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Exploring the diversity of fossil hominin dental patterns in the western Indonesian archipelago during the Quaternary by Geometric Morphometric Analysis. Application on second upper and lower molars.

Approche de la diversité des patrons dentaires des hominines fossiles de l'archipel indonésien occidental au Quaternaire par analyse en Morphométrie Géométrique. Application sur les deuxièmes molaires supérieures et inférieures.

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Abstract

Islands of the western part of the Indonesian archipelago were impacted by climatic and sea-level changes during Pleistocene, which affected the dispersals and/or isolation of hominins in this region. This study aims to characterize the diversity of ancient human populations in the Sundaland based on dental collections from several localities in Sumatra and Java. The material consists of 111 teeth, 57 from Pleistocene hominins and 54 from Holocene *Homo sapiens*. The study of external morphology was done by geometric-morphometric analysis on the occlusal surface of the upper (N=47) and lower second molars (N=64). We observe group clustering among the samples. There are at least four groups (dental types) of hominins during Pleistocene times. Result suggest that there is an overlapping among them throughout the Lower and early Middle Pleistocene; another group persists until the Late Pleistocene, and two other groups of *Homo sapiens* are present during the Holocene. The implication of this study sheds light on the history of ancient human occupation (continuity/rupture) in Island Southeast Asia during the Quaternary period.

Keywords: *Homo erectus*, Sundaland, Quaternary, teeth, Procrustes analysis

Résumé

Les îles de la partie ouest de l'archipel indonésien ayant été affectées par les changements du climat et le niveau marin, les hominines ont migré et se sont parfois trouvés isolés au cours du Pléistocène. Le but de cette étude est de caractériser la variabilité des anciennes populations humaines dans la région de Sundaland à partir du matériel dentaire fossile provenant de plusieurs sites de Sumatra et de Java. L'échantillon comprend 111 dents dont 57 d'hominines pléistocènes et 54 d'*Homo sapiens* holocènes. Cette étude est basée sur une approche en morphométrie géométrique des faces occlusales des secondes molaires inférieures (N=64) et supérieures (N=47). Les résultats ont permis d'observer quatre groupes (types dentaires) parmi les hominines pléistocènes et deux pour les *Homo sapiens* holocènes. Parmi les premiers (*Homo erectus*), une continuité morphologique est observée entre le Pléistocène inférieur et le début du Pléistocène moyen. Un autre groupe ne présente pas de rupture dans l'expression des caractères jusqu'au Pléistocène supérieur. Enfin, deux groupes d'*Homo sapiens* ont été identifiés pour l'Holocène. Ainsi, cette recherche contribue à préciser les modalités des peuplements humains (continuité/rupture) en Asie du Sud-Est insulaire pendant le Quaternaire.

Mots clé : *Homo erectus*, Sundaland, Quaternaire, dents, analyses Procrustes

1 Introduction

Teeth are the most frequently preserved part in the skeleton. More directly affected by the forces of natural selection, teeth reflect genotype changes (Rathmann et al., 2017; Rathmann and Reyes-Centeno, 2020). Moreover, they are easy to process by quantitative methods (Brace et al., 1987). Teeth have been the subject of numerous paleoanthropological studies for a long time. They provide a wealth of information on humans, including: cultural habits, pathology, morphological variation, and biological development. An understanding of dental morphological variation among living humans has proven to be important for assessing biological relationships between recent groups (for a recent review, see Bailey and Hublin, 2007).

The study of hominin teeth in Indonesia began when the two molars from Trinil discovered in 1891 were published by Dubois in 1924 and attributed to a human relative

named *Pithecanthropus erectus* (Dubois, 1924). Subsequently, Miller (1923), Weidenreich (1937) and von Koenigswald and colleagues (1940) suggested the teeth belong to an orangutan. Hooijer (1948) studied the prehistoric human teeth from Padang Highland, Western Sumatra which were found by Dubois during his first exploration (1888-1890). He stated that the teeth from Lida Ajer cave near Pajakombo do not allow a definitive determination, but it is less likely that they come from a European or African population than from an Asian population (Hooijer, 1948).

Based on the analysis of several mandibular and maxillary teeth from Sangiran, von Koenigswald and Weidenreich mentioned four different taxa: *Meganthropus palaeojavanicus*, *Pithecanthropus mojokertensis*, *P. dubius* and *P. robustus* (von Koenigswald, 1950; Weidenreich, 1945). Von Koenigswald (1954; 1960) and Tobias (1967) studied the *Pithecanthropus* and *Meganthropus* dental and mandibular remains from the Sangiran dome. The latter tried to understand the evolutionary trends within hominid teeth, including *Australopithecus*, *Homo habilis*, *Sinanthropus*, and *Pithecanthropus* from Java. He concluded that four degrees of hominization could be recognized in African and Asian samples from Lower to early Middle Pleistocene (Tobias, 1967): 1) *Australopithecus*, 2) *H. habilis* and *Meganthropus*, 3) *Telanthropus*, *P. mojokertensis* and *P. robustus*, and 4) *Atlanthropus*, *P. erectus* and *Sinanthropus pekinensis*.

Korenhof studied a large number of the 'prehistoric' *Homo sapiens* teeth collected from Sangiran dome by von Koenigswald between 1935-1940. Most of the specimens lack roots, and a significant percentage of the dentine is lost, probably because of the weathering under tropical conditions. Indeed, fragile dentine can be eliminated while preserving the enamel cap. Korenhof made comparative observations of the outer and inner structures of molars, such as the primary cusps, marginal ridges, foveas, and crista (Korenhof, 1961; 1966; 1978; 1982). His observations on the enamel-dentine separation plane laid the groundwork for present-day endostructural dental studies using high-resolution techniques.

Also at that time, Jacob (1967) studied the history of Indonesian populations based on skeletal and dental remains, and stated that *Pithecanthropus soloensis* came to an extinction while the modern populations of *Homo sapiens* were descending from *H. wajakensis*. This paleoanthropological work was continued by Widiyanto (1991; 1993), who studied the diversity and evolution of the hominin fossils from Java. He evidenced the evolution of Javanese hominins from the Early to the Middle Pleistocene through examination of the robustness index. From *H. erectus* to *H. sapiens*, the robustness of the upper canines decreased while the upper fourth premolars became more robust and the lower teeth remained unchanged. Both the upper and lower second molars show the same pattern of evolution, becoming smaller, while the first molars have increased in size over time (Widiyanto, 1991). In another cranio-dental study, Widiyanto suggested that over its one-million-year history, Indonesian *H. erectus* could be divided into "Robust", "Trinil-Sangiran", and "Solo" groups. However, this hypothesis cannot be supported by the dental remains of the Solo group (Widiyanto, 1993), because there is no dental collection from this latter group.

In the context of the description of *Homo erectus* definition between Africa vs Asia, Grine (1984) compared African and Asian deciduous teeth to try to understand their evolutionary history. Then, Grine and Franzen (1994) did a comprehensive morphological and metric description of the fifty-two isolated permanent teeth that von Koenigswald found on the surface of the Sangiran dome between 1937 and 1941. These teeth are now housed in the Naturmuseum Senckenberg, Frankfurt, and were catalogued as Sangiran 7 (7.1 – 7.52) by Jacob (1975). The specimens which came from the Pucangan/Djetis beds (Lower Pleistocene) are catalogued as Sangiran 7a and those from the Kabuh/Trinil beds (Middle Pleistocene) Sangiran 7b.

Various researchers have sought to catalogue Indonesian collections of human fossils. Jacob (1975) did the first comprehensive catalogue of early hominins and *Homo sapiens* fossils. This work was built upon by Aziz (2001), who added the Sartono's dental collection stored in the Geological Research and Development Center, Bandung. Indriati (2004) catalogued the collection of Jacob housed in the Laboratory of Paleoanthropology and Bioanthropology, Gadjah Mada University, Yogyakarta. However, with the exception of the study of Grine and Franzen (1994), most of these efforts consist only of brief descriptions lacking morphological and morphometric detail. The last catalogue with comprehensive morphological descriptions was compiled by Schwartz and Tattersall (2003).

Kaifu and his colleagues made a comprehensive study of the mandibular (N=8) and dental (N=84) remains from the Sartono's collection found in Java between 1952 and 1986. They examined morphological differences between older and younger chronological groups, and also investigated their affinities with African and Eurasian hominins. They traced the evolutionary history, specialization and extinction of Javanese *Homo erectus*. Their results indicate that 1) there are remarkable morphological differences between the different chronological groups; 2) the older group has some primitive features shared with the early African *H. erectus*; and 3) the younger group is morphologically advanced, showing a degree of dentognathic reduction similar to that of the Middle Pleistocene Chinese *H. erectus* (Kaifu et al., 2005b, 2005a).

Zanolli (2011) explored the endostructural characters of Indonesian *Homo erectus* (N=17) using a high-resolution technique and compared his results with contemporary specimens from Africa. In 2013, he added supplementary evidence for a marked degree of size variation and time-related structural reduction in Javanese *H. erectus* (Zanolli, 2013). Subsequently, Zanolli et al. (2014) identified the Arjuna 9 specimen as a ponginae on the basis of its endostructural characters, but then referred to it as a *Meganthropus palaeojavanicus* (Zanolli et al., 2019). This study actually restored Widiyanto's (1993) previous identification of this specimen as a robust *Homo erectus*.

Noerwidi (2012; 2017) reconstructed the latter part of the history of the Java population from a comparative morphometric study of prehistoric and recent mandibular teeth. He suggested a hypothesis of multiple migration to Java from the Late Pleistocene to the Late Holocene with the successive arrivals of: An Australo-Melanesian population (Latest Pleistocene), a Southeast Asian or 'Southern *Mongoloid*' population (Neolithic Austronesian, 3000 BP), and a 'gracile' population (early AD, perhaps from India). The Song Keplek 5 specimen from Gunungsewu was considered to be the first representative of the island's Austronesian language speaker.

Based on these previous studies, the human population of Indonesian archipelago shows a great diversity in temporal and spatial distribution. Studies on the dental evidence are still few, and the aim of this paper is to assess human variability in this region from the Lower Pleistocene to the Holocene based on teeth. For this purpose, a geometric morphometric approach has been used. This approach allows to compare fossils on the basis of their dental shape, i.e. by isolating first the individual size factor.

2 Material and Methods

2.1 Material

This research brings together a comprehensive database of all human dental collections from Java, whose specimens are housed in 7 different institutions in Indonesia and Europe: The Sangiran Museum, Balai Arkeologi Yogyakarta, Geological Museum Bandung,

Gadjah Mada University Yogyakarta, Institute of Technology Bandung, Naturmuseum Senckenberg Frankfurt, and National Museum of Natural History Leiden. These specimens include 17 maxilla and 19 mandibles (mostly fragmentary) as well as 62 isolated teeth. They come from the following Pleistocene sites (Fig.1): Sangiran and Patiayam (Central Java), Trinil and Wajak (East Java), Lida Ajer (West Sumatra). For comparative purpose the study will also include *Sinanthropus* teeth, which are the Pleistocene hominins from the Zhoukoudian Lower Cave (China), the nearest Mainland Asia region. We used a little-known collection of *Sinanthropus* dental casts housed in the Institut de Paléontologie Humaine, Paris.

The Holocene *Homo sapiens* teeth come from the Insular Sundaland (Fig.1) region (Java and Sumatra), including Tamiang and Sukajadi shellmidden sites (Northern Sumatra), Gua Harimau (South Sumatra), Gua Pawon (West Java), Gua Kidang (Central Java), Gua Braholo and Song Tritis (western part of Southern Mountains), also Song Keplek and Song Terus (eastern part of Southern Mountains). The original Holocene *H. sapiens* collections are housed in Museum Si Pahit Lidah (South Sumatra), Balai Arkeologi Bandung (West Java), Balai Arkeologi Yogyakarta, Gadjah Mada University Yogyakarta, and Laboratory of Gunung Sewu, Pacitan (East Java). The Holocene *H. sapiens* samples used in this study are important because, in contrast to specimens referred to *H. erectus*, some have only been superficially studied and most are unpublished.

Fig. 1.

In total, this study includes 111 teeth, consisting of 57 teeth from Pleistocene hominins and 54 teeth from Holocene *Homo sapiens* (Table 1). This work uses only the second lower and upper molars (M2) of Javan hominins. These teeth are part of a larger sample (N=725) used in previous study by Noerwidi (2020). We have chosen the M2 because this tooth class is the most abundant in the sample available and among the most significant in terms of evolutionary anthropology. Its importance on the study of human diversity and evolution in the Island of Southeast Asia was highlighted previously by some studies e.g., Widiyanto (1991; 1993) and Kaifu *et al.* (2005). They noted that the Pleistocene Javan hominin teeth, especially the second molar, reflected evolutionary changes through time. Furthermore, a study by Noerwidi (2012) added more about the significance of the second molar on the identification of the difference between populations in the region during the Holocene.

Table 1 summarizes the correspondence between the stratigraphy record and the chronometric dating suggested from previous studies for dental remains used in this study.

No.	Sites	Chronology	Reference	No. of Teeth
Early Hominins				
1	Trinil	0.5 Ma	(Joordens et al., 2015)	1
2	Sangiran - Pucangan Fm.	1.6 - 1.16 Ma	(Matsu'ura et al., 2020; Sémah et al., 2000; Suzuki et al., 1985)	11
3	Sangiran - Grenzbank Layer	0.97 - 0.9 Ma	(Hyodo et al., 1993; Matsu'ura et al., 2020)	5
4	Sangiran - Kabuh Fm.	0.78 - 0.7 Ma	(Falguères, 2001; Suzuki et al., 1985; Swisher et al., 1994)	28
5	Sangiran - Notopuro Fm.	0.49 - 0.25 Ma	(Hyodo et al., 1993; Suzuki et al., 1985)	-
6	Zhoukoudian	0.5 - 0.23 Ma	(Zhao et al., 1985)	8
Late Pleistocene <i>Homo sapiens</i>				
1	Lida Ajer	73 - 63 Ka	(Westaway et al., 2017)	1

2	Wajak 1 & 2	37.4 - 28.5 Ka	(Storm <i>et al.</i> 2013)	4
Early Holocene <i>Homo sapiens</i>				
1	Tamiang Shellmidden	12 - 4 Ka	(Wiradnyana, 2016)	2
2	Sukajadi Shellmidden	7 - 5 Ka	(Bronson and Glover, 1984)	7
3	Gua Harimau (Lower Level)	14 - 5 Ka	(Simanjuntak, 2016)	5
4	Gua Pawon	9.5 - 5.5 Ka	(Yondri, 2005)	6
5	Gua Braholo	12 - 4 Ka	(Simanjuntak, 2002)	8
6	Song Terus	9330 ± 90 BP	(Sémah <i>et al.</i> , 2004)	5
7	Song Tritis	6 - 3 Ka	(Widianto, 2004)	1
8	Song Keplek (Preneolithic)	5900 ± 180 BP	(Simanjuntak, 2002)	3
9	Wajak - Holocene	10.5 - 6.6 Ka	(Shutler Jr <i>et al.</i> , 2004)	5
Late Holocene <i>Homo sapiens</i>				
1	Song Keplek (Neolithic)	3053 ± 65 BP	(Noerwidi, 2012)	2
2	Gua Harimau (Upper Level)	2.800-1.800 BP	(Simanjuntak, 2016)	10

Table 1. Chronological attributions of the sites and dental remains used in this study.

Tableau 1. Attributions chronologiques des sites et restes dentaires utilisés dans cette étude.

2.2 Method

This study applies 2D Geometric-Morphometric Analysis (GMA) on teeth to assess the diversity and evolutionary history of ancient human populations in the western Indonesian archipelago. The landmark-based GMA is used to work on the shape space and to explore intra- and inter- taxon variation with an approach that allows the size effect to be excluded. The occlusal surface of all upper and lower molars was digitized in the same anatomical orientation recording, respectively, 24 and 18 landmarks.

2.2.1 Limitations

Following the procedure of Quam *et al.* (2009) and Gomez-Robles *et al.*, (2011), we have selected for our analysis the teeth corresponding to the following conditions:

- Only teeth in good condition. Are excluded from the analysis: teeth that were suffering from crown wear higher than grade 4 of Molnar (1971), or damage that has erased the fissure pattern or breakage that has disturbed an accurate assessment of the crown area.
- Only molars that preserves the four main cusps or more.
- Preferably the right lower premolar/molar and the left upper premolar/molar (when both teeth for the same individual are preserved). Otherwise, the tooth best preserved and/or with the least worn condition was used.

2.2.2 Recording protocol

To undertake such GM analysis, a picture of the occlusal surface of the tooth is required. The protocol used is adapted from the procedure of Bailey (2002), as follows:

- A Nikon™ D70S digital camera with AF-S Nikkor DX 18-70 mm lens f/3.5-4.5G ED was used to capture images of the occlusal surface of the tooth. The camera was attached to a tripod and was levelled horizontally and vertically. The pictures were taken with a manual setting using 50 mm (standard) magnification, 200 ISO, with a narrow aperture and low speed, which is supposed to be provided a natural and sharp picture.
- Isolated teeth were mounted on plastiline and positioned in anatomical position so that the plane of occlusion was vertical to the visual axis of the camera lens. For tooth *in*

situ, the cranium or mandible was manipulated in such way that the occlusal surface of the tooth in question is perpendicular to the camera's optical axis. A millimetre scale was included in each image for calibration, placed parallel to the lens and at the same distance from it as the occlusal plane.

2.2.3 Positioning the landmarks

The protocol of documentation and the condition of the teeth used for GMA are adapted from Bailey (Bailey, 2004), Quam *et al.*, (2009) and Gomez-Robles *et al.*, (2011). Some additional information come from the protocol of Martinon-Torres *et al.* (2006), Gomez-Robles *et al.* (2007, 2008, 2011, 2012), Bae *et al.* (2014), Xiao *et al.* (2014). We observed the following conditions:

- The landmarks located on the tips of the main cusps were visually located in the images by examining the original fossil.
- When the tip of the main cusp showed little wear, the landmarks were located in the center of the wear facet.
- On the casts, landmarks were marked with a soft pencil before the documentation process.
- Landmarks on the groove and fovea were marked at the deepest part of the fissure. The specimen was excluded of the analysis in case of unclear location of the landmarks.
- The original shape was estimated by reference to the overall crown shape and the buccolingual extent of the wear facets following the protocol of Bailey and Lynch (2005), for the mesial and/or distal borders of the teeth that are affected by interproximal wear.

Fig. 2.

The position of the 18 landmarks position on the lower second molar (Fig. 2, left) are described in the following Table 2:

<i>No</i>	<i>Landmark</i>	<i>Reference</i>
1	Peak of Metaconid (C2)	1
2	Lingual end of anterior fovea	2
3	Central intersection of anterior fovea	3
4	Buccal end of anterior fovea	4
5	Peak of Protoconid (C1)	5
6	Mesial end of Protoconulid (buccal accessories cusp)	6
7	Lingual end of Protoconulid (buccal accessories cusp)	7
8	Distal end of Protoconulid (buccal accessories cusp)	8
9	Mesial end of the contact between Metaconid/Protoconid with Hypoconid/Entoconid	9
10	Distal end of the contact between Metaconid/Protoconid with Hypoconid/Entoconid	10
11	Mesial end of Metaconulid (C7)	11
12	Buccal end of Metaconulid (C7)	12
13	Distal end of Metaconulid (C7)	13
14	Peak of Hypoconid (C3)	14
15	Buccal end of Hypoconulid (C5)	15
16	Mesial end of Hypoconulid (C5)	16

17	Lingual end of Hypoconulid (C5)	17
18	Peak of Entoconid (C4)	18

Table 2. Position of the 18 landmarks on LM2

Tableau 2. Position des 18 points de repère sur la M2 inférieure

The position of the 24 landmarks on the upper second molar (Fig. 2, right) are described in the following Table 3:

<i>No</i>	<i>Landmark</i>	<i>Reference</i>
1	Peak of Protocone (C1)	1
2	Lingual end of mesial accessories tubercle	2
3	Distal end of mesial accessories tubercle	3
4	Buccal end of mesial accessories tubercle	4
5	Lingual end of anterior fovea	5
6	Intersection of anterior fovea	6
7	Buccal end of anterior fovea	7
8	Peak of Paracone (C2)	8
9	Mesial end of buccal accessories cusp	9
10	Lingual end of buccal accessories cusp	10
11	Distal end of buccal accessories cusp	11
12	Central fossa	12
13	Distal triangular fossa	13
14	Mesial end of lingual accessories cusp	14
15	Buccal end of lingual accessories cusp	15
16	Distal end of lingual accessories cusp	16
17	Peak of Metacone (C3)	17
18	Buccal end of Metaconule (C5)	18
19	Mesial end of Metaconule (C5)	19
20	Lingual end of Metaconule (C5)	20
21	Buccal end of posterior fovea	21
22	Intersection of posterior fovea	22
23	Lingual end of posterior fovea	23
24	Peak of Hypocone (C4)	24

Table 3. Position of the 24 landmarks on UM2.

Tableau 3. Position des 24 points de repère sur la M2 supérieure.

2.2.4 Digitizing landmarks

At the beginning of the digitizing process, each tooth has to be oriented in the same direction with the mesial and distal sides horizontally parallel to the x-axis, and the buccal and lingual sides vertically parallel to the y-axis, with the buccal side facing to the right. We use the right lower teeth and the left upper teeth.

TpsDig2 version 2.16 (Rohlf, 2010) was used to digitize the landmarks. They were always digitized in the same clockwise direction starting with the first point being the lingual cusp for premolar, the protocone for the upper molar and the metaconid of the lower molar. In order to minimize the bending energy between each point of the landmarks (Bookstein, 1991; Gunz et al., 2006), these landmark points were then slid and connected using TpsUtil and tpsRelw (Rohlf, 2010).

Subsequently, Generalized Procrustes Analysis (superimposition of landmark configurations) was performed in tpsRelw (Rohlf, 2010). The procrustes residuals (deviation of a configuration of Procrustes coordinates from the consensus configuration, see Mitteroecker and Gunz (2009) were analyzed using the Relative Warps Analysis function in

tpsRelw. The relative warp output is the same as the Principal Component output. TPS-grids were also evaluated to better observe the degree of variation at the edges of the different principal components (Bookstein, 1997). The principal components plots and TPS-grids were generated in tpsRelw (see Martín-Torres *et al.*, 2006; Gómez-Robles *et al.*, 2007, 2008, 2011, 2012; Bae *et al.*, 2014; Xiao *et al.*, 2014).

3 Result

This work will present geometric morphometric analysis (GMA) on the second lower and upper molars (LM2 and UM2) of Javan hominins. The PCAs express the diversity of the sample and we can visualise the changes in conformation between the fossils along the axes through the deformation grids. In a second step, we observe whether the distribution of fossils in the analysis corresponds to the groups we defined in a previous analysis based on morphological characters (Noerwidi, 2020).

3.1 Geometric Morphometric Analysis on LM2

For this analysis, 64 LM2 were considered. Among them, 34 correspond to Pleistocene hominins (26 from Sangiran, 6 from Zhoukoudian, 2 from Wajak) and 30 to Holocene *Homo sapiens* (4 from Northern Sumatra, 9 from Gua Harimau, 4 from Gua Pawon, 9 from Gunungsewu, 3 from Wajak Holocene caves, 1 from Gua Kidang). The 2 coordinates of 18 landmarks were recorded on the occlusal surface, delivering 36 point of X and Y coordinates used as 36 Principal Component Analysis (PCA) factors. The first two factors of the PCA have eigenvalue value which are 10.55 or 43.39 % for the Axis 1 and 7.21 or 29.64 % for the axis 2 (totalizing 73.03 %).

Fig. 3

The first axis of the PCA based on Procrustes residuals after superimposing sets of landmarks on LM2 (Fig. 3) shows a tendency to separate *Homo erectus* from *H. sapiens*. The *H. erectus* pattern is more complex (crenulation, marked fissures, crest, and accessories tubercle) while the *H. sapiens* pattern is simple and presents a bucco-lingual enlargement. The second axis of the PCA trends to separate the *H. erectus* teeth (Groups 1, 2-3 and the Zhoukoudian specimens). In the former, the LM2 is square in shape while in the latter, it is more elongated mesio-distally.

Based on such results and on our direct observations of the teeth (Noerwidi, 2020), we can describe the main differences as follows:

- All Pleistocene hominins from Java and Zhoukoudian show a complex occlusal pattern, with large anterior and posterior fovea, also a lingual accessory tubercle. This pattern also survived in **SKJ X**, **SKJ 4a**, and **SK 4** of G 5 Early Holocene *H. sapiens* and **HRM 12**, **HRM 21**, and **HRM 23** of G 6 Late Holocene *H. sapiens*.
- All of G 4 Pleistocene hominins and *Homo sapiens*, including **Sangiran 37** and **Sangiran 33** of G 3 Javan *H. erectus*, and **Sp 45** of Zhoukoudian *H. erectus*, display a simpler occlusal formation with narrow or absent anterior and posterior fovea, also absence of lingual accessory tubercle.
- G 1-2 Pleistocene hominins, **Wajak 2**, **Abimanyu 1**, **NG 92 D6**, **NG 92.4**, and **NG 0802.2** of G 4 Pleistocene hominins, also **HRM 23** of G 6 Late Holocene *H. sapiens* have mesio-distal elongated shape
- G 6 Late Holocene *H. sapiens*, Zhoukoudian *Homo erectus*, including **Sangiran 9**, **S 25**, **S 7-64** of G 2 Javan *H. erectus*, **NG 8503**, **S 0089**, **S 7-78**, and **S 7-84** of G 3 Javan

H. erectus, also **Wajak 1**, **NG 92.1**, **NG 92.3**, and **NG 0802.1** of G 4 Pleistocene hominins, have square shape

- G 5 Early Holocene *H. sapiens* from Sukajadi, Gua Braholo, Song Keplek, Song Terus, Song Tritis, Goea Ketjil and Djimbe have mesiodistal elongated shape, but other specimens from Tamiang, Gua Harimau lower level, Gua Pawon, and Gua Braholo have square shape.

3.2. Geometric Morphometrics on UM2

For this analysis, 47 UM2 were considered. Among them 22 correspond to Pleistocene hominins (17 from of Sangiran, 2 from Zhoukoudian, 1 from Lida Ajer, 2 from Wajak) and 25 to Holocene *Homo sapiens* (4 from Northern Sumatra, 6 from Gua Harimau, 3 from Gua Pawon, 9 from Gunungsewu, 2 from Wajak Holocene caves, 1 from Gua Kidang). The 2 coordinates of 24 landmarks were recorded on the occlusal surface, delivering 48 point of X and Y coordinates used as 32 factors for PCA. The first two factors of the PCA have eigenvalue value which are 44.22 or 47.97 % for the Axis 1 and 22.35 or 24.24 % for the Axis 2 (totalizing 72.21 %).

Fig. 4

The first axis of the PCA based on Procrustes residuals after superimposing of the sets of landmarks on UM2 (Fig. 4) shows a tendency to separate *Homo erectus* and *Homo sapiens*. The *H. erectus* pattern is more complex (crenulation, marked fissures, crest, and accessories tubercle) while the *H. sapiens* pattern is simple and presents a bucco-lingual enlargement. The second axis of the PCA clearly separates the *H. erectus* (Groups 1-2) from *H. sapiens* on the one hand and from the Zhoukoudian specimens on the other hand. In the former, mesial margin accessory tubercle and distal cusp are developed while they are reduced in the latter. Note the overlap between *H. sapiens* and G 3 – Javan *H. erectus*.

Based on such results and on our direct observations of the teeth (Noerwidi, 2020), we can describe the main differences as follows:

- All the Pleistocene hominins from Java and Zhoukoudian display a complex occlusal pattern, with large anterior and posterior fovea, also buccal accessory tubercle. This pattern also presented in **Wajak 1** of G 4 Late Pleistocene *H. sapiens*.
- All of *H. sapiens* and G 4 Late Pleistocene hominins show a simpler occlusal pattern with narrow to absent anterior and posterior fovea, also absent buccal accessory tubercle.
- G 1-2 Pleistocene hominins, including **S 7-3c** of G 3 Javan *H. erectus*, **Wajak 2**, **NG 91 G 10**, **NG 1989**, and **S 0087** of G 4 Late Pleistocene hominins, also **HRM 10** of G 6 Late Holocene *H. sapiens*, have developed mesial margin accessory tubercle and distal cusp.
- G 3 Javan *H. erectus*, Zhoukoudian *H. erectus*, and G 6 Late Holocene *H. sapiens* including **PDS 0712**, **LA 11472**, and **S 0086** of G 4 Late Pleistocene hominins, have reduced mesial margin accessory tubercle and distal cusp.
- Specimens of G 5 Early Holocene *H. sapiens* show more or less developed mesial margin accessory tubercle and distal cusp.

We only present here the results obtained on upper and lower M2. In a previous work (Noerwidi, 2020), we have performed GMA also on premolars and M1 and M3, and the main observations are summarized on Table. 4 for lower teeth, and Table. 5 for upper teeth.

Tooth	Separation between early hominins and <i>Homo sapiens</i>	Separation among early hominins	Separation among <i>Homo sapiens</i>
LP3	No clear separation	Clear separation for G-1 A tendency to separate between G-2, G-3, and the Zhoukoudian specimens	No separation
LP4	No clear separation	Clear separation for G-1 Clear separation between G-2, G-3, and the Zhoukoudian specimens	Clear separation between G-4, G-5 and G-6
LM1	A tendency to separate	A tendency to separate between G-1, G-2 and G-3 Clear separation of the Zhoukoudian specimens	A tendency to separate between G-4, G-5 and G-6
LM2	Almost clear separation	A tendency to separate between G-1, G-2 and G-3, also with the Zhoukoudian specimens	A tendency to separate between G-5 and G-6
LM3	Almost clear separation	A tendency to separate between G-1, G-2, and G-3 Clear separation of the Zhoukoudian specimens	A tendency to separate between G-5 and G-6

Table 4. Summary of the results obtained by GMA on the lower premolars and molars (for details see Noerwidi, (2020).

Tableau 4. Résumé des résultats obtenus par analyses en morphométrie géométrique sur les prémolaires et molaires inférieures (pour plus de détails, voir Noerwidi, (2020).

Tooth	Separation between early hominins and <i>Homo sapiens</i>	Separation among early hominins	Separation among <i>Homo sapiens</i>
UP3	No clear separation	Clear separation for G-1 No tendency to separate for the rest early hominins	No separation
UP4	A tendency to separate	A tendency to separate between G-1, G-2, G-3, and Zhoukoudian <i>Homo erectus</i>	A tendency to separate between G-5 and G-6
UM1	No clear separation	A tendency to separate between Javan <i>Homo erectus</i> , and Zhoukoudian <i>Homo erectus</i>	No separation
UM2	Almost clear separation	A tendency to separate between G-1, G-2, G-3, and Zhoukoudian <i>Homo erectus</i>	No separation
UM3	A tendency to separate	A tendency to separate between G-1 and G-2 with G-3 and Zhoukoudian <i>Homo erectus</i>	A tendency to separate between G-5 and G-6

Table 5. Summary of the results obtained by GMA on the upper premolars and molars (for details see Noerwidi, (2020).

Tableau 5. Résumé des résultats obtenus par analyses en morphométrie géométrique sur les prémolaires supérieures et les molaires (pour plus de détails, voir Noerwidi, (2020).

4 Discussion

4.1 Dental Pattern Diversity

The results of the GMA on M2 from the western Indonesian fossil record, have documented the differences between dental patterns within the 6 groups of hominins defined on chronological basis (see Fig. 5-8). Such groups represent the dental record diversity and are not directly correlated to the hominin population diversity. However, we observe that the variability of the dental type groups is higher than expected.

Fig. 5.

Fig. 6.

Group 1 (Fig. 5 and 6), named here “Meganthropus” type, includes Early Pleistocene hominins formerly named Sangiran 4, Sangiran 5, Sangiran 6a & b, Sangiran 27, Arjuna 9, and other isolated teeth of S-7a from Early Pleistocene layers of the Sangiran Dome. Such specimens are characterized by the following features: large size, asymmetric shape of premolar, square shape of LM and rhombus shape of UM, also a complex occlusal morphology with pronounced developed accessories of LM and UM.

Group 2 (Fig. 5 and 6), named here “Mojokertensis” type, includes specimens such as Sangiran 1b, Sangiran 8, Sangiran 9, Sangiran 15a, Sangiran 37, Tjg 1993.05, Bpg 2001.04 and other hominins found in Early to Mid-Pleistocene layers in the Sangiran Dome. Such specimens are characterized by the following features: medium size, less symmetric shape of premolar, rectangular shape of LM and rhombus shape of UM, also a less complex occlusal morphology with developed accessories of UM and LM.

Group 3 (Fig. 5 and 6), named here “Sangiran” type, consists of Sangiran 1a, Sangiran 7-3, Sangiran 7-17, Sangiran 15b, Sangiran 17, Sangiran 22b, Sangiran 33, Sangiran 39, and NG 8503 also hominins from Early to Mid-Pleistocene from Sangiran. Such specimens are characterized by the following features: small size, less symmetric shape of premolar, square shape of LM and rhombus and rhomboid shape of UM, also a less complex occlusal morphology with less developed accessories of UM and LM.

The comparative sample from mainland Asia (Zhoukoudian) is distributed between Groups 2 “Mojokertensis” and 3 “Sangiran” type (Fig. 7). This condition can be explained by the stratigraphic distribution of the fossils (in different levels) and/or it represents the high variability of the Zhoukoudian *Homo erectus* group.

Fig. 7.

Group 4 (Fig. 5 and 6), named here “Wajak” type, includes several hominins from Mid-Pleistocene in Sangiran and *Homo sapiens* ‘*wajakensis*’ from the Late Pleistocene. Such specimens are characterized by the following features: moderate size, symmetric shape of premolar, square shape of LM and rhomboid shape of UM, also simple occlusal morphology represented by the reduction of accessories characters.

Group 5 (Fig. 8, left), named “Preneolithic” type, includes the *Homo sapiens* fossils from Early to Mid-Holocene. They are characterized by the following features: small size,

symmetric shape of premolar, square shape of LM and rhomboid shape of UM, also simple occlusal morphology represented by the absent of accessories characters.

Group 6 (Fig. 8, right), named here “Neolithic-Paleometallic” type, groups the Late Holocene *H. sapiens*. They are characterized by the following features: small size, symmetric shape of premolar, rectangular shape of LM and rhomboid shape of UM, also less complex occlusal morphology with lightly developed of accessories characters.

Fig. 8.

4.2 Chronology of human occupation

We summarized the attribution of the fossils to one of the 6 groups in parallel with their chronological estimation (Table 6). Groups were determined by clustering analysis based on morphological pattern (for details see Noerwidi et al., 2019 and Noerwidi, 2020). With the exception of group 6, no group is limited to a chronological period but, on the contrary, there is a significant overlap.

<i>Chronology</i>	<i>Hominin Fossils</i>
<i>Early Pleistocene</i> <i>(1.6 to 1.2 Ma)</i>	<ul style="list-style-type: none"> • Group 1: Sangiran 4, Sangiran 5, Sangiran 6a, Sangiran 6b, Sangiran 27 • Group 2: Sangiran 1b, Sangiran 9, Sangiran 15a • Group 3: Sangiran 1a, Sangiran 22b
<i>Late of Early Pleistocene</i> <i>(0.9 Ma)</i>	<ul style="list-style-type: none"> • Group 1: Arjuna 9 • Group 2: Sangiran 8, Bpg. 2001.04 • Group 3: Sangiran 33
<i>Middle Pleistocene</i> <i>(0.78 to 0.5 Ma)</i>	<ul style="list-style-type: none"> • Group 2: Sangiran 37, Tjg 93.05 • Group 3: Sangiran 15b, Sangiran 17, Sangiran 33, Sangiran 39, NG 8503 • Group 4: Isolated teeth of NG 91 610, NG 92.01, NG 92.03, NG 92.04, NG 92 D6, PDS 0712, NG 0802.3, Abimanyu 1
<i>Late Pleistocene to Early Holocene</i> <i>(125 to 12 Ka)</i>	<ul style="list-style-type: none"> • Group 4: Wajak 1 & 2, Lida Ajer • Group 5: Braholo 4
<i>Early to Mid-Holocene</i> <i>(10 to 5 Ka)</i>	<ul style="list-style-type: none"> • Group 5: Song Terus from Keplek Layer, Song Keplek 1 & 4, Braholo (except BHL 4), Song Tritis, Wajak Holocene caves, Gua Kidang, Gua Harimau lower layer, Northern Sumatra Shellmidden
<i>Late Holocene (3 Ka)</i>	<ul style="list-style-type: none"> • Group 6: Song Keplek 5 and Gua Harimau upper layer

Table 6. Diachronic position of the hominins in Sundaland during the Quaternary
Tableau 6. Position diachronique des hominines dans le Sundaland pendant le Quaternaire

Similarly, we observed that the dental pattern diversity exceeded the chronological distribution of specimens (Fig. 9). In other words, dental diversity is not strictly following the chronology, which means that the variability is higher than previously expected and evolutionary processes are more complex.

Fig. 9

The earliest hominin occupation in Island Southeast Asia occurred during the Early Pleistocene at least at 1.6 Ma (e.g. Sémah et al., 2000). This period yields fossils of Group 1 “Meganthropus” type from the Lower Pleistocene Pucangan layers. The Group 2 “Mojokertensis” type is also found in the middle of Pucangan series. In a higher part of the Pucangan series, around 1.2 Ma (Suzuki and Wikarno, 1982), fossils belonging to Group 1 “Meganthropus” type are still found. Group 2 “Mojokertensis” type is also found in these levels, while other fossils show characters of Group 3 “Sangiran” type.

Near the boundary between Early and Middle Pleistocene (around 0.9 Ma), the Grenzbank layer yields hominin fossils. We find here the last specimens belonging to Group 1 “Meganthropus” type. Group 2 “Mojokertensis” and Group 3 “Sangiran” type” also exist at this level. In the early Middle Pleistocene Kabuh series (c. 0.8 Ma), Group 2 “Mojokertensis” type is documented. Fossils from Group 3 “Sangiran” type are more frequent, and new dental characters of Group 4 “Wajak” type appear in the Kabuh layers at the same time.

The Zhoukoudian *Homo erectus* who lived at the same period in Mainland Asia share some morphological characters with Group 2 and Group 3. Based on these records, there might be a genetic contact between Island Southeast Asia and Mainland Asia during the Middle Pleistocene. Previous studies based on cranial anatomy show a relationship between Zhoukoudian and Javan *Homo erectus*, especially the Solo derived group (Jacob, 1981; Santa Luca, 1980; Weidenreich, 1951, 1943).

The Late Pleistocene (since 125 ka) dental record in the western Indonesian archipelago is still poor. We studied here the Lida Ajer fossil, recently claimed to date back c. 73-63 Ka (Westaway *et al.*, 2017), and the Wajak hominins (37.4 to 28.5 ka, Storm *et al.* 2013). The two specimens included in this research belong to the Group 4 “Wajak” type.

At the very end of the Pleistocene and during the first part of the Holocene, the western part of Indonesian archipelago was occupied by *Homo sapiens* of Group 5 “Preneolithic” type. This group is represented by a huge amount of specimens coming from shellmidden and cave sites in Sumatra and Java. The Group 6 “Neolithic-Paleometallic” type is only documented during the Late Holocene, including specimens of Gua Harimau upper layer, and the Neolithic burial of Song Keplek 5.

In summary, our results make it possible to identify at least four groups of hominins during the Pleistocene, and two groups of hominins during the Holocene. They suggest that there are groups that seem to overlap and appear chronologically throughout the Lower and early Middle Pleistocene, that another group presents a dental pattern that is found also during the Late Pleistocene, and that two other groups of *Homo sapiens* were present during Holocene. The implication of this study sheds light on the actually complex history of ancient human occupation in Island Southeast Asia during the Quaternary period.

5 Conclusion

Teeth are the most abundant anatomical parts represented among hominin fossils collections, especially from Indonesia. Some fossils were found *in situ* in archaeological or palaeontological excavations, others have a more or less reliable stratigraphical context, and

others are surface finds. That means that the identification of the material and the documentation of their chrono-stratigraphical context is not always possible. It has to be taken into account in any study attempt.

We tried to compile quite scattered data and to build an updated comprehensive reference collection: some of the analyzed teeth have been subject to detailed previous studies, some were only partly or not studied; a large part of the *Homo sapiens* collection included in this study were never studied in detail before. The latter collection had therefore a twofold role in our research: using the fossils as reference collection (i.e. comparing quite recent *H. sapiens* sample with older hominins) and also describing the diversity of late Pleistocene to late Holocene populations in Western Indonesia in the light of the dental record, in order to present a comprehensive and updated approach of Quaternary prehistoric human remains in the area.

The conclusions propose to discriminate 6 dental type groups and to correlate, partly or as a whole, each of them with the hominin groups who occupied the western part of the Indonesian archipelago. This approach, both regarding dental type diversity and chronology must be deepened and enlarged in the future in several important ways: the exploration of teeth internal characters by CT-Scan acquisition (which has begun on several fossils); the inclusion of deciduous teeth in the study (such an approach can be critical for several sites, e.g. in Gunung Sewu area); the comparative approach between the dental material and other anatomical cranial and post-cranial characters.

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Légendes

Fig. 1. Geographical distribution of the palaeoanthropological sites used in this study (Zhoukoudian is not shown on the map). Color: Square = Early-Mid. Pleistocene, Diamond = Late Pleistocene, Circle = Holocene.

Fig. 1. Répartition géographique des sites paléanthropologiques utilisés dans cette étude (Zhoukoudian non indiqué sur la carte). Symboles : Carré = Pléistocène inférieur et moyen, Diamant = Pléistocène Tardif, Cercle = Holocène.

Fig. 2. Location of the 18 and 24 landmarks on LM2 (left) and UM2 (right). Picture sources: White and Folkens (2005), with modification.

Fig. 2. Localisation des 18 et 24 points de repère sur les M2 inférieure (gauche) et M2 supérieure (droite). Sources d'images : White et Folkens (2005), avec modification.

Fig. 3. PCA on lower second molars, Axis 1 (43.39%) and axis 2 (29.64%). The deformation grids show the change in shape along the axis. On the upper right: picture of the occlusal surface of a right LM2 showing the landmarks recorded (Up = Mesial edge, Right = Buccal edge).

G-1 = robust *Homo erectus*, G-2 and G-3 = Javan *H. erectus*, G-C = Zhoukoudian *H. erectus*, G-4 = Late Pleistocene *H. sapiens*, G-5 = Early Holocene *H. sapiens*, and G-6 = Late Holocene *H. sapiens*.

Fig. 3. ACP sur les secondes molaires inférieures, axe 1 (43.39%) et axe 2 (29.64%). Les grilles de déformation montrent le changement de forme le long de l'axe. En haut à droite : photographie de la surface occlusale d'une M2 inférieure droite montrant les points de repère enregistrés (Haut = bord mésial, droite = bord buccal).

G-1 = Homo erectus robuste, G-2 et G-3 = H. erectus de Java, G-C = H. erectus de Zhoukoudian, G-4 = H. sapiens de la fin du Pléistocène, G-5 = H. sapiens du début de l'Holocène, et G-6 = H. sapiens de l'Holocène Tardif.

Fig. 4. PCA on upper second molars, Axis 1 (47.97 %) and axis 2 (24.24 %). The deformation grids show the change in shape along the axis. On the upper left: picture of the occlusal surface of a right UM2 showing the landmarks recorded (Up = Mesial edge, Right = Buccal edge).

G-1 = robust *Homo erectus*, G-2 and G-3 = Javan *H. erectus*, G-C = Zhoukoudian *H. erectus*, G-4 = Late Pleistocene *H. sapiens*, G-5 = Early Holocene *H. sapiens*, and G-6 = Late Holocene *H. sapiens*.

Fig. 4. ACP sur les secondes molaires supérieures, axe 1 (47.97 %) et axe 2 (24.24 %). Les grilles de déformation montrent le changement de forme le long de l'axe. En haut à gauche : photographie de la surface occlusale d'une M2 supérieure droite montrant les points de repère enregistrés (Haut = bord mésial, droite = bord buccal).

G-1 = Homo erectus robuste, G-2 et G-3 = H. erectus de Java, G-C = H. erectus de Zhoukoudian, G-4 = H. sapiens de la fin du Pléistocène, G-5 = H. sapiens du début de l'Holocène, et G-6 = H. sapiens de l'Holocène Tardif.

Fig. 5. Lower teeth of Group 1-4 (Pleistocene hominins).

Fig. 5. Dents inférieures des Groupes 1-4 (Hominines pléistocènes)

Fig. 6. Upper teeth of Groups 1-4 (Pleistocene hominins).

Fig. 6. Dents supérieures des Groupes 1-4 (Hominines pléistocènes)

Fig. 7. Similarities between Zhoukoudian and Javan *Homo erectus*. e.g. Mandible of Sp F1 close to Sangiran 37 (Group 2) and Mandible of Sp G1 close to Sangiran 22b (Group 3)

Fig. 7. Similitude entre les Homo erectus de Zhoukoudian et de Java. La mandibule de Sp F1 est similaire à celle de Sangiran 37 (Group 2) et la mandibule de Sp G1 est similaire à celle de Sangiran 22b (Group 3)

Fig. 8. Lower and upper teeth of Group 5-6 (Holocene *Homo sapiens*).

Fig. 8. Dents inférieures et supérieures des Groupes 5-6 (Homo sapiens de l'Holocène)

Fig. 9. Hypothesis of the chronology of human occupation in the Sundaland during Pleistocene (after Noerwidi, 2020)

Fig. 9. Hypothèse de chronologie de l'occupation humaine dans le Sundaland pendant Pléistocène (d'après Noerwidi, 2020)

Table 1. Chronological attributions of the sites and dental remains used in this study.

Tableau 1. Attributions chronologiques des sites et restes dentaires utilisés dans cette étude.

Table 2. Position of the 18 landmarks on LM2

Tableau 2. Position des 18 points de repère sur la M2 inférieure

Table 3. Position of the 24 landmarks on UM2.

Tableau 3. Position des 24 points de repère sur la M2 supérieure.

Table 4. Summary of the results obtained by GMA on the lower premolars and molars (for details see Noerwidi, (2020).

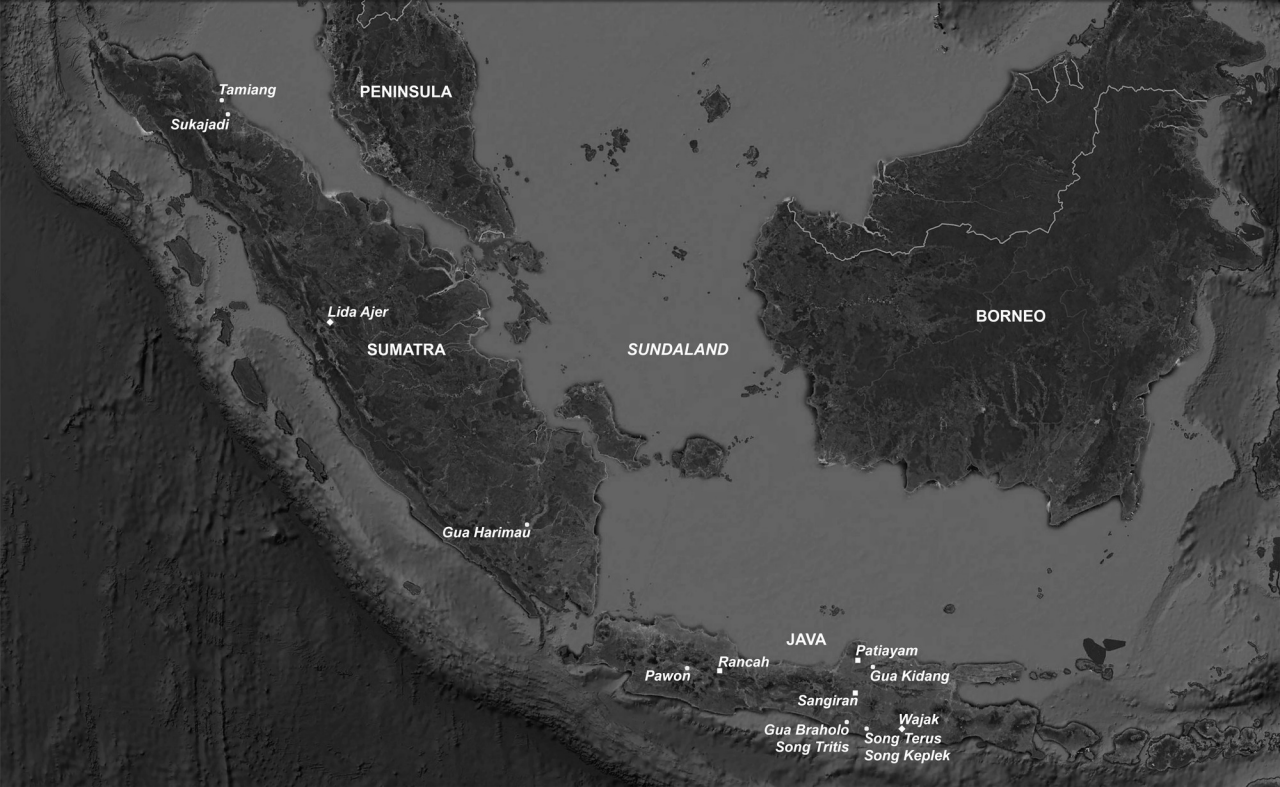
Tableau 4. Résumé des résultats obtenus par analyses en morphométrie géométrique sur les prémolaires et molaires inférieures (pour plus de détails, voir Noerwidi, (2020).

Table 5. Summary of the results obtained by GMA on the upper premolars and molars (for details see Noerwidi, (2020).

Tableau 5. Résumé des résultats obtenus par analyses en morphométrie géométrique sur les prémolaires supérieures et les molaires (pour plus de détails, voir Noerwidi, (2020).

Table 6. Diachronic position of the hominins in Sundaland during the Quaternary

Tableau 6. Position diachronique des hominines dans le Sundaland pendant le Quaternaire



Tamiang

Sukajadi

PENINSULA

Lida Ajer

SUMATRA

SUNDALAND

BORNEO

Gua Harimau

JAVA

Pawon

Rancah

Patiayam

Gua Kidang

Sangiran

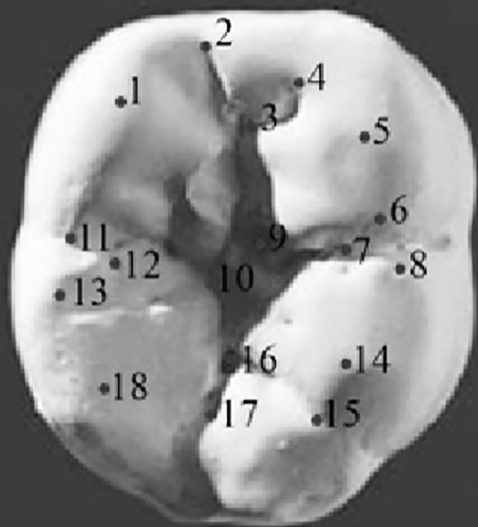
Gua Braholo

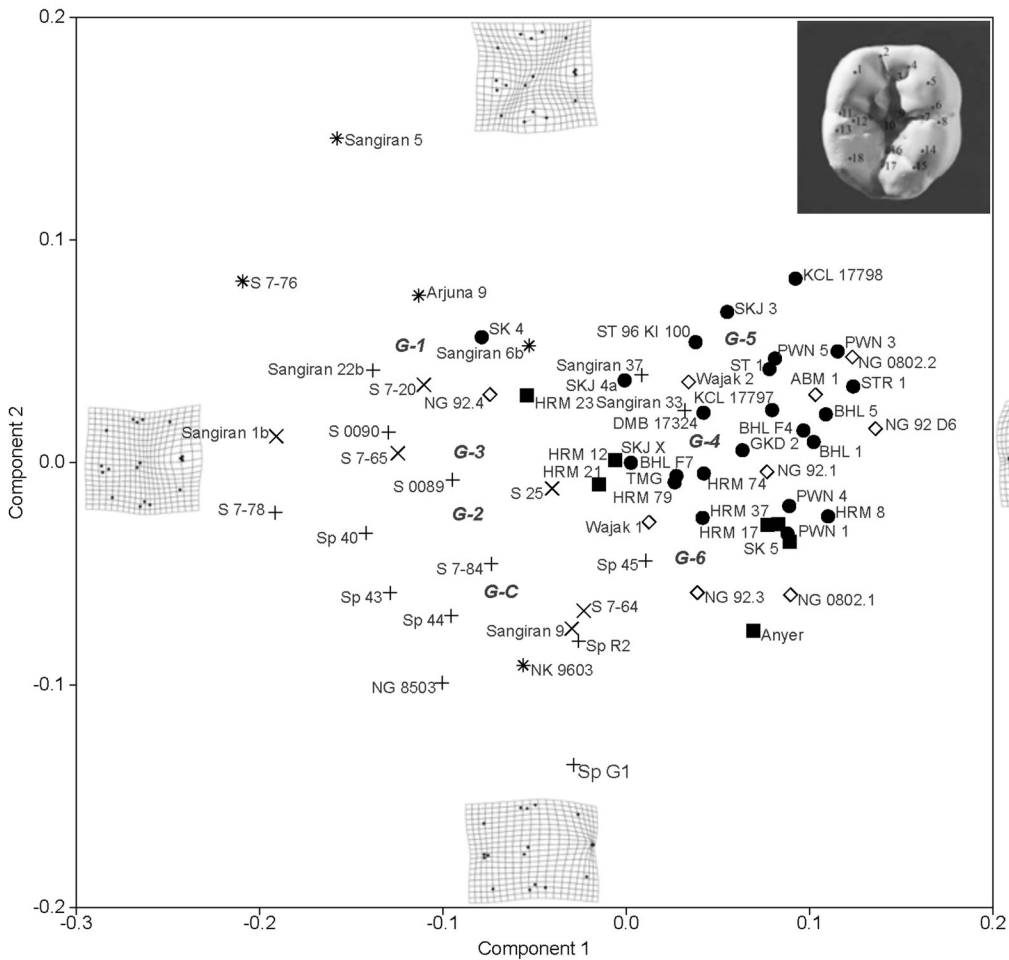
Song Tritis

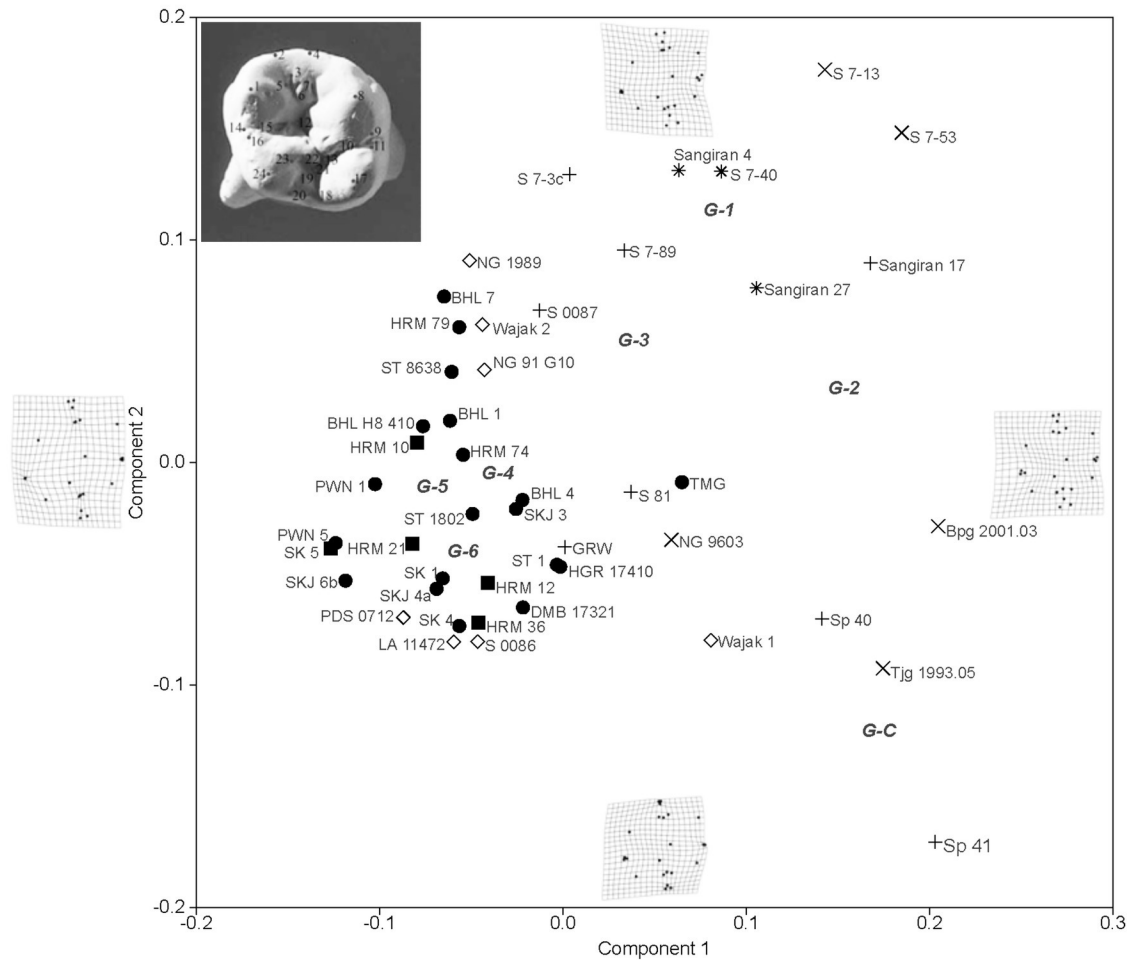
Wajak

Song Terus

Song Kepek









Sangiran 6a



Sangiran 9



Sangiran 37

Group 2



Sangiran 22b

Group 3



Wajak 2

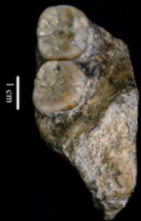


1 cm
NG D6



1 cm
ABM 1

Group 4

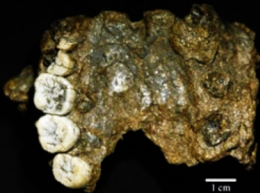


Arjuna 9

Group 1



Sangiran 4
Group 1



Tjg 93.05
Group 2



Sangiran 17
Group 3



Wajak 2



NG G10



ABM 2

Group 4



Sp F 1



Sp G 1



Sangiran 37
Group 2



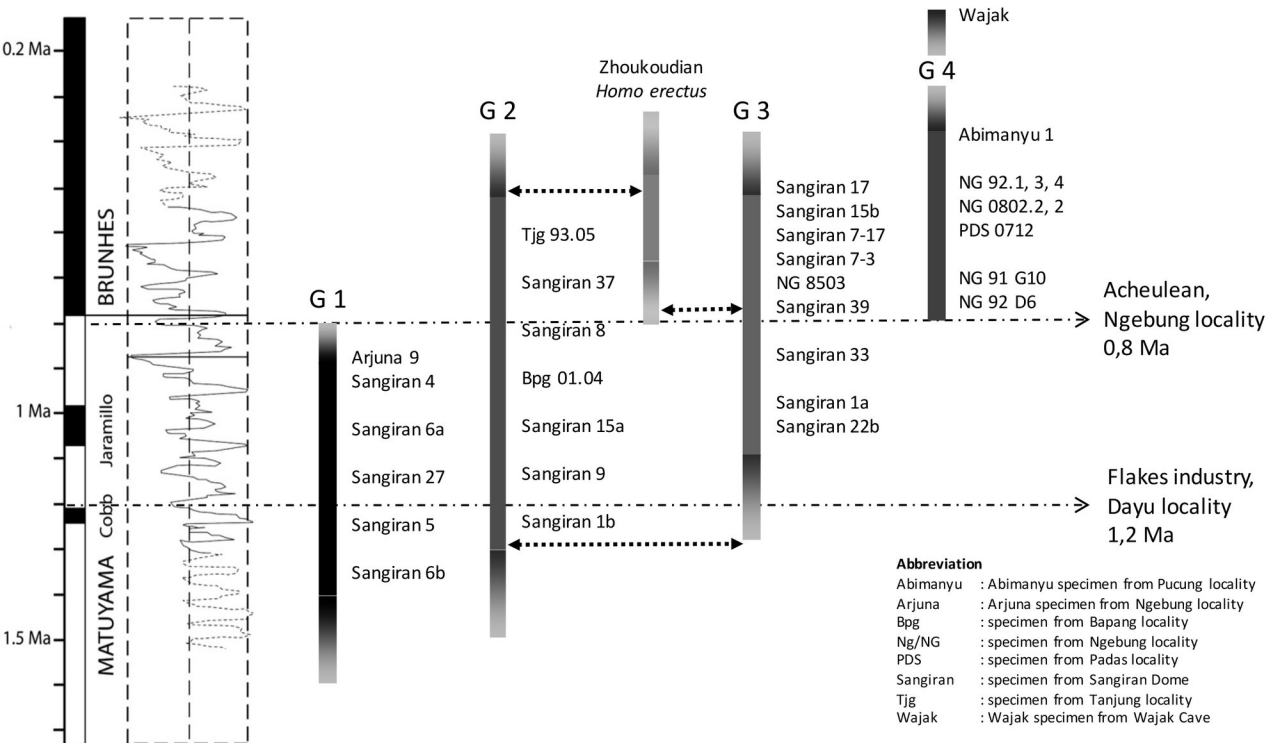
Sangiran 22b
Group 3



Group 5



Group 6



* All specimens came from Sangiran site, except Wajak