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**The Position of Holocene Crania from Braholo Cave,
Song Keplek, and Song Terus within Modern
Indonesian Cranial Variation: A 3D Geometric
Morphometrics Approach**

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*What is life without heartache?
Every downfall builds and teaches us some new things every day
Now this is faith
It does conquer
And it gives you strength and hope to carry on*

-I'll be fine, by: Monita Tahalea-

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"Tinallik dulang tampak dohot aekna, pinungka hata ulaon unang langlang di tagetna"

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ABSTRACT

This study evaluates whether Holocene cranial vaults from the Gunung Sewu karst, Braholo Cave, Song Kepek, and Song Terus express continuity or shift relative to modern Indonesian cranial variation. We built an Indonesian reference shape space from 3D landmark data and projected the fossils as supplementary specimens. Analytically, we applied a vault-focused landmark protocol, Generalized Procrustes Analysis (GPA), Principal Component Analysis (PCA), and thin-plate spline (TPS) imputation to assess robustness under missing data. The reference shows a structured morphospace, with PC1 modulating parietal prominence and distinguishing Javanese more clearly within the Indonesian range. Within this frame, SK4 plots inside the central overlap, supporting early–mid Holocene continuity in the Kepek horizon; ST1 occupies an inner edge position along positive PC1, consistent with a high-dome tendency in the early Holocene Kepek Layer. By contrast, BHL2 and BHL5 extend beyond the densest modern sector across PC planes (outside/edge), in opposing PC3 directions, highlighting site-specific heterogeneity in the Braholo sequence. These placements remain stable across PC1–PC2, PC1–PC3, and PC2–PC3 views and after TPS imputation, indicating that the inside/edge/outside pattern is not an artifact of landmark loss. Taken together, Gunung Sewu preserves a mosaic: SK4 and ST1 uphold local continuity within the Indonesian range, whereas Braholo yields low-frequency variants at or beyond the edge of that range.

Keywords: Holocene; Gunung Sewu; geometric morphometrics; cranial vaults

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LIST OF ABBREVIATIONS

¹⁴ C	Carbon-14 (radiocarbon)
2D	Two-dimensional
3D	Three-dimensional
a.s.l.	above sea level
bgPCA	between-group Principal Component Analysis
BP	Before Present
BRIN	<i>Badan Riset dan Inovasi Nasional</i>
c.	circa
CVA	Canonical Variates Analysis
e.g.	exempli gratia
ESR	Electron Spin Resonance (dating)
GMM	Geometric Morphometrics
GPA	Generalized Procrustes Analysis
ID	Identifier
IDE	Integrated Development Environment
ISEA	Island Southeast Asia
ka	kiloannum
LIG	Last Interglacial
M3	third molar
MNHN	<i>Muséum national d'Histoire naturelle</i>
NA	Not Available
PC	Principal Component
PCA	Principal Component Analysis
Puslit Arkenas	<i>Pusat Penelitian Arkeologi Nasional</i>
TPS	Thin-plate Spline
U-series	Uranium-series dating

INTRODUCTION

In Island Southeast Asia (ISEA), the Indonesian archipelago conserves a layered record of Late Pleistocene to Holocene *Homo sapiens* populations relevant to their history (Détroit, 2002, 2006). Regional studies suggest Holocene heterogeneity across the archipelago, characterized by a combination of local continuity and interactions, as well as, in some contexts, the discovery of new affinities (Noerwidi, 2020; Widiyanto & Noerwidi, 2023a). Taken together, these conditions motivate a brief historiography of Indonesian paleoanthropology.

For more than a century, Indonesia has been an essential contributor to Southeast Asian Paleoanthropology. This history began when B.D. van Rietschoten reported the discovery of a fossilized *Homo sapiens* skull in Wajak (Tulungagung, East Java) in 1888. He attracted the attention of E. Dubois, who traveled to Java with the ambition of finding older humans (Storm, 1995). In 1891–1892, he discovered a cranial calotte and femur in Trinil, which he later named *Pithecanthropus erectus*, now placed within *Homo erectus*. Détroit (2002) review, supplemented by updates by Noerwidi (2012, 2020), positions Java as the basis for the study of human evolution in Southeast Asia. This history frames how scholars have traditionally read the Southeast Asian fossil record.

Since that time, the human fossil record in this region has often been understood as branched: 1) older hominins (*Homo erectus*), abundant in Java; and 2) late Pleistocene to Holocene *Homo sapiens*, mostly found through excavations in caves and rock shelters. However, the stratigraphic and archaeological contexts in Holocene materials are often fragmented, and their evolutionary and population-biological relationships have long remained unresolved. Since the early 1990s, Gunung Sewu has become an important laboratory for refining the chronology and context through systematic excavations studies of karst sediments linking Pleistocene and Holocene layers, and for confirming the continuity of long-term occupation, as well as the variability of burial practices (Détroit, 2002, 2006; Noerwidi, 2012, 2020; Simanjuntak, 1999, 2002; Widiyanto & Noerwidi, 2023b) Taken together, these sequences define the stratified Holocene context against which morphological variability can be compared.

Against this background, the Holocene record of Indonesia is read not as uniform but as heterogeneous. Previous studies have concluded that the early Holocene in Indonesia exhibits Australo-Melanesian affinities, with later evidence of East Asian-related cranio-dental characteristics (Noerwidi, 2012, 2020; Widiyanto & Noerwidi, 2023a). As part of this structure,

studies in Indonesia highlight the morphological heterogeneity of the Holocene, with traces of local continuity and Australo-Melanesian dimensions in the early Holocene, followed by indications of East Asian-related affinities in some later contexts. Thereafter, cranio-dental studies and a review of populations in Java and Sumatra associated with cultural complexes revealed a mosaic of biocultural interactions throughout the Holocene (Noerwidi, 2012, 2020; Widiyanto & Noerwidi, 2023b, 2023a) Especially for Java, the studies by Noerwidi (2020) and Widiyanto & Noerwidi (2023a) emphasize that reading early Holocene Australo-Melanesian patterns versus East Asian-related traits in some later contexts should be treated as descriptively operational (rather than typological) when mapping fossil positions inside, at the edge of, or outside the modern Indonesian range of variation.

In this thesis, the Australo-Melanesian term is used descriptively to refer to the cranio-dental pattern attributed to early Holocene Indonesian *Homo sapiens*, in comparison with East Asian-related traits (Widiyanto & Noerwidi, 2023a). This descriptive-operational usage underpins our inside/edge/outside mapping.

Set against this clarified terminology, we state the problem that guides this study. In this analysis, we reassess cranial morphological variability at Braholo Cave, Song Keplek, and Song Terus in relation to the range of modern Indonesian cranial shape to evaluate continuity versus shift. To make this assessment concrete, we anchor the analysis in a single karst region.

The south of Java contains extensive karst regions; the Gunung Sewu karst preserves stratified Holocene deposits. Gunung Sewu is well-documented for its long-term Holocene occupation and burial activity (Détroit, 2002; Simanjuntak, 1999). Archaeological sediments here record late Pleistocene-Holocene occupation with traces of human activity and burial practices in several cultural horizons (Détroit, 2006; Handini & Widiyanto, 1998, 1999; Simanjuntak, 1999, 2002; Widiyanto & Noerwidi, 2023b). It establishes Java as a locality for Holocene *Homo sapiens*, with documented craniofacial variability and diversity in burial practices (Détroit, 2006). In these circumstances, Gunung Sewu gives a relevant context for examining Holocene cranial variation in southern Java. Excavations at Braholo Cave, Song Keplek, and Song Terus yield Holocene individuals ranging from nearly complete skeletons to cranio-dental fragments suitable for morphometric analysis (Détroit, 2006; Noerwidi, 2012, 2020).

This thesis examines whether Holocene cranial vaults from the Gunung Sewu karst reflect continuity or a shift in relation to modern Indonesian cranial morphology. Specifically, it characterizes variation in the modern reference, places each fossil within that space, quantifies proximity, and assesses robustness to data limitations. To implement these aims, we define the

materials and analytical scope as follows. Here, “crania” is used in a general sense; the analytical scope is the cranial vault. The study considers Holocene *Homo sapiens* crania from three sites in the Gunung Sewu karst (Braholo Cave, Song Keplek, Song Terus). It compares them with a modern Indonesian reference (Java, Kalimantan, Sulawesi). Analyses employ a geometric morphometrics approach with a landmark-based protocol to locate each fossil within a shape space derived from the modern series and to classify positions as inside, at the edge of, or outside that range. The scope is limited to Holocene material, comparisons among the three sites, and cranial domes recorded using a uniform landmark scheme. Accordingly, the study is guided by the following questions:

1. What is the distribution and structure of cranial variation in modern Indonesian populations used as a reference for comparison?
2. Where do the Holocene crania from Braholo Cave, Song Keplek, and Song Terus fall relative to that range (inside/edge/outside), and what does this placement imply for continuity or shift?
3. Do these classifications and interpretations remain stable when considering data limitations (e.g., fragmentary specimens and missing landmarks)?

In the first chapter, we set the Gunung Sewu and site contexts, review prior work, and frame the research questions. In the second chapter, we detail the materials and methods for constructing the modern reference shape space and projecting the fossils (specimens and 3D data), including landmarking and Procrustes, as well as proximity metrics and robustness checks. In Chapter three, we present the reference PCA and fossil placements, along with distance-based evaluations and associated uncertainties. Chapter four interprets the anatomical meaning of the reference axes and situates each fossil, site by site, within an inside/edge/outside framework. Chapter five synthesizes the findings as a Gunung Sewu mosaic within the modern Indonesian frame.

CHAPTER I: STATE OF THE ART

1.1. Region and Sites Description

1.1.1. Gunung Sewu

The southern mountains, also known as the “Thousand Mountains” (Gunung Sewu in Javanese), are a Miocene limestone belt in southeastern Java that extends approximately 80 km from Pacitan (East Java) in the east to the Oyo–Wonosari area (Central Java) in the west. To the northwest lie the Bantul graben, the Solo depression, and the Wonogiri–Baturetno depressions, while to the south, the hills are bounded by the Indian Ocean (Simanjuntak, 1999, 2001, 2002). After the Quaternary uplift, the Wonosari Formation limestone underwent deep karstification, producing hundreds of hemispherical hills, dolines, and extensive cave-rock-shelter systems. These caves were occupied during prehistory and preserve continuous sedimentary sequences from the Late Pleistocene into the Holocene (Sémah et al., 2004; Simanjuntak, 1999, 2001, 2002). Stratigraphically, cave records in the area are commonly organized into the Terus–Tabuhan–Keplek stratigraphic units that link Late Pleistocene to Holocene contexts. Key sites studied in this research include Braholo Cave (Yogyakarta), Song Keplek and Song Terus (Pacitan) (Figure 1). Gunung Sewu is an essential landscape for tracking environmental change, presence, and burial practices during the Holocene in Java, due to the combination of a coherent karst belt and high, consistent cave stratigraphy (Sémah et al., 2004; Simanjuntak, 1999, 2001, 2002).



Figure 1. Location of Braholo Cave, Song Keplek, and Song Terus in the Gunung Sewu karst. Basemap: Google Earth (imagery date: August 28, 2025) processed by the author; inset shows the regional setting on Java Island.

1.1.2. Braholo Cave

Braholo Cave is the richest prehistoric site in the western sector (Figure 2). The name “Braholo” is associated with the meaning statue in local belief; the cave’s remote location was thought to contain statues (Simanjuntak, 2002). The cave is located in Semugih, Rongkop, Gunungkidul, Yogyakarta. The mouth of the cave is around 40 m wide and faces southwest, sitting about 15 m above the foot of the hill. This configuration provides good lighting and air circulation (Détroit, 2002; Handini & Widiyanto, 1999; Simanjuntak, 2002).

Excavations by the National Archaeological Research Center (Puslit Arkenas) (1997-2001) opened 17 squares, two of them (O8, G6) reached a depth of around 7.3 m. The sequence was dated by approximately 17 ^{14}C radiocarbon dates (charcoal), with traces of occupation dating back to around 33–3 ka BP and several horizons of fireplace-ash accumulation (Détroit, 2002; Simanjuntak, 2002). According to Noerwidi (2020), there are at least five cultural horizons: 1) Neolithic (pottery, polished choppers, shells), 2) transitional with rare Neolithic artifacts, 3) thick Pre-Neolithic with many hearths and volcanic ash (c. 10–4 ka), 4) Pleistocene-Holocene boundary (c. 12 ka BP), and 5) older units poor in artifacts and without human remains. The artifact found in Braholo Cave, but not in the eastern Gunung Sewu sites, is notable for its use of limestone flakes, modified *Tridacna* shells, and double-point bone needles (Noerwidi, 2020). The fauna record is very abundant (c. 425,000 fragments; predominantly mammals, including *Macaca*), providing a broad ecological context for cave habitation (Amano et al., 2016).



Figure 2. Entrance of Braholo Cave. (Source: Jogja Travel, 2024)

At Braholo Cave, an initial study by Widiyanto (2002) identified eight individuals in primary (mostly flexed and one circular) and secondary contexts with strong associations with hearth ash horizons. This strongly suggests a burial activity between approximately 9–4 ka BP and identifies them as having Australo-Melanesian affinities in the early–middle Holocene Widiyanto (2002). A following study by Détroit (2002) provided detailed anatomical descriptions, including calvarial reconstructions, and documented a variety of primary and secondary burial practices. This confirms the richness of Holocene human finds at Braholo Cave.

Furthermore, Noerwidi (2020) stated that the study conducted in 2014 was an inventory update and increased the MNI to approximately 24. Taken together, these studies establish Braholo Cave as a long, well-dated burial sequence anchoring the western Gunung Sewu record. Recent research by Widiyanto & Noerwidi (2023a) highlights that the individuals from Braholo Cave show a dolichocephalic and often gracile pattern, characterized by a relatively robust chewing apparatus and a tendency for stratigraphically younger materials to appear more gracile.

1.1.2.1. Braholo 2 (BHL2)

Based on Widiyanto (2002), BHL2 originated from box L8 in the hearth horizon. Identified elements comprise portions of the skull and pelvis; their arrangement indicates secondary burial. The position is inverted, with the cranial and pelvic components lying in close association with small-mammal remains (especially *Macaca sp.*), and bone artifacts (including a spatula) are present in the same context. The dating of charcoal (^{14}C) from the area around the skeleton gives $8,760 \pm 170$ BP (Simanjuntak, 2002). This value reflects the age of the layer, which was likely excavated when the pit was formed, so the individual's age is probably younger than the layer's date.

Widiyanto (2002) notes that secondary deposition is indicated by the fragmentary character of the remains: cranial vault and mandible, right coxa and sacrum attached; two upper cervical vertebrae preserved. The skull is elongated (dolichocephalic), with marked prognathism. The superciliary arches are visible but not prominent, and the temporal line is visible on the frontal bone, extending to the temple. Cranial sutures were largely unexposed during excavation, except the left lambdoid, which shows no advanced synostosis. On the frontal squama, the orbital part is prominent, and the orbit tends to be rounded. The nuchal plane is smooth, suggesting modest muscular insertion. Détroit (2002) reconstructed the calvaria of BHL2 from large fragments (the right parietal is almost complete, while the left

parietal is composed of nine fragments connected to the frontal, temporal, and left occipital regions) (Figure 3). A “band” of bone along the sagittal axis (nasion–lambda) is missing. Overall, the neurocranium is small, gracile, and thin-boned.

The maxilla is robust; the palate is broad and deep. The mandibular body is lower than BHL1, and the alveolar portion is markedly thicker than the basilar portion. The distinct alveolar plane observed in BHL1 is absent in BHL2. The mandible is lower and slender, with well-developed buccal–lingual relief. In general, the masticatory apparatus appears robust. The pelvis (comprising the coxa and sacrum) remains in situ and exhibits a broad and “open” morphology, characterized by a broad pelvic cavity and a wide greater sciatic notch. Based on cranial and pelvic morphology, BHL2 is interpreted as female. The tooth eruption and wear indicate an age at death of more than 50 years.

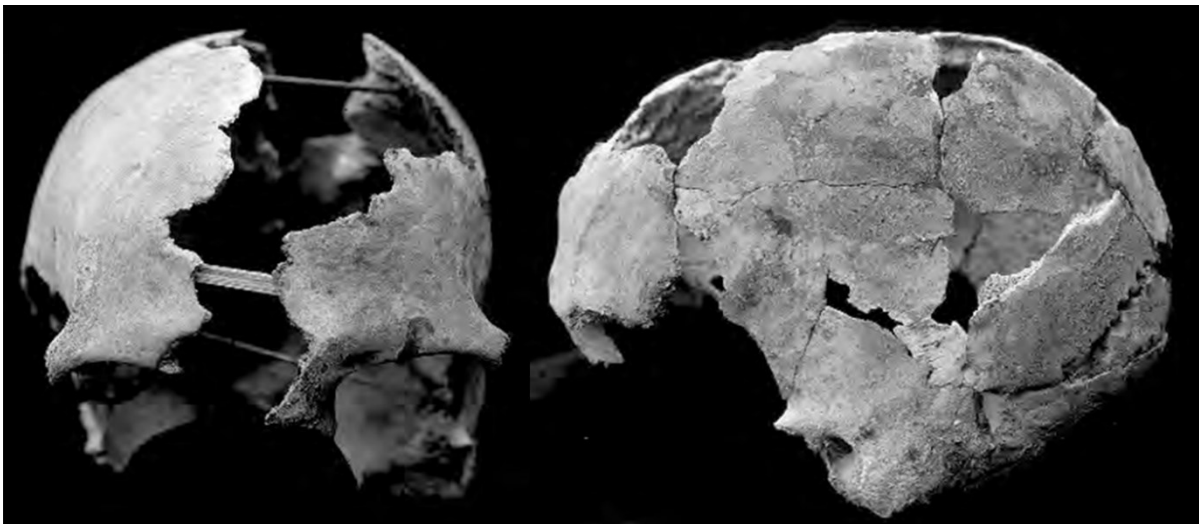


Figure 3. BHL2 cranial vault after the 2000 reconstruction: anterior view (Left) and lateral view (Right)
(Source: Déroit, 2002)

1.1.2.2. Braholo 5 (BHL5)

Based on Widianto (2002), BHL5 (Figure 4) is represented by a skull with mandible from box H8 at a depth of c. 270 cm, clearly associated with a secondary burial. Four cervical vertebrae remain attached to the cranial base. The skull is generally complete but very fragile and severely deformed; the calvaria is most affected, with the vault cracking along sutures and fractures in the squama (frontal, parietal, temporal, and occipital) extending to the cranial base. Even so, the facial region is comparatively well preserved (orbits, zygomatics, maxilla, teeth), and the mandible remains articulated with the maxilla in the occlusal plane. The cranium is

dolichocephalic, with an occipital protrusion and a depression around lambda; muscle insertion marks are well-developed.

The teeth are parallel, with relatively large crowns and roots. The upright frontal squama, distinct supraorbital margin, and minimal relief of the nuchal plane and mandible indicate an Australo-Melanesian female in the ^{14}C contextual $9,780 \pm 230$ BP. Age estimation using the Masset formula yields 39.08 ± 15.50 years ($\approx 23\text{--}54$ years), consistent with M3 eruption status and Broca's wear grade 2 (Widianto & Noerwidi, 2023a).



Figure 4. BHL5 cranial vault at the time of study: anterior view (Left) and lateral view (Right).
(Author's documentation).

1.1.3. Song Keplek

Song Keplek is a cave in Pagersari, Punung (Pacitan, East Java), c. 300 meters southwest of the Wonogiri–Pacitan highway and about 3 km from Song Terus (Figure 5) (Handini & Widianto, 1998; Simanjuntak, 2002). “Song” means a rock-shelter or cave with two opposing entrances, and “Keplek” in the Javanese language refers to domino gambling, reflecting the local use of the shelter prior to archaeological work (Noerwidi, 2020; Simanjuntak, 2002). This site is located at the foot of a hill at an elevation of 333 m above sea level (a.s.l.). The entrance is 20 m wide; the main chamber faces northeast to southeast, and much of the deeper interior is filled with large blocks from ceiling collapse (Simanjuntak, 2002). The archaeological record is dense between approximately 21,000–700 BP, indicating repeated occupation from the Upper Pleistocene into the Holocene (Détroit, 2006; Simanjuntak, 2002). Within the Keplek horizon, stratified dates and cultural markers anchor a long Holocene sequence that is directly comparable to the upper units of Song Terus (Handini & Widianto, 1998; Noerwidi, 2020).

Culturally, the Keplek horizon is marked by a rich flint industry (rijang-dominated), intensive hearth activity, and broad faunal exploitation (Bovidae, Suidae, Cervidae, Cercopithecidae, chelonians, molluscs), together with both flexed and extended burial practices (Noerwidi, 2012; Simanjuntak, 2002). Within a regional context, Keplek is cautiously aligned with the “Sampungian” (strong bone industry) as a late pre-Neolithic phase in East Java. Technologically, Keplek lithics differ from those of the Toalean or Hoabinhian and suggest continuity of flaking from older layers at Song Terus (Noerwidi, 2012; Simanjuntak, 1999). Faunal and artefactual associations at Keplek fit the broader eastern-Java pattern (e.g., targeted primate exploitation and occasional burial use of faunal items), reinforcing its role in early–mid Holocene subsistence and ritual systems (Ingicco, 2012; Noerwidi, 2020; Simanjuntak, 1999).

Human remains recovered comprise five individuals: SK1–SK3, represented by distributed cranio-dental fragments, and SK4–SK5, by complete skeletons in burial contexts (Détroit, 2006; Widiyanto, 2002). In this part, the description is limited to the individuals used in the analysis, namely SK4. Critically, SK4 (early–mid Holocene) exhibits Australo-Melanesian affinities within a pre-Neolithic context, whereas SK5 (late Holocene) aligns with Southeast Asian (Austronesian-related) traits in a Neolithic context; thus, Song Keplek documents a biocultural transition at the site scale (Noerwidi, 2012, 2020).

1.1.3.1. Song Keplek 4 (SK4)

SK4 was discovered in 1996 from box LU2, located near the southern wall of the cave, along with stone flakes and faunal remains (Figure 6) (Noerwidi, 2020; Widiyanto, 2002; Widiyanto & Noerwidi, 2023a). The skeleton, located in a brown clay layer with charcoal dating (^{14}C) from the surrounding context, gives a date of $5,900 \pm 180$ BP (Handini & Widiyanto, 1998; Widiyanto, 2002). The completeness of the elements indicates primary burial with a right-facing flexed position: the right leg placed over the body, the right hand on the chest or jaw, the left at the left chin, and the knees raised (Widiyanto, 2002). This placement falls within the Keplek cultural horizon and is consistent with the flexed funerary template recognized for early–mid Holocene Java (Handini & Widiyanto, 1998; Noerwidi, 2020).

According to Widiyanto (2002), the skeletal elements remain in situ. The vertebral column (cervical–thoracic–lumbar) is relatively complete and continuous to the sacrum, articulated with the coxae and both femora; the femoral head is still within the acetabulum. In the upward-flexed position, the distal femur contacts the proximal tibia; the patella is absent. At the ankle, the calcaneus and phalanges are identifiable. The posture indicates the soles positioned behind the pelvic bones.



Figure 5. Entrance of Song Keplek (Source: Gunawan, 2022).

Widianto (2002) notes a dolichocephalic cranium. In the lateral view, the contour descends to a prelambda depression with an occipital prominence; the parietal wall is fairly vertical, and the temple region rounded. The superior–inferior temporal lines are not visible (obscured by sediment). The mastoid process is small. The occipital bone is relatively intact, whereas the basilar portion and occipital condyles are not visible; cranial sutures are indistinct. On the left, the temporo–parietal suture area appears convex; facial prognathism is marked. On the right, the superior orbital apex on the zygomatic is sharp, and the orbit is relatively rounded. The mandible appears robust, with a wide ramus and a large condylar process. The dentition is generally strong and nearly complete.

Sex identification as female is supported by the small mastoid process, orbital form, and a relatively sharp supraorbital margin; the superciliary arch is flat, and muscular relief on the nuchal plane is slight. The pelvis shows broad dimensions, with a wide pelvic cavity, a large greater sciatic notch, and a broad obturator foramen (Noerwidi, 2020; Widianto, 2002; Widianto & Noerwidi, 2023a). Based on the M3 eruption and molar wear reaching dentin, the individual's age is estimated to be greater than 50 years. In sum, SK4 anchors the Australo-Melanesian morpho-signature in the Keplek horizon and provides a point of comparison for later Holocene material at the same site.

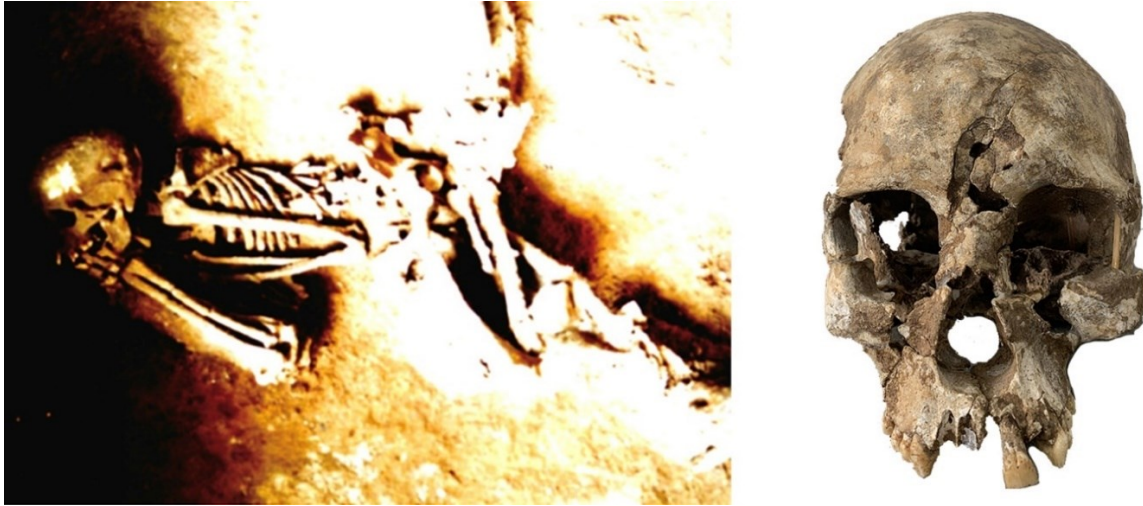


Figure 6. SK4 *in situ* documentation by Harry Widiyanto (Left) and cranial vault at the time of study: anterior view (Right) (Author's documentation).

1.1.4. Song Terus

Song Terus is a tunnel cave in the small karst hills of Werung, Punung (Pacitan, East Java), oriented west–east with the main entrance facing west. In the local language, the term “Terus” refers to a passageway that penetrates a hill from one side to the other (Figure 7). The cave is believed to have had two entrances (west and east) before the eastern part was sealed off by a large limestone boulder (Budiman, 2009; Noerwidi, 2020). The passage resembles a long tunnel, approximately 60–70 m in length; the width of the opening is generally 10–20 m. The western mouth is semicircular with a width of 15.5 m and a height of 5–6 m from the ground, while the eastern part is now blocked by boulders (Budiman, 2009). Indications of its use as a prehistoric dwelling are observed mainly at the western entrance (Noerwidi, 2020). The research history notes that primary excavations began in 1953 by Soejono and Basoeki, and were subsequently continued from 1994 through a French-Indonesian collaboration (Noerwidi, 2020; Sémah et al., 2004).

Stratigraphically, the sequence from bottom to top consists of the Terus, Tabuhan, and Keplek Layers (Sémah et al., 2004). The Terus Layer is dated by U-series/ESR to the Middle Pleistocene to early Late Pleistocene (c. 341–80 ka) and is characterized by riverine alluvial deposits together with a flint industry (core, flake, scraper, denticulates) (Hameau et al., 2007; Sémah et al., 2004). The upper part of the Terus Formation indicates the earliest cave habitation in the ISEA region (c. 125–80 ka) (Détroit, 2002). Overlying it, Tabuhan is followed by Keplek, which is radiocarbon dated to 9,400–5,700 BP; carbonate laminations recorded between Tabuhan and Keplek mark the Pleistocene-Holocene transition (Hameau et al., 2007; Noerwidi, 2020; Sémah et al., 2004). Characteristics of the Keplek Layer at Song Terus include a rich flint

industry, an abundance of Cercopithecidae (*Macaca*, *Trachypithecus*), large mammals (Bovidae, Suidae, Cervidae, Ursidae, Rhinocerotidae, *Elephas*), and aquatic fauna (molluscs, turtles) (Amano et al., 2016; Ansyori, 2010; Ingicco, 2012).



Figure 7. Entrance of Song Terus (Source: Gunawan, 2022).

1.1.4.1. Song Terus 1 (ST1)

At least one human skeleton was recorded at Song Terus in a flexed primary burial position (Détroit, 2002). ST1 was found in 1991 in box J9, Keplek Layer, attached to the northern wall of the cave (Figure 8) (Budiman, 2009; Détroit, 2002). An arrangement of limestone blocks surrounded the skeleton. The parallel upper and lower limb positions, as well as hyperflexion, may reflect the wrapping of the body during burial (Budiman, 2009; Détroit, 2002). As noted later, Noerwidi (2020), the body lay on its right side in a north–south orientation, with the head to the north and the face directed south, consistent with a tightly wrapped “hyperflexed” interment Noerwidi (2020).

Détroit (2002) states that the left tibia shows a burnt spiral fracture; the 90° rotation indicates involvement by fire, despite the presence of soft tissue. In the cranial section, post-excavation conservation revealed a disturbance of a small tunnel cavity in the head area; fragments of the face and vault were dislocated and fused by concretions, consistent with a male individual showing Australo-Melanesian affinities. The postcranial skeleton was relatively

complete with traces of trauma or pathology: a poorly healed fracture of the right ulna and an anomaly at the proximal end of the left femur, accompanied by a noticeable difference in length compared to the right femur.

Artefacts found in situ include flint flakes near the face, a bone point, and a retouched flake on the left hand. Facial bones of Cercopithecidae (mainly *Macaca*, *Trachypithecus*), *Elephas* molars, *Suidae* teeth, porcupine remains, small carnivores, and molluscs were interpreted as grave goods, although the direct relationship of each find to burial practices needs to be considered with caution (Détroit, 2002, 2006; Noerwidi, 2020; Sémah et al., 2004). Radiocarbon (^{14}C) dating of mollusc shells directly above the burial structure yielded an age of $9,330 \pm 90$ BP. In this stratigraphic context, this is considered an estimate of the burial age (Détroit, 2002). Thus, ST1 is among the earliest documented flexural burials in the ISEA region.

Regionally, Song Terus connects the long Pleistocene-Holocene sequence and provides a comparative context for the upstream sites of Punung (e.g., Song Keplek) and Braholo Cave in the west. Evidence of deciduous teeth from the upper Terus, lower Tabuhan, and Keplek layers indicates changes in settlement intensity in line with climate dynamics from the Last Interglacial (LIG) to the Holocene; this pattern suggests that ST1 emerged during a phase of repeated settlement in the early Holocene (Noerwidi, 2020; Sémah et al., 2004).



Figure 8. *ST1 in situ documentation by Détroit (2002) (Left) and cranial vault at the time of study: anterior view (Right) (Author's documentation).*

As a closure to the site descriptions, Table 1 compiles the key attributes such as remains completeness, age estimate, sex, morphological affinities, and associated ^{14}C ages (BP) to provide a comparable baseline across Braholo Cave, Song Keplek, and Song Terus.

Table 1. Summary of individuals from Braholo Cave, Song Keplek, and Song Terus.

ID	Remains	Age	Sex	Affinity	Dating (BP)*
BHL2	Almost complete skeleton	> 50	Female	Australo-Melanesian	8,760 ± 170
BHL5	Almost complete skeleton	≈23-54	Female	Australo-Melanesian	9,780 ± 230
SK4	Almost complete skeleton	> 50	Female	Australo-Melanesian	5,900 ±180
ST1	Almost complete skeleton	> 55	Male	Australo-Melanesian	9,330 ± 90

*All ¹⁴C ages are contextual (not direct bone dates) and uncalibrated.

1.2. Positioning the Present Study

At the close of this chapter, we summarize what previous work at Braholo Cave, Song Keplek, and Song Terus has done and how this study is positioned to extend it. We read the Holocene record operatively, not typologically, which means specimens are placed inside, at the edge of, or outside the modern Indonesian range of variation. Within this framework, previous research on Gunung Sewu consistently reports early Holocene Australo-Melanesian dimensions, with later contexts in some sites indicating East Asian-related traits; the terminology is used descriptively to denote position in shape space, not identities (Noerwidi, 2020).

At Braholo Cave, early Holocene individuals with Australo-Melanesian affinities have long been recognized; together with Keplek and Terus, the western–eastern transect of Gunung Sewu offers a coherent, stratified context in which to assess cranial variation against a modern Indonesian reference. This thesis builds directly on that rationale by fixing analysis in a single karst region and by treating affinities as descriptive positions in a defined morphometric space (Détroit, 2002).

At Song Keplek, the paired burials SK4 and SK5 remain a keystone. Noerwidi (2012) analyses progress from univariate and bivariate comparisons to multivariate exploration, including Principal Component Analysis (PCA) with log-shape ratios, revealing that SK4 (early–mid Holocene) is closer to the Australo-Melanesian series, and SK5 (late Holocene) is trending toward Southeast Asian or Austronesian-related groups. At the site scale, this pattern documents a biocultural transition without fixing specimens into essentialized types; it is a positional reading that we adopt in this thesis (Noerwidi, 2012)

At Song Terus, the ST1 burial (Keplek Layer) provides one of the earliest flexed interments in ISEA and a reference point for early Holocene morphology. The grave architecture concentrations of small limestone blocks around the body and the hyperflexed posture are well-documented stratigraphically. Morphological assessment places ST1 within

the broad Australo-Melanesian range, establishing an early Holocene standard in the same karst system (Budiman, 2009; Détroit, 2002).

Methodologically, the relevant precedents converge on geometric morphometrics (GMM). For cranial vaults, (Détroit, 2002) established a now-standard path, Generalized Procrustes Analysis (GPA) to remove non-shape effects, projection to the tangent space, PCA on Procrustes residuals, and Canonical Variates Analysis (CVA) for group separation applied to calottes and to frontal/posterior subsets when preservation requires it. This approach legitimizes reading breadth and edges of vault variation in a quantitative shape space (Détroit, 2002). For dentitions, (Noerwidi, 2020) research formalizes a two-dimensional (2D) GMM protocol (GPA → PCA → bgPCA/CVA) and, importantly, fixes the operational use of “Australo-Melanesia or East Asian–related” as positional descriptors rather than labels, an interpretive stance we retain here. Within ISEA, Cosalan (2017) on the frontal bone shows the benefit of combining anatomical landmarks with sliding semilandmarks on three-dimensional (3D) scans under a Procrustes–PCA/CVA framework, particularly when shape is controlled by subtle curvature; this offers a technical reserve for elements whose contours demand denser sampling.

Taken together, previous work yields three empirical points that this study carries forward. First, early Holocene continuity is visible in Braholo, SK4, and ST1, read as inside or near the edge of a broadly Australo-Melanesian field. Second, later Holocene shifts are documented at the site scale in Keplek (SK5), which trends toward East Asian–related configurations. Third, the appropriate lens is operational: positions in a calibrated shape space are the claim, not essences (Noerwidi, 2012)

Position of the present study, we reconstruct a modern Indonesian vault shape space (Java, Kalimantan, Sulawesi) and project the Gunung Sewu Holocene domes into it as supplementary points, classifying each as inside/edge/outside across multiple Principal Component (PC) planes. This design answers directly what earlier studies imply but did not test with a vault-focused, Indonesia-specific reference: whether Braholo Cave, Song Keplek, and Song Terus crania uphold local continuity or indicate shifts when read against a controlled modern baseline and whether those readings are stable under fragmentary conditions, including subset landmarks, Thin-plate Spline (TPS) guided imputations. In doing so, we integrate Détroit’s vault protocol, Noerwidi’s operational diction, and Cosalan’s ISEA GMM practice within one karst system to evaluate continuity versus shift as empirical positions rather than fixed types (Cosalan, 2017; Détroit, 2002; Noerwidi, 2020).

CHAPTER II: MATERIALS AND METHODS

This chapter describes the comparative materials and analytical methods used to examine morphological variation in *Homo sapiens*, with a focus on 3D cranial comparisons between fossil specimens and modern human reference collections. Fossil data consist of high-resolution 3D surface meshes (.ply format) derived from structured-light scanning of cranial remains recovered from Braholo Cave, Song Keplek, and Song Terus. The comparative dataset includes digitally captured cranial models from Java, Kalimantan, and Sulawesi. Data collection was conducted using landmark-based GMM, where landmark coordinates were placed on the digital models using MorphoDig software to capture and analyze shape variation in 3D space.

2.1. Materials

2.1.1. Fossil Specimens

This study utilized 3D cranial models of specimens from the Braholo Cave, Song Keplek, and Song Terus, located in the Gunung Sewu area of Java, Indonesia. These specimens were selected because they represent *Homo sapiens* groups that lived during the Holocene period, which is relevant for understanding human morphological variation in Indonesia. The selection of these fossil specimens aims to identify variations in *Homo sapiens* cranial shape in the geographical and temporal contexts of Indonesia. Table 2 shows the details of the fossil specimens used in this study.

Table 2. List of fossil specimens and the descriptions based on 3D scan descriptions.

Fossil specimens	3D scan descriptions
Braholo 2	Fragmentary skullcap.
Braholo 5	Fragmentary skullcap.
Song Keplek 4	Fragmentary cranium, but well-preserved.
Song Terus 1	Fragmentary cranium, but well-preserved.

These fossil specimens serve as a morphological reference in this study, providing the main insights into cranial shape variation in Holocene populations in the Gunung Sewu region.

2.1.2. Comparative Modern Human Collection

Given the goal of evaluating fossil morphology within the broader context of Indonesian population variation, the inclusion of regionally diverse modern crania was essential. The 3D models were acquired by Andrea D. Cosalan during her Master 2 (Cosalan, 2017) from

specimens in the collections of the Muséum national d’Histoire naturelle (MNHN), Paris, representing populations from Java, Kalimantan, and Sulawesi. Group labels followed the original collection metadata and were standardized for analysis.

Cosalan’s (2017) study, which uses these Indonesian groups, explains how group labels are assigned. She states that the label “Dayak” (n = 11) is understood as an umbrella ethnonym that emerged during the Dutch colonial period and loosely refers to the interior communities of Kalimantan, separate from Malay. She adds that several entries are marked as the ‘Trophy of the Dayak’, leading her to mark them as ambiguously provenanced. Cosalan (2017) also notes that the term “Sopulit” (n = 2) is unknown in recent literature and is described as “Sepulut” in British colonial reports. This form is rarely used outside of toponymy and may refer to the “Sapulut” linguistic group. For Java, she mentions two labels: “Javanese” (n = 10) and “Java-Malay” (n = 15). For the “Java-Malay” label, the MNHN curatorial notes use the code JMa with the historical annotation “Malay from Java,” which needs to be read carefully: Is it really referring to a Malay from Java, or a Javanese with characteristics that, according to the collector, are considered Malay? Sulawesi is represented by “Bugis” (n = 4), “Makassar” (n = 1), and an unspecified entry labeled “Sulawesi” (n = 5). All labels are retained as in the curatorial metadata, standardized into analytical codes, and used solely as operational markers in the analysis.

This reference dataset (Table 3) provided a wide regional morphological baseline and a comparative framework to analyze shape variation and morphological proximity between the Gunung Sewu fossils and present-day Indonesian populations, thereby enabling an assessment of morphological continuity or differences between prehistoric and modern Indonesians.

Table 3. *Distribution of reference collection.*

Population	Origin	Specimen ID	Number of specimens (n)
Javanese	Java	Jav	10
Java-Malay	Java	JMa	15
Dayak	Kalimantan	Day	11
Sulawesi	Sulawesi	Sul	5
Bugis	Sulawesi	Bug	4
Borneo	Kalimantan	Bor	2
Sopulit	Kalimantan	Sop	2
Makassar	Sulawesi	Mak	1
Total			50

2.1.3. 3D Scanning and Data Acquisition

The fossil specimens used in this study were previously stored in a museum storage facility near the discovery site, part of the regional archaeological collection management. The collection was then transferred and consolidated to the Cibinong Science Center, owned by the National Research and Innovation Agency (BRIN), in West Java, Indonesia, for long-term conservation. Indonesia's vision is to centralize and document its ancient human fossil collections, carefully implementing this relocation process. Due to relocation and storage, some specimens have undergone anatomical changes. It led the researcher to conduct a reconstruction before scanning (Figure 9), which involved gathering the separated fragments to ensure they were in the correct anatomical position. This process was carried out carefully with the assistance and supervision of experts.



Figure 9. Reconstruction of fossil specimens prior to 3D scanning.

The researcher conducted reconstruction and 3D scanning from May 22 to 30, 2025, at the Cibinong Science Center, with official permission from the Center for Archaeometry Research and the Deputy for Scientific Collection Management, BRIN. The researcher reconstructed and scanned specimens from the Braholo Cave, Song Keplek, and Song Terus sites.

The 3D scanning was carried out using the Shining 3D EinScan-SP V2, which captures detailed data for complete surface acquisition and high-quality mesh generation (Figure 10). Each specimen required a varying amount of scanning time; however, on average, the complete

scanning process for one specimen took between 25 and 45 minutes, including full rotation and underside scanning. The researcher discovered that certain surfaces, particularly teeth, were overly reflective and interfered with the scanner's light output during the scanning process. A thin layer of Marcks talcum powder was applied to reduce surface reflections during 3D scanning, and it is removable and does not alter the surface morphology of the fossil. The talcum powder acts as a matte coating that disperses light more evenly, ensuring better surface capture without altering the underlying anatomical features. This method has also been commonly used in previous studies, as noted by Imran & Rogers (2020). This process was carried out carefully with the assistance and supervision of experts.

The 3D scanning process was carried out using EXScan S software version 3.1.4.3. Each specimen was placed on an automatic turntable and activated in full 360° rotation mode, with distance and lighting settings adjusted based on the shape and color of the surface. Of the six individuals scanned (consisting of crania), only four were used in this study. Two individuals were excluded due to their fragmented condition and the loss of important landmarks.



Figure 10. 3D scanning process using the Shining 3D EinScan-SP V2.

2.1.4. Digital Tools and File Management

The researcher collected and processed digital data derived from 3D surface meshes (.ply format) of fossil specimens. This study employed a combination of software tools for

digital model cleaning, landmark acquisition, and statistical analysis, supported by a structured digital file storage system. The software used included:

- **EXScan S version 3.1.4.3**, the default software for the Shining 3D EinScan-SP V2 scanner, was used for pre-processing of the 3D surface meshes (Figure 11). Following the manual guide (Shining 3D, 2024), the researcher performed the following steps: 1) removal of noise and floating artifacts using the selection tool; 2) global alignment to refine the spatial consistency of multiple scans; 3) automated registration and merging of scan segments; 4) generation of surface meshes in non-watertight mode to preserve anatomical fidelity; 5) hole filling (only when necessary) to repair topological gaps; 6) surface sharpening and smoothing; and 7) export of finalized 3D surface meshes in .ply format for morphometric analysis.

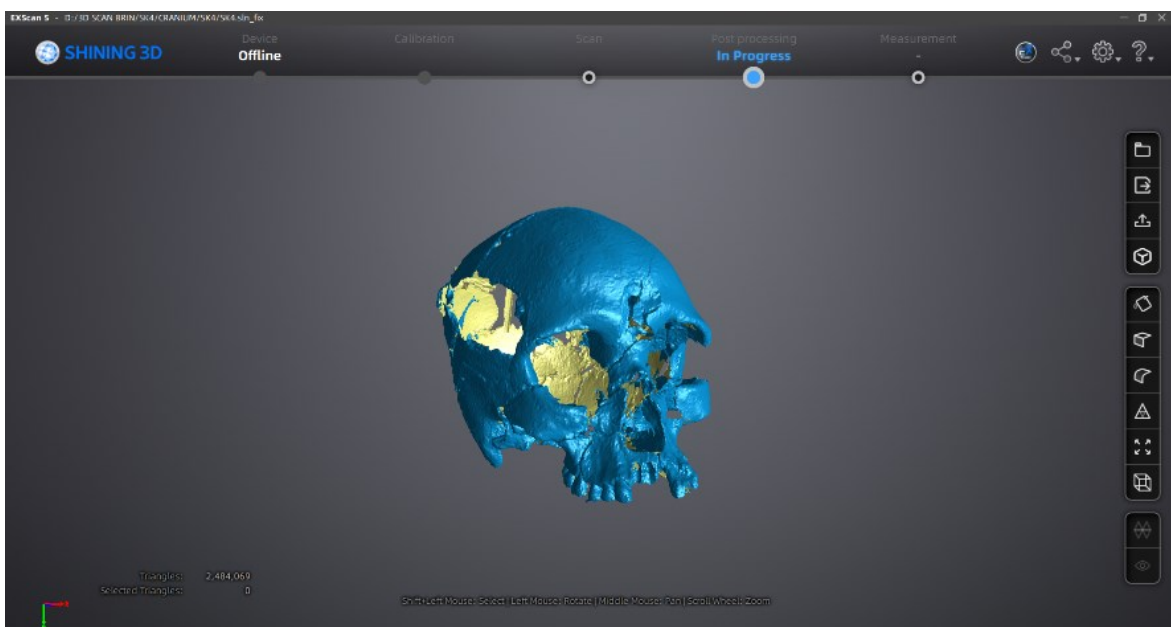


Figure 11. Post-processing of a 3D scan in EXScan S software.

- **MorphoDig version 1.6.9**, an open-source software developed for 3D comparative anatomical studies (Lebrun, 2022), was used to place anatomical landmarks directly onto the 3D surface meshes (.ply). The landmarks used follow a predetermined numerical sequence corresponding to anatomical points. Then, the landmark coordinates are exported in .fcsv format, recording the spatial values (x, y, z) at each point. MorphoDig included functions that facilitate the accurate placement of landmarks on complex skull structures, such as interactive model rotation, surface shading, and transparency settings.

- Analyses were conducted in **R version 4.5.0** using **RStudio** as the integrated development environment (IDE). The open-source R language was utilized for: 1) importing and transforming landmark coordinates (.fcsv) into 3D arrays suitable for morphometric analysis; 2) managing missing data with transparent, script-based imputation methods; 3) performing shape analysis through GPA and PCA; and 4) generating both 2D and 3D visualizations for morphospace exploration.

This study applied an organized digital file management system to continue analytical transparency and facilitate reproducibility. Raw 3D surface meshes (.ply) were stored in a separate folder from their associated landmark files (.fcsv). All files were consistently named using specimen ID codes for smooth data integration during statistical analysis. It enabled efficient tracking of the input-output workflow and ensured the integrity of the analytical pipeline.

2.2. Methods

2.2.1. Landmark Description and Protocol

This study employed a GMM approach, a 3D landmark method, to quantitatively measure the shape of the cranium in *Homo sapiens* specimens from the Braholo Cave, Song Keplek, and Song Terus sites. This approach is used to preserve the geometric information from the analyzed anatomical structures, in contrast to classical morphometric approaches that rely more on linear or angular distances (Slice, 2007).

This study used 36 craniometric landmarks (Table 4), comprising 10 unpaired landmarks and 13 paired landmarks, and the placement was performed manually using MorphoDig, with guidance based on Lebrun (2022). The distribution of landmarks is illustrated in Figure 12. The selection and placement of landmarks in this study were based on anatomical standards (White et al., 2012), the classification of landmarks by Bookstein (1991), and morphometric practices in paleoanthropological studies (Gunz et al., 2005). This landmark placement method was also applied in the analysis of human population variation in Southeast Asia (Grimaud-Hervé et al., 2012). The three categories stated by Bookstein (1991) were based on their structural position and biological relevance, including:

- **Type I** is the meeting point of three anatomical structures, namely sutures, which are highly stable and biologically informative (e.g., bregma, lambda).

- **Type II** is the point of maximum curvature or structural prominence, namely a bony prominence or anatomical boundary that forms a peak (e.g., inion).
- **Type III** is the spatial extreme point, namely the outermost point of a given segment or diameter, for which information is limited to one dimension (e.g., glabella, opisthion).

For transparency and reproducibility, the Bookstein (1991) type assigned to each landmark is reported in Table 4. Landmark data were exported in .fcsv and .ply formats, then prepared for statistical analysis in R using RStudio.

During the acquisition process, not all landmarks could be completely identified in all specimens, particularly the fossil specimen from the Braholo Cave, which consists of a fragmentary skullcap. Therefore, the researchers used a subset of landmarks that were preserved and homologously identifiable, by common practice in GMM studies of fossil material (Bookstein, 1991; Slice, 2007). This approach adheres to established guidelines to ensure comparative validity and minimize bias resulting from missing data in fragmentary fossils. The use of reduced landmark configurations is a widely accepted practice when dealing with taphonomically incomplete hominin material, as it enables robust statistical comparisons across partial specimens.

The choice of landmarks is also supported by previous research that maintains consistency in fossil material originating from Indonesia. A study by Kaifu et al. (2015) on the Ngawi 1 calvaria applied measurements of landmarks such as the glabella, bregma, and opisthocranion and used them in a log-ratio-based PCA for the distinctive morphology of *Homo erectus* in Java. Meanwhile, a study by Zeitoun et al. (2010) conducted a GMM analysis based on 17 calvaria landmarks to differentiate *Homo erectus* groups in Java, China, and Kenya, using the principal components of shape. Other studies by Grimaud-Hervé et al. (2012) on Bukuran calvaria and Détroit (2002) on Sangiran and Sambungmacan specimens also strengthen the framework for landmark selection in this study. Therefore, the landmark placement protocol used in this study was developed not only based on theoretical principles but also considering comparative continuity with existing Indonesian paleoanthropological research. After the landmarks are determined (Section 2.2.1), the next stage is the acquisition process and visual checking using the MorphoDig software (Section 2.2.2)

Table 4. List of Craniometric Landmarks

No.	Code	Landmark Name	Bookstein (1991) Types	Definition
Unpaired Landmarks				
1	pr.	Prosthion	III	The midline point is at the most anterior point on the alveolar process of the maxilla.
2	ns.	Nasospinale	III	The point where a line tangent to the inferiormost points of the two inferior curves of the anterior nasal aperture margin crosses the midline.
3	n.	Nasion	I	The midline point where the two nasal bones and the frontal bone intersect.
4	g.	Glabella	III	The most anterior midline point on the frontal bone, usually above the frontonasal suture.
5	b.	Bregma	I	The ectocranial point is where the coronal and sagittal sutures intersect.
6	l.	Lambda	I	The ectocranial midline point is where the sagittal and lambdoid sutures intersect.
7	op.	Opisthocranium	III	The ectocranial midline point at the farthest chord length from the glabella is determined instrumentally at the rear of the cranium.
8	i.	Inion	II	The ectocranial midline point is at the base of the external occipital protuberance.
9	o.	Opisthion	III	The midline point is at the posterior margin of the foramen magnum.
10	ba.	Basion	III	The midline point on the anterior margin of the foramen magnum; location may vary based on measurement type (e.g., cranial height or basion-prosthion).
Paired Landmarks				
11,24	zm.	Zygomaxillare	III	The most inferior point on the zygomaticomaxillary suture.
12,25	al.	Alare	III	The most lateral point on the margin of the anterior nasal aperture.
13,26	or.	Orbitale	III	The lowest point on the orbital margin.
14,27	ec.	Ectoconchion	III	The most lateral point on the orbital margin is determined instrumentally.
15,28	fmo.	Frontomalare orbitale	I	The point where the frontozygomatic suture crosses the inner orbital rim.
16,29	sn.	Supraorbital notch (center)	II	Midpoint of the notch or foramen on the superior orbital rim.
17,30	d.	Dacryon	I	The point where the maxillofacial suture meets the frontal bone.
18,31	ft.	Frontotemporale	III	The point where the temporal line reaches its most anteromedial position on the frontal.
19,32	zy.	Zygion	III	The point of maximum lateral extent of the zygomatic arch is determined instrumentally.
20,33	eu.	Euryon	III	The instrumentally determined ectocranial point of most extraordinary cranial breadth.
21,34	po.	Porion	III	The uppermost point on the margin of the external acoustic meatus.
22,35	ms.	Mastoidale	III	The most inferior point in the mastoid process.
23,36	ast.	Asterion	I	The point where the lambdoid, parietomastoid, and occipitomastoid sutures meet.

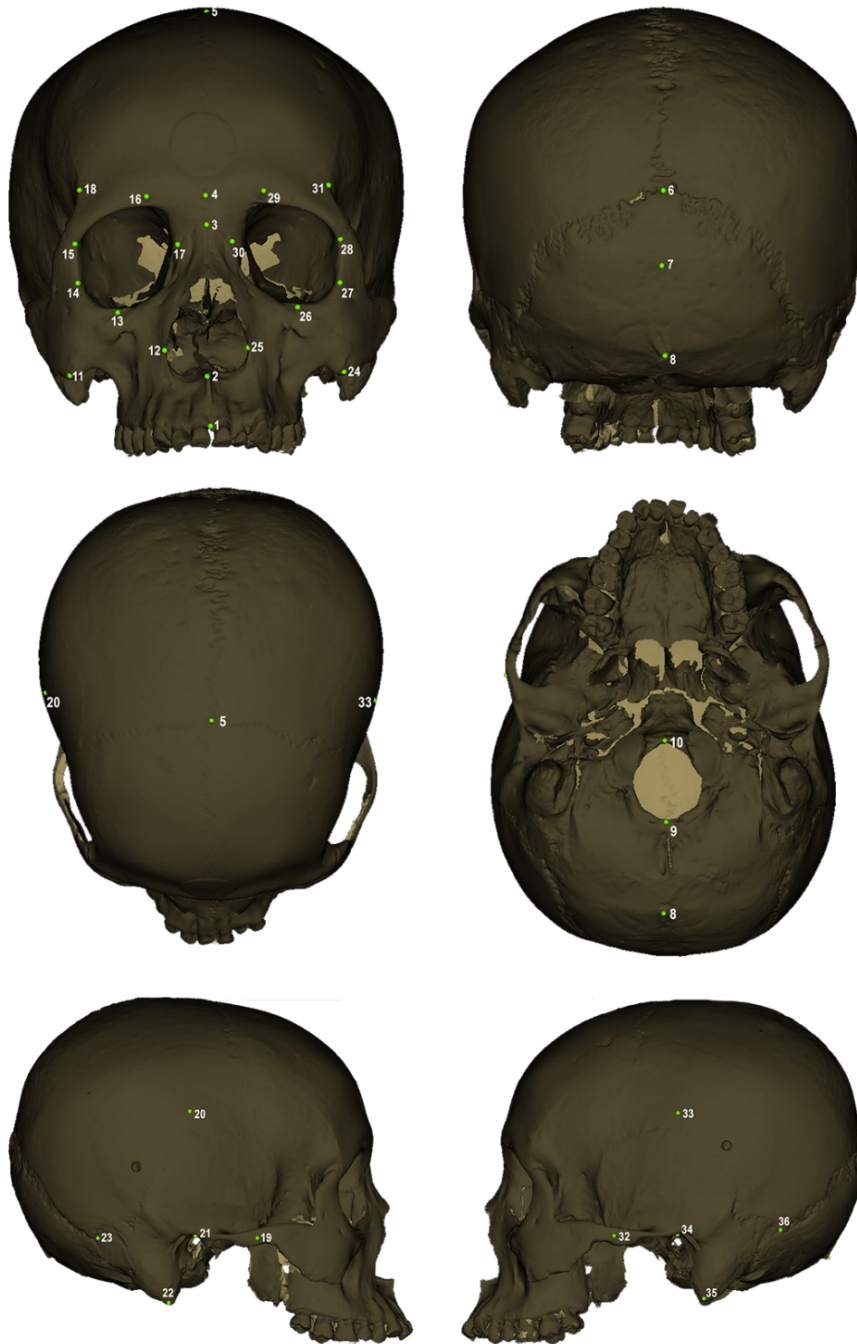


Figure 12. Visualization of cranial landmark placement on the surface of a 3D model.
 (The image was created using MorphoDig v1.6.9 on a modern reference specimen)

2.2.2. Landmark Acquisition

The landmark acquisition was performed manually using MorphoDig. Digital models of the cranium in .ply format were loaded into the software, and the researchers analyzed them individually.

The next step was to align the models to standard anatomical orientations using the transformation toolbar. The 3D model was adjusted so that the cranial surfaces faced anteriorly, superiorly, laterally (left and right), posteriorly, and inferiorly. This process was essential to ensure uniform orientation throughout the specimen before landmark placement.

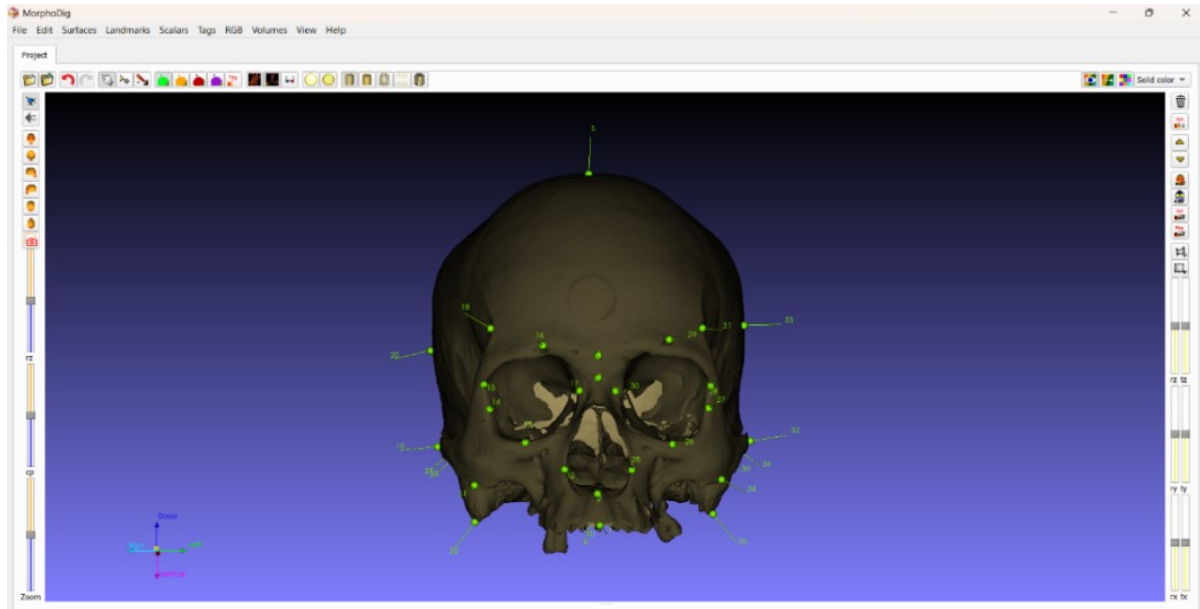


Figure 13. View of the cranium model in MorphoDig with manually placed landmarks, shown in anterior orientation.

Landmarks were then placed using the “Digitize → Create Normal Landmark” feature. Landmark placement by researchers was performed manually in a consistent order following the landmark protocol (see Section 2.2.1). This process was also assisted by other features such as interactive zoom and rotation to improve accuracy, especially when dealing with fragmented surfaces. We were unable to place landmarks at their proper points in some fragmented specimens, so landmark placement was skipped, but the numerical sequence was maintained to ensure the .fcsv file structure was consistent with other configurations. Unavailable points were marked as “not available” (NA) to ensure the data array remained compatible for multi-specimen analysis in RStudio without disrupting the processing sequence and functionality.

After all landmarks were placed, researchers evaluated and corrected landmark positions using the “push landmarks to closest surface vertex” feature. This feature adjusts the position of each landmark to align with the mesh surface, thereby helping to avoid errors caused by placing landmarks outside the mesh. This process is supported by additional verification using a landmark table (Table 4) and a software visual display (Figure 13), which ensures the correct number and order of landmarks before exporting the data. The resulting landmarks were saved in two formats:

- .fcsv, the main file containing the three-dimensional coordinates (x, y, z) of each landmark, which will be used for statistical analysis in RStudio.
- .ply (landmarked), a copy of the 3D model with landmarks used for visualization and documentation.

For compatibility purposes in statistical analysis using RStudio, we modified the specimen file names to conform to their original format. This adjustment aims to ensure consistency in naming the .fcsv and .ply files described in Section 2.1.4. This section emphasized that control over specimen ID uniformity is crucial to avoid data reading errors between analysis stages. A list of specimens that experienced ID changes from the original version to the working version is presented in Table 5. This naming was done systematically to facilitate data retrieval in R scripts and interpretation of the visualization graph results. All name changes are documented and traced back to the original saved files. This process confirmed that the entire dataset remains interoperable across different software environments and that all specimens can be accurately compared within a standardized analytical framework. In narrative text we use BHL2, BHL5, SK4, ST1, data files and figure labels use BHL02, BHL05, SKP04, STR01.

Table 5. *Specimen name customization for analysis in R.*

Fossil specimens	Name used in analysis
Braholo 2	BHL02
Braholo 5	BHL05
Song Keplek 4	SKP04
Song Terus 1	STR01

All landmark placement and data export procedures follow the technical guidelines from Lebrun (2022) to ensure consistency, precision, and reproducibility in data processing. After obtaining and exporting the landmark data, the next step involved importing it into RStudio and pre-processing to handle missing landmarks and prepare the data array for statistical analysis.

2.2.3. Data Import and Missing Data Handling in R

All statistical analyses were performed in R using RStudio (R Core Team, 2025; RStudio Team, 2024), with the assistance of the main packages, including *Morpho* (Schlager, 2017), *geomorph* (Baken et al., 2021), *Rvcg* (Schlager, 2017), *rgl* (Murdoch & Adler, 2025), and *ggsci* (Xiao, 2024). Landmark data exported to .fcsv format in MorphoDig was imported into RStudio and organized into directories according to the analysis groups. The researcher conducted three types of analyses based on variations in specimen combinations and landmark completeness (Table 6). To maintain consistency, all .fcsv files were automatically imported into a 3D array with the following structure: number of landmarks (k), spatial coordinates (x , y , z), and individuals (n).

The parameter $lm = 36$ is used when forming the 3D array ($k \times 3 \times n$), so that each specimen is indexed at the same sequence of landmarks. Each specimen name is derived from the file name and used as the third identifier in the array. Some landmarks could not be identified due to the fragmented condition of the cranium, namely in fossil specimens BHL02, BHL05, SKP04, and STR01. In these cases, missing landmarks were manually marked as NA using the row index and specimen name. This process is crucial for maintaining the alignment of landmark sequences between specimens, even when some landmarks are missing. A complete list of missing landmarks for each is included in Appendix A.1.

Analysis B compared BHL02 and BHL05 using only the six shared landmarks that were previously identified as preserved and homologous (Section 2.2.1). It ensured that shape variation was assessed only from equivalent anatomical structures across specimens. Furthermore, in analysis C, which included STR01 and SKP04, landmark imputation was performed using the TPS method. TPS-based imputation is a well-established technique for estimating missing landmark coordinates, particularly in paleoanthropological and fragmentary contexts (Gunz et al., 2005). The results of the TPS imputation (DataNA) were used as input for the GPA and all subsequent shape analyses, as detailed in Section 2.2.4. This step completes the data preparation phase, ensuring that even fragmented fossil specimens can be included in standardized shape comparisons.

In Analysis A, three modern human specimens were excluded due to missing values at one or more landmarks, resulting in the use of only 47 of the 50 reference specimens. Meanwhile, in Analysis B and C, all 50 reference specimens were retained because they included only six familiar landmarks that were still available across all three crania.

Table 6. Morphometric analysis dataset composition.

Analysis	Reference specimen	Fossil specimens involved	Number of landmarks used	Handling of missing landmarks
A	47 reference specimens	None	36	3 reference specimens were excluded due to missing landmarks
B	50 reference specimens	BHL02, BHL05	6 (common landmarks)	Manual removal (NA)
C	50 reference specimens	BHL02, BHL05, STR01, SKP04	6 (common landmarks)	Landmark imputation with TPS

2.2.4. Generalized Procrustes Analysis (GPA)

GPA is an important process in GMM analysis that aims to eliminate non-shape variability, namely specimen size, orientation, and initial position. By using this process, differences between specimens originating from different body sizes or positions can be controlled. This enables more precise analysis of shape variations, eliminating irrelevant factors such as size or orientation differences. Through GPA, landmark configurations across specimens are aligned by translating, rotating, and scaling them to the same size and orientation. The result is data that represents pure shape differences, enabling more accurate and biologically meaningful morphological comparisons (Bookstein, 1991; Slice, 2007). For example, in cranial morphometric studies, GPA enables the comparison of skull shapes from individuals of different body sizes. This is achieved by aligning the skull shapes so that only shape variations are measured and not differences in size or position.

In this study, the researcher employed two approaches to the GPA process, tailored to the type and needs of the data being analyzed. The *procSym()* function from the *Morpho* package was used to process data in the form of 3D arrays. In contrast, the *gpagen()* function from the *geomorph* package was used when the analysis needed to be directly integrated into an advanced statistical workflow.

The result of this process is a standardized landmark configuration and a consensus shape across all specimens in a single dataset. These aligned data were then used in further analyses, namely PCA (discussed in Section 2.2.5) and modeling of shape changes along the principal axes of morphological variation (Section 2.2.6). The researcher applied GPA separately to three dataset scenarios:

- Analysis A (reference collection), conducted on 47 *Homo sapiens* specimens from the reference collection, excluding three specimens with NA values at several important landmarks.
- Analysis B (reference collection + BHL02 and BHL05), conducted on 50 reference specimens and two fossil specimens from Braholo Cave, but using only a subset of landmarks ($n = 6$) available on both specimens. This dataset, called `specimens_common`, was used to ensure configuration consistency under data limitations.
- Analysis C (reference collection + fossil specimens), conducted after imputing missing landmarks using TPS on data containing NA. The imputation results were stored as a `DataNA` array, which then served as input for GPA, using a subset of landmarks ($n = 6$) available on fossil specimens from Braholo Cave.

The resulting GPA configuration was then used to construct a shape space free of non-shape variables, allowing quantitative exploration of shape in PCA. The GPA approach has been widely applied for consistently comparing the shape of modern and fossil specimens (Bookstein, 1991; Slice, 2007). While this study focuses on cranial shape, similar landmark-based GMM approaches have been applied to dental morphology (Noerwidi, 2020), highlighting its value in assessing morphological variation in Holocene *Homo sapiens* populations from Java, Indonesia. The GMM approach was also employed by Baab & Zaim (2017) to analyze cranial shape variation in *Homo erectus* specimens from Sangiran and Ngandong, demonstrating the relevance of GPA and shape space analysis in understanding long-term evolutionary patterns in Indonesia. Thus, the GPA serves as a precondition for downstream analyses, such as PCA and TPS deformation, ensuring that shape comparisons remain biologically meaningful across both modern and fossil specimens with varying preservation quality.

2.2.5. Principal Component Analysis (PCA) and Shape Space Visualization

After the GPA process, PCA was performed on the aligned landmark configuration. PCA is a statistical technique used to reduce the complexity of data and extract the primary axes of variation, enabling researcher to visually and quantitatively understand morphological differences. This technique is advantageous in comparing cranial shape variations between populations, as it reveals how specific groups differ in their overall cranial morphology. For example, PCA can show whether modern populations, like those from Java or Sulawesi, exhibit

shape features that overlap with or diverge from fossil specimens in Gunung Sewu. These visualizations help identify morphological patterns that may not be immediately apparent from raw measurements, offering a more intuitive way to interpret shape differences and similarities across populations.

In this study, PCA was performed using the results of *procSym()* from the *Morpho* package, which automatically computes PCA scores from GPA output. These scores were then plotted in various axis combinations to construct the shape space. Visualizations were tailored to each analysis scenario:

- Analysis A (the reference collection): A 2D projection between PC1 and PC2 illustrated variation among modern *Homo sapiens* specimens from various regions.
- Analyses B and C: Additional plots showing PC1 vs PC2, PC1 vs PC3, and PC2 vs PC3 were used to evaluate the position in morphospace of fossil specimens (BHL02, BHL05, STR01, SKP04) within the reference shape variation.

Each specimen was color-coded by population group, with consistent coding across analyses. Individual ID labels were displayed at each point to facilitate tracking and interpretation. Convex hulls were drawn around each group using outermost points in shape space to define morphospacial boundaries.

The PCA results were then used to analyze the direction of shape change in each principal component, which will be explained in Section 2.2.6. Overall, PCA transforms high-dimensional shape data into interpretable axes, providing a statistical framework for detecting patterns of cranial variation and fossil affinities across regional populations.

2.2.6. Consensus Morphology along Principal Axes

The consensus shape refers to the average configuration of all aligned landmarks and acts as a baseline for comparing shape differences between specimens or groups. To visualize these differences, TPS deformation grids were used to show how certain anatomical regions expand or contract along a specific principal component.

For example, changes along PC1 generally indicate variation in cranial vault height and length, while PC2 and PC3 may reflect differences in frontal projection or occipital curvature. Using TPS grids, the researcher was able to assess whether fossil specimens such as BHL02, BHL05, STR01, and SKP04 followed or diverged from the variation pattern seen in modern

Homo sapiens. This visualization method offers an intuitive way to interpret shape variation that may not be obvious from numerical PCA results alone. The deformation grids and consensus shape visualizations used in this study were generated from aligned and, when needed, imputed landmark data (see Section 2.2.3). By linking statistical outcomes with anatomical understanding, this approach supports meaningful interpretations of evolutionary or population-level shape differences.

2.2.7. Software and Analytical Environment

All data processing and statistical analysis were performed in R (v4.5.0) using RStudio as the IDE. The main R packages included *geomorph* for geometric morphometric procedures, *Morpho* for procrustes alignment and TPS deformation, *Rvcg* for 3D mesh manipulation, and *rgl* for interactive 3D visualization. Additional visual enhancements were applied using *ggsci* to maintain consistent and publication-ready color schemes. Mesh preparation and cleaning were performed in EXScan S software version 3.1.4.3, as part of the standard post-processing workflow provided by Shining 3D, prior to landmarking in MorphoDig version 1.6.9, as described in Section 2.1.4

Software versions and package details are described in Sections 2.1.4 and 2.2.7 to support full reproducibility. Using open-source software and modular scripts improves the ability to replicate the analysis and supports future development of morphometric research on Southeast Asian fossil collections.

2.2.8. Reproducibility and Documentation

All analytical workflows were implemented using structured and well-documented R scripts, covering data import, pre-processing, GPA, PCA, and TPS deformation. The complete code is available in Appendix A.2-A.4. As noted in section 2.2.2, consistent file naming and directory structure were applied to ensure traceability. This reproducible framework enhances scientific transparency and provides a referential model for future morphometric studies on fossil hominins in Indonesia and beyond.

CHAPTER III: RESULTS

In this chapter, we report three complementary analyses under a single reading frame. First, a reference-only PCA on the 36-landmark Indonesian sample defines the pooled convex hull and depicts between-group structure. Second, a six-landmark PCA computes the reference space and projects BHL02 and BHL05 as supplementary points. Third, a TPS-imputed model harmonises landmark sets to jointly place BHL02, BHL05, SKP04, and STR01 in the same space. Fossil point positions are read against the pooled hull on PC1–PC2, PC1–PC3, and PC2–PC3 as inside (within), edge (on/visually touching; qualitative or visual assessment), or outside (beyond). Analyses are descriptive (procedures in Chapter 2). The panels show the whole cranium for orientation, but the PCs reflect variation of the cranial-vault landmarks; non-vault warps are not interpreted. Inference is limited by the available configuration, chiefly six vault landmarks.

3.1. Indonesian Modern Populations

In the reference-only shape space, the first two axes summarize variation: PC1 = 13.00%; PC2 = 10.74%. The scatter shows a stratified pattern expressed in three tendencies:

1. A horizontal excursion on PC1 that places Java (Jav) toward the positive side, resulting in an elongated and relatively separate hull.
2. A vertical dispersion on PC2 that is most pronounced in Dayak (Day), whose hull extends upward; and
3. A central overlap is formed by Bugis (Bug), Sulawesi (Sul), Sopolit (Sop), and Makassar (Mak). By contrast, the Borneo (Bor) and Java Malay (JMa) group is on the negative side of PC1 with compact dispersion.

The distribution of the reference sample in the PC1–PC2 plane is shown in Figure 14. Java shows a positive PC1 excursion with limited overlap against other groups, whereas Dayak shows the vertical dispersion along PC2 (including individuals in the PC2+ sector) at the between-group level. Bugis, Sulawesi, Sopolit, and Makassar moderate overlap around the origin. Borneo and Java Malay occupy the lower-left quadrant as a compact cluster. Qualitatively, the centroid order along the PC1 gradient follows Bor/JMa (PC1–) to Bug/Sul/Sop/Mak (central) to Jav (PC1+), while Dayak bears the strongest spread along PC2.

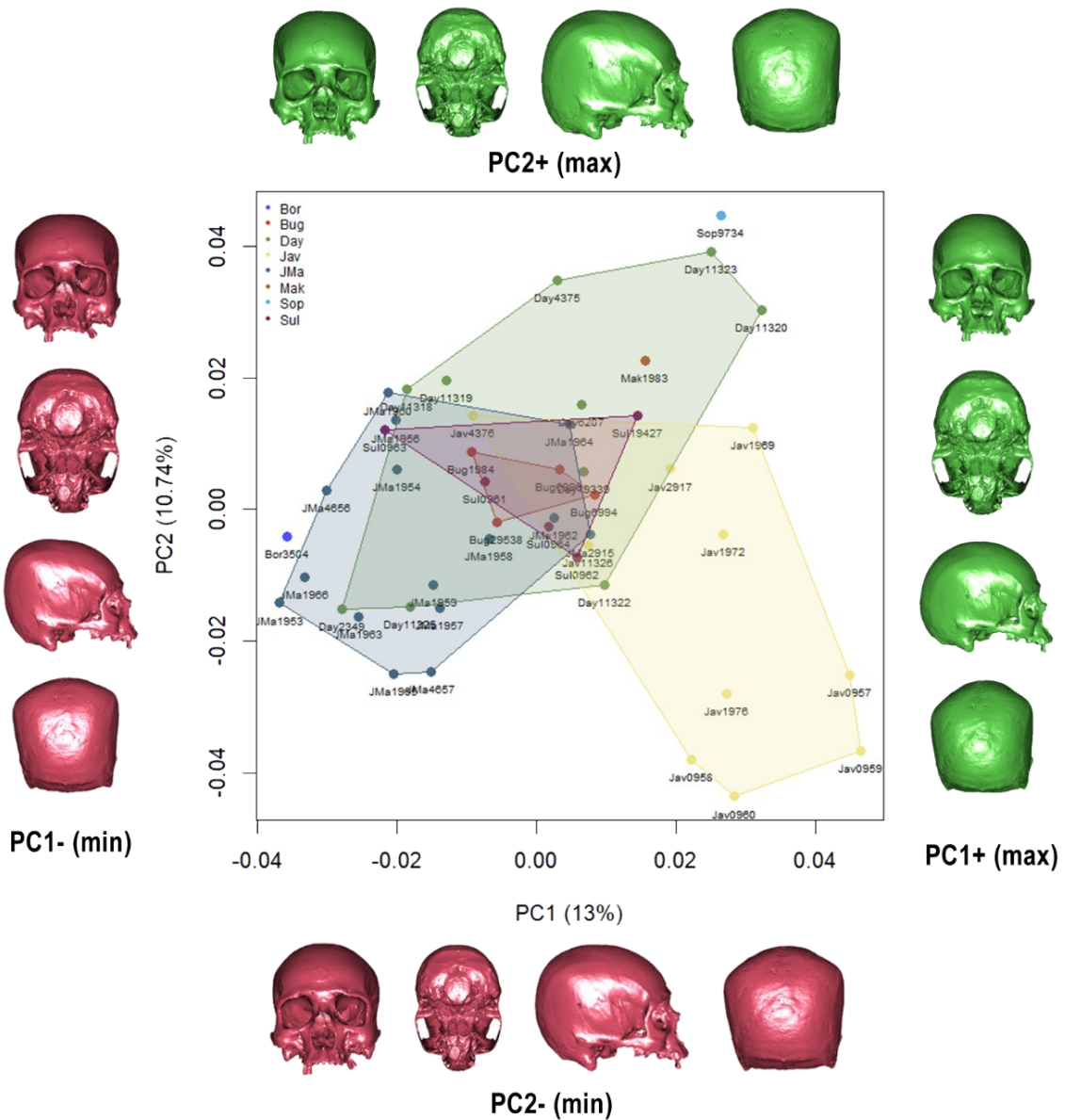


Figure 14. PC1–PC2 plot of the Indonesian modern reference sample (36-landmark). Along PC1, the expression of the parietal bump characterizes the axis: PC1– shows a squared, projected parietal bump, whereas PC1+ reduces that expression; this cue differentiates Jav from the other groups.

Morphological panels at the plot margins aid orientation. Along PC1, vault shape grades from an anteroposteriorly elongated, squarer parietal eminence (PC1–) to a taller, rounder dome with an attenuated eminence (PC1+). PC2 captures frontal curvature versus flatness together with occipital rounding (taller vs flatter vault). Together, these axes frame the horizontal separation on the reference plot: the Javanese hull drifts toward PC1+, whereas Bor/JMa cluster toward PC1–.

From the explanation above, the modern population distribution in Indonesia is not homogeneous. Java is the most horizontally separated (PC1+), Dayak shows the broadest vertical expansion (PC2+), Bugis, Sulawesi, Makassar, and Sopolit form a central overlap zone, and Bor/JMa cluster on PC1- with small dispersion. The PC1-PC2 plane explains approximately 23.7% of the variance.

3.2. Braholo in the Indonesian Reference PCA

The analysis used six landmarks to ensure compatibility with the fossils. The PCA was computed on the Indonesian reference ($n = 50$), with BHL02 and BHL05 projected as supplementary points. Axis variances are PC1 = 31.59%, PC2 = 20.12%, PC3 = 18.42% (PC1-PC2 = 51.71%; PC1-PC3 = 50.01%; PC2-PC3 = 38.54%). The explanation is complete with the consensus morphology and serves as an orientation key for reading shape change.

PC1-PC2, as shown in Figure 15, is the main map of Indonesian modern reference data distribution and Braholo positions. Here, the modern distribution shows an orderly structure with persistent overlap near the centre. Java (Jav) occupies a positive PC1 data distribution with a relatively compact hull to the right. Bugis (Bug), Sulawesi (Sul), Sopolit (Sop), Makassar (Mak) form a central overlap zone, whereas Borneo (Bor) and Java Malay (JMa) tend toward negative PC1. On the other hand, BHL05 plots close to the centroidal cloud (slightly -PC1, PC2 = 0) and inside the combined hull. BHL02 falls in the lower-left quadrant (-PC1, slight -PC2), lying at the edge of the modern variation. Figure 15 also features the consensus morphology. PC1 retains the same fundamental gradient observed in the reference model: from a comparatively elongated vault (PC1-) to a taller, more domed vault (PC1+). Although the six-landmark subset yields a coarser depiction of shape, the polarity of PC1 remains stable and negative scores accentuate antero-posterior extent and a lower cranial arc, whereas positive scores accentuate superior arching around bregmatic regions. The consensus shapes at the axis extremes summarize these tendencies for the reduced configuration. PC2 chiefly modulates overall vertical arching and the frontal rise, with higher values indicating stronger superior contouring.

PC1-PC3, in Figure 16, shows the Braholo separation along PC3. Here, the PC1 structure of the modern sample remains evident; however, PC3 introduces the dimension that distinguishes the two fossils: BHL05 is elevated on PC3+, whereas BHL02 lies on PC3-. From the consensus morphology, PC3 captures parietal–occipital contouring or the vertical component of the vault orthogonal to PC1. Accordingly, the internal separation of the Braholo crania is driven more by PC3 than by PC1. BHL05 lies outside the modern variation on the PC3+ side, and BHL02 is outside/edge on the PC3- side.

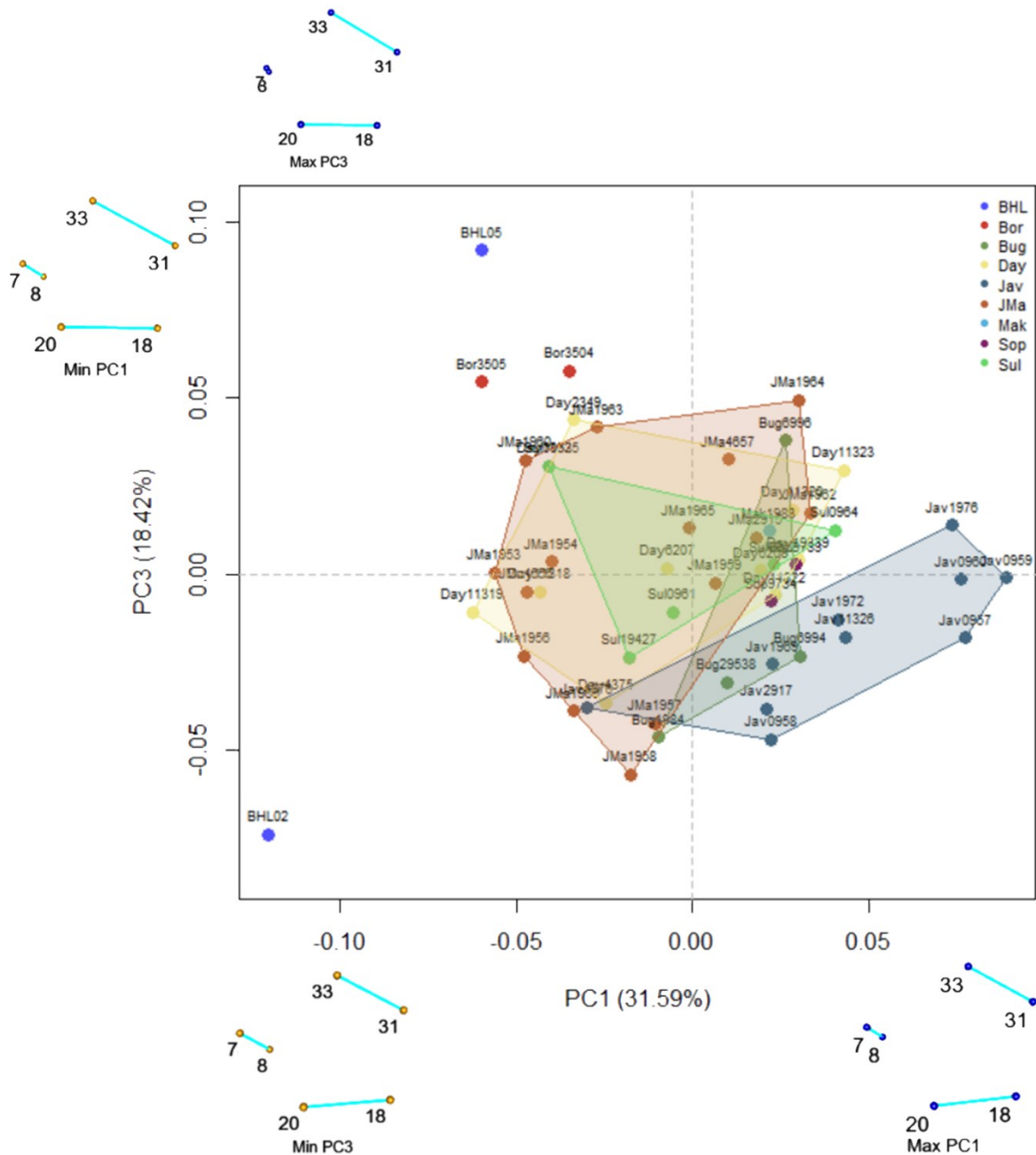


Figure 16. PC1–PC3 (50.01%) shows BHL05 at PC3+ (outside), BHL02 at PC3- (outside/edge).

PC2-PC3 in Figure 17 becomes a complementary plane that reinforces the pattern. Here, BHL05 remains high on PC3+ with PC2 near neutral, while BHL02 is at PC3- with slight PC2-. Modern groups continue to overlap near the centre, and Dayak expresses a relative spread toward PC2+. This pattern corroborates that the BHL05–BHL02 separation is structured primarily along PC3, with PC2 providing a secondary gradient.

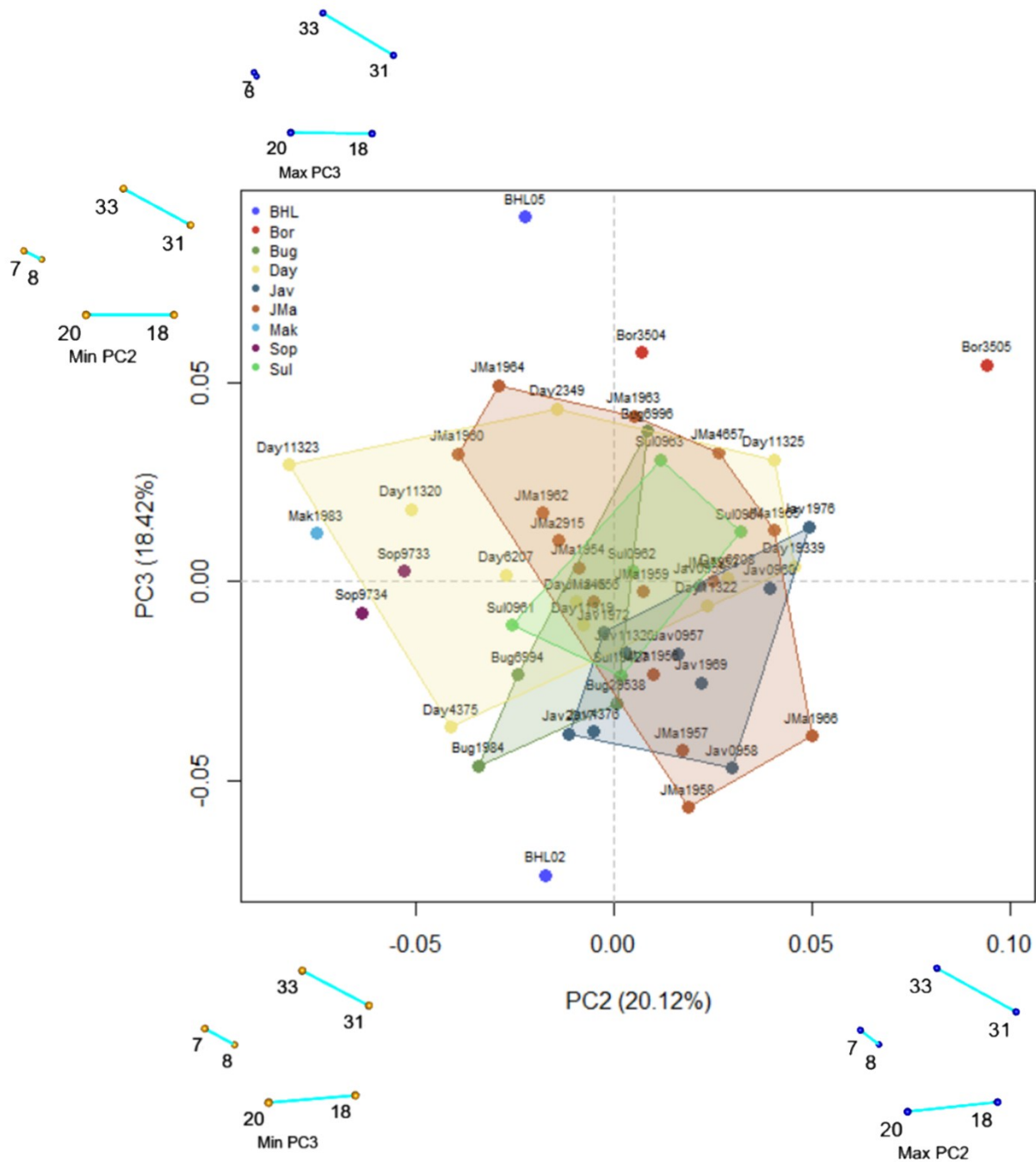


Figure 17. PC2–PC3 (38.54%) shows BHL05 remains high at PC3+ and BHL02 at PC3– with slight –PC2.

Within the six-landmark, reference-computed PCA, BHL05 plots inside the combined Indonesian hull near the centroid on PC1–PC2, whereas BHL02 sits at the edge of the variation on PC1–PC2. Along PC3, the Braholo pair separates in opposite directions. BHL05 at PC3+ outside and BHL02 at PC3– outside/edge, indicating an axis-specific departure that primarily concerns the vertical contour of the vault.

3.3. Placement of Braholo, Song Keplek, and Song Terus in the Indonesian Reference PCA (Imputed Model)

In line with Section 3.2, the PCA was computed on the Indonesian reference sample. However, the difference here is that TPS imputation was applied to complete the missing points, allowing for the joint evaluation of STR01 and SKP04 together with BHL02 and BHL05. The first three axes summarize a large share of variation (PC1 = 31.74%, PC2 = 20.72%, PC3 = 17.51%), and the reference distribution employs a stratified yet overlapping structure around the center of shape space.

PC1-PC2, in Figure 18, shows that the reference shape space retains a layered yet overlapping structure. Java (Jav) extends an elongated, relatively discrete hull toward PC1+, Dayak (Day) drives dispersion along PC2+, while Bugis (Bug), Sulawesi (Sul), Makassar (Mak), Java Malay (JMa) occupy the overlap zone near the origin, and a Borneo (Bor) outlier plots on PC2+. Here, BHL02 falls in the PC1– or PC2– quadrant, far from the center and outside the reference hull. BHL05 is nearer but remains at the edge to outside of the lower-left sector. STR01 lies on PC1+ with PC2 near zero, at the edge (or slightly beyond) the Jav hull, whereas SKP04 sits within the central overlap and thus inside the reference variation. The vector sketches at the panel margins indicate the direction of shape change along PC1-PC2 and are consistent with the Jav elongation on PC1. Figure 18 also shows the consensus morphology: PC1 preserves the same polarity observed in the preceding analyses, a gradient from a comparatively antero-posteriorly elongated vault (PC1–) to a relatively taller, more domed vault (PC1+). Thin-plate spline completion harmonizes landmark sets and slightly regularizes local curvature. However, it does not alter the axial meaning that negative PC1 scores emphasize a lower cranial arc and extended frontal–occipital distance, whereas positive PC1 scores emphasize superior arching and vertical elevation around bregmatic regions. PC2 chiefly modulates superior–inferior arching and the frontal rise, with higher PC2 indicating stronger vertical contouring.

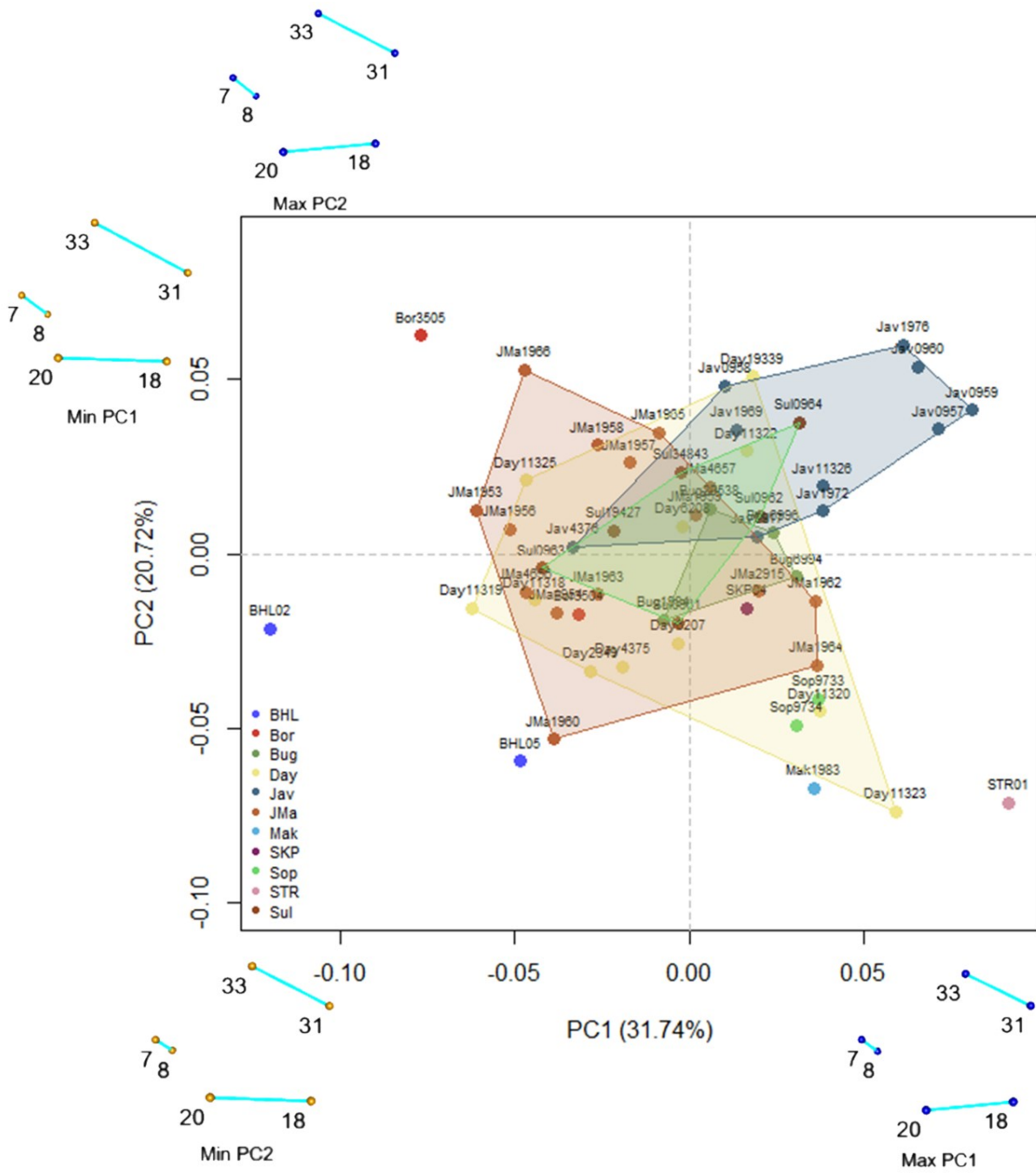


Figure 18. PC1-PC2 (52.46%). *BHL02* and *BHL05* fall in the lower-left sector outside/at the edge, *STR01* lies on the PC1+ boundary of the Jav hull, and *SKP04* sits inside the central overlap.

PC1–PC3, in Figure 19, shows the elongation of the Java (Jav) distribution along PC1+ is again evident, helping to situate the fossils relative to that axis. BHL02 lies on both PC1- and PC3-, clearly outside the reference variation and far from the central overlap. BHL05 is also occupied in PC1- but rises on PC3-, remaining outside the main variation with a marked elevation along the third axis. STR01 plots on the PC1+ near the boundary of the Jav hull, effectively on the edge and in places just beyond it on the right-hand sector. SKP04 returns to the center of the configuration within the area where reference groups overlap.

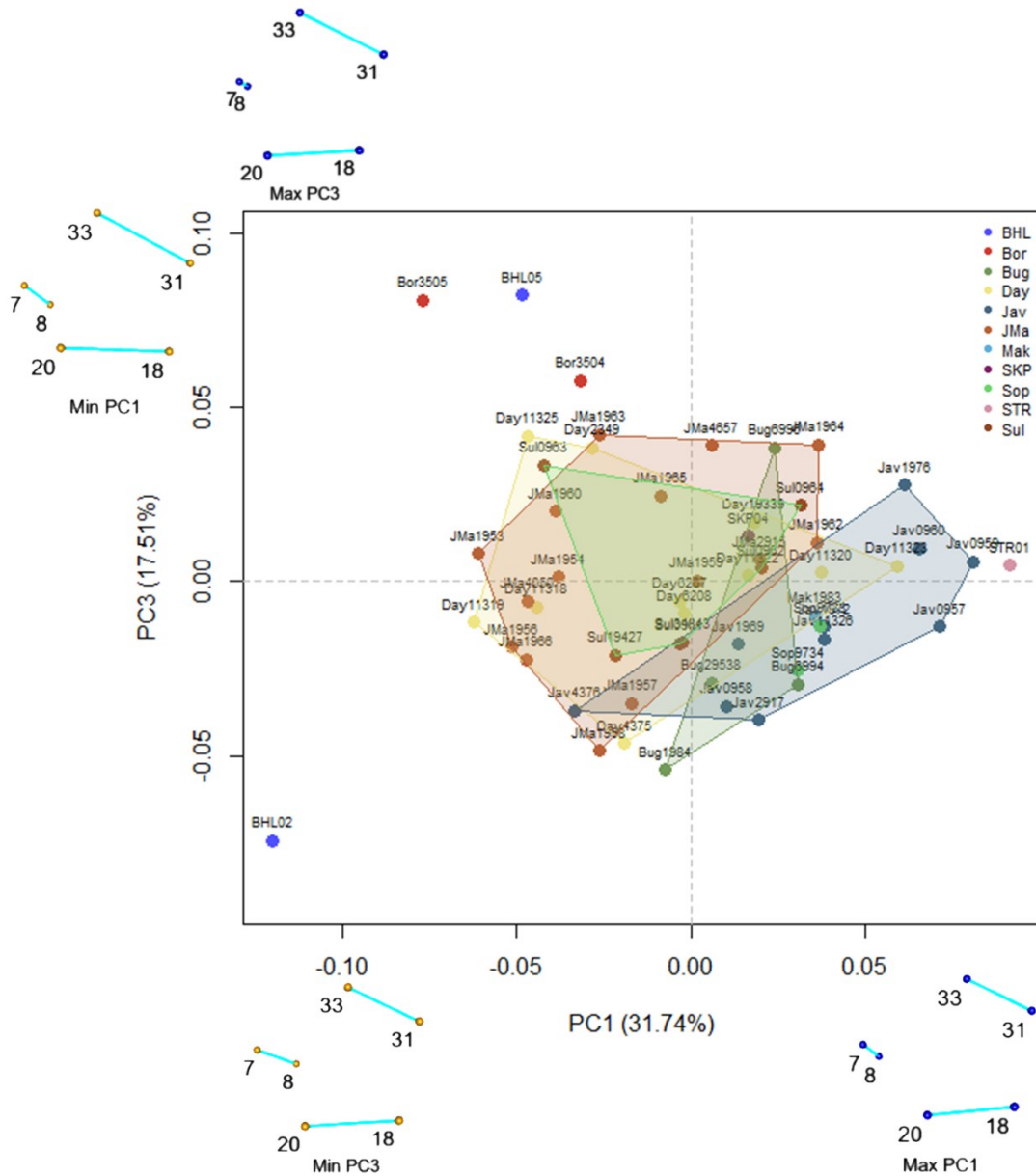


Figure 19. PC1-PC3 (49.25%). BHL02 is outside on negative PC1 and negative PC3, BHL05 is outside on negative PC1 and positive PC3, STR01 lies at the positive-PC1 edge of the Jav hull, and SKP04 remains inside the central overlap.

PC2-PC3, in Figure 20, shows that Dayak (Day) continues to extend the spread toward positive PC2, while the Bugis (Bug), Sulawesi (Sul), Makassar (Mak), and Java Malay (JMa) core fills the central region. The main contrast lies along PC3, which BHL05 trends toward the PC3+ in the upper-left sector, whereas BHL02 trends toward the PC3- in the lower-left sector, and both plots are outside the principal variability. STR01 and SKP04 remain near the center and STR01 at the inner edge of the hull, and SKP04 clearly inside, preserving the qualitative inside/edge/outside classifications observed in the non-TPS model. In sum, the third axis accentuates vertical contrast in the Braholo fossils without altering the inter-group structure of the modern reference.

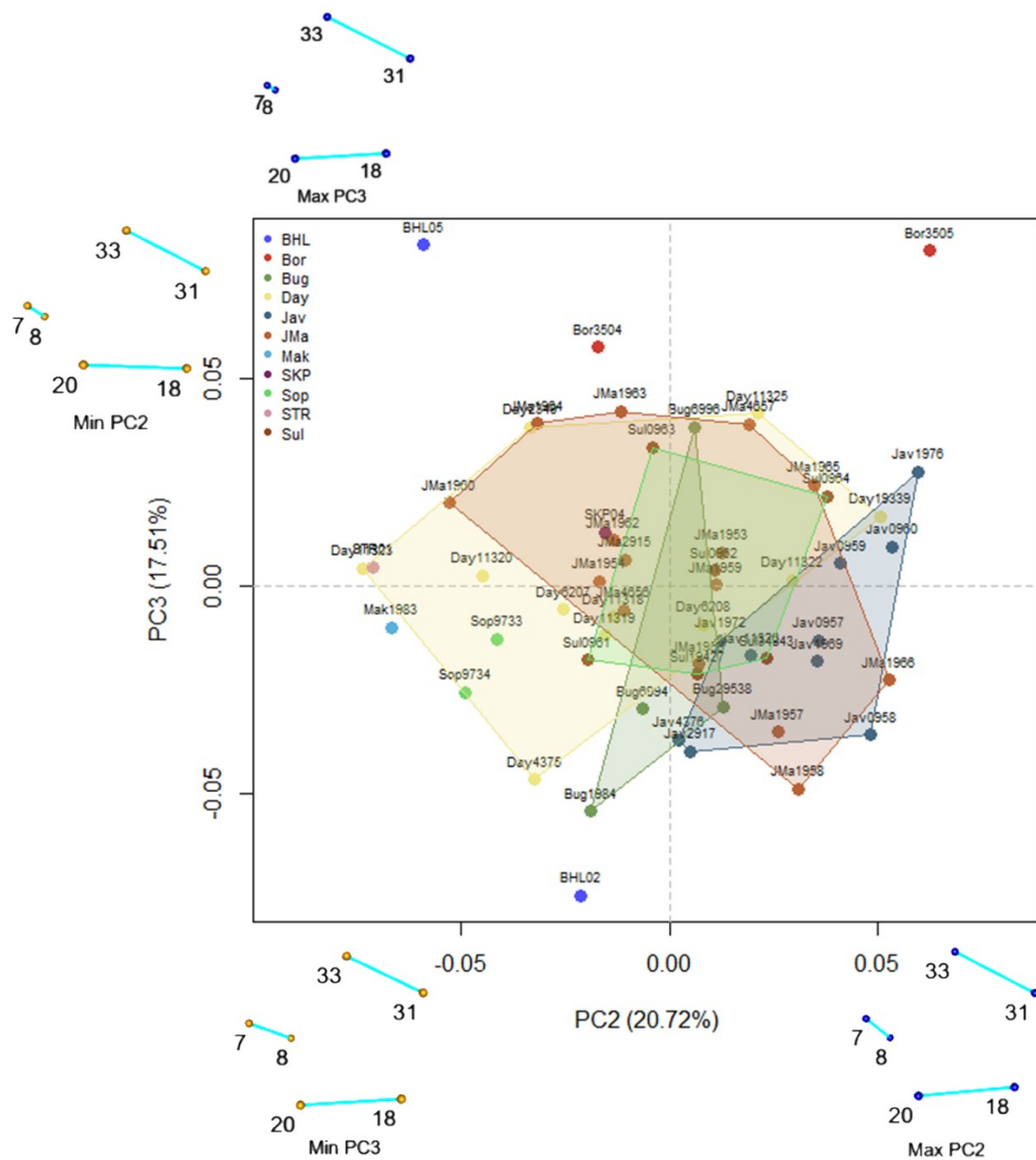


Figure 20. PC2-PC3 (38.23%). BHL05 trends high on PC3 in the upper-left, BHL02 low on PC3 in the lower-left (both outside the principal), STR01 remains near the inner edge, and SKP04 remains inside.

Table 7 summarizes the projected positions of the four fossils on the PC1–PC2, PC1–PC3, and PC2–PC3 biplots (B–C analysis), classified as inside/edge/outside with respect to the reference convex hull. The “Nearest group (visual)” column indicates the nearest reference sector, while “Notes” highlights the characteristic axis behavior. In summary, BHL02 is consistent outside (especially along PC3–), BHL05 tends to be central but deviates on PC3+, STR01 is on the Java boundary (PC1+), and SKP04 is stable inside.

Table 7. Summary of fossil placements across analyses and PC planes

Fossil	Analysis	PC1–PC2	PC1–PC3	PC2–PC3	Nearest group (visual)	Notes
BHL02	B	Edge (PC1–, slight PC2–)	Outside/edge (PC1–, PC3–)	Outside/edge (PC3–, slight PC2–)	Bor / JMa sector	Axis-specific departure mainly along PC3–
	C	Outside (lower-left sector)	Outside (PC1– & PC3–)	Outside (PC3–)	Bor / JMa sector	Consistent with non-TPS; remains outside on principal planes
BHL05	B	Inside (near centroid)	Outside (PC3+)	Outside (PC3+)	Central overlap	Inside on PC1–PC2; separates along PC3+
	C	Edge → Outside (lower-left)	Outside (PC1– & PC3+)	Outside (PC3+)	Central or left sector	Edge/outside on PC1–PC2; persistent PC3+ outlying
STR01	C	Edge (PC1+ boundary)	Edge (PC1+ boundary)	Inner edge / near center	Java (Jav) hull	Consistently at/near the Jav boundary
SKP04	C	Inside (central overlap)	Inside (central overlap)	Inside (near center)	Central overlap	Stable “inside” across PC planes

CHAPTER IV: DISCUSSION

The cranial vaults recovered from Braholo Cave, Song Keplek, and Song Terus provide a unique opportunity to explore early Holocene variation within the Gunung Sewu karst of Java (for readability, we refer to BHL2, BHL5, SK4, and ST1; file codes: see Table 5). What distinguishes this region is not only the density of human burials but also the finely resolved stratigraphy of the Terus–Tabuhan–Keplek sequence. This stratigraphic framework provides a secure chronological anchor against which morphological variation can be read horizon by horizon rather than through fixed typological categories. In this discussion, we situate the Gunung Sewu fossils relative to a modern Indonesian comparative series, with particular attention to the vault anatomy that underlies statistical placements (i.e. geometric morphometrics approach), and evaluate their significance in light of earlier osteological and morphometric studies. In particular, fossils are projected onto a modern Indonesian reference and its pooled convex hull (corresponding to its shape range of variation), then classified as inside, edge, or outside, with checks for robustness on fragmentary fossils. This follows the practice of Cosalan (2017), emphasizing landmark consistency and clear assumptions for partial specimens.

4.1. Morphological Variation of the Indonesian Reference Sample

The modern Indonesian comparative series exhibits structured variation that can be described in anatomical terms. At one end of the variation spectrum, crania present a higher, more rounded dome: the vault rises steeply, the parietal eminence is less pronounced, and the transition between frontal and parietal bones is smooth. In these cases, the parietal walls converge gradually with the temporal squama, producing a compact cranial contour. At the opposite end, crania exhibit a longer, lower dome: the cranial vault extends antero-posteriorly, the parietal bulge projects laterally to form a squarer outline, and the occipital contour is more prominent. The parietal–temporal junction is sharper, and the dome reads as elongated rather than rounded. These two poles represent the main morphological contrast in the Indonesian series, corresponding to what is observed for the variation along the PC1 axis in the results of the geometric morphometrics (Figure 14). Importantly, the parietal eminence, expressed as a localized lateral swelling on the parietal wall, serves as a reliable anatomical marker of this polarity. Independent of this main axis, additional variation can be described:

- Frontal curvature vs. flatness and occipital rounding (PC2), which determines whether the vault presents a taller, globular profile or a flatter one (Figure 14).
- Balance between parietal and temporal regions (PC3 minor, not analyzed in the main PC1–PC2 results), modulating the relative prominence of the lateral vault walls.

These features have been highlighted in prior morphometric analyses of Southeast Asian crania by Cosalan (2017), whose consistent landmarking shows that even subtle differences in frontal curvature and parietal–temporal balance are diagnostic. Applied to the Indonesian groups, this anatomy reads as follows:

- Javanese more often show a higher, rounder dome with a less pronounced parietal eminence.
- Borneo/Java-Malay more often show a longer, lower dome with a squarer parietal outline and a sharper parietal–temporal junction.
- Dayak spans the widest range, from relatively flatter vaults to more globular crania with stronger frontal curvature/occipital rounding.
- Bugis, Sulawesi, Makassar, and Sopolit occupy intermediate proportions.

These tendencies should be read with caution (Table 3) because collection labels are historical and inconsistently applied; see Cosalan (2017) for a detailed discussion of label usage. Thus, the Indonesian reference is not a typological template but a morphological frame of variation against which fossil vaults can be positioned.

4.2. Fossil Placements within this Frame

4.2.1. Braholo Cave (BHL2, BHL5)

The Braholo series, by contrast, often falls outside the modern Indonesian range along the PC2–PC3 axes (See Figure 17 for non-TPS analysis, Figures 20 for TPS model). Morphologically, this corresponds to vault shapes at the extremes of the Indonesian spectrum: either a longer, lower dome with a sharper parietal–temporal junction and stronger posterior projection, or a higher, rounder dome with a smoother frontal–parietal transition and reduced lateral parietal swelling. BHL2 exhibits a thin-walled, elongated dome. BHL5 illustrates the second, preserving an upright forehead, rounded orbits, a protruding occiput, and a relatively

gracile calvaria. Because both Braholo crania are preserved primarily as vaults, no specimen-specific facial inferences are made here.

The critical point is that along certain axes, particularly those modulating frontal curvature and parietal–temporal balance, these crania extend beyond the observed variation in the modern comparative sample. This pattern is consistent with a local morphological variant within the Braholo sequence. An alternative, non-biological explanation exists for BHL2: the physical reconstruction described by Déroit (2002) on which the current model is based joined the right and left vault halves essentially at the occipital because a sagittal bony strip is missing from nasion to lambda, leaving few anterior cross-side contacts; such geometry could make the anterior arc slightly too narrow and bias width-sensitive axes (PC2–PC3). Even with this condition, site reports document heterogeneity, “primitive” and “gracile” individuals, across multiple burials at Braholo, which remains compatible with a genuine local variant (Noerwidi, 2020; Widiyanto & Noerwidi, 2023a).

Contextual evidence reinforces this interpretation: Braholo records a long sequence of primary and secondary burials interstratified with hearth layers, bone tools, and abundant small primate remains. Radiocarbon ages around 8.7 ka BP anchor BHL2 in the early Holocene, situating its morphology within a mosaic of variation that coexisted with broader regional continuity. BHL5 derives from contemporary early-Holocene deposits within the same mortuary horizon, reinforcing that these variant vault expressions are coeval rather than sequential.

4.2.2. Song Keplek (SK4)

The cranium SK4, recovered in a tightly flexed burial within the Keplek horizon, consistently plots inside the modern Indonesian comparative range. SK4 was found near the southern wall of the cave, in a brown clay layer with stone flakes and animal remains, securing its context. Anatomically, SK4 displays an elongated dome (Figure 21), relatively upright parietal walls, a marked occipital prominence, and only light muscular relief on the nuchal plane. The vault morphology accords with the Australo-Melanesian profile repeatedly documented for early Holocene Java: dolichocephalic proportions, distinct occipital contour, and a robust masticatory apparatus (Widiyanto, 2002; Noerwidi, 2020).

The anatomical reading is reinforced by its archaeological context: a primary burial, and associations with a dense flake industry and aquatic fauna characteristic of the Keplek Layer. Radiocarbon ages around 5.9 ka BP from associated charcoal (Handini & Widiyanto, 1998) support the placement. Integrating archaeological context with its PCA placement, SK4

lies within the modern Indonesian comparative range and exemplifies early-Holocene–present continuity, consistent with attribution by Noerwidi (2020) of Australo-Melanesian affinity in a pre-Neolithic context. It occupies the central overlap on PC1–PC2 and PC1–PC3 and remains inside after TPS, indicating the classification is not influenced by missing data (Figures 18-20).

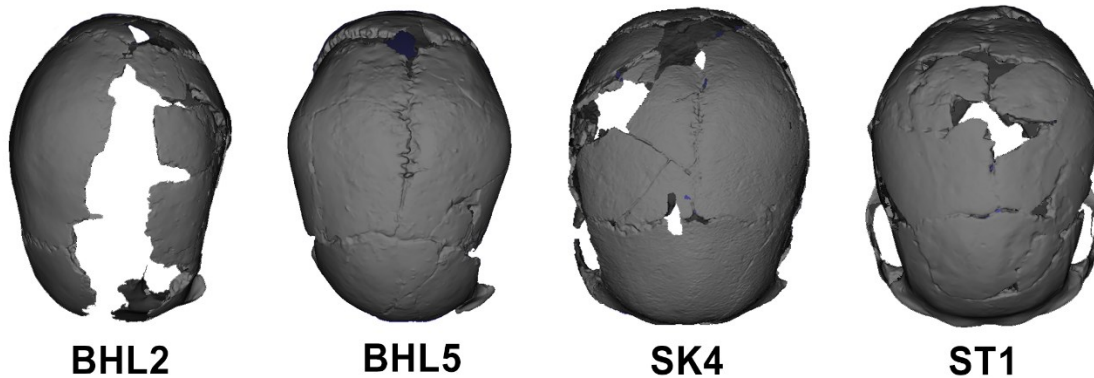


Figure 21. Superior views (anterior at top) of the four cranial vaults.

4.2.3. Song Terus (ST1)

The ST1 cranium, also from the Keplek Layer, consistently plots at the edge of the modern Indonesian range. This position reflects a higher, rounder dome with a reduced lateral parietal eminence. In anatomical terms, ST1 is at the high-dome end: the top of the skull rises higher around the bregma, the curve from the forehead to the top is smoother, the sides bulge less, and the overall vault looks more rounded. While still within the Indonesian variation range, the vault does not overlap with its densest sector, but instead occupies a marginal position. This position was tested for sensitivity to landmark absence and TPS-based imputation; it remains at the edge, indicating that this result is likely not a reconstruction artifact. The stratigraphic and archaeological context of ST1, flexed burial, enclosed by small limestone blocks, associated chert flakes, fauna, and a radiocarbon date of ~9.3 ka BP from overlying shells (Détroit, 2002; Budiman, 2009), aligns with the morphological reading of ST1 as a transitional profile. ST1 is also among the earliest documented flexed posture burials in ISEA (Détroit, 2002). Regionally, ST1's edge placement and rounded-dome tendency refine earlier descriptions of Song Terus burials as Australo-Melanesian (Détroit, 2002; Widiyanto, 2002) by situating the specimen at the margin of Indonesian variation.

4.3. Regional Implications

Bringing the data from the three sites together, SK4 at Song Keplek provides a strong case for early Holocene continuity within the modern Indonesian range. Its elongated dome, upright parietal walls, and robust craniofacial complex express a morphological package that remains consistent with the comparative frame. By contrast, ST1 from Song Terus illustrates a marginal, high, rounded dome profile, a form that makes sense with its stratigraphic situation at a transitional node between the Pleistocene and Holocene layers. Braholo presents yet another picture: the individuals BHL2 and BHL5 highlight how site-specific heterogeneity can extend vault morphology beyond the limits of the modern comparative range, producing a local mosaic of dolichocephalic and gracile forms that is possibly distinctive to the western Gunung Sewu.

In interpretive terms, the inside/edge/outside categories may have different meanings: inside signals local continuity with the modern range, edge marks low-frequency variants or local population structure without necessarily assuming admixture, and outside points to vault shapes that fall beyond the modern range but shift in a consistent anatomical direction. In this study, we interpret these categories at the Keplek-horizon level; the broader Terus–Tabuhan–Keplek sequence serves only as regional context and is not directly tested.

At the scale of Island Southeast Asia, these results resonate with literature that treats the Holocene as a heterogeneous period: local continuity is visible at some sites (Keplek), transitions at others (Terus), and extreme variants at still others (Braholo). The terms Australo-Melanesian and East Asian-related remain useful as positional markers in morphometric space, but they should not be understood as typological identities (Noerwidi, 2012, 2020; Widiyanto & Noerwidi, 2023a).

Equally important is the link between statistical axes and anatomical features: the parietal eminence as a marker of PC1, and frontal/occipital curvature as markers of PC2, provide a bridge between geometric morphometrics and traditional anatomy. This ensures that placements (inside, edge, outside) can be interpreted as biological clues rather than procedural artifacts, in line with best GMM practice (Cosalan, 2017).

4.4. Limitations and prospects

Equally important is the link between statistical axes and anatomical features: the parietal eminence as a marker of PC1, and frontal/occipital curvature as markers of PC2, provide a bridge between geometric morphometrics and traditional anatomy. This ensures that placements (inside, edge, outside) can be interpreted as biological clues rather than procedural

artifacts, in line with best GMM practice (Cosalan, 2017). However, several limitations must be acknowledged. First, the focus on the cranial vault excludes signals from the face and cranial base, which may express different trajectories of continuity or change. Second, the modern Indonesian reference derives from historical collections (e.g., MNHN) whose ethnogeographic labels (e.g., “Java-Malay,” “Dayak”) must be treated cautiously when linked to biology (Cosalan, 2017). Third, fossil reconstruction strategies, landmark imputation, and TPS reflection while shown here to be robust, should be complemented in the future by higher-resolution 3D surface models and cross-method validation.

CONCLUSION

This thesis investigated the cranial vault morphology of four Holocene individuals from the Gunung Sewu karst, Java, Indonesia (BHL2, BHL5, SK4, and ST1) within a comparative framework of modern Indonesian populations. Using a 3D landmark-based geometric morphometric protocol, the aim was to evaluate whether these fossils reflect local continuity, marginal transitional forms, or shifts beyond the range of modern variation, and whether these results remain stable under conditions of fragmentation and thus of missing landmarks.

The first research question addressed the structure of cranial variation in the modern Indonesian reference. The comparative sample revealed a broad but coherent space of variation, marked by a contrast between higher, rounder domes with attenuated parietal eminence and longer, lower vaults with stronger lateral parietal projection. This provided a reference frame within which fossils could be positioned without presupposing fixed biological types.

The second research question concerned the position of the Holocene fossils relative to this range. The results show a spectrum of placements. SK4 from Song Keplek consistently falls inside the modern Indonesian range, confirming Hypothesis 1 (continuity). ST1 from Song Terus occupies a marginal position, with a higher, rounder dome profile consistent with its slightly older age, and supports Hypothesis 2 (marginal). The two Braholo crania diverge from one another but tend toward heterogeneity outside the common modern range: BHL05 remains close to the centroid on primary axes, while BHL02 consistently departs along orthogonal dimensions, together supporting Hypothesis 3 (shift). Taken together, these placements indicate that within the same karst belt, continuity, transitional forms, and site-specific variability coexisted during the Holocene.

The third research question asked was whether these classifications remain stable under the effects of missing data and reconstructions. Across reduced-landmark and thin-plate spline procedures, the inside–edge–outside ordering held, confirming Hypothesis 4 (stability). This demonstrates that the morphological signals obtained in our study are not artifacts of fragmentation or reconstruction but reflect observable anatomical patterns of vault shape.

Beyond the specific hypotheses, several broader conclusions can be drawn. First, the Holocene record of Gunung Sewu does not present a uniform picture but rather a mosaic of persistence and change. At Song Keplek, continuity with modern forms is present; at Song Terus, a transitional morphology is expressed, consistent with its slightly older age; and at Braholo Cave, distinct local variation extends beyond the comparative frame. Second, these results align with previous studies that describe early Holocene Indonesian cranial morphology

as predominantly Australo-Melanesian in pattern, later intersecting with East Asian-related features, while cautioning that such terms should be treated as descriptors of affinities rather than fixed identities.

Limitations must also be acknowledged. The analysis was restricted to cranial vaults, thus, facial and basicranial regions remain to be examined. The comparative reference draws on historical collections, where labels are operational rather than biologically precise. And while radiocarbon ages anchor interpretations chronologically, additional direct dating and finer contextual control are needed to link morphological signals to specific depositional events.

Looking forward, three perspectives emerge. First, future work should expand landmark coverage to the face and cranial base, testing whether the observed continuity, edge, and heterogeneity extend across other cranial regions. This is a clear objective but is presently difficult, as very few Holocene specimens preserve the face or basicranium sufficiently for reliable landmarking. Second, the comparative dataset should be broadened with contemporary, well-documented modern samples, with harmonized protocols and ethically governed data-sharing frameworks to enable replication and inter-laboratory refinement. Third, closer chronological integration (through AMS dating and micro-stratigraphic provenience) will allow more precise correlations between morphology and archaeological horizons.

To conclude, this study demonstrates that the Holocene cranial vaults of Gunung Sewu can be read within a comparative and stratigraphically anchored framework as evidence for both local continuity and structured heterogeneity. Continuity and change appear not as mutually exclusive categories but as intertwined dynamics that shaped the populations of southern Java during the Holocene.

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APPENDIX

Appendix A.1.

A complete list of missing landmarks for each material

Specimen ID	Missing Landmark number	n missing
BHL02	1,2,3,6,9,10,11,12,13,14,15,17,19,21,22,23,24,25,26,27,28,29,30,32,34,35,36	27
BHL05	1,2,3,4,5,9,10,11,12,13,14,15,16,17,19,21,22,24,25,26,27,28,32	23
SKP04	4,6,17,20,23,27,30,35	8
STR01	33	1
Sul34843	6, 27, 28, 33	4
Bor3505	13	1
Day6208	9, 10, 32	3
Sop9733	3, 32	2

Appendix A.2.

Complete R Code for Geometric Morphometric Analyses A

```
library(ggsci)
library(Morpho)
library(rgl)
library(Rvcg)
library(geomorph)

###definition du dossier de travail
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/REF SKUL (.FCSV)")
### to see if it reads the file right
read.csv(file="Jav0957.fcsv", skip=2, header=T)[,2:4]

###Choice of the number of landmarks
lm<-36

## search automatically how many specimens there are in the folder
dir()
files <- dir()
dim <- 3 # 3D
n<-length(files) # nb de specimens total

#### building an array with all the specimens
specimens<-array(NA,c(lm,dim,n))

for (i in 1:n) {
  temp<-as.matrix(read.csv(files[i],header=T, skip=2)[,2:4])
  specimens[,i]<-temp[c(1:lm),]
}

###adding the name of the specimens from the files name
id<-substr(files,1,c(nchar(files)-5))
specimens<-array(specimens,c(lm,dim,n),dimnames=list(NULL,NULL,id))

###creating a grouping
group<-as.factor(substr(id,1,3)) #### put the first 3 letters of the file name with the group

##color for groups##
col.gp <- pal_igv(palette = c("default", "alternating"), alpha = 1)(9) ##the last number
correspond to the number of group
names(col.gp) <- levels(group)
col.gp <- col.gp[match(group, names(col.gp))]

##Test on a 3D mesh
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/REF SKUL (.PLY)") ##change work directory
ref<-file2mesh("Jav0957.ply") #save the mesh in a file
#you need to save the meshes in ply with modified position in morphodig
shade3d(ref,color="beige",rglopen=T) #la visualizzo
spheres3d(specimens[,,"Jav0957"], col="orange", radius=3);rgl::rglwidget() #aggiungo i suoi
landmarks

#####
###RUN ONLY IF Missing Data###
#####
setNA <- specimens #creation of a copy of the data
#need to convert missing landmarks to NA. The format of my data is a 3D array, meaning it
consists of three dimensions:
#a series (k) of matrices with the same dimensions.
#So the function setNA[line (landmark number), column (x, y, z), individual] will be used to
assign NA values.
#setNA[c(4,6,17,20,23,27,30,35), , "SKP04"] <- NA ### here i change the line XX of the
individual
#setNA[33, , "STR01"] <- NA
```

```

#setNA[c(1,2,3,6,9,10,11,12,13,14,15,17,19,21,22,23,24,25,26,27,28,29,30,32,34,35,36), ,
"BHL05"] <- NA
#setNA[c(1,2,3,4,5,9,10,11,12,13,14,15,16,17,19,21,22,24,25,26,27,28,32), , "BHL02"] <- NA
#setNA[c(6, 27, 28, 33), , "Sul34843"] <- NA
#setNA[13, , "Bor3505"] <- NA
#setNA[c(9, 10, 32), , "Day6208"] <- NA
#setNA[c(3, 32), , "Sop9733"] <- NA

###Fix NA by TPS##
#fixLMtps ##chiedi cosa fai questa funzione
#DataTPS <- fixLMtps(setNA, comp=7, weight=TRUE) #new dataset
#DataTPS$out
#DataNA <- as.array(DataTPS$out) #trasform new table in an array
#####

###GPA##
gpa <- procSym(specimens) ##if missing landmarks, replace specimens by DataNA, everywhere
from now on.
####visualizzare tutti i landmark di tutti gli individui sovrapposti
plotAllSpecimens(gpa$orpdata, mean=TRUE, label=TRUE,plot_param =list(pt.bg=col.gp,
pt.cex=0.5, mean.bg=5, mean.cex=5))

#x11()
#plot(gpa$PCscores[,c(1,2)],pch=21, xlab=paste("PC1
(",round(gpa$Variance[1,2],2),"%"),ylab=paste("PC2
(",round(gpa$Variance[2,2],2),"%"),
asp=1,col=col.gp,bg=col.gp)
#text(gpa$PCscores[,c(1,2)],labels = id,pos=1,asp=1)
#abline(a = NULL, b = NULL, h = 0, v = 0,col = "darkgray", lty=3)
#legend("topleft", as.vector(unique(group)), pch=20, col = unique(col.gp), bty="n")

#plot with convex hull - Must be adjusted in function of the number of group (with the
excluded specimens,
#here there with 8 groups) and the number of individual in a group, I have excluded the group
with less that 3 individuals
pca<-procSym(specimens)
plotAllSpecimens(pca$orpdata, mean=TRUE, label=TRUE,plot_param =list(pt.bg=col.gp,
pt.cex=0.5, mean.bg=5, mean.cex=5))
par(pty="s")
xlab=paste("PC1",paste("(",round(pca$Variance[1,2],2),"%"),sep=""))
ylab=paste("PC2",paste("(",round(pca$Variance[2,2],2),"%"),sep=""))
zlab=paste("PC3",paste("(",round(pca$Variance[3,2],2),"%"),sep=""))
plot(pca$PCscores[,c(1,2)],cex=1,xlab=xlab,ylab=ylab, pch=21,col=col.gp,bg=col.gp)
text(pca$PCscores[,c(1,2)], labels = id, pos = 1, asp = 1, cex = 0.5)
legend("topleft", as.vector(unique(group)), pch=20, col = unique(col.gp), bty="n", cex =
0.6)
PCx<-1
PCy<-2

sel<-which(group=="Bug") # select the group "Bug"
mat<-pca$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
col=adjustcolor(unique(col.gp)[2],alpha.f=0.2),border=unique(col.gp)[2])
#assigning the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-pca$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3])

sel<-which(group=="Jav")
mat<-pca$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

```

```

sel<-which(group=="JMa")
mat<-pca$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="Sul")
mat<-pca$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[8],alpha.f=0.2),border=unique(col.gp)[8])

#####
####Consensus shape PC min/max####
#####
pc1min<-restoreShapes(min(gpa$PCscores[,1]),PC = gpa$PCs[,1],mshape = gpa$mshape)
pc1max<-restoreShapes(max(gpa$PCscores[,1]),PC = gpa$PCs[,1],mshape = gpa$mshape)
pc2min<-restoreShapes(min(gpa$PCscores[,2]),PC = gpa$PCs[,2],mshape = gpa$mshape)
pc2max<-restoreShapes(max(gpa$PCscores[,2]),PC = gpa$PCs[,2],mshape = gpa$mshape)
pc3min<-restoreShapes(min(gpa$PCscores[,3]),PC = gpa$PCs[,3],mshape = gpa$mshape)
pc3max<-restoreShapes(max(gpa$PCscores[,3]),PC = gpa$PCs[,3],mshape = gpa$mshape)

REFSUR<- ref
pc1min_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc1min)
pc1max_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc1max)
pc2min_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc2min)
pc2max_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc2max)
pc3min_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc3min)
pc3max_sur<-tps3d(REFSUR,specimens[,,"Jav0957"],pc3max)

##3D all'estremità degli assi PCs
layout3d(matrix(1:6,ncol=2,byrow = TRUE),sharedMouse = T)
shade3d(pc1min_sur,col=2)
next3d()
shade3d(pc1max_sur,col=3)
next3d()
shade3d(pc2min_sur,col=2)
next3d()
shade3d(pc2max_sur,col=3)
next3d()
shade3d(pc3min_sur,col=2)
next3d()
shade3d(pc3max_sur,col=3)

```

Appendix A.3.

Complete R Code for Geometric Morphometric Analyses B

```
library(ggsci)
library(Morpho)
library(rgl)
library(Rvcg)
library(geomorph)

###definition du dossier de travail
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/SKULL + BHL (.FCSV)")
### to see if it reads the file right
read.csv(file="Jav0957.fcsv", skip=2, header=T)[,2:4]

# search automatically how many specimens there are in the folder
lm <- 36 # max landmark
files <- dir()
dim <- 3
n <- length(files)
specimens <- array(NA, c(lm, dim, n))

for (i in 1:n) {
  temp <- as.matrix(read.csv(files[i], header=TRUE, skip=2)[,2:4])
  specimens[, ,i] <- temp[1:lm,]
}

id <- substr(files, 1, nchar(files)-5)
dimnames(specimens) <- list(NULL, NULL, id)

# === Define missing landmarks manually === #
setNA <- specimens

# Manual NA assignment for fossils
setNA[c(1,2,3,6,9,10,11,12,13,14,15,17,19,21,22,23,24,25,26,27,28,29,30,32,34,35,36), ,
"BHL05"] <- NA
setNA[c(1,2,3,4,5,9,10,11,12,13,14,15,16,17,19,21,22,24,25,26,27,28,32), , "BHL02"] <- NA

# === Find common landmarks between BHL02 and BHL05 === #
lm_bhl02 <- which(!is.na(setNA[,1,"BHL02"]))
lm_bhl05 <- which(!is.na(setNA[,1,"BHL05"]))
common_lm <- intersect(lm_bhl02, lm_bhl05)

cat("Total common landmarks:", length(common_lm), "\n")
cat("The same landmarks are available in BHL02 and BHL05:\n")
print(common_lm)

# === Subset all specimens based on common landmarks === #
specimens_common <- setNA[common_lm, , ]

##Test on a 3D mesh with only 6 common landmarks
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/SKULL + BHL (.PLY)")
ref <- file2mesh("Jav0957.ply")
shade3d(ref,color="beige",rglopen=T) #la visualizzo
#you need to save the meshes in ply with modified position in morphodig
spheres3d(specimens[common_lm, , "Jav0957"], col = "red", radius = 3);rgl::rglwidget()
text3d(specimens[common_lm, , "Jav0957"], texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)

# === Run GPA and PCA === #
gpa_common <- procSym(specimens_common)

# === Plot PCA (PC1 vs PC2) === #
group <- as.factor(substr(id,1,3))
col.gp <- pal_igv("default")(length(levels(group)))
names(col.gp) <- levels(group)
col.gp <- col.gp[match(group, names(col.gp))]
```

```

xlab <- paste("PC1 (", round(gpa_common$Variance[1,2],2), "%)", sep="")
ylab <- paste("PC2 (", round(gpa_common$Variance[2,2],2), "%)", sep="")
zlab <- paste("PC3 (", round(gpa_common$Variance[3,2],2), "%)", sep="")

# === PC1 PC2 === #
x11()
plot(gpa_common$PCscores[,1], gpa_common$PCscores[,2],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = xlab, ylab = ylab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,1], gpa_common$PCscores[,2],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("topright", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Sul")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === PC1 PC3 === #
x11()
plot(gpa_common$PCscores[,1], gpa_common$PCscores[,3],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = xlab, ylab = zlab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,1], gpa_common$PCscores[,3],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("topright", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"

```

```

mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Sul")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === PC2 PC3 === #
x11()
plot(gpa_common$PCscores[,2], gpa_common$PCscores[,3],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = ylab, ylab = zlab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,2], gpa_common$PCscores[,3],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("topleft", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)

```

```

polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Sul")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === MIN MAX PCs === #
max_1<-restoreShapes(max(gpa_common$PCscores[,1]),gpa_common$PCs[,1],gpa_common$mshape)
min_1<-restoreShapes(min(gpa_common$PCscores[,1]),gpa_common$PCs[,1],gpa_common$mshape)
max_2<-restoreShapes(max(gpa_common$PCscores[,2]),gpa_common$PCs[,2],gpa_common$mshape)
min_2<-restoreShapes(min(gpa_common$PCscores[,2]),gpa_common$PCs[,2],gpa_common$mshape)
max_3<-restoreShapes(max(gpa_common$PCscores[,3]),gpa_common$PCs[,3],gpa_common$mshape)
min_3<-restoreShapes(min(gpa_common$PCscores[,3]),gpa_common$PCs[,3],gpa_common$mshape)

open3d()
layout3d(matrix(1:6,ncol=2,byrow = T),sharedMouse = T)

spheres3d(min_1,col="orange",radius=0.02,rglopen=T)
lineplot(min_1,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(min_1,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(min_1,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(min_1, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Min PC1")
rgl::rglwidget()

next3d()
spheres3d(max_1,col="blue",radius=0.02)
lineplot(max_1,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(max_1,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(max_1,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(max_1, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Max PC1")
rgl::rglwidget()

next3d()
spheres3d(min_2,col="orange",radius=0.02)
lineplot(min_2,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(min_2,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(min_2,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(min_2, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Min PC2")
rgl::rglwidget()

next3d()
spheres3d(max_2,col="blue",radius=0.02)
lineplot(max_2,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(max_2,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(max_2,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(max_2, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Max PC2")
rgl::rglwidget()

next3d()
spheres3d(min_3,col="orange",radius=0.02)
lineplot(min_3,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(min_3,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(min_3,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(min_3, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Min PC3")
rgl::rglwidget()

next3d()

```

```
spheres3d(max_3,col="blue",radius=0.02)
lineplot(max_3,point=c(1,2),col = "cyan",add = TRUE,lwd=3)
lineplot(max_3,point=c(3,4),col = "cyan",add = TRUE,lwd=3)
lineplot(max_3,point=c(5,6),col = "cyan",add = TRUE,lwd=3)
text3d(max_3, texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)
title3d("Max PC3")
rgl::rglwidget()
```

Appendix A.4.

Complete R Code for Geometric Morphometric Analyses C

```
library(ggsci)
library(Morpho)
library(rgl)
library(Rvcg)
library(geomorph)

###definition du dossier de travail
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/SKULL + BHL + SKP04 + STR01 (.FCSV)")
### to see if it reads the file right
read.csv(file="Jav0957.fcsv", skip=2, header=T)[,2:4]

# search automatically how many specimens there are in the folder
lm <- 36 # max landmark
files <- dir()
dim <- 3
n <- length(files)
specimens <- array(NA, c(lm, dim, n))

for (i in 1:n) {
  temp <- as.matrix(read.csv(files[i], header=TRUE, skip=2)[,2:4])
  specimens[:,i] <- temp[1:lm,]
}

id <- substr(files, 1, nchar(files)-5)
dimnames(specimens) <- list(NULL, NULL, id)

# === Define missing landmarks manually === #
setNA <- specimens

# Manual NA assignment for fossils
setNA[c(1,2,3,6,9,10,11,12,13,14,15,17,19,21,22,23,24,25,26,27,28,29,30,32,34,35,36), ,
"BHL05"] <- NA
setNA[c(1,2,3,4,5,9,10,11,12,13,14,15,16,17,19,21,22,24,25,26,27,28,32), , "BHL02"] <- NA

# === Fix missing landmarks using TPS (if any missing) === #
setNA[c(4,6,17,20,23,27,30,35), , "SKP04"] <- NA
setNA[(33), , "STR01"] <- NA
setNA[c(6,27,28,33), , "Su134843"] <- NA
setNA[(13), , "Bor3505"] <- NA
setNA[c(9,10,32), , "Day6208"] <- NA
setNA[c(5,32), , "Sop9733"] <- NA

# Fix the missing landmarks using TPS
DataTPS <- fixLMtps(setNA, comp = 7, weight = TRUE)
gpa_common <- procSym(DataTPS$out)
DataTPS$out
DataNA <- as.array(DataTPS$out)

# === Find common landmarks between BHL02 and BHL05 === #
lm_bhl02 <- which(!is.na(setNA[,1,"BHL02"]))
lm_bhl05 <- which(!is.na(setNA[,1,"BHL05"]))
common_lm <- intersect(lm_bhl02, lm_bhl05)

cat("Total common landmarks:", length(common_lm), "\n")
cat("The same landmarks are available in BHL02 and BHL05:\n")
print(common_lm)

# === Subset all specimens based on common landmarks === #
specimens_common <- DataTPS$out[common_lm, , , drop = FALSE]

##Test on a 3D mesh with only 6 common landmarks
setwd("C:/NASUTION/DEVI TESSINA/R STUDIO ANALYSIS/SKULL + BHL + SKP04 + STR01 (.PLY)")
```

```

ref <- file2mesh("Jav0957.ply")
shade3d(ref,color="beige",rglopen=T) #1a visualizzo
#you need to save the meshes in ply with modified position in morphodig
spheres3d(specimens[common_lm, "Jav0957"], col = "red", radius = 3);rgl::rglwidget()
text3d(specimens[common_lm, "Jav0957"], texts = common_lm, adj = c(1.2, 1.2), cex = 1.2)

# === Run GPA and PCA === #
gpa_common <- procSym(specimens_common)

# === Plot PCA (PC1 vs PC2) === #
group <- as.factor(substr(id,1,3))
col.gp <- pal_igv("default")(length(levels(group)))
names(col.gp) <- levels(group)
col.gp <- col.gp[match(group, names(col.gp))]

xlab <- paste("PC1 (", round(gpa_common$Variance[1,2],2), "%)", sep="")
ylab <- paste("PC2 (", round(gpa_common$Variance[2,2],2), "%)", sep="")
zlab <- paste("PC3 (", round(gpa_common$Variance[3,2],2), "%)", sep="")

# === PC1 PC2 === #
x11()
plot(gpa_common$PCscores[,1], gpa_common$PCscores[,2],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = xlab, ylab = ylab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,1], gpa_common$PCscores[,2],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("bottomleft", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Su1")
mat<-gpa_common$PCscores[sel,c(PCx,PCy)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === PC1 PC3 === #

```

```

x11()
plot(gpa_common$PCscores[,1], gpa_common$PCscores[,3],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = xlab, ylab = zlab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,1], gpa_common$PCscores[,3],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("topright", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Su1")
mat<-gpa_common$PCscores[sel,c(PCx,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === PC2 PC3 === #
x11()
plot(gpa_common$PCscores[,2], gpa_common$PCscores[,3],
     pch = 21, col = col.gp, bg = col.gp,
     xlab = ylab, ylab = zlab, asp = 1, cex = 1.2)
text(gpa_common$PCscores[,2], gpa_common$PCscores[,3],
     labels = id, pos = 3, cex = 0.6)
abline(h = 0, v = 0, lty=2, col="gray")
legend("topleft", legend=levels(group), pch=21, pt.bg=unique(col.gp), col=unique(col.gp),
      bty="n", cex=0.7)

PCx<-1
PCy<-2
PCz<-3
sel<-which(group=="Bug") # select the group "Bug"
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[3],alpha.f=0.2),border=unique(col.gp)[3]) #assigning
the 2nd color corresponding to Bug color

sel<-which(group=="Day")

```

```

mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[4],alpha.f=0.2),border=unique(col.gp)[4])

sel<-which(group=="Jav")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[5],alpha.f=0.2),border=unique(col.gp)[5])

sel<-which(group=="JMa")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[6],alpha.f=0.2),border=unique(col.gp)[6])

sel<-which(group=="Sul")
mat<-gpa_common$PCscores[sel,c(PCy,PCz)]
conv<-chull(mat)
polygon(mat[c(conv,conv[1]),],
        col=adjustcolor(unique(col.gp)[9],alpha.f=0.2),border=unique(col.gp)[9])

# === 7. Calculate and show Procrustes distance between BHL02 and BHL05 === #
fossil_pair <- specimens_common[,c("BHL02","BHL05")]
proc_dist <- sqrt(sum((fossil_pair[,1] - fossil_pair[,2])^2))
cat("Procrustes Distance between BHL02 and BHL05:", round(proc_dist, 4), "\n")

```