekkeri*, *Rusa* sp., *Duboisia santeng*, *Sus* sp., *Manis palaeojavanica*, *Panthera tigris*, and *Crocodylus ossifragus*. The Butak bonebed is several hundred meters stratigraphically below the Kabuh Formation at Kedungbrubus (SI I-36, -41, -42). Huffman et al. (2006) found *Duboisia santeng* in the relocated Perning bonebed, the source of the Mojokerto *Homo erectus* child skull, and *Rhinoceros* was collected on the surface near the Perning bonebed outcrop (SI I-43). Huffman et al. (2010a, b) and Rizal et al. (2020: Supplement Table 3) give the assemblage known from Ngandong *Homo erectus* bonebed. See van der Geer et al. (2018) regarding canids. An otter maxillary fragment that Dubois (1908) described was reclassified as *Lutrogale palaeoleptonyx* (Willemsen 1986), and it differs slightly from the extant *L. perspicillata* (Willemsen 1986).

[4] Dubois (1908) indicates no hippopotamus fossils had been found at Trinil, and this has long been held to be true, but Kriele and de Winter state the presence of lower jaw of a hippopotamus with 2 molars attached in a letter of October 19, 1891 (SI II-6) and the taxonomy was confirmed by Hooijer (1950).

[5] Five taxa occur throughout the *S.-H.e.* (● *Axis lydekkeri*, *Hexaprotodon sivajavanicus*, *Stegodon trigonocephalus*, *Panthera tigris-Panthera* sp., and *Homo erectus*). Four additional taxa are in three of the faunas (● *Muntiacus muntjak*, *Bibos palaesondaicus*, *Bubalus palaeokerabau*, and *Macaca* sp.). Certain species are represented by different subspecies in some biostratigraphic units (for example, the increasing numbers of molar ridges that define *S. trigonocephalus praecursor*, *S. t. trigonocephalus* and *S. t.* ngandongensis; van den Bergh 1999; van der Geer 2010). Tiger was the only persistent large-mammal carnivore in the *S.-H.e.* (Hertler and Volmer 2008). The large mammal/carnivore cohort in Java was markedly more limited than those associated with *Homo erectus* in China (Rabett 2012) and mainland Asia generally. According to Larick et al (2001: 4866), the "upper units [of the Pucangan Formation at Sangiran Dome] … have yielded *Homo erectus* fossils" (also, Matsu'ura et al. 2020), such as the specimens known as *Pithecanthropus* B ('S1') and *Pithecanthropus* IV ('S4;' Aziz et al. 1995). Bettis et al. (2009: 13) note that the hominins were "one component in the fully terrestrial and endemic island-type fauna known as Ci Saat," as described in de Vos et al. (1994). Brasseur et al. (2015: 86) caution: "Several authors (e.g., Watanabe and Kadar, 1985) think that human fossils first appeared in the Upper Sangiran [Pucangan] member, a position disputed by other researchers."

[6] A faunal turnover took place in Java during the Late Pleistocene; the corresponding biostratigraphic unit is the Punung or *Homo sapiens-Pongo* fauna, which contains Asian Elephant, orangutan, and gibbon, among other rainforest-adapted introductions from China (de Vos 1983, 1996a; de Vos and Long 2001; Storm and de Vos 2006; Storm et al. 2005; van der Geer et al. 2010; Westaway et al. 2007, 2017). The change-over from the *S.-H.e.* was not complete until after the deposition of the Ngandong *Homo erectus* bonebed (SI I-40). A Holocene fauna with *Homo sapiens* is known from the East Java Wajak site that Dubois collected in 1890 (Dubois 1920, 1921; Storm 1995). The assemblage dates to ~40 ka and contains tropical rainforest mammals such as *Pongo* and *Hylobates* (Storm et al. 2013). While Punung fauna species are uncommon or missing in the *S.-H.e.*, large ungulates (e.g., bovids, cervids, suids, *Rhinoceros*) and carnivores (*Panthera tigris*) do occur in the Punung assemblages as well as those in the *S.-H.e.* In 1887–1890, Dubois already had collected in karstic caves (and possibly other associated contexts) of the Sumatra's volcanic Padang Highlands (elevations of 500–2800 m, de Vos 1983; Hooijer 1948b). The collecting produced two anatomically modern human teeth, and the remains of *Muntiacus muntjak* (N=167*), *Pongo pygmaeus* (143*), *Sus scrofa* (>100*), *Hystrix brachyura* (>100; Malayan porcupine*), *Rusa* sp. (43*), *Tapirus indicus* (32), large bovids (28*), *Rhinoceros* sp. (22*), *Presbytis*/*Trachypithecus*/*Macaca* (16*), *Elephas* (8*) *Ursus malayanus* (6) and *Naemorhedus*/*Capricornis* sp. (gorals/serows); "a few" teeth each were found of *Hylobates* sp., *Arctonyx collari* (Hog badger), *Panthera pardus*, *Panthera tigris*, *Catopuma temminckii* (Asiatic Golden Cat), *Cuon alpinus* (Asian Dhole), *Paradoxurus hermaphoditus*, and *Rattus* sp. (Westaway et al. 2017: Supplementary Table 2; the *s indicates species that are both in the Dubois Collection and materials that Westaway et al. found in recent fieldwork; also, Louys et al. 2017, 2021; Wirkner and Hertler 2019). Hooijer described large bovid material from the Padang Highland as *Bos javanicus* subsp., a variety of the historic Banteng cattle (de Vos 1983). The diminished abundance of large bovids in the Punung fauna compared to the *S.-H.e.* has yet to be reconciled precisely to the 'glacial' drier climate and more expansive lowlands that often have been inferred to have existed during Late Pleistocene periods of low sea level (SI I-49, -50).

the uplands of the drainages were dominated by montane rainforest (SI I-34). One palynological sample collected near the main bonebed stratigraphic level on the left bank contained more pollen of woody taxa than did samples from the underlying Pucangan, and less dryland-tree signal than samples from the overlying Kabuh Formation, leading to a suggested up-section shift toward wetter paleo-landscapes through the period of main bonebed accumulation (Polhaupessy 1990, 2002, 2006).

LITHOFACIES

Archival accounts contain less information about the lithofacies of the main bonebed than they do on its bioclastic content. However, Dubois and the Selenka geologists offered key lithological observations, and most helpfully, identified modern depositional analogs for the main bonebed.

In 1895, Dubois (Dubois 1896b: 251) summarized the lithologies he saw in 1891–1893 (SI II-227):

> *Bones are present within beds of tight and hardened volcanic tuffs, consisting of clay, sand and lapilli rocks. These tuffs suggest a fluvial origin, especially indicated so by a strong general presence of fresh water animals* [such as molluscs] *and by certain fluvial structures that English geologists call current bedding* [crossbedding or -lamination].

The "hardened" rock fits other firsthand reports of indurated beds during excavation (e.g., SI II-42, -183, -190 to -193; also, SI II-54, -55, -58).

The endocranial space of the Skullcap was filled with the indurated pebble conglomerate, which consisted of fresh, very poorly sorted, volcanic minerals and rock fragments within a fine-grained matrix (see Figure 2c, d). The clastic materials adhering to other Trinil fossils in the DC range from very fine-grained volcaniclastic sandstone to granule-pebble conglomerate (SI I-20 to -23; also, Huffman et al. 2018). Complete long bones tend to have finer-grained- and partial-infills of clastic material, whereas bones that were broken *in situ* tend to have coarser-grained fills and adhering sediment (Hill et al. 2015; M. Hill and L. Todd, personal communication, 2015). Labile minerals in the sandstone affixed to the specimens include plagioclase, hornblende, and pyroxene, indicating that volcanoes in the Trinil paleo-river uplands were shedding fresh rocks, crystals, and glass.

Right up to the moment of deposition of the main bonebed, the Trinil paleo-river carried a mixture of shelly and vegetal bioclasts along with gravel, sand, and volcanic ash. The bioclasts represent the concurrent deposition of hydrodynamically different elements of Voorhies (1969) dispersal groups (e.g., craniums with long bones). The competence of the flow is evident in the cobbles and boulders of hard andesite, pumiceous gravel, rip ups of *"clayey marl cobbles"* and clots of entwined antlers that the **HK** contained (e.g., Berkhout and Huffman 2021: 38 and 73; Carthaus 1911b: 14; Oppenoorth 1908a; SI II-245; Oppenoorth 1911: xxxiv). The tusks, tree trunks, and very large bioclasts of more equant shapes appear to have been rafted into place amidst a dense fluvial load of mud, sand, pebbles, gravel, and smaller bioclasts.

The lithofacies of the bonebed fits transport *en masse* under suspended- and traction-movement attained during a sediment-heavy flooding, as opposed to common modes of episodic river-channel sedimentary transport and deposition. The main bonebed might be thought of as a bioclast-rich diamicton wherein biotic- and lithic-materials were emplaced simultaneously (see Pantin 1967 for types of diamictons). The cross-bedded **LB-HK** seen today along the left bank (e.g., SI I-2b) and the cross-laminated **LB-HK** that Kriele observed in 1900 must have formed by traction transport of sand, but the oversized vertebrate bioclasts that characterize the main bonebed probably were carried to Trinil by hyperconcentrated flow.

Not all the main bonebed was conglomeratic sandstone, judging from Oppenoorth's reports on 1907. He (1908b) saw fossiliferous *"bluish volcanic tuff, which reminds me of a very soft sandstone,"* and reported that the **HK** *"consists of three portions …* [in which] *finer-grained grades into a coarser-grained layer"* containing cobbles and perhaps small boulders *"a few decimeters"* in diameter (SI II-246). *"Fine blue clay with harder clay concretions"* made up the upper **HK** (Berkhout and Huffman 2021: 35; Oppenoorth 1911: xxxiv). According to the 1907 Listing, the **HK** in Selenka Pit I did have three vertical subunits with spatially varying bioclast densities (see Table 2; SI I-11c). Although the sedimentary and paleontological differences in the main bonebed suggest that variable flow conditions occurred from moment-to-moment and place-to-place during the responsible depositional events, firsthand reporting lacks descriptions suggesting that there was a long cessation of accumulation during the formation of the main bonebed.

MODERN DEPOSITIONAL ANALOGS

Ideas that Dubois and the Selenka's geologists expressed about the origin of the main bonebed draw from historic fluvial volcaniclastic deposition around the active volcanoes of Java. Even without modern descriptive and analytical skills, these workers could make visual comparisons of the bonebed to historic laharic sediments and evaluate how sedimentary processes in modern lahar-prone drainage basins might apply to Trinil (Figure 11). Their inferences benefitted from leading scientific levels of vulcanological knowledge in Java (e.g., Neuman van Padang 1983; Voight et al. 2000; also, van Gorsel 2022j).

In mid-1892, when Dubois (1982b) considered the origin of the **LB** vertebrate fossils deeply, he wrote, *"only a catastrophe, and a volcanic catastrophe at that, comparable to, but on a larger scale than, those that accompanied eruptions of the Salak (1699), Galungung (1822) and Kelud (1848)* [stratovolcanoes in Java] *can explain … these accumulations"* of the lapilli-bearing fossil beds (SI II-180; also, SI I-163). Dubois (1892a; SI II-166) had concluded that generally:

> *The fossil-bearing sediments* [of the Kendeng Hills] *…. appear to have been deposited in the same manner* [as the Recent

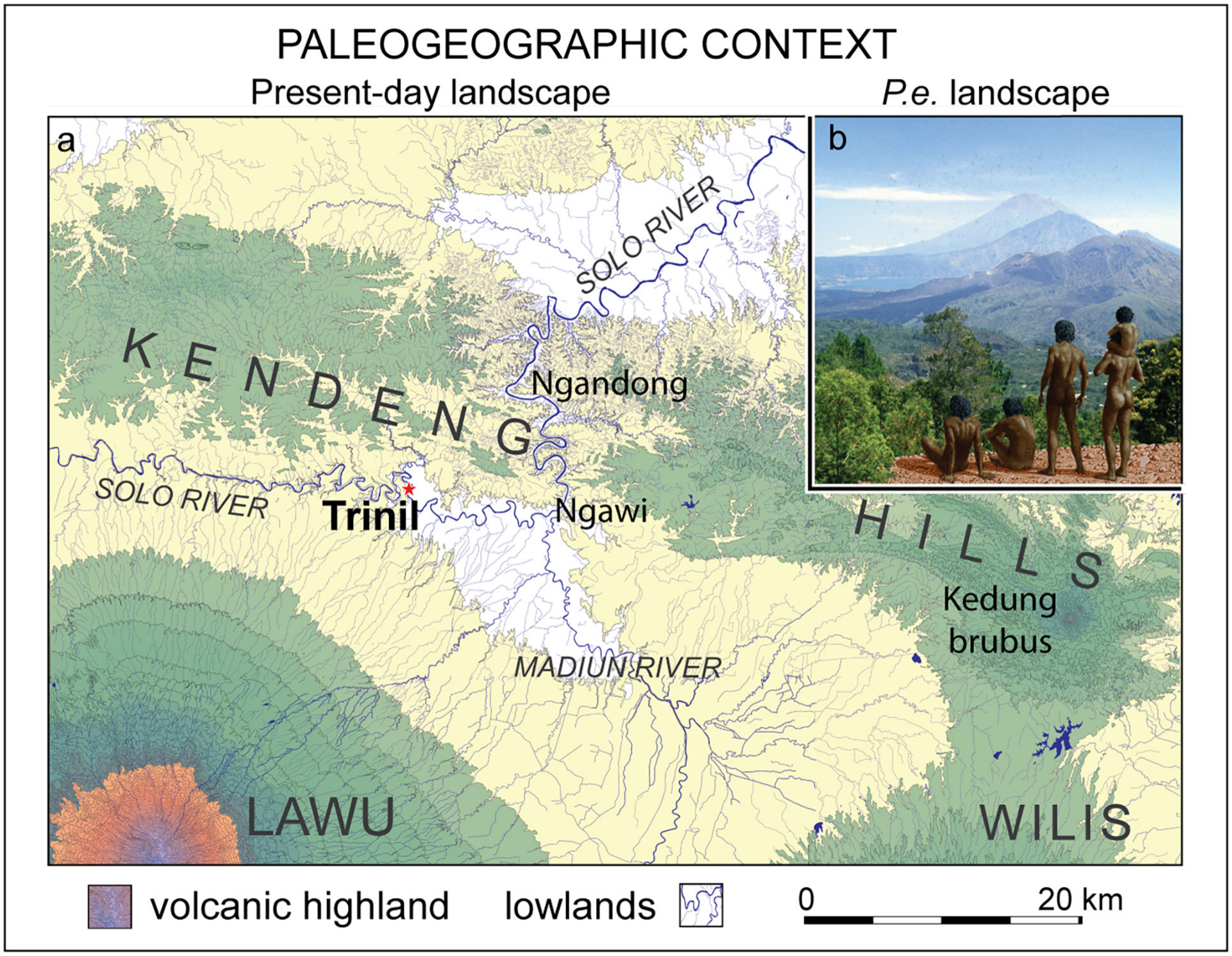


Figure 11. Dubois (1894, 1895a) attributed the fossils excavated in 1891–1893 (see Figure 2a) to taphonomic and depositional events in a Pleistocene valley and understood that the Pithecanthropus erectus *(*P.e.*) lived in and the main bonebed formed in paleogeographic conditions, which were much like those in modern stratovolcanic terrains of eastern Java. The lowland near Trinil today is less than 50m above sea level; to the south, Lawu stratovolcano rises above 1000m along a dense parallel network of drainages (green) into forested highlands (red) which crests at 3118m. The drainage contains biotopes of fine-scale complexity and carries volcaniclastic materials and biotic remains into the lowlands (SI I-37). Paleocurrent information indicated to Dubois (1894, 1895a) that the paleoriver in the time of* P.e. *flowed in an opposite direction to that of the modern Solo River. The river now flows from west to east along the southern edge of the Kendeng Hills, shifts course sharply at Ngawi to join the Madiun River tributary, and then traverses the Hills through a deeply incised valley (Solo River gap), where the Ngandong* Homo erectus *site is located (SI I-40). The Madiun watershed covers 9827km^2 (~7% of the total for Java). Part of (b) is modified from a Turner and Antón (2004) illustration.*

sedimentary] *… rocks of the lowlands. Historical eruptions of the Kelud that delivered products to the Kediri lowlands* [along the Brantas River drainage]*, consisting of sands, sometimes hardened to sandstone, tuffs and breccias,* [which are] *indistinguishable from the Pleistocene on the Kendeng slopes. Sedimentary rock material that encloses the remains of the Pleistocene Java fauna has undoubtedly similarly been carried to its destination by an eruption. This would have been partly in dry condition as volcanic sand, lapilli and bombs etc., but especially during heavy rains that mixed with them in the form of heavy slurry flowing down the slope* [lahars]*. The animals would have perished in the same manner that the inhabitants of the Kelud slope can now tell us about during the historical eruptions of this volcano. After the last eruption, many cadavers of pigs, kidangs, deer, bantengs, tigers and other forest animals were found on and within the volcanic sand etc.*

Carthaus also called attention to 19th century events in the Kediri lowlands of the Brantas River (East Java), which drains the active Kelud volcano in East Java (see Figure 1b). For Carthaus (1911b: 27–28,), floods on the Brantas *"are quite appropriate to explain the rich occurrence of animal bones and pieces of wood in the main bonebed of Trinil"* (Berkhout and Huffman 2021: 86).

Carthaus (1911b: 27) gave an example of a man carried by *"lahar sand flow during the last eruption"* of Kelud volcano who *"did not suffer any hard knocks from the rocks … in a flowing mass of very thick slurry"* (Berkhout and Huffman 2021: 86). Carthaus (1911b: 16) concluded that *"the main bonebed of Trinil is the … product of an extraordinary large lahar flow, which originated from* [an emptying of] *an erstwhile western*

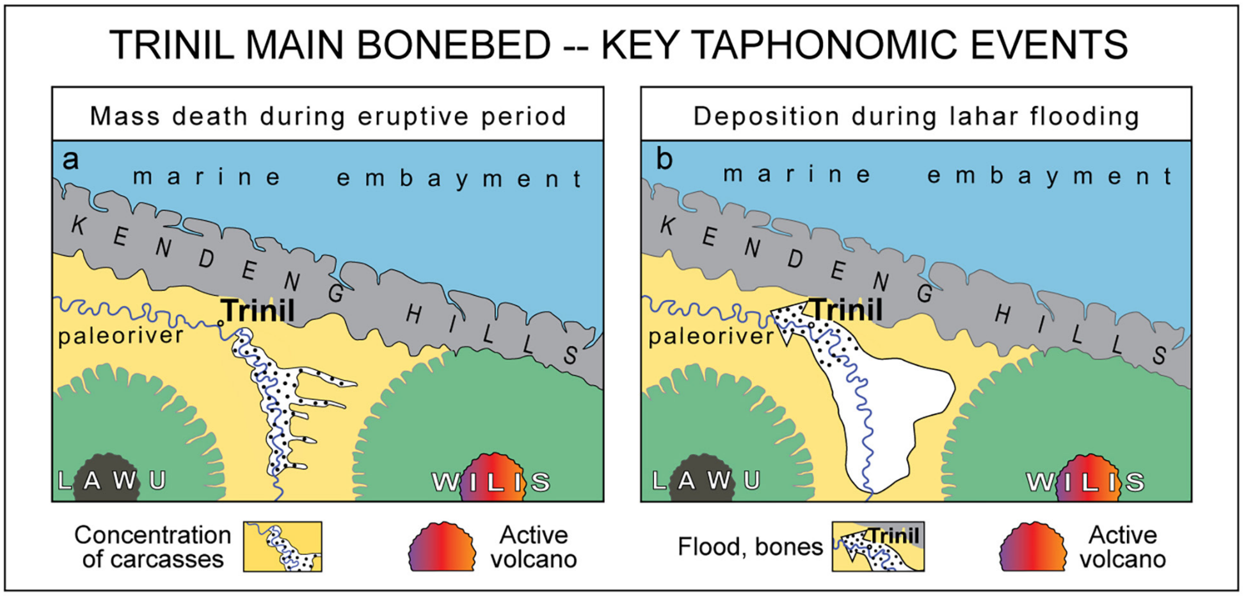


*Figure 12. We propose that Trinil main bonebed developed in two stages (partially after Huffman et al. 2010a, b, 2012b, 2018). (**a**) Accumulation of the main bonebed was preceded by a mass death of ungulates along a floodplain upriver of Trinil; the resulting carcasses were skeletonized, but the bones were not severely weathered. (**b**) Lahar flooding entrained the bony remnants and carried them (with those of aquatic reptiles, molluscs, and plants) to a point of accumulation at Trinil. Corollary proposals and comments are in SI I-25. Other* H. erectus *sites in eastern Java also formed in stratovolcanic watersheds (this figure and Figure 13; SI I-38 to -47), as did archaic fossil hominin sites in Flores, Sulawesi, and Luzon.*

crater of the Wilis," analogous to the historically active volcanoes at Kelud and Semeru (see Figure 1b; Berkhout and Huffman 2021: 76). Dozy (1911b: 21) imagined the slurry *"loose volcanic material, mainly ash and lapilli"* (Berkhout and Huffman 2021: 80). Carthaus (1911b: 14, 27) referred several times to *"sand flows"* to emphasize the dense sandy flux in lahar flooding that he envisioned responsible for the **HK** (Berkhout and Huffman 2021: 75, 86).

Carthaus' (1911b: 29) thinking was influenced by catastrophic deaths near the Semeru stratovolcano of East Java, where in 1909 *"more than 500 people lost their life"* in *"an immense tuff mudflow which,* [took place] *during an enormous rainfall in the upper regions …* [concurrent with] *incessant ash, lapilli, pumice and volcanic bombs … from the volcano"* (Berkhout and Huffman 2021: 88, footnote; also, Cool 1909). Semeru has produced deadly lahars regularly since that year (Lavigne and Suwa 2004). A 1919 event around Kelud also illustrates the potential for lahars to produce mass death where large-mammal populations concentrate; when lahars descended a thckly populated Kelud drainage that year, the flooding killed 5110 humans and 1571 livestock (B. Voight in Huffman et al. 2010b).

Carthaus (1911b: 2) further surmised: *"The Trinil conglomerate* [underlying the **HK**] *may thus possibly be the product of the first outpouring of enormous tuff mudflows from the giant western crater of the Wilis that was probably filled by a huge lake* [such as the one in the Kelud caldera of 1909]*"* (Berkhout and Huffman 2021: 80). *"The overlaying main bonebed … arrived in the vicinity of Trinil during continuation of the eruption either through the same channel as the prior tuff mudflow or in a different one created by damming"* (Carthaus 1911b: 2).

Dubois and the Selenka geologists seem to have viewed the main bonebed, and perhaps also the overlying strata, as a continuation of the laharic paleogeographic regime that is so prominent in diamictons of the Pucangan Formation underlying the Kabuh Formation around Trinil (SI I-16). These men were perceptive to focus on long-run out lahar flows as a mechanism for transportation and accumulation of the main bonebed (Huffman et al. 2012b). Subsequent research on lahars amplifies the broad spectrum of geological conclusions relevant to Trinil that one might draw from the identification of lahar deposits within a sedimentary sequence (SI I-37).

PALEOGEOGRAPHIC SETTING

Two Pleistocene stratovolcanoes that lay south of the *Pithecanthropus erectus* site in the Trinil paleo-river valley were the source for the Pucangan Formation lahars. Smaller nonvolcanic watersheds were situated within the Kendeng Hills to the north of the paleo-valley (see Figure 13 below). Wilis Pleistocene stratovolcano, located southeast of Trinil, is particularly relevant to the regional paleogeography (see Figure 11; Figure 12; also, SI I-25). Laharic breccia comprise most of a 275m-thickness of the Pucangan Formation near Kedungbrubus, where the Pucangan and Kabuh combined have 765m stratigraphic thickness of volcaniclastic deposits (SI I-41, -42). The exposed relationships in an ~35km-long outcrop on the southern side of the Kendeng Hills make for an open-air cross-section of the cone-shaped northern flank

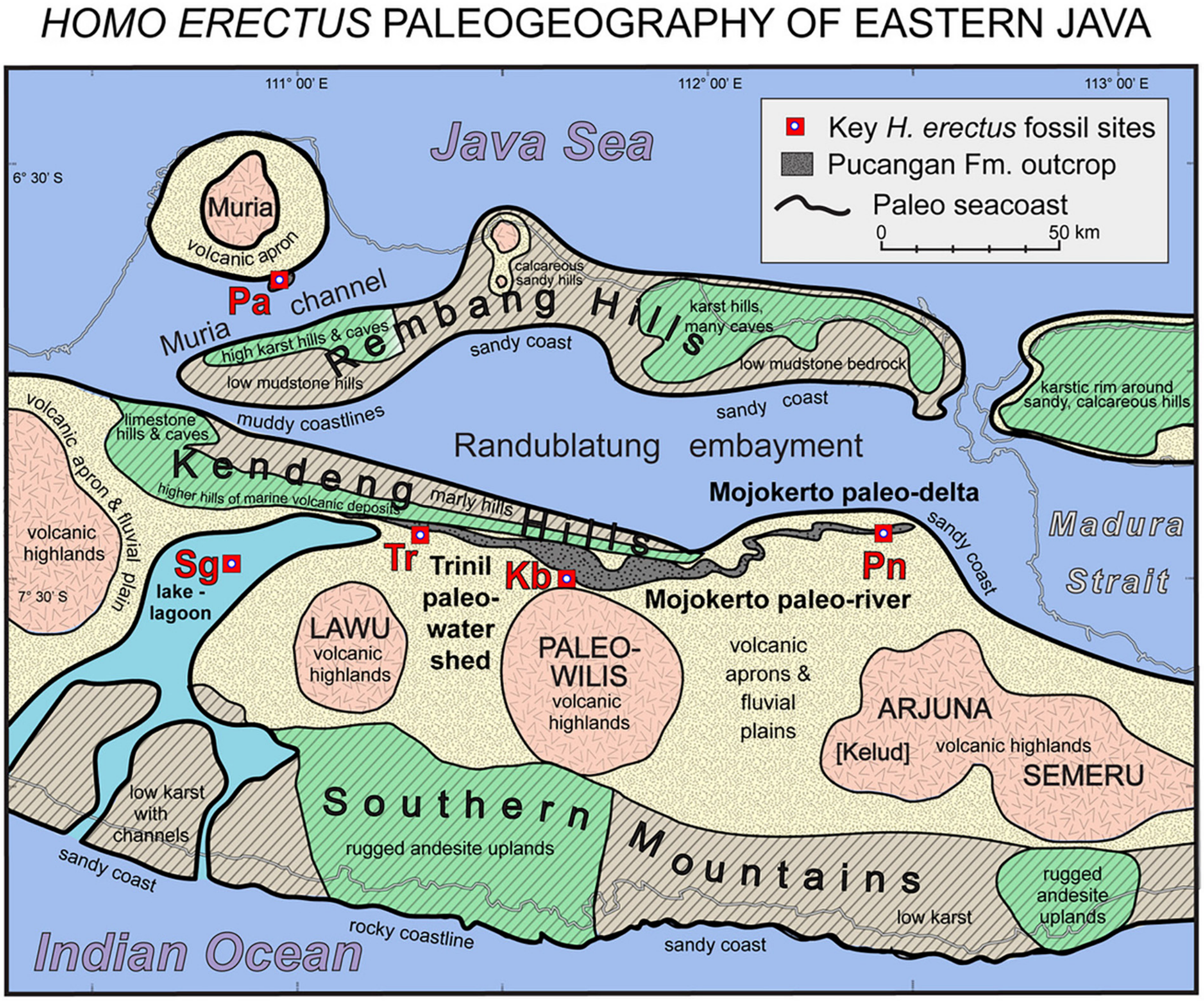


Figure 13. A broad variety of potential habitats were available to the Pithecanthropus erectus *population of eastern Java due to the presence of high-standing stratovolcanoes, hilly pre-Pleistocene carbonate- and volcanic-bedrock terranes, large- and small-rivers, various seacoasts, and islands reachable by short sea crossings, as illustrated here in a generalized paleogeographic map (after Huffman 1997, 1999a, b, 2001a, 2020; Huffman et al. 2000). Shown for reference is the outcrop distribution of the Pucangan Formation volcaniclastic facies, a key to interpreting the stratovolcanic paleo-watersheds in which* Homo erectus *fossils accumulated (the facies was mapped by van Es [1931]; Duyfjes [1936, 1938a-d], summarized in Huffman 2020: 23–35 and 41; also, De Genevraye and Samuel [1972]; Huffman et al. [2006]; I.J.J.S.T. [1992]; Lunt [2013: Fig. 135]; Watanabe and Kadar [1985] and multiple unpublished geological studies done for petroleum exploration noted in Huffman et al. [2000]).*

of the immense Pleistocene paleo-Wilis stratovolcano (Figure 13; also, Huffman 2020). Volcaniclastic sands and lahars originating from the center spanned 150km east west and reached both Trinil and Mojokerto (SI I-38, -43). The west-flowing drainage apparently was part of the Trinil paleo-watershed (see Figure 12).

FORMATIONAL EVENTS

A central issue in assessing the origin of the main bonebed is to explain how thousands of large, disarticulated, and little-abraded vertebrate bioclasts and numerous other biotic remains became concentrated (with certain internal irregularities) within a thin, localized, poorly sorted gravelly volcaniclastic sand along a lowland section of a large perennial river (SI I-25).

The biofacies and lithofacies, as evaluated above, lead to a plausible hypothesis. The main bonebed fossil assemblage (see Table 1) represents the catastrophic death of multiple large-ungulate species, notably *Bibos*, *Bubalus*, and *Axis*, which typically live in herds (see Table 4). The bony fossils of these and other terrestrial animals exhibit evidence of neither substantial weathering by surface exposure nor abrasion or bioclast sorting from river transport, and include large bioclasts, such as *Stegodon* skulls and tusks. The terrestrial species co-occur with the remains of forest animals, aquatic-vertebrates, molluscs, and plants, giving further information on the formational conditions. We explain these features and the lithofacies of the main bonebed by proposing the simultaneous death of hundreds of ungulates in one section of the Trinil paleo-river watershed surrounding a stratovolcano followed by *en masse* transport of the skeletonized, little-weathered remains by lahar flooding, which resulted in little bioclast-damage and -sorting (as explained more fully in SI I-25).

Ungulate populations in the Trinil hinterland doubtless inhabited wide areas across the flanks and lowlands of the stratovolcanoes (see Figure 11). Periods of intense eruption or drought plausibly forced hundreds of ungulates towards areas with plentiful water and forage. One refuge for *Axis*, cattle, water buffalo, *Stegodon*, *Duboisia*, *Sus*, and *Rhinoceros* (see Tables 1 and 2) was in the floodplain of the trunk Trinil paleo-river or lowland tributary (see Figure 12a). Tigers and a few dogs presumably also inhabited the refuge, as did at least three adult *Pithecanthropus erectus*.

Grass and forbs were sufficiently widespread there to sustain the deer herd long enough for many males to shed antlers. Reed grounds or the woody forest undergrowth presumably offered safe harbor. The water courses passing through the refuge had the same diverse suite of riverine reptiles, fish, and molluscs as existed in other perennial tributaries and standing water bodies of the watershed.

Catastrophic mortality decimated the ungulates. Almost all the carcasses decayed to the point of skeletonization, but the bones were not substantially weathered or damaged by biotic taphonomic processes. A lahar flood inundated the paleo-river floodplain, sweeping up thousands of decomposed skeletal remains, and had sufficient hydrodynamic competence to suspend and carry nearly whole *Stegodon* and large-bovid craniums.

At Trinil, a pulse carrying the 1891–1893 *Pithecanthropus erectus* Skullcap and Femur I and hundreds of other large mammal bioclasts followed an initial flood surge, which had carried fewer bioclasts and more cobbly gravel. Over the course of hours or days, internal streams and pulses of the flood waters segregated bioclasts and lithic materials sufficiently to create internal lithic and bioclastic facies within the **LB**, **LB-HK**, and **HK** deposit. The four *Pithecanthropus erectus* femora from the 1900 excavation might have accumulated a few hours or days earlier or later than the first *P.e.* remains. The *Pithecanthropus erectus* population in Trinil paleo-lowland used lithic tools so sparingly that no flakes or artifacts came to be embedded with the voluminous amounts of granules and pebbles excavated from the bonebed.

Several meters of sandy volcaniclastic deposits events representing the same conditions as those expressed in the main bonebed might have accumulated after it. This is the situation in the terrace deposits containing the Ngandong *Homo erectus* bonebed, which is a bony concentration in the lower portion of the ~3m thick deposit that formed by lahar flooding and includes an unambiguous diamicton facies above the bonebed (see Table 5; SI II-40).

PALEOGEOGRAPHIC IMPLICATIONS

Eugène Dubois considered *Pithecanthropus erectus* and associated Trinil fossils in broad paleobiogeographic context. Following this tradition, we highlight several roles that the main bonebed currently plays in understanding the *Homo erectus* paleogeography of southern Sundaland (Java, Java Sea portion of the Sunda Shelf, southern Sumatra, and southern Borneo). Table 5 and Figures 13 and 14 summarize our conclusions about key *H. erectus*-fossil beds and sites containing the *Stegodon-Homo erectus* faunal association species (also, SI I-36 to -50).

The hominin populations known from existing *Homo erectus* fossil discoveries lived in stratovolcanic watersheds. The regional conditions are illustrated in Figure 13, a generalized paleogeographic map of the Early-Middle Pleistocene as inferred from the upper Pucangan Formation and lithostratigraphically correlative strata. Included for orientation is the outcrop of the Pucangan Formation volcaniclastic facies, noted because it contains gravelly volcanic diamicton deposits important for the paleogeographic reconstruction. The volcaniclastic facies was traced along the south side of the Kendeng Hills from the greater Trinil area through Kedungbrubus to Mojokerto (see Figure 13). The diamicton component was thickest in the Kedungbrubus-Butak area (Kb, Bk) north of present-day Wilis-Liman volcano, indicating Pleistocene paleo-Wilis was a major source of the lahar flows responsible for the diamictons and other volcaniclastic sand and gravel materials (SI I-36, -41, -42).

Volcaniclastic deposits are the discovery contexts at the consequential hominin-fossil sites of Ngandong, Kedungbrubus, Mojokerto, Sangiran Dome, and Trinil, and dominate the lithofacies of the hominin-fossil bearing formations of eastern Java (SI I-37). Indeed, all *Homo erectus* fossils so-far discovered in the region accumulated in paleo-watersheds that drained high-standing stratovolcanoes, much like the circumstances for *Pithecanthropus erectus* (Huffman 2017). Before *H. erectus* arrived in Java, most of its large-scale physiographic features were present (compare Figure 1b to Figure 13). Figure 14 summarizes the broad range of potential habitats that *H. erectus* could have occupied.

The large-mammal species in the main bonebed define the Trinil fauna (see Table 3). It anchors the *Stegodon-Homo erectus* faunal association that characterizes the volcaniclastic formations containing the *Homo erectus* fossil remains (see Table 5). The *S.-H.e.* embodies a paleobiogeographic link between *H. erectus* and certain lineages of large bovids, cervids, proboscideans, rhinoceros, suids, and tiger (de Vos 1995b). *Axis lydekkeri*, *Panthera tigris* (or *P.* sp.), and *Stegodon trigonocephalus* were present during the whole period of known *H. erectus* occupation (see Table 5). *H. erectus* populations seem to have been as widespread as those of other temporally persistent *S.-H.e.* lineages. Ubiquitous and persistent also were the inhabitants of large river systems, *Crocodylus*, Testudines, and molluscs. Both terrestrial and aquatic fossils are common in the *H. erectus*-bearing formations and consistently situate the riverine faunas in the same volcanic watersheds as the hominins.

Radiometric dating at the Ngandong *Homo erectus* site and several sites at Sangiran Dome provide a geochronological framework for the life and death of the hominin populations in the stratovolcanic paleo-watersheds. The

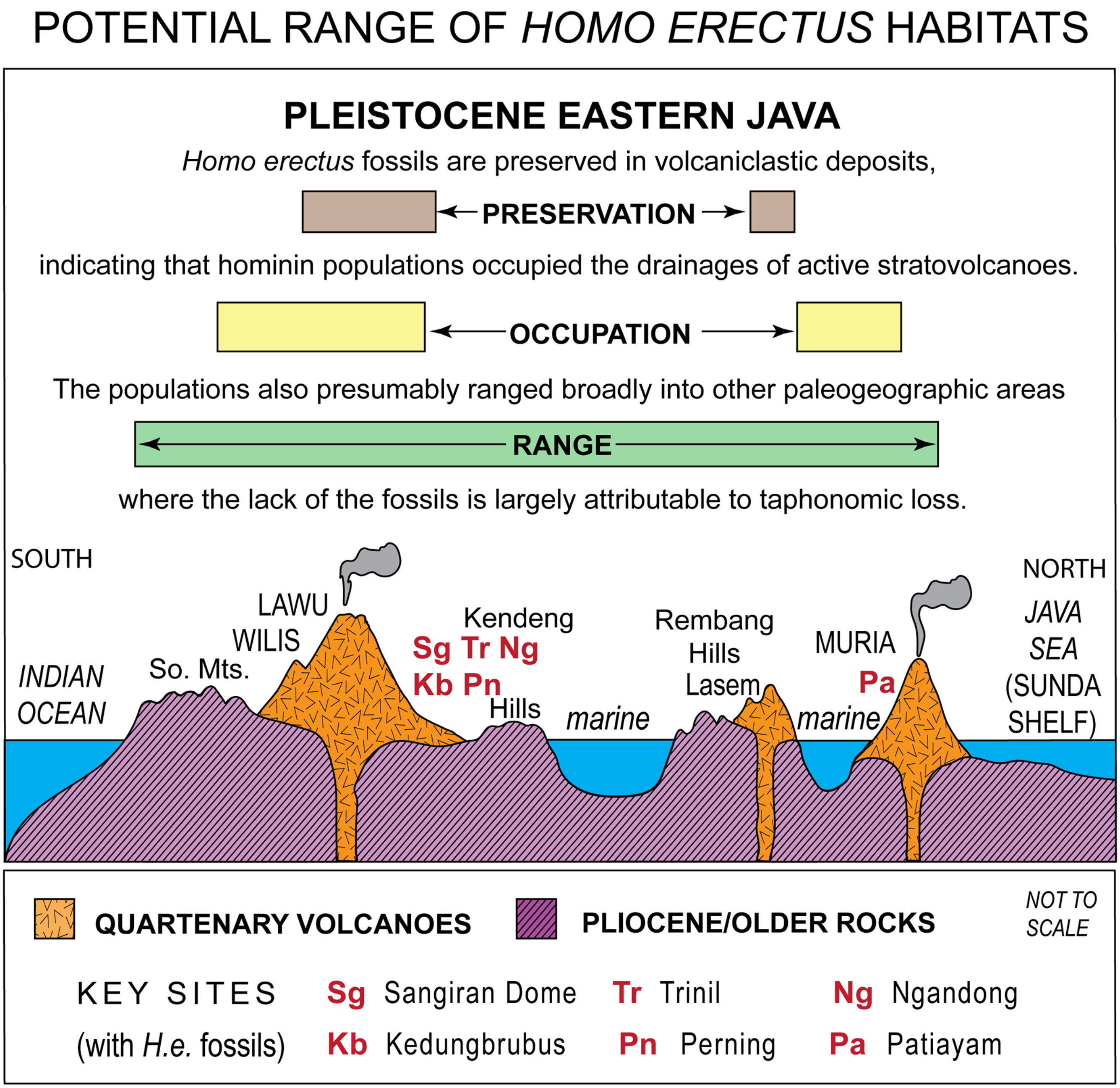


Figure 14. Homo erectus *fossil sites situated in the stratovolcanic paleo-watersheds of eastern Java displayed in a north-south schematic transect (Kb to Tr; see also Figures 1b and 13). These discoveries strongly suggest that archaic hominins also occupied or frequented terranes where none of their fossils have been discovered, including in the Kendeng Hills, Rembang Hills, and Southern Mountains (So. Mts.; Huffman 1999b, 2001a; also, SI I-38 to -48). Volcaniclastic accumulation in these uplands apparently was insufficient to preserve archaic hominin skeletal remains (after Huffman et al. 2012a, b). The abbreviations for discovery sites, such as Tr, are the same as in Table 5 and Figures 1b and 13. Deep seas in the Indian Ocean formed a persistent barrier to southward terrestrial migration (this figure), but during periods of Pleistocene sea levels that were below present day, vast areas of the Sunda Shelf were potentially inhabited by* H. erectus *and other large mammals (SI I-38, -49 to -52). The uplands and volcanoes of Java and the submerged Sunda Shelf to the north are Neogene back-arc tectonic terranes related to lithospheric plate subduction evident in the deep oceanic trench lying south of Java (SI I-38).*

oldest-known hominin fossils at Sangiran Dome are late Early Pleistocene; that is, ≥0.9 Ma and more likely <1.3 Ma than <1.5 Ma (SI I-45, -46). The Ngandong *Homo erectus* bonebed is early Late Pleistocene in age, modelled to be ~0.1 Ma (117 to 108 ka; SI I-40; the Pleistocene sub-epochs are used in the sense shown in SI I-49). Thus, archaic hominin populations inhabited eastern Java for >0.8 Ma and perhaps ~1.4 Ma.

Comparing Ngandong to the youngest Sangiran *Homo erectus* leaves an apparent lacuna of ~0.8 Ma. Radioisotopic dating at Trinil is taken by some to indicate that the main bonebed is ~0.5 Ma (Joordens et al. 2015) or even ~0.1 Ma (about the same age as the Ngandong terrace deposit according to Berghuis et al. 2021; SI I-35). A more accepted chronology relates Trinil to radiometric results and biostratigraphic data from Sangiran Dome. The large-mammal assemblage in the Grenzbank *H. erectus* bonebed at the Dome represents the Trinil fauna (see Table 5; SI I-45). Since the Grenzbank is >0.9 Ma, the Trinil fauna was present in eastern Java by the end of the Early Pleistocene. This inference is supported by the ~0.8 Ma age of Ngebung hominin bed, which overlies the Grenzbank and has a somewhat evolved Trinil fauna (see Table 5 [footnote 3] and SI I-46). The Trinil fauna is clearly older in biostratigraphic terms than the Ngandong fauna (see Table 5).

Another paleontological inference arises from comparing the Grenzbank and Trinil bonebeds. Terrestrial vertebrate fossils in the Grenzbank are reworked bioclasts that were produced over a protracted period of geological time, in contrast to shorter-term pre-depositional taphonomic development of the fossils in the Trinil main bonebed (see Figure 12; SI I-42, -45). The faunal similarity between the two bonebeds, one having reworked bioclasts and the other not, suggests that the more rapidly formed Trinil main bonebed and the palimpsestic Grenzbank *Homo erectus* unit both had fossils representing most of the large mammals present then in stratovolcanic watersheds of eastern Java (see Table 5), if not across the region's non-volcanic uplands also (e.g., see Figure 14).

Even though the Ngandong and Trinil bonebed are distinguishable because of their differing large-mammal faunas and geological ages (see Tables 2 and 5), the two bonebeds had similar taphonomic and sedimentological histories. Both bonebeds formed after the (i) an aggregation of ungulates in a floodplain of a major stratovolcanic drainage, (ii) decimation within the population concentration, (iii) skeletonization of remains without severe bone destruction (such as biotic damage, weathering, and pervasive fragmentation), (iv) transport of tens of thousands of bones downriver by laharic flooding, and (v) local concentration of skeletal materials by a large river (see Figures 11 and 12; SI I-42, -45; Huffman et al. 2010a, 2012b). Each set of events took place over a short geological period (perhaps, just a few months or years), and therefore, both terrestrial-fossil assemblages appear to closely approximate the large-mammal fauna present in the respective stratovolcanic paleo-watersheds (see Figure 11).

The stratovolcanic paleo-drainages in which both the Ngandong and Trinil bonebeds formed were dominated by the same large-scale topographic features; that is, Pleistocene versions of the Kendeng Hills, Lawu volcano, and Wilis volcano (see Figures 1b and 11). Paleo-Wilis was a massive- and long-lasting stratovolcano (see Figure 13; SI I-38). Geological evidence of its size and long period of activity is clear from its northern flank in the Kedungbrubus-Butak area. There, hundreds of meters of gravelly laharic diamicton accumulated in the Pucangan Formation, as mentioned above (SI I-16 to -18). Fossils of large-bodied vertebrates have been found in lower portion of diamicton-bearing sequence, so that a diverse fauna of terrestrial- and aquatic species was present around paleo-Wilis early in its eruptive history (see Table 5; Butak bonebed, SI I-36, -42).

The watersheds on the west side of paleo-Wilis fed the Solo River where the Ngandong bonebed accumulated ~0.1 Ma (see Figure 13; SI I-38). Discharge from paleo-Wilis headwaters might have previously drained to Trinil (see Figure 12). The watershed to the east of paleo-Wilis clearly fed the Mojokerto paleo-delta where the Mojokerto *Homo erectus* child skull was deposited near the shoreline of a marine delta (see Figure 13; SI I-38, -43). Viewed broadly, the Mojokerto, Ngandong, Sangiran Dome, and Trinil discovery sites represent different proximal-to-distal positions along Pleistocene stratovolcanic drainages extending as far as marine shore zones (see Figure 14).

Profound temporal environmental and geographic changes took place during the period when *Homo erectus* occupied eastern Java. The youngest-documented hominin fossil at Sangiran Dome dates to ~0.8 Ma (SI I-44), making the minimum span of *Homo erectus* inhabitation in the paleo-Solo Basin >0.5 Ma. This particular time span corresponds approximately to the global Mid-Pleistocene Transition (MPT). Episodes of glacio-eustatic change intensified during the MPT compared to older Pleistocene patterns (SI I-49a). The oldest hominins in the Sangiran area probably arrived before the MPT or during its earliest phases, when the large-mammal fauna of Java (Ci Saat fauna) had less taxonomic diversity than did the Trinil fauna (see Table 5). Periods of lower global sea levels during the MPT doubtless exposed more land between Java and mainland Asia (Sunda Shelf) and afforded the Trinil fauna terrestrial lineages greater access to southern Sundaland (SI I-50).

Little is known about the impact that specific glacio-eustatic fluctuations had on the populations of *Homo erectus* and associated *S.-H.e.* species, but the youngest well-dated *S.-H.e.* deposit, the Ngandong *Homo erectus* bonebed, provides a fruitful reference point. Ngandong *H. erectus* paleodeme and associated Ngandong fauna flourished in the Javan interior ~113 ka (SI I-40). Ten- to fifteen-thousand years earlier, ancestor populations would have lived in relative geographic isolation during the last interglacial sea-level highstand (Marine Isotopic Stage 5e, MIS 5e). During the preceding glacial period (MIS 6; SI I-49a), older *S.-H.e.* populations would have had the opportunity to expand enormously across landscapes in the Sunda Shelf that greatly depressed sea levels exposed (SI I-50).

Thus, late in their occupation of Java, the *Homo erectus* and certain non-hominin *S.-H.e.* lineages appear to have adjusted successfully to profound glacio-eustatic changes in landscape and climate. Perhaps the replacement of the Kedung Brubus fauna by the Ngandong fauna (see Table 5) reflects the extreme paleoenvironmental conditions of the last-interglacial highstand or the preceding glacial lowstand, but Middle Pleistocene sea-level and paleoenvironmental fluctuations before this might also have led to the faunal changes (SI I-49a). Judging from the continuity of large mammal lineages in the *S.-H.e.* (see Table 5), *H. erectus* included, no glacio-eustatic fluctuations led to hominin speciation in Java or a complete displacement of *S.-H.e.* populations from southern Sundaland.

The ability of *Homo erectus* and other long-lasting *S.-H.e.* species had to persist through a range of hydroclimates, including glacio-eustatic extremes, is evident in paleoclimatic information from several key fossil sites in eastern Java. In particular, the Mojokerto-child *H. erectus* population appears from paleobotanical information to have lived in a drier climate than was present in the Trinil paleo-river valley during the time of *P. erectus* (SI I-43); and paleopedological and palynological studies of the *H. erectus*-section at Sangiran Dome reveals fine-grained hydroclimatic and vegetation variations, some involving severely dry conditions (SI I-44 to -46).

Recent climatic patterns suggest a potential explanation for faunal continuity in the *S.-H.e.* Historic Java varied from dry-monsoonal to ever-wet climate from eastern to western portions of the island and from south to north coasts, lowlands to mountains, and watershed to watershed (SI I-49b). When the *S.-H.e.* lineages inhabited Java, there was a similar range of physiographic provinces, doubtless similar island-scale variations in climate, and presumably a commensurate diversity of associated vegetation- and mammalian-biotopes. Quite plausibly therefore *H. erectus* and other long-lasting *S.-H.e.* species persisted across southern Sundaland because of their capacity to relocate within Java and the Sunda Shelf and thereby exploit the variety of shifting lowland, coastal, and montane biotopes that the region offered (see Figures 13 and 14; Huffman 1999a, b, 2001a). Habitat flexibility in *H. erectus* is reasonably supposed to have played a critical role in its >0.8 Ma occupation of southern Sundaland.

Despite its long-term prior success, the *S.-H.e.* failed to survive into the second half of the Late Pleistocene. A faunal turnover is evident from teeth of *Homo sapiens* and mountain-forest vertebrate species in the Sumatran cave that Dubois discovered (see Table 5, note 5). Recently, fossil-bearing breccia at his Lida Ajer cave of Sumatra has been dated to 63–73 ka (Westaway et al. 2017). This places a fauna with *H. sapiens* in a mountainous peripheral sector of Sundaland during MIS 4 (71–50ka). MIS 4 included an episode of very low sea level (e.g., de Deckker et al. 2019; Schneider et al. 2013) when the modern humans might have dispersed widely across the Sunda Shelf and Sunda islands and replaced all *H. erectus* populations (SI I-50b). *H. sapiens* teeth are also reported from among the 128 ka ± 15 ka rain-forest faunal remains recovered from Punung rock shelter in the Southern Mountains of eastern Java (SI I-48). If so, *H. sapiens* took over some sectors of southern Sundaland, such as these Mountains, while *H. erectus* and other *S.-H.e.* large mammals inhabited other sectors, such as the Ngandong paleo-watershed.

S.-H.e. occurrences outside of the stratovolcanic watersheds of mid-island eastern Java supports broadening the inferred paleogeographic range of *Homo erectus* (see Figure 14). Hominin fossils occur with abundant remains of *S.-H.e.* species ~100km north of Trinil at Patiayam (see Figure 1b; SI I-47). This collection area, which was on the flank of an Early to Middle Pleistocene stratovolcanic island, lay across the Kendeng Hills and Randublatung marine embayment from the *H. erectus* discovery area of medial Java (see Figure 13). *S.-H.e.* mammals must have crossed the seaways that separated the paleo-island from the Kendeng Hills and Rembang Hills (SI I-38).

Archaic hominins reached into the Southern Mountains, where artifacts at the Song Terus cave record a presence during the Middle Pleistocene (SI I-48). The lack of *Homo erectus* skeletal fossils in the Southern Mountains, Rembang Hills, and Kendeng Hills (except for the volcaniclastic Kedung Brubus bedrock and Ngandong terrace deposit) should not be taken to mean that Pleistocene populations were absent across the broad extent of these uplands, just that destructive taphonomic conditions generally prevailed in them (see Figure 14). Erosional paleo-landscapes in these uplands apparently accumulated too little volcaniclastic material to preserve bony remains (see Figure 13; Huffman et al. 2012b). The skeletal materials of hominins and other large mammals might have been destroyed systematically on the ground surface or in corrosive subsurface settings in these mountains.

The Patiayam and Song Terus localities are not the only sites indicative of broad paleogeographic distribution of *S.-H.e.* species. Several sites west of Sangiran Dome and Patiayam have archaic hominin skeletal or dental remains (SI I-49). The type of area for the oldest fauna of the *S.-H.e.*, the Ci Saat fauna (see Table 5), is in Central Java, ~200km west of Sangiran. The western-most known *S.-H.e.* occurrence is a Trinil fauna pig jawbone in a non-marine sequence cored near the Java Sea coast at Jakarta, ~450km west of Patiayam (Marks 1956; Yulianto et al., date unknown; SI I-49). Evidence at hand suggests that many *S.-H.e.* species, such as its bovids, cervids, suids, rhinoceros, and tiger, had sufficient ecological flexibility to attain wide distribution in southern Sundaland.

The potential for *S.-H.e.* dispersal north of Java also is evident from the paleo-landscapes that sub-bottom seismic data reveal beneath the present-day Java Sea. Modelling Pleistocene paleogeography (e.g., Salles et al. 2021) benefit critically from close attention to marine-geophysical resources (Alqahtani et al. 2015; Darmadi et al. 2007; Huffman et al. 2012a, 2013, 2018). For example, in the Java Sea north of the eastern Java *Homo erectus* discovery area (see Figure 1b) seismic profiles reveal widespread Pleistocene paleo-landscape features, as do interpreted '3-D' data volumes in the westernmost and easternmost Java Sea (SI I-51).

The seismic data demonstrate that immense river-valley systems developed across the Sunda Shelf during multiple periods of the Pleistocene. Valley systems are clearest for low-stand episodes when the Shelf terrane was the largest. Conversely, marine beds in Java attest to the likelihood that portions of Sunda Shelf continued to be inundated periodically during the Early and Middle Pleistocene. Geological indications are clear that severe paleogeographic fluctuations occurred while the *S.-H.e.* persisted to inhabit southern Sundaland during the Middle Pleistocene.

The 3-D data particularly permit spatiotemporal (four-dimensional) analysis of the paleogeomorphology, greatly increasing confidence in environmental interpretation of the landscapes that formed under lower-than-present sea level (SI I-49c). In Central Java, many north-draining Pleistocene watersheds fed directly into the low-sea level river valleys of the Sunda Shelf, and some onshore watersheds have *S.-H.e.* fossils (SI I-49, -50). Large-mammal populations potentially expanded down the former valleys and interfluves during periods of depressed sea level and contracted back into the Javan core as sea level rose.

In the western portion of Java, Pleistocene highlands drained into the Sunda paleo-watershed that emptied into the Indian Ocean via Sunda Strait. The northern headwaters of this watershed abutted low-sea-level drainage divides and headwaters now under the western Java Sea situated between Sumatra, west Borneo, and the Malay Peninsula (SI I-50). During lowered sea level, these Pleistocene territories would have afforded *S.-H.e.* populations pathways into the Sunda uplands of Borneo, Sumatra, and Malaysia, and account for the arrival of new Asian mainland taxonomic lineages in the Trinil fauna and Kedung Brubus fauna (see Table 5).

Hominin and other terrestrial mammals might well have inhabited seemingly peripheral parts of southeasternmost Sundaland. The stratovolcanic valleys of the type which the Mojokerto *Homo erectus* inhabited continued for ~250km east of Perning, as did coastal lowlands bordering Madura Strait. The Pleistocene upland of the Rembang Hills extended for hundreds of kilometers through Madura Island towards the Kangean archipelago at a southeastern corner of the Sunda Shelf. Between Madura and Kangean islands, Pleistocene rivers, which had flowed for hundreds of kilometers across the Shelf, exited into the deep-water of the Bali-Flores Sea or areas north of the Kangean archipelago (SI I-50b, -51c). Quite plausibly when depressed sea-level stood at elevations below the continental shelf edge, large braided-river systems carried voluminous clastic materials for hundreds of kilometers across the Sunda lowlands from headwaters in central Borneo towards the coasts that lay on the easternmost shelf (SI I-50b).

To summarize the paleogeographic conclusions we draw: Dubois claimed reasonably that the Skullcap and Femur I, along with thousands of other fossils, came from one sedimentary deposit, and established that *Pithecanthropus erectus* (*P.e.*) lived in a biotically rich stratovolcanic watershed. The *H. erectus* occurrences in Java are profitably viewed as samples of hominin populations that broadly inhabited southern Sundaland. The Trinil fauna anchors the *Stegodon-Homo erectus* large-mammal faunal association (*S.-H.e.*), which often occurs at *H. erectus* fossil sites in eastern Java (see Table 5; see Figure 1b) and links *S.-H.e.* paleogeographically to watersheds of stratovolcanoes (see Figure 13; SI I-38 to -47). Radiometric dating at Sangiran Dome and Ngandong establishes hominin residency in this setting from 0.9 Ma to 0.1 Ma and suggests a longer geological time span of occupation. Glacio-eustatic fluctuations of sea level and climate, which were prominent during this period, presumably impacted the distribution of suitable hominin habitats throughout Java and adjacent Sunda Shelf and led to interchange of terrestrial biota with other Sunda islands and mainland Asia (SI I-49, 50). *Homo erectus* survived even the harshest apparent conditions in southern Sundaland until the Late Pleistocene.

CONCLUSIONS

Sparse remnants of *Pithecanthropus erectus* discovery bonebed (**LB**) apparently still occur in the middle of the Solo River near its left bank, but modern work has yet to describe the deposit at this spot, and the overlying strata were removed entirely during 1891–1893. Firsthand records of Dubois and his field supervisors from those years endure as documentation of the stratigraphic context. These records, evaluated here in conjunction with later work at Trinil and non-hominin fossils from the site, persuasively support Eugène Dubois' determination that the *Pithecanthropus erectus* (*P.e.*) Skullcap and Femur I came from a single stratum (see Figures 2 and 10). Dubois' later excavation of the bonebed evidently produced the femora of at least two more *P.e.* individuals and the great preponderance of non-hominin vertebrate fossils from the left bank (see Tables 1 and 2).

The hominin remains and diverse paleobiota of the Trinil main bonebed continue to contribute greatly to the *Homo erectus* record of Java (see Table 3). The large mammal species from the bonebed are the basis for the biostratigraphic Trinil fauna, a central component of the *Stegodon-Homo erectus* fauna association (*S.-H.e.*). Every known bony *H. erectus* fossil from eastern Java is like *Pithecanthropus erectus* in the sense of having been embedded in a stratovolcanic drainage as part of stratigraphic sequence containing large mammalian fossils of the *S.-H.e.* (see Table 5).

The provenience observations on the 1891–1892 *Pithecanthropus erectus* discoveries benefitted from being excavated in an indurated flat-lying stratum with an unmistakable concentration of large-sized vertebrate fossils. These conditions were already evident when the Skullcap was unearthed in October 1891 from the Lapilli bed (**LB**) and Femur I was discovered in 1892 from the **LB** at "approximately the same depth [elevation]" 12 meters away (see Figures 2 and 3). Judging from the archival record, when site supervisors G. Kriele and A. de Winter transmitted this account to Dubois, all three had sufficient technical expertise to assess discovery provenience in the geological and operational circumstances involved.

After the Femur I trench was enlarged in late 1892 and further expanded in 1893 (see Figure 3a), the discovery subunit of the **LB** was followed in exposure from the immediate vicinity of the Skullcap Pit to the Femur I discovery spot and beyond. Moreover, the **LB** was exposed stratigraphically at the base of excavated backwalls eight-to-nine-meters high and tens of meters long in lale 1892 and again in 1893. Dubois had the site photographed in 1894 and later annotated the image to show the Skullcap and Femur I findspots relative to rocky remnants of the 1891–1893 excavations (see Figure 3c).

In 1895–1896, Dubois illustrated and described the **LB** as occurring stratigraphically beneath sandy strata that held up the incised Solo River embankment topped by a soil (see Figure 2a). The soil had developed on a terraced upland of largely erosional origin, much as is seen in the 1894 photograph (see Figure 4a). Dubois' prediction that the strata he had witnessed in 1891–1893 would extend under the embankment to the south was confirmed by excavations in 1895–1908, as firsthand reporting and site photographs document (see Figures 5, 7, and 10).

Contemporaneous reporting also substantiates the direct stratigraphic association of the Trinil fauna species with 1891–1893 *Pithecanthropus erectus* fossils (see Table 1). The **LB** Skullcap Pit produced large bioclasts that are attributable to *Axis lydekkeri*, *Bubalus palaeokerabau*, *Duboisia santeng*, and *Stegodon trigonocephalus*. Femur I originated from a portion of the 25-m Trench in which the **LB** yielded *Bibos palaesondaicus*, *Duboisia santeng*, *Stegodon trigonocephalus*, and possibly *Gavialis bengawanicus* and *Sus brachygnathus*. The **LB** in the 40-m-Trench, largely dug adjacent to the 25-m Trench (see Figure 3a), contained *A. lydekkeri*, *Crocodylus siamensis*, *D. santeng*, and *S. trigonocephalus*, Testudines, shells, and wood.

Large skeletal remains of the same ungulate and reptile species continued to occur near the seasonal low-water level in the great expansion of left-bank excavation in 1895–1900 (see Table 1, see Figure 3a). Comparison of the 1894 image of the site to three 1900 site photographs shows that the new pits and trenches, portions of which were adjacent to those of 1891–1893, penetrated the same near-horizontal stratal succession across several thousand square meters of excavated area (see Figures 4 and 5). Firsthand reporting and 1907 photographs of the Selenka Trinil Expedition confirm the persistence of the main bonebed near the seasonal low-river level (their 'Hauptknochenschicht,' **HK**), while at higher elevations in Pit II, the Selenka crew encountered the same eight-to-nine meters of hardened strata that Dubois' excavators had (see Figures 7 and 8).

Dubois' 1894 photograph can be overlain precisely on a photograph of the site taken in 1926. The superposition relates the context of the *Pithecanthropus erectus* discovery, as Dubois noted on the 1894 photograph, to the landscape as it was long after the historic excavations were finished. The scars and baulks of the bonebed, which spoils had blanketed when the 1900 and 1907–1908 excavations were underway, were clearly visible in 1926 when the first geological mapping of the area began. For decades thereafter, geologists considered the stratal remnants on the left bank to be bedrock. Since 1936, these strata have been assigned to the bedrock Kabuh Formation (SI I-16 to -19). Some or all beds that overlay the **HK** in the 1907 Pit II doubtless occur under the soil and vegetation of the present-day left bank (see Figure 6d; SI I-18).

Besides documenting the site stratigraphy and taxonomic paleontology, Dubois' and Selenka photographs and geological descriptions offer indispensable observations on the sedimentary and taphonomic conditions leading to the formation of the main bonebed (**LB**, **HK**, and the bioclast-rich stratum of 1895–1900, termed **LB**-**HK** here). Judging from firsthand accounts, thousands of large, disarticulated, and irregularly distributed bioclasts of terrestrial vertebrate species were concentrated in this thin, poorly sorted, gravelly volcaniclastic stratum, which also contained the remains of freshwater molluscs, reptiles, trees, and sedges. Most of the larger bioclasts in theh bonebed appear to have been matrix-supported gravel embedded in a partially stratified diamicton. The longest bioclasts, such as proboscidean tusks and logs, would have lain approximately parallel to the horizontal bedding and the biggest bioclasts, such as large ungulate skulls, would have taken up the whole bonebed. No clear evidence of a lacuna fluvial accumulation was reported.

The vertebrate and plant fossils ranged in size from small teeth and leaves to large crania and logs, as is indicated by both original descriptions and museum collections. While the skeletal specimens were commonly broken, levels of abrasion attributable to fluvial transport were rare. Fine surface preservation and uniform fossilization of bony materials, including Femur I, add to a picture of an isotaphonomic assemblage of terrestrial remains. Because the main bonebed varied in horizontal and vertical bioclast density, the deposition of the bioclasts appears to have occurred during multiple surges of river flow that followed the same general sequence of taphonomic events.

Straightforward analogies with historic lahar deposition surrounding active volcanoes in Java led Dubois' and Selenka's geologists to postulate further about the origin of the main bonebed. These workers rightly focused on long-run out lahar flows as a mechanism for transport and accumulation in the instance of the main bonebed. The biota had been living in the Pleistocene stratovolcanic watershed upriver of Trinil when the ungulate populations were decimated. What Dubois and Selenka geologists suspected a century ago is now supported by analysis of museum collections—the formation of the main bonebed involved the penecontemporaneous deaths of more than one hundred ungulate individuals (see Table 4). After the resulting carcasses were skeletonized, the remains were transported fluvially to Trinil (see Figure 12). The very poor size sorting of both lithic- and biotic-clasts in the main bonebed fits transport *en masse* by a sediment-heavy flood (SI I-25).

Proposals such as these are testable by further field, museum, archival, and analytical research. Trinil fossils at Naturalis and Museum für Naturkunde continue to be incompletely exploited as a paleontological resource for evaluating the formation of the bonebed and the paleoecology of the watershed in which it originated. However, new geological field investigations of the 1891–1908 excavations face considerable hurdles. Remnants of the **LB** constitute a small fraction of what existed prior to excavation. This calls for an all-inclusive interlinking of the features still observable at the mid-river discovery site to archival accounts of the 1891–1893 excavations.

The record of the left-bank excavations at Trinil, as presented here, contradicts the suggestion that strata excavated on the left bank included Late Pleistocene valley fill (SI II-35). The main bonebed Trinil fauna (see Table 3) correlates on biostratigraphic criteria with ~0.8–0.9 Ma beds at Sangiran Dome (e.g., Grenzbank and Ngebung bonebeds), not with the early Late Pleistocene Ngandong fauna (see Table 5). The cranial form of the *Homo erectus* in the Ngandong bonebed is widely acknowledged to be more derived anatomically than the *Pithecanthropus erectus* crania.

The lithofacies and biofacies of the main bonebed are essential to evaluating the long archaic hominin prehistory in the stratovolcanic drainages of eastern Java and southern Sundaland more broadly. Radiometric dating at the Sangiran Dome and Ngandong discovery sites establishes hominin residency in this setting from 0.9 Ma to 0.1 Ma, if not also suggesting hominin occupation of Java over a longer geological time span.

Glacio-eustatic fluctuations of sea level and climate, which were prominent in the Middle and Late Pleistocene, presumably impacted the distribution of suitable hominin habitats in Java and the Sunda Shelf and led to interchange of terrestrial biota with other Sunda islands and mainland Asia. *Homo erectus* survived the harshest apparent conditions that southern Sundaland had to offer.

Eugène Dubois ventured to Sumatra and Java thinking of paleobiogeography in expansive ways. Once in the Indies, he applied geology and paleontology to rock outcrops and caves to search for fossil specimens of early ancestor species. The premier product of Dubois' efforts in Java, the discovery of *Pithecanthropus erectus* at Trinil, offers future avenues for explication of regional Pleistocene paleobiogeography, most particularly when the site is viewed in conjunction with the many archaic hominin discoveries in Indonesia and the Philippines that followed Dubois' lead.

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