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journal homepage: [www.elsevier.com/locate/jhevol](http://www.elsevier.com/locate/jhevol)Naming *Homo erectus*: A reviewEduard Pop<sup>a,b,\*</sup>, Sofwan Noerwidi<sup>c</sup>, Fred Spoor<sup>d,e</sup><sup>a</sup> Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, the Netherlands<sup>b</sup> Faculty of Archaeology, Leiden University, P.O. Box 9514, 2300 RA, Leiden, the Netherlands<sup>c</sup> Research Center for Archaeometry, National Research and Innovation Agency, Jl. Condet Pejaten 4, Pasar Minggu, Jakarta Selatan 12510, Indonesia<sup>d</sup> Centre for Human Evolution Research, Natural History Museum, Cromwell Road, SW7 5BD London, United Kingdom<sup>e</sup> Department of Human Origins, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

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## ABSTRACT

Following the discovery of hominin fossils at Trinil (Java, Indonesia) in 1891 and 1892, Eugène Dubois named a new species, now known as *Homo erectus*. Although the main historical events are well-known, there appears to be no consensus regarding two important aspects of the naming of the species, including what constitutes the original publication of the name, and what is the name-bearing type specimen. These issues are addressed in this paper with reference to original sources and the International Code of Zoological Nomenclature. Our review confirms earlier studies that cite the published quarterly fieldwork report covering the 3rd quarter of 1892 as the original publication naming the species *erectus*. However, until recently, the correct publication year of 1893 has consistently been cited as 1892, and it has rarely been recognized that the author of the publication was anonymous, even though the author of the species is specifically named. Importantly, Dubois assigns all three hominin fossils found at Trinil up to that moment to the new species, explicitly stating that they belong to a single individual. The three fossils, a molar, a calotte, and a femur, therefore jointly constitute the original holotype. However, the femur most likely derives from younger strata than the other hominins and shows fully modern human-like morphology, unlike subsequently discovered *H. erectus* femora. Moreover, there is no consensus over the affinities of the molar, and if it is *H. erectus* rather than an extinct ape, there is no evidence that it belongs to the same individual as the calotte. Excluding these two fossils from the holotype, the calotte is the appropriate fossil to retain the role as name-bearing specimen.

## 1. Introduction

The discovery of hominin fossils at Trinil (Java, Indonesia) in 1891 and 1892 and their attribution by Eugène Dubois to the species now known as *Homo erectus* is a major landmark in the study of human evolution as it represents the first active search for early fossil evidence, followed by systematic excavation and publication of the findings. The broader historical context of these events is well documented (e.g., Theunissen, 1989), but as will be discussed below, there seems to be no consensus on 1) what constitutes the original publication of the species name, and 2) the name-bearing type specimen or specimens. With this contribution, we would like to address these issues, with reference to the 4th edition of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature [ICZN], 1999), and the original sources directly relevant to the species designation. For each aspect, the factual information will be reviewed first, followed by a

discussion of how this was interpreted in the literature. Names and citations in Dutch are given as published at the time, followed by our English translation. The first five Trinil fossils, directly relevant in the context of the current paper, are numbered following Jacob (1975), noting that for some of the subsequent specimens different numbering systems have been proposed (Table 1). Reviewing the naming and type specimen(s) of *H. erectus* is timely because new research has rekindled the debate over the affinities of some of the key fossils (Smith et al., 2009, 2018; Ruff et al., 2015; Zanolli et al., 2019; Huffman et al., 2022; Hilgen et al., 2023; Pop et al., 2023).

2. The publication naming *Homo erectus*

Central to the naming of *H. erectus* are six publications. The first four of these were progress reports of the paleontological fieldwork on Java and particularly at the Trinil site, which Dubois submitted to the director

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of the Departement van Onderwijs, Eeredienst en Nijverheid ('Department of Education, Religious Affairs and Industry') of the Dutch East Indies government (Dubois, 1894; Theunissen, 1989). They were included in quarterly issues of Verslag van het Mijnwezen ('Report of the Mining Industry') under the section heading Palaeontologische Onderzoekingen op Java ('Paleontological investigations on Java'). These formal government publications are anonymous throughout and written in passive voice, but Dubois' authorship of the paleontological reports is clear from the content, his own statements (Dubois, 1894: footnotes pp. 1–2), and the handwritten drafts from mid-1889 to mid-1895 held in the Dubois archive at Naturalis (Leiden, The Netherlands; archive no. MM774C-000050-041 to –096). To the best of our knowledge, these reports were mostly or only disseminated as Extra-bijvoegsel der Javasche Courant ('Extra supplement' to the official government newspaper) and this apparently happened a little after formal publication. Hence, in some cases the year of publication, shown on the cover jointly with the publisher (Landsdrukkerij, Batavia; see Fig. 1), precedes the year an issue was distributed with the newspaper. The latter is marked with an additional line in a smaller font on the external cover (Fig. 1). In libraries, the Verslag van het Mijnwezen can be found archived jointly with the Javasche Courant, or as separate offprints, marked on the external cover as Overdruk uit de Javasche Courant ('Reprint from the official government newspaper'; see Supplementary Online Material [SOM] S1 for an example).

The six key publications are:

**Anonymous (1891a)**, which discusses the Trinil fieldwork during the 3rd quarter of 1891, and reports the discovery of a right hominin M<sup>3</sup> (Trinil 1; Fig. 2A) and its attribution to *Anthropopithecus*, the genus name that was mostly used at the time for the extant chimpanzee.

**Anonymous (1891b)**, which discusses the Trinil fieldwork during the 4th quarter of 1891, and reports the discovery of a hominin calotte (Trinil 2; Fig. 2B) in October of that year and its attribution to the genus *Anthropopithecus*.

**Anonymous (1893)**, which discusses the Trinil fieldwork during the

3rd quarter of 1892 (Fig. 1) and reports the discovery of a left hominin femur (Trinil 3; Fig. 2C) in August of that year and the attribution of all three fossils (Trinil 1–3; Table 1) to the new species *Anthropopithecus erectus* EUG. DUBOIS. It should be noted that this phrasing unambiguously identifies Dubois as the person proposing the new species name.

**Anonymous (1894)**, which discusses the Trinil fieldwork during the 4th quarter of 1893, and reports that a small monument has been erected to mark the discovery site. The explanation of the inscription states that it includes the initials P.e. of the "nader *Pithecanthropus erectus* te noemen anthropoied" (Anonymous, 1894: 14), which best translates as 'the anthropoid soon to be named *Pithecanthropus erectus*'. This phrasing amounts to a conditional proposal of the genus name *Pithecanthropus*, but when proposed before 1961 such names can be available (ICZN, 1999: Art. 15.1).

**Dubois (1894)**, a monograph which describes the Trinil 1–3 fossils. It starts with establishing a new primate family Pithecanthropidae, followed by the heading "PITHECANTHROPUS ERECTUS, genus novum, species nova" (Dubois, 1894: 1). Dubois explains in an attached footnote that the species was briefly described as *Anthropopithecus erectus* in an earlier report (i.e. Anonymous, 1893), thus contradicting the 'species nova' of the heading. This monograph was published in August 1894 (Theunissen, 1989), and postdates the publication of Anonymous (1894), which was distributed on 5 January and thus first proposed *Pithecanthropus*.

**Weidenreich (1940)**, a short review paper which considers the hominin fossil record known at the time. In his conclusion, the author proposes a simplified classification, transferring both *Pithecanthropus erectus* and *Sinanthropus pekinensis* to *Homo erectus*.

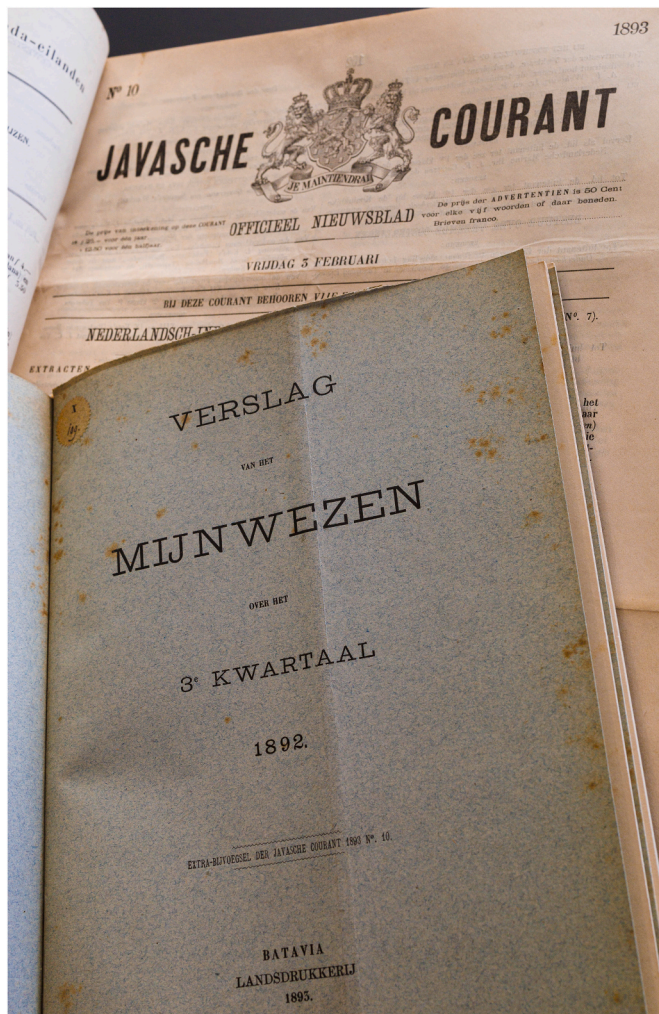
In summary, the species *erectus* was named by Dubois in 1893, and the publication in which he did so is Anonymous (1893). It is worth noting that anonymity of a publication from before 1951 does not prevent the availability of a name (ICZN, 1999: Art. 14), and that a person can name a species in a publication without being an author of that publication (ICZN, 1999: Art. 50.1.1). Within different genera the full

**Table 1**

Fossils from Trinil attributed by Dubois to *Pithecanthropus erectus*. The listed Trinil numbers follow Jacob (1975), as well as an alternative given in de Lumley (1993), Grimaud-Hervé et al. (1994) and Indriati (2004). The latter includes a Femur VI from Trinil, but Dubois (1935) emphasized that it is not from Trinil and the specimen may not be hominin (Day and Molleson, 1973).

Reg. number	Found	Species attribution			Other key sources	Trinil number		Femur number	Remarks
		Source	Fossil <sup>a</sup>	Species		Jacob (1975)	de Lumley (1993)		
RGM.1332451	Sept. 1891	Anonymous (1893)	Right M <sup>3</sup>	<i>Anthropopithecus erectus</i>	First description in Anonymous (1891a) as <i>Anthropopithecus</i> ; in Dubois (1894) as <i>Pithecanthropus erectus</i>	Trinil 1	Trinil 1		Previously registered as DUB.11620
RGM.1332450	Oct. 1891	Anonymous (1893)	Calotte	<i>Anthropopithecus erectus</i>	First description in Anonymous (1891b) as <i>Anthropopithecus</i> ; in Dubois (1894) as <i>Pithecanthropus erectus</i>	Trinil 2	Trinil 2		
RGM.1332452	Aug. 1892	Anonymous (1893)	Left femur	<i>Anthropopithecus erectus</i>	In Dubois (1894) as <i>Pithecanthropus erectus</i>	Trinil 3	Trinil 3	Femur I	
RGM.1394730	Oct. 1892	Dubois (1896a)	Left M <sup>2</sup>	<i>Pithecanthropus erectus</i>	Dubois (1896b), 1924a, 1924b, 1924c	Trinil 4	Trinil 4		Previously registered as DUB.11621
RGM.1394731	1897	Dubois (1899)	Left P <sub>3</sub>	<i>Pithecanthropus erectus</i>	Dubois (1924a), 1924b, 1924c	Trinil 5	Trinil 5		
RGM.1332453	1900	Dubois (1932a)	Right femur fr.	<i>Pithecanthropus erectus</i>	Dubois (1932b)	Trinil 6	Trinil 6	Femur II	
RGM.1332454	1900	Dubois (1932a)	Left Femur fr.	<i>Pithecanthropus erectus</i>	Dubois (1932b)	Trinil 7	Trinil 7a	Femur III	
RGM.1332455	1900	Dubois (1932a)	Right femur fr.	<i>Pithecanthropus erectus</i>	Dubois (1932b)	Trinil 8	Trinil 8	Femur IV	
RGM.1332456	1900	Dubois (1934)	Left femur fr.	<i>Pithecanthropus erectus</i>		Trinil 9	Trinil 7b	Femur V	

<sup>a</sup> Fr. = fragment.



**Fig. 1.** The Anonymous (1893) issue of *Verslag van het Mijnwezen* in which Dubois names the species *Anthropopithecus erectus*. The cover indicates that 1893 was the year of publication (bottom), that it reports on the 3rd quarter of 1892 in the title, and in smaller print in the middle, that this copy was distributed as a special supplement of the *Javasche Courant* number 10, 1893. That issue of the newspaper, published on 3 February, is shown in the background.

species name is:

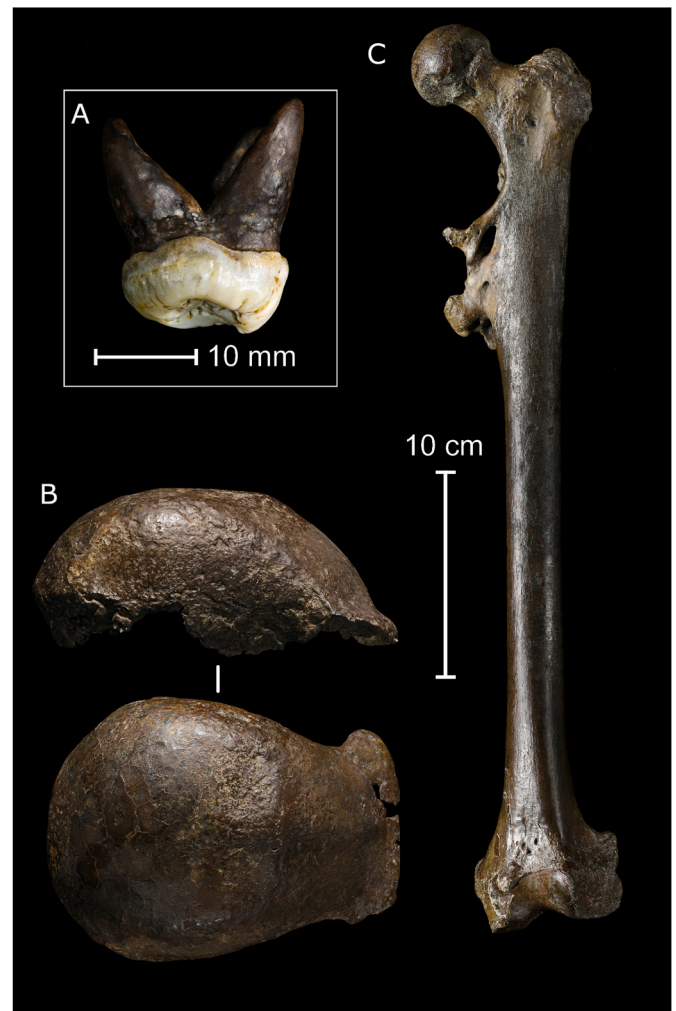
*Anthropopithecus erectus* Dubois, 1893

*Pithecanthropus erectus* (Dubois, 1893) [Dubois]<sup>1</sup>, 1894

*Homo erectus* (Dubois, 1893) Weidenreich, 1940.

Following the publication and widespread distribution of Dubois (1894), it is this monograph that is initially cited in the literature to reference the newly proposed species (e.g., Schwabe, 1899; Weinert, 1928; von Koenigswald, 1940), and some recent studies still do so (e.g., Huffman et al., 2022; Antón and Middleton, 2023). Apart from Dubois himself (Dubois, 1894: p.1, footnote 1) it seems that Campbell (1963) first identified the actual publication naming the species. However, the year of publication is given as 1892 instead of 1893, and subsequently, this incorrect year is commonly cited (e.g., Campbell, 1963, 1965; Jacob, 1975; Szalay and Delson, 1979; Day, 1986a; Groves, 1989; Wood and Collard, 1999; Schwartz and Tattersall, 2003; Wood and Lonergan, 2008). Based on a detailed biography of Dubois (Theunissen, 1989),

<sup>1</sup> The square brackets indicate that the name of the person transferring the species to *Pithecanthropus* in Anonymous (1894) is inferred from external evidence (ICZN, 1999: Art. 51).



**Fig. 2.** The holotype of *Homo erectus* as published by Dubois in Anonymous (1893), consisting of A) the molar Trinil 1, B) the calotte Trinil 2, and C) the femur Trinil 3.

Meikle and Parker (1994) realized that 1892 might not be the correct year, and 1893 eventually started to be used (MacLatchy et al., 2010; Anonymous, 2011; Wood, 2020). Anonymous (2011) specifically explains that the 1892 given in the title, is the year when the relevant excavations were carried out, rather than the year of publication (Fig. 1), but 1892 continues to be cited (e.g., Henke and Hardt, 2011; Schrenk et al., 2015; Schwartz, 2016; Urciuoli et al., 2022; Reed et al., 2023).

Apart from the year of publication, a second issue is that from at least Campbell (1965) onwards, the author of the species (Dubois) is consistently taken as the author of the publication. Hence, Anonymous (1893) is cited as ‘Dubois (1892)’ or ‘Dubois (1893)’. It is likely that this misunderstanding not only follows from the unusual situation where a specified author names a species in an anonymous publication but also from the difficulty to consult that publication directly. Here we hope to improve accessibility by providing the original publication of Anonymous (1893) in original format (SOM S1), as well as our English translation side-by-side with the Dutch text (SOM S2), noting that a translation has previously been published (Meikle and Parker, 1994).

### 3. The name-bearing type of *Homo erectus*

In Anonymous (1893) Dubois attributed three fossils to *Anthropopithecus erectus*: the  $M^3$  (Trinil 1) and the calotte (Trinil 2), both found

in 1891, and the femur (Trinil 3) found in 1892. In particular, the four crucial statements and sections are:

p. 10: "... het linker dijbeen van den *Anthropopithecus*, van welken, een jaar geleden, door eene kies en den schedelkap het bestaan gebleken was" ('... the left thigh bone of the *Anthropopithecus*, whose existence had been shown a year ago by a molar and the skullcap'), which assigns all three fossils to *Anthropopithecus*.

p. 10: "Uit die bevinding en uit het vergelijkend onderzoek blijkt, dat de drie skeletdeelen aan eenzelfde individu hebben toebehoord" ('These findings and comparative analysis show that the three skeletal parts belonged to the same individual'), which attributes all three fossils to a single individual.

p. 11: "Door ieder van de drie gevonden skeletdeelen nadert *Anthropopithecus erectus* EUG. DUBOIS meer tot den mensch dan eenige andere anthropoïed" ('For each of the three discovered skeletal parts *Anthropopithecus erectus* EUG. DUBOIS is closer to humans than any other anthropoid'), which names the species, identifies the person naming it, and indicates that the name-bearing specimen is the Trinil individual represented by three skeletal parts.

p. 11–13: Dubois discusses the comparative morphology of the calotte, the molar, and the femur, thus providing a required description (ICZN, 1999: Art. 12.1).

Thus, the specimen (individual) represented by Trinil 1, 2, and 3 is the nominated holotype of the species *erectus*, rather than that these three fossils are syntypes. Dubois did not specifically use the term 'type' in Anonymous (1893), but this is not required as long as it is implied (ICZN, 1999: Art. 73.1.2), noting also that these events took place before internationally recognized rules were first established (ICZN, 1905). Subsequently, Dubois attributed two additional fossils to the name-bearing specimen (Table 1). These are Trinil 4, a left M<sup>2</sup> found in 1892, but first described in Dubois (1896a, 1896b)<sup>2</sup>, and Trinil 5, a left P<sub>3</sub> found in 1897, and described in Dubois (1899, 1924).

None of the steps taken by Dubois fall outside common practice of contemporary zoology, including the routine designation of holotypes that consist of multiple body parts of what is assumed to be a single individual (e.g., skin and skeleton of extant taxa, or multiple skeletal elements of extinct ones). Importantly, if it is subsequently found that one or more parts do not belong to the same individual, these can be excluded from the holotype "by appropriate citation" (ICZN, 1999: Art. 73.1.5). Conversely, elements can be added if these are found to be from the same individual, noting that exclusion and addition both represent scientific opinions that may or may not receive wider acceptance based on the strength of the arguments. Within the study of human evolution, an apt example is the OH 7 holotype of *Homo habilis* which was published by Leakey et al. (1964) as a partial mandible, an isolated upper molar, parietals, and hand bones of a juvenile individual. Subsequently, the upper molar was excluded because of its incompatible developmental age (Tobias, 1991), the matching right M<sub>2</sub> was found and added (Clarke, 2012), and the hand bones may eventually be excluded, because of ongoing doubts whether they belong to the same individual (Grine et al., 2022). Thus, fossils can be excluded from Dubois' name-bearing specimen, as long as it is based on the argument that more than one individual is represented, whether based on their morphology or on stratigraphic placement.

Reviewing the hominin fossil record, Weidenreich (1940: 376) reiterated Dubois' interpretation that "The type consists of a skull cap found by Eug. Dubois near Trinil, a femur and three teeth presumed to belong to one and the same individual", despite believing himself that the teeth should not be included (Weidenreich, 1937). In contrast, subsequent

reviews of the species single out the Trinil 2 calotte as the type specimen, citing Dubois (1894) or Anonymous (1893)<sup>3</sup>, but without referencing the exclusion of the femur and teeth (Campbell, 1965; Jacob, 1975; Howell, 1978; Groves, 1989; Meikle and Parker, 1994; Wood and Collard, 1999; Dunsforth and Walker, 2002; Schwartz and Tattersall, 2003; Antón et al., 2007; Wood and Lonergan, 2008; MacLachy et al., 2010; Anonymous, 2011; Baab, 2015; Antón and Middleton, 2023; Pop et al., 2023). Of these, Schwartz and Tattersall (2003) do exclude the molars as probably not hominin, but not the femur. By contrast, Grün and Stringer (2023) do not question the affinities of the molars but nevertheless exclude Trinil 1, on the mistaken assumption that Dubois (1894) defined the species based on the calotte and femur only.

The notion of Trinil 2 as the single type may go back to the 1965 'definitive list of named Hominid taxa' which records for *H. erectus*: "Lectotype: calotte ('Pithecanthropus I', in Dubois, 1894)" (Campbell, 1965:15). However, the same work also refers to "the Trinil holotype - *Pithecanthropus erectus*" (Campbell, 1965: 27) and it is not explained why the calotte is seen as a lectotype. In their review of hominin taxonomy, Meikle and Parker (1994: 36–37) address this issue, stating: "the type specimen for the name *erectus* Dubois is the calotte, not the femur. Because Dubois indicates no type specimen in this paper a lectotype could later be designated. The calotte is viewed as the lectotype by Campbell (see selection 18) on account of its description by Dubois as 'Pithecanthropus I' in 1894". The importance of Dubois in 1893 considering all three Trinil fossils as one individual is thus not recognized here. Moreover, the suggested reason for selecting the calotte as lectotype cannot be correct because Dubois never used the informal name 'Pithecanthropus I'. It was introduced in von Koenigswald (1940) to distinguish Trinil 2 from newly found Sangiran crania following the initial use of 'Pithecanthropus skull I' in von Koenigswald and Weidenreich (1939). Campbell (1965) likely used the name in that context.

Most recently, an extensive historical review of the Trinil excavations observed that Dubois (1894) "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." (Huffman et al., 2022: 270). Noting that syntypes cannot also be a holotype (ICZN, 1999: Art. 73.2), we do agree that no valid lectotype has been assigned because a holotype has been available since 1893.

#### 4. The affinities of the Trinil holotype fossils

Dubois' interpretation that Trinil 1–3 represent a single individual is a key element of naming the species *erectus* and it is therefore of interest to consider how this assumption has been viewed since, also with regards to Trinil 4 and 5 that were subsequently assigned by him to the same individual (Dubois, 1896a, 1896b, 1899). The publication of Dubois (1894) instantly triggered an intense debate in which the critical stance that the three fossils belong to more than one individual, and possibly more than one species, was frequently expressed (see Theunissen, 1989 for a review). With only extant taxa and some Neanderthal fossils for comparison, the arguments at the time questioned the compatibility of ape-like and human-like features, as well as the stratigraphic position of the specimens in the Trinil excavations. As more *H. erectus* fossils were discovered, both in China and elsewhere on Java (e.g., Black, 1931; Dubois, 1932a, 1934; Oppenoorth, 1932; Weidenreich, 1937, 1941, 1943; von Koenigswald, 1940), the morphology of the species became better known, thus providing an improved comparative context to assess the original Trinil fossils.

Concerning the Trinil 1 and 4 upper molars (Dubois, 1894, 1896a, 1896b, 1924a), some studies supported the proposed association with the calotte and femur as one species and individual (Gregory and

<sup>2</sup> Jacob (1975) incorrectly states that Trinil 4 was attributed to *A. erectus* in Anonymous (1893).

<sup>3</sup> Cited as 'Dubois (1892)' or 'Dubois (1893)'.

Hellman, 1923; Weidenreich, 1928), but a majority concluded that the molars should be attributed to an ape species (e.g., Miller, 1923; Weidenreich, 1937, 1945; von Koenigswald, 1940; Hooijer, 1948). Subsequently, however, von Koenigswald (1967) attributed the molars to *Meganthropus palaeojavanicus*, envisaged by him as an *Australopithecus*-like hominin distinct from *H. erectus*, but widely seen as a junior synonym of *H. erectus* (Campbell, 1963). Likewise, Smith et al. (2009, 2018) support an attribution to *H. erectus* rather than *Pongo*, based on enamel morphology and histology. Recently, Zanolli et al. (2019) re-examined the external and internal morphology and assigned the two molars<sup>4</sup> to *M. palaeojavanicus*, not as the hominin species as first described (Weidenreich, 1945; von Koenigswald, 1950), but as an extinct ape. Lastly, Noerwidi (2020) included Trinil 1 and 4 as hominin in a comprehensive study of dental crown morphology in the Indonesian fossil record. They are described as different from *Meganthropus*, a genus considered close to early hominins from Africa as originally proposed by Robinson (1953, 1955) and Tobias and von Koenigswald (1964).

The Trinil 5 P<sub>3</sub> has received less attention than the molars, but being non-sectorial and lacking a canine/P<sub>3</sub> honing wear facet, it was readily accepted as having hominin rather than ape affinities (e.g., Weidenreich, 1937, 1945; von Koenigswald, 1940, 1967; Hooijer, 1948; LeGros Clark, 1955; Schwartz and Tattersall, 2003). Based on comparisons with Zhoukoudian and Sangiran specimens, Weidenreich (1937, 1945) considered the P<sub>3</sub> too modern human-like to be *H. erectus*. Accepting that Trinil 5 is not ape-like, Hooijer (1948) nevertheless thought it was not characteristically human either. Whereas von Koenigswald (1940) had agreed with Weidenreich (1937) that the premolar was modern human-like and not *H. erectus*, he subsequently concluded that there is no doubt that it should be attributed to *H. erectus* (von Koenigswald, 1967). His re-evaluation received support from a geometric morphometric analysis of P<sub>3</sub> crown shape in hominins (Gómez-Robles et al., 2008). It found that Trinil 5 clusters with specimens from Sangiran and Zhoukoudian, and this Asian sample shows close similarities to early *Homo* from Africa and is distinct from modern humans. Likewise, Noerwidi (2020) found that analyses of morphological traits and crown shape associate Trinil 5 with *H. erectus* rather than with *Homo sapiens*.

The recent research findings in Zanolli et al. (2019) have indirect bearing on the affinities of Trinil 5. This study not only attributed the Trinil 1 and 4 molars to *M. palaeojavanicus* as an ape species but also the Sangiran 6a mandible. As the latter has a non-sectorial P<sub>3</sub>, Zanolli et al. (2019) logically had to conclude that the inferred ape species shows this typically hominin dental morphology. If correct, the well-accepted hominin status of Trinil 5, based on non-sectorial morphology, would be less conclusive. Recognizing that their novel interpretation of *Meganthropus* would require substantial convergence on hominin-like morphology, Zanolli et al. (2019) refer to *Gigantopithecus* and *Indopithecus* as other extinct ape species where this happened. However, the P<sub>3</sub>s of these taxa retain a mesiobuccal honing facet, reflecting the small but interlocking upper canine (Zhang and Harrison, 2017). Consistent with hominin affinities, Trinil 5 clearly does not show this type of wear, and given the crown shape (Gómez-Robles et al., 2008; Noerwidi, 2020), attribution to *H. erectus* remains most plausible. More broadly, the reinterpretation of *M. palaeojavanicus* as an ape species will need further scrutiny, including the evaluation of non-dental fossil evidence.

The Trinil 3 femur has been central to the issue of relatedness among the Trinil fossils. From the publication of the Dubois (1894) monograph onwards, skepticism has been expressed about the combination of a primitive cranial vault and a modern-looking femur (e.g., Cunningham, 1895; Manouvrier, 1895; Hepburn, 1896; see Theunissen, 1989 for a detailed review). In the 1930s, four additional partial hominin femora were discovered in previously unopened boxes of the Dubois collection

that came from the 1900 excavations at Trinil (Table 1). With all four femora attributed to *P. erectus* (Dubois, 1932a, 1934), the hard evidence for multiple hominin individuals in the Trinil deposits was seen as a clear indication that Trinil 1–5 did not have to belong to the same individual either (e.g., von Koenigswald, 1940). Furthermore, at Zhoukoudian, crania similar to the Trinil calotte were found associated with femora of apparently different morphology, thereby questioning the taxonomic association between the Trinil fossils (Weidenreich, 1938, 1941).

More recently, in an analysis that included *H. erectus* femora from China and Africa, Day and Molleson (1973) could not distinguish any of the five Trinil femora anatomically from those of modern humans; a conclusion similar to that of Kennedy (1983) with regards to the four additional Trinil femora (Trinil 3 was not interpreted taxonomically because of its shaft pathology). In contrast, Ruff et al. (2015) concluded on the basis of CT scans and structural and density characteristics that the four additional femora can be attributed to *H. erectus*, whereas Trinil 3 does not show any of the characteristics of early *Homo* and fits comfortably within *H. sapiens*.

Another point of contention has been Dubois' interpretation that Trinil 1–5 share the same stratigraphic provenance (Dubois, 1894, 1896a, 1896b, 1899, 1924a). Although doubts regarding the provenance of the fossils were voiced from the beginning, i.e. in terms of circumstances of discovery and potential disturbance or transport (Theunissen, 1989), it would take time before Dubois' assertion was seriously questioned. Early studies were based on chemical analysis of the fossils that not only included the Trinil 2 calotte and Trinil 3 femur but also the four newly discovered femora. Based on their analysis, Bergman and Karsten (1952) suggested a similar Middle Pleistocene age for the fossils. While chemical analysis by Day and Molleson (1973) yielded inconclusive results, Day (1986b) later found significant differences in heavy element composition between the Trinil 3 femur on the one hand, and the calotte and the additional femora on the other, explained as a potential difference in provenance and/or age. Around the same time, the stratigraphy itself was also considered, with some maintaining that the fossil material collected from the lower level at Trinil (including Trinil 1–5) constituted a single faunal assemblage (de Vos and Sondaar, 1982; Sondaar et al., 1983) while others observed terrace deposits in low positions at and around Trinil and suggested that Dubois must have excavated through those younger deposits as well (Bartstra, 1982, 1983). Chemical analyses continued to play an important role, with Matsu'ura (1986) obtaining similar results for all five femora, but singling out the calotte as an outlier because of a different stratigraphic origin or contamination. In contrast, Bartsiokas and Day (1993) found Trinil 3 to be the outlier which must have originated from a younger stratigraphic layer than the Trinil 2 calotte and the other four femora.

New fieldwork and comprehensive geochronological studies at and around Trinil in 2018 and 2019 showed that the Trinil site is stratigraphically more complex than previously assumed, with deposits of five different ages ranging from Early to Late Pleistocene situated at low water level within the historical excavation area (Berghuis et al., 2021; Hilgen et al., 2023), thereby confirming earlier suspicions of younger (terrace) deposits situated at low water level (Bartstra, 1982). By combining these results with detailed studies of Dubois' historical documentation of the site (Pop et al., 2023), the provenance of the hominin fossils could be reconstructed in relation to the stratigraphy. The calotte and three teeth (Trinil 1, 2, 4, 5) can be confidently placed within the Early to Middle Pleistocene deposits, while the femur (Trinil 3) was probably recovered from a channel related to Late Pleistocene terrace deposits that cut through the older, inclined stratigraphy. This interpretation is consistent with the chemical analysis of Bartsiokas and Day (1993). By contrast, Huffman et al. (2022) argue that archival material, including reports from his on-site supervisors, memoranda, field accounts, and annotated photographs, demonstrates that the skullcap and femur came from the same stratigraphic unit. However,

<sup>4</sup> This study refers to these molars as 'paratypes' of *Homo erectus*, but it is recommended practice that paratypes should only be designated in the publication naming the species (ICZN Recommendation 73D).

their stratigraphic model and positioning of the fossils therein are at odds with the complex, field-based stratigraphy of Hilgen et al. (2023) and the reconstructions of Pop et al. (2023). The stratigraphic position of the four additional femora is uncertain, as they are said to originate from the 1900 excavation (Dubois, 1932a, 1934), of which the pit ran along the full length of the historical excavation area (Pop et al., 2023).

In summary, the Trinil 3 femur is an outlier because it probably derives from younger strata than the other Trinil hominins, differs in chemical composition, and is the only specimen showing fully modern human-like morphology. Moreover, there is no consensus over the affinities of the Trinil 1 molar, and if it is *H. erectus* instead of an extinct ape, there is no evidence that it belongs to the same individual as Trinil 2. Thus, the three original holotype fossils could actually represent three individuals of two or three different species, depending on the attribution of Trinil 1. The uncertain affinities of the Trinil 4 molar mirror those of Trinil 1, and although the Trinil 5 premolar and the four additional partial femora are probably conspecific with the Trinil 2 calotte, no convincing case can be made that any of these derive from the same individual. Given our current understanding as outlined here, it seems prudent to exclude two of the three originally nominated fossils from the holotype as long as no new evidence emerges for individual associations, for example, based on ancient DNA or protein signature. In doing so, the question is raised which fossil should remain connected with the name *erectus*. The descriptions of the Trinil 2 calotte (Anonymous, 1891b, 1893; Dubois, 1894) undoubtedly include the most meaningful diagnostic features characterizing the species *erectus*. In contrast, the Trinil 3 femur is *H. sapiens*-like, and thus lacks diagnostic features of a separate species, whereas the Trinil 1 molar provides very limited and taxonomically ambivalent morphological information. Hence, it should be Trinil 2 that retains its role as holotype. In all, the pioneering discoveries at Trinil may no longer be interpreted as Dubois envisaged, but they are testimony of a rich and diverse paleoanthropological record that continues to inspire challenging stratigraphic fieldwork and advanced methodological approaches to analyze enigmatic hominid fossils.

### CRedit authorship contribution statement

**Eduard Pop:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Sofwan Noerwidi:** Writing – review & editing. **Fred Spoor:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization.

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### Supplementary Online Material.

Supplementary Online Material for this article can be found online at <https://doi.org/10.1016/j.jhevol.2024.103516>.

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