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Research Article

Mandibular Characteristics to Determine Quaternary Proboscideans of Indonesia

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ABSTRACT
Proboscideans (order Proboscidea) are a group of mammals known for their distinctive proboscis or trunk. During the Pleistocene Epoch, proboscideans thrived globally, including the Indonesian Archipelago. Most taxonomic determination for proboscidean fossils primarily relies on molar analysis. Mandible analysis for determining Quaternary proboscidean taxa in Indonesia is still rarely utilized, despite its potential for taxonomic identification. Therefore, this research aims to identify the diagnostic characters of Quaternary proboscideans found in Indonesia based on their mandibular characteristics. Quantitative morphometrical analysis and qualitative morphological observations were conducted in determining the diagnostic characters of each taxon. Mandible specimens of modern Asian elephant (*Elephas maximus*) were also used as a comparison to fossil specimens. The values obtained by morphometric measurements were then analyzed using the Principal Component Analysis (PCA) method in PAST 4.12b. In addition, qualitative morphological characters obtained were described to further support the PCA results. The results showed that the mandibles of each taxon observed have their own distinguishable characteristics, thus can be used to determine the taxa of Quaternary proboscideans found in Indonesia.

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INTRODUCTION

Proboscideans (order Proboscidea) are commonly known by their distinctive proboscis or trunk. Today, this order is represented solely by the family Elephantidae, which includes three extant species. They are: Asian elephant (*Elephas maximus*), African savanna elephant (*Loxodonta africana*), and African forest elephant (*L. cyclotis*). Currently, the African savanna elephant and Asian elephant are considered endangered by the IUCN, while the African forest elephant is considered as critically endangered. Their populations are facing significant threats from habitat loss and fragmentation, poaching, wildlife trade, and human-elephant conflict (Riddle et al. 2010; Hammond et al. 2022; Sukmasuang et al. 2024).

During the Pleistocene Epoch, approximately 2.6 million to 11,700 years ago, large bodied mammals (megafauna) were widespread across the globe (Carlton 2019). Within the Indonesian Archipelago, fossil evidence dating back to the Pleistocene has revealed a diverse assemblage of megafauna, including giant tortoises, buffalos, hippopotamuses, tigers, hyenas, and giant pangolins (van den Bergh et al. 2001; Setiyabudi 2016). During this period, proboscideans also shaped the biodiversity of megafauna in the region. According to Wibowo et al. (2015), there are six genera of proboscideans from Pleistocene Indonesia: *Sinomastodon*, *Palaeoloxodon*, *Stegolophodon*, *Stegoloxodon*, *Stegodon*, and *Elephas*, with at least 14 described species. However, in the present day, only two proboscideans can be found in Indonesia: the Sumatran elephant (*E. m. sumatranus*) and a very small population of Bornean elephant (*E. m. borneensis*) in North Kalimantan (Riddle et al. 2010; Sharma et al. 2018; Feldhamer 2020).

The taxonomic determination of most extinct mammalian taxa primarily relies on cranial analysis, especially the teeth (Prothero & Williams 2017). Proboscideans have a unique type of molar termed lophodont (Feldhamer 2020). However, there are some differences and variations among the molars of proboscideans. The molars of three proboscidean families found in the Indonesian Archipelago each have their own characteristics. Gomphotheriidae members are characterized by low-crowned molars (brachyodont) with blunt and conical cusps arranged in transverse rows (lophs for upper molars; lophids for lower molars), termed as bunolophodont. Stegodontidae and Elephantidae members are characterized by lophodont molars in which the cusps and loph(id)s multiplied along with the thinning of the enamel to form more incised ridges. The difference between the two latter families is in their crown height. Elephantidae members evolved to have a heightened tooth crown, termed hypsodont, whereas Stegodontidae members retained the brachyodonty of gomphotheres (Zhang et al. 2017). Besides their crown height (hypsodonty), the increasing number of lophs is also a general indicator of more modern or progressive taxa (Sukumar 2003).

Proboscidean mandibles have been used to analyze their diets and feeding adaptations, mastication mechanisms, and evolutionary history (Todd 2010; Ferretti & Debruyne 2011; von Koenigswald 2016; Li et al. 2023). From a taxonomic perspective, the mandible could be a potential component in determining proboscidean taxa. Todd (2010) analyzed the mandibles of the three extant species from both sexes and found some characteristics that could be used as diagnostic characters. For Indonesian specimens, several mandibular characteristics of extinct proboscideans from Java, the Lesser Sunda Islands, and Sulawesi have been described by van den Bergh (1999). However, there is still no identification key on mandible specimens for Quaternary proboscideans of Indonesia. Identification through analyzing mandibular characteristics is also rarely conducted, despite the substantial number of specimens found at various paleontological sites in Indonesia. Therefore, this research aims to identify the diagnostic characters of Quaternary proboscideans in Indonesia based on their mandibular characteristics through quantitative morphometrical analysis and qualitative morphological observation. These diagnostic characters were then made into an identification key that could be used as a practical guide, alternative to molar analysis.

MATERIALS AND METHODS

Materials

In this study, we examined 21 proboscidean mandibles from five institutions: Museum of Biology, Universitas Gadjah Mada (MB-UGM); Laboratory of Bioanthropology and Palaeoanthropology, Faculty of Medicine, Public Health, and Nursing, Universitas Gadjah Mada (LBP-UGM); Laboratory of Mammals Biosystematics, Museum Zoologicum Bogoriense, National Research and Innovation Agency (MZB-BRIN); Bandung Geological Museum (MGB); and Sangiran Early Man Museum (MMPS). We analyzed the mandibles of the modern Asian elephant (*Elephas maximus*; n=8), *Elephas hysudrindicus* (n=1), *Sinomastodon bumiajuensis* (n=1), *Stegodon elephantoides* (n=1), *Stegodon trigonocephalus* (n=1), *Stegodon florensis* (n=2), *Stegodon sondaari* (n=1), *Elephas* sp. from Sangiran (n=1), and *Stegodon* sp. from Sangiran (n=5). The specimens used in this study were in a complete or near-complete condition from approximately the same age. The age estimation analysis was based on the research by Lee et al. (2011) on African savanna elephant (*Loxodonta africana*) age determination from their mandibular teeth.

Two specimens were treated as an exception in the qualitative morphological observation, namely *Elephas hysudrindicus* (EH) and *Stegodon florensis* (SF2), as both specimens had been reconstructed because of their damaged condition. The EH mandible underwent extensive reconstruction, leaving the teeth as the main visible part of the original fossil. The reconstruction itself was based on a Sumatran elephant (*Elephas maximus sumatranus*) specimen (U. P. Wibowo, personal communication, January 8, 2024). Additionally, the SF2 mandible underwent reconstruction as well, particularly on the posterior part of the mandibular ramus. Therefore, the morphological characteristics of both specimens could not be observed, since their original morphology had been altered by the reconstruction process.

Methods

The methods used in this study were quantitative morphometrical analysis based on van den Bergh (1999) with the addition of one new parameter in the form of a ratio (see parameter M26 in Table 1) and qualitative morphological observation. The morphometrical data were then analyzed using Principal Component Analysis (PCA) in PAST 4.12b. PCA was used to figure out specimens grouping and determine characters that could potentially be used as diagnostic characters. The qualitative data obtained from morphological observation was not included inside the PCA and treated separately as descriptive characters. Morphological observation was conducted on the angle between the mandibular ramus and the mandibular corpus, the orientation of mandibular condyles from lateral view, the shape of the mandibular condyles, and the curvature of the mandibular notch. The dominant mandibular characteristics for each taxon, obtained from both PCA and morphological observation, were then compiled to create a dichotomous key for a more practical identification guide.

RESULTS AND DISCUSSION

PCA Results on the Mandibles

Morphometrical parameters could be easily measured on complete and undamaged specimens. However, several specimens in this study were damaged or incomplete, preventing several parameters from being measured. Based on

Table 1. Morphometrical parameters used to determine the diagnostic characters of the mandibles.

No.	Code	Characters
Parameters based on van den Bergh (1999)		
1.	M1	Maximum length of the mandible in a plane defined by the basal points of support and parallel to the median plane
2.	M2	Total height of the mandible perpendicular to its basal plane
3.	M3	Total length of the mandibular ramus
4.	M4	Height between the basal plane and the coronoid apophyses
5.	M5	Height of the mandibular corpus measured at the level of the anterior border of the dental alveoli
6.	M6	Height of the mandibular corpus measured at the level of the anterior onset of the mandibular ramus
7.	M7	Length of the interalveolar crest
8.	M8	Height between the inferior border of the mandibular foramen and the base of the mandibular condyle
9.	M9	Horizontal distance of the mandibular ramus posteriorly of the posterior border of the mandibular condyle
10.	M11	Maximum width of the mandible measured between the external borders of the condyles
11.	M12	Width between the internal borders of the condyles
12.	M13	Largest (transverse) diameter of the condyle
13.	M14	Smallest (antero-posterior) diameter of the condyle
14.	M15	Width of the mandible at the level of the onset of the mandibular ramus
15.	M16	Width of the mandible between the external borders of the coronoid apophyses
16.	M17	Distance separating the internal borders of the mandibular corpus at the level of the onset of the mandibular ramus
17.	M18	Maximum transverse diameter of the mandibular corpus
18.	M19	Distance separating the internal borders of the mandibular corpus at the level of the anterior border of the dental alveoli
19.	M20	Minimum transverse diameter of the mandibular corpus
20.	M21	Antero-posterior length of the mandibular symphysis
21.	M22	Distance between the superior terminations of the interalveolar crests
22.	M23	Minimum distance between the internal borders of the mandibular corpus
23.	M24	Length of the occlusal wear surface
24.	M25	Maximum width of the occlusal wear surface
Parameter added in this study		
25.	M26	Ratio between the maximum width of the mandible (M11) against the maximum length of the mandible (M1)

the observation, the most frequently damaged parts were the tip of the mandibular symphysis, the mandibular condyles, the coronoid process, the mandibular ramus, and the anterior part of the molars. Because of that, parameters associated with the parts mentioned could not be measured thoroughly on several specimens. Therefore, the PCA method used in this study should minimize the effects of incomplete measurements data when analyzing the potential diagnostic characters and grouping the specimens to their respective taxa.

The PCA method produced a total variance value of 82.316 % from the sum of Principal Component 1 (PC1=71.258 %) and Principal Component 2 (PC2=11.058 %). The value of each Principal Component (PC) can be seen in Table 2. Furthermore, all morphometrical parameters, except for M9, were positively correlated with PC1, indicating a size-based grouping along the x-axis (see Figure 1). The grouping of specimens along the y-axis was potentially based on four significant parameters within PC2: M6, M12, M20, and M26 (see Figure 2). This is because the loading values of those parameters were either above +0.5 (M12 and M26) or below -0.5 (M6 and M20).

Based on the x-axis (PC1) in Figure 3, *Stegodon sondaari*, the smallest specimen observed, was placed on the far-left side of the x-axis. Meanwhile, *Stegodon elephantoides*, the largest specimen observed, was placed on the far-right side of the x-axis. In the middle, there are specimens of medium sizes: *Elephas maximus*, *Stegodon trigonocephalus*, *Elephas* sp. from Sangiran, and *Stegodon* sp. from Sangiran. Therefore, the x-axis reflects the size differences among the observed specimens (see Figure 4 for size comparison of each taxon). On the y-axis (PC2), the *Stegodon-Sinomastodon* group was placed on the more positive axis, while the *Elephas* group was placed on the more negative axis. As mentioned before, the grouping of specimens along the y-axis was potentially influenced by parameters M6, M12, M20, and M26.

Table 2. Eigenvalue and % Variance for all Principal Components.

PC	Eigenvalue	% Variance
1	17.8144	71.258
2	2.76451	11.058
3	1.50689	6.0276
4	1.09713	4.3885
5	0.863605	3.4544
6	0.647223	2.5889
7	0.218398	0.87359
8	0.0878436	0.35137

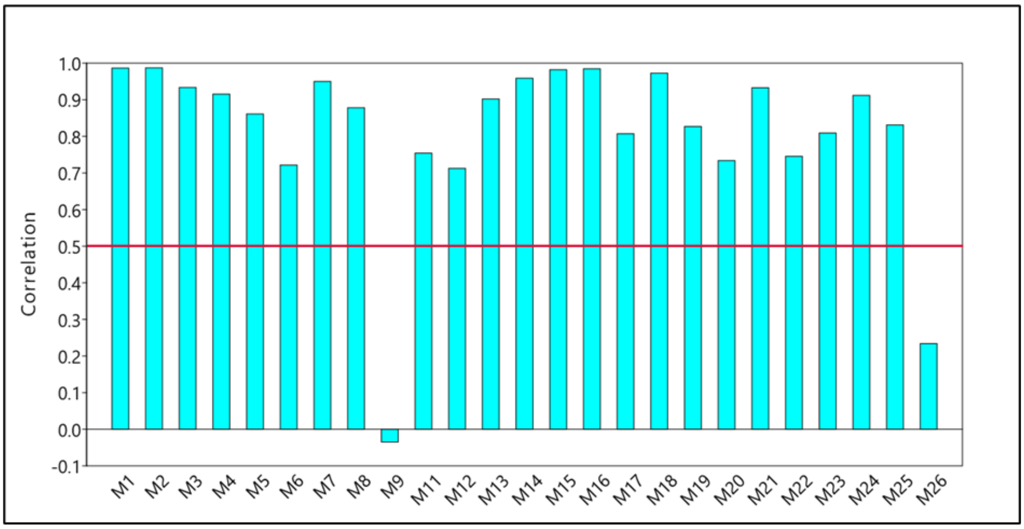

Figure 1. Loading plots of PC1. The red line marks the threshold at +0.5.

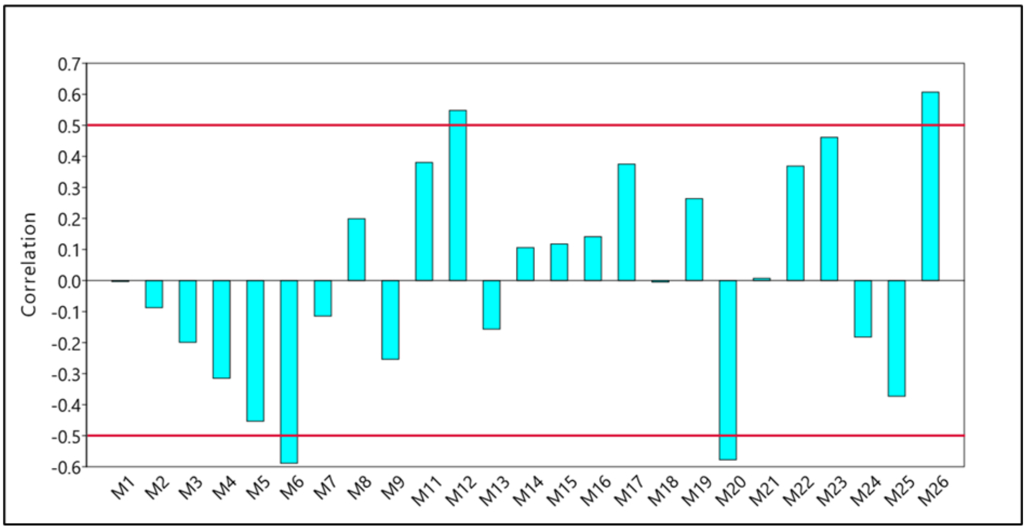

Figure 2. Loading plots of PC2. The red lines mark the threshold at +0.5 (upper) and -0.5 (lower).

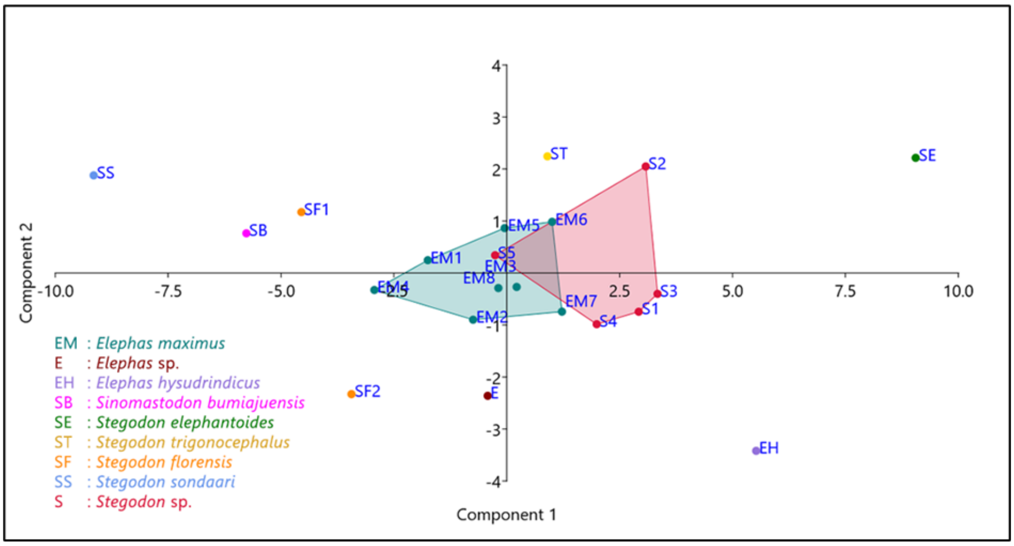

Figure 3. PCA results on the measured mandibles.

Mandibular Characteristics of Each Taxon

The *Stegodon-Sinomastodon* group in the PCA was characterized by a more positive correlation to M12 (width between the internal borders of the condyles) and M26 (ratio between the maximum width of the mandible (M11) against the maximum length of the mandible (M1)). From the dorsal view, the genus *Stegodon* has a wider mandible appearance compared to the genus *Elephas* or *Sinomastodon*. Therefore, increasing the measurement values of M12 and M26. Mandibles from the genus *Elephas* have an intermediate distance between the internal borders of the condyles when compared to the other two genera. Meanwhile, the only specimen of *Sinomastodon* mandible was missing its left condyle. Through shape and size estimation based on the right condyle, the *Sinomastodon* mandible likely has a shorter distance between the internal borders of the condyles than *Stegodon* or *Elephas*. Therefore, based on parameter M12, the distance between the internal borders of the condyles from smallest to largest, is as follows: *Sinomastodon*, *Elephas*, and *Stegodon* (see Figure 5).

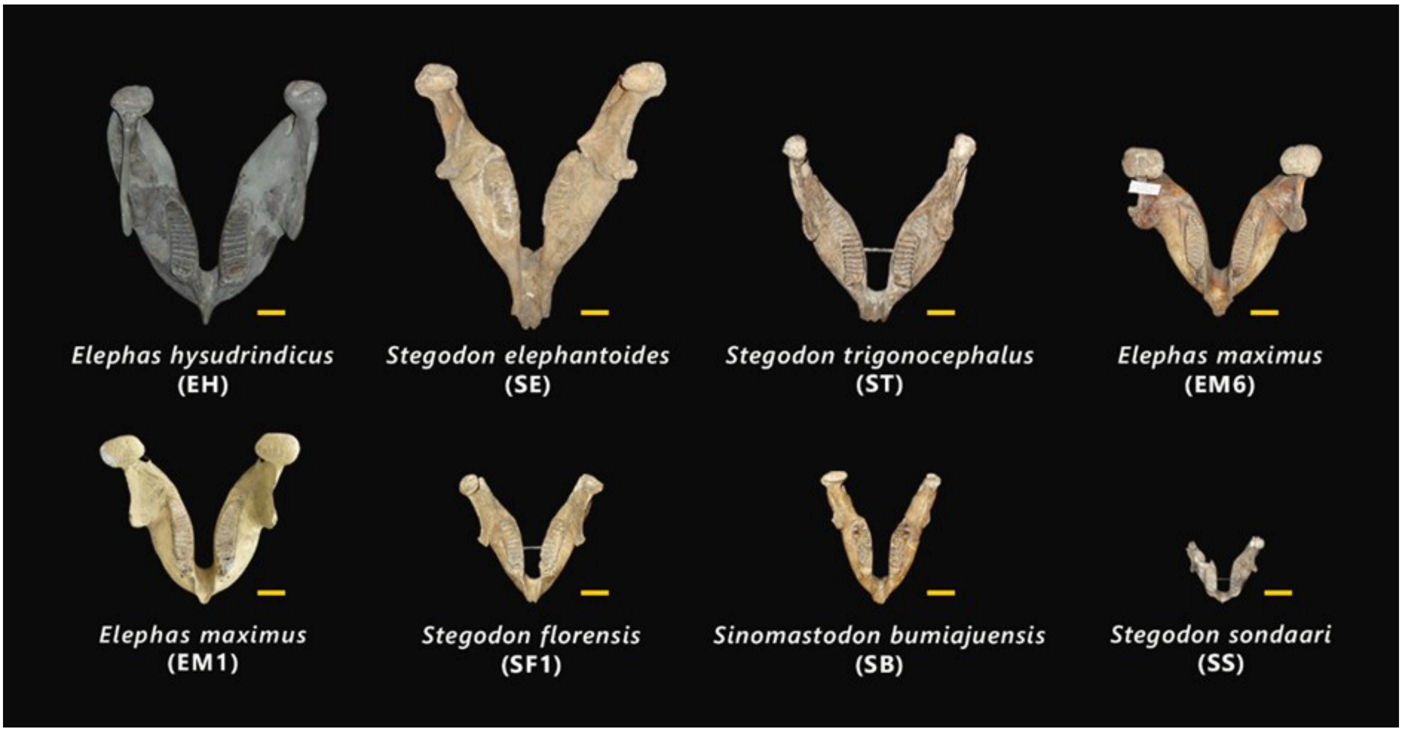

Figure 4. Dorsal view of the Quaternary proboscidean taxa observed in this study, represented by eight specimens. Scale bars: 10 cm.

The *Elephas* group in the PCA was characterized by a more positive correlation to M6 (height of the mandibular corpus measured at the level of the anterior onset of the mandibular ramus) and M20 (minimum transverse diameter of the mandibular corpus). Both parameters were potentially influenced by their molar type. As previously stated, members of the family Elephantidae, such as *Elephas*, possess high-crowned molars or hypsodont. To accommodate this feature, the Elephantidae members likely evolved a higher mandibular corpus, indicated by a positive correlation with parameter M6. In contrast to *Elephas*, *Stegodon* and *Sinomastodon* still possess low-crowned molars (brachyodont), which resulted in smaller M6 values. In addition, the buccal side of the mandibular corpus in the genus *Elephas* have a more “swollen” appearance than *Stegodon* and *Sinomastodon* specimens. This characteristic likely caused the M20 values of *Elephas* mandibles to be higher than the other two genera.

In this study, qualitative morphological observations were also conducted to determine other characters that could distinguish the mandibles of each taxon apart from the morphometrical parameters. The results showed that there are several characters that could be used to distinguish the mandible of Quaternary proboscideans of Indonesia at the genus level, namely the angle between the mandibular ramus and the mandibular corpus, the orientation of the mandibular condyles from lateral view, the shape of the mandibular condyles, and the curvature of the mandibular notch.

Measurement of the angle between the mandibular ramus and the mandibular corpus was done by drawing the horizontal line parallel to the molar surface and the vertical line along the direction of the masseteric fossa. From these measurements, the angle of *Elephas* mandibles tends to be at ± 90° (right angle). Meanwhile, the genus *Stegodon* has a mandibular angle of ± 100°. The genus *Sinomastodon* showed the highest value of mandibular angle, which is 113.6° (Figure 6). These characters were also mentioned by van den Bergh (1999), who stated that the genus *Stegodon* has a wider mandibular angle than the genus *Elephas*. However, the publication did not mention the an-

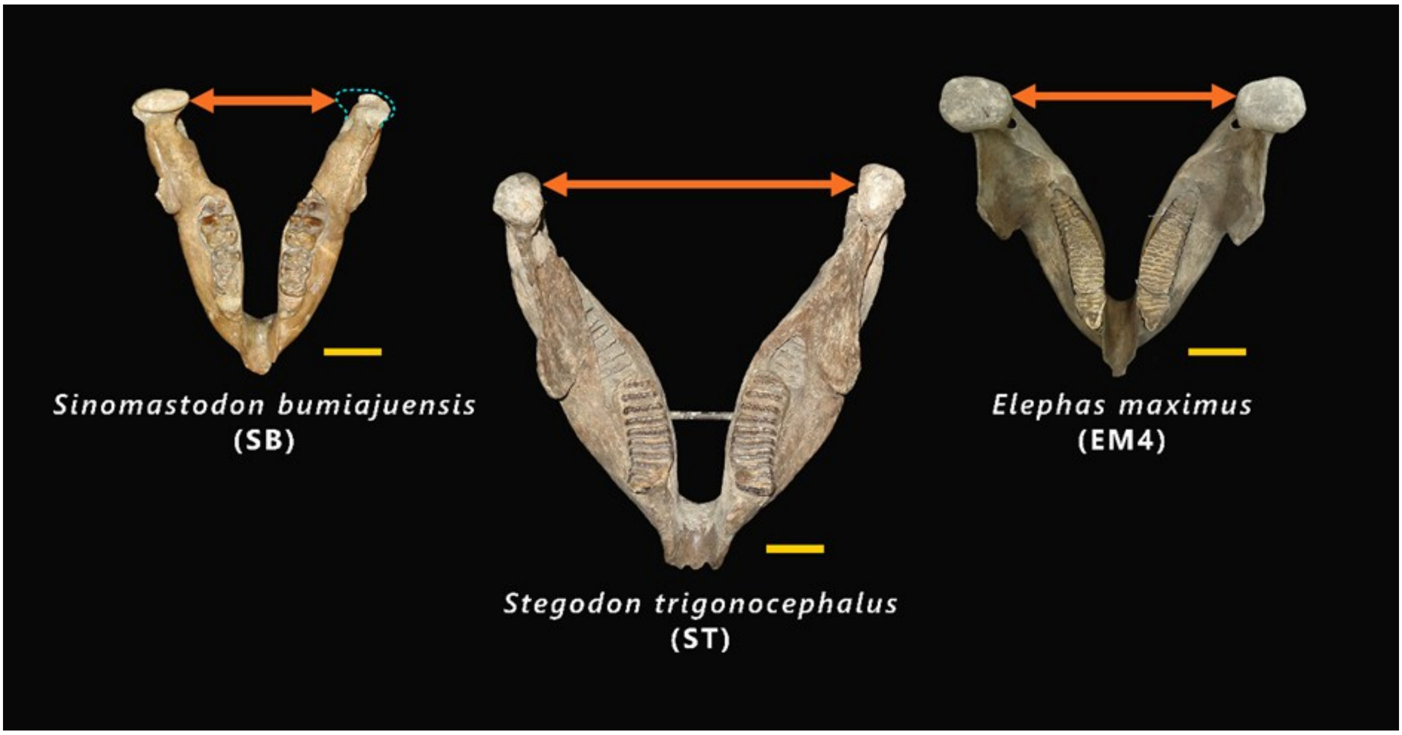

Figure 5. Dorsal view between the three genera of proboscideans found in Indonesia, represented by *Sinomastodon bumiajuensis*, *Stegodon trigonocephalus*, and *Elephas maximus*. The cyan dashed line on specimen SB is an estimation for the missing left condyle, while the orange lines in the three specimens illustrate the measurement of parameter M12. Scale bars: 10 cm.

gle value of those mandibles, nor the mandibular angle of the genus *Sinomastodon*. Therefore, this study provides new insights for the mandibular angle of Quaternary proboscideans found in Indonesia.

The orientation of the mandibular condyles also differs between the *Stegodon-Sinomastodon* group and the *Elephas* group. In Figure 6, the mandibular condyles of *Stegodon* and *Sinomastodon* face straight upwards. Meanwhile, the mandibular condyles of the genus *Elephas* tilt slightly to the anterior side. The shape of the mandibular condyles from each genus also showed differences. In the genus *Sinomastodon*, the condyle is rather oval and flattened antero-posteriorly. The genus *Stegodon* possesses condyles that are generally circular or oval. In dwarf stegodonts, namely *Stegodon florensis* and *S. sondaari*, the condyles tend to be slightly more circular than stegodonts from Java. The condyles of *Stegodon trigonocephalus* and *Stegodon* sp. from Sangiran showed a variety of shapes, such as rectangular (latero-medial) with blunt corners or oval. However, due to the majority of the condyles being damaged, the shape of the condyles for *Stegodon trigonocephalus* and *Stegodon* sp. from Sangiran could not be certainly determined. In *Stegodon elephantoides*, the condyles are relatively oval and antero-posteriorly wider than the condyle of *Sinomastodon bumiajuensis*. The condyles of the genus *Elephas* share a similar shape with those of a *Stegodon* sp. from Sangiran (S3), being rectangular (latero-medial) with blunt corners. However, the condyles of the genus *Stegodon* tend to be antero-posteriorly wider on the lingual side. In the genus *Elephas*, the condyles tend to be antero-posteriorly wider on the buccal side. The shape differences of the condyles between the three genera can be seen in Figure 7.

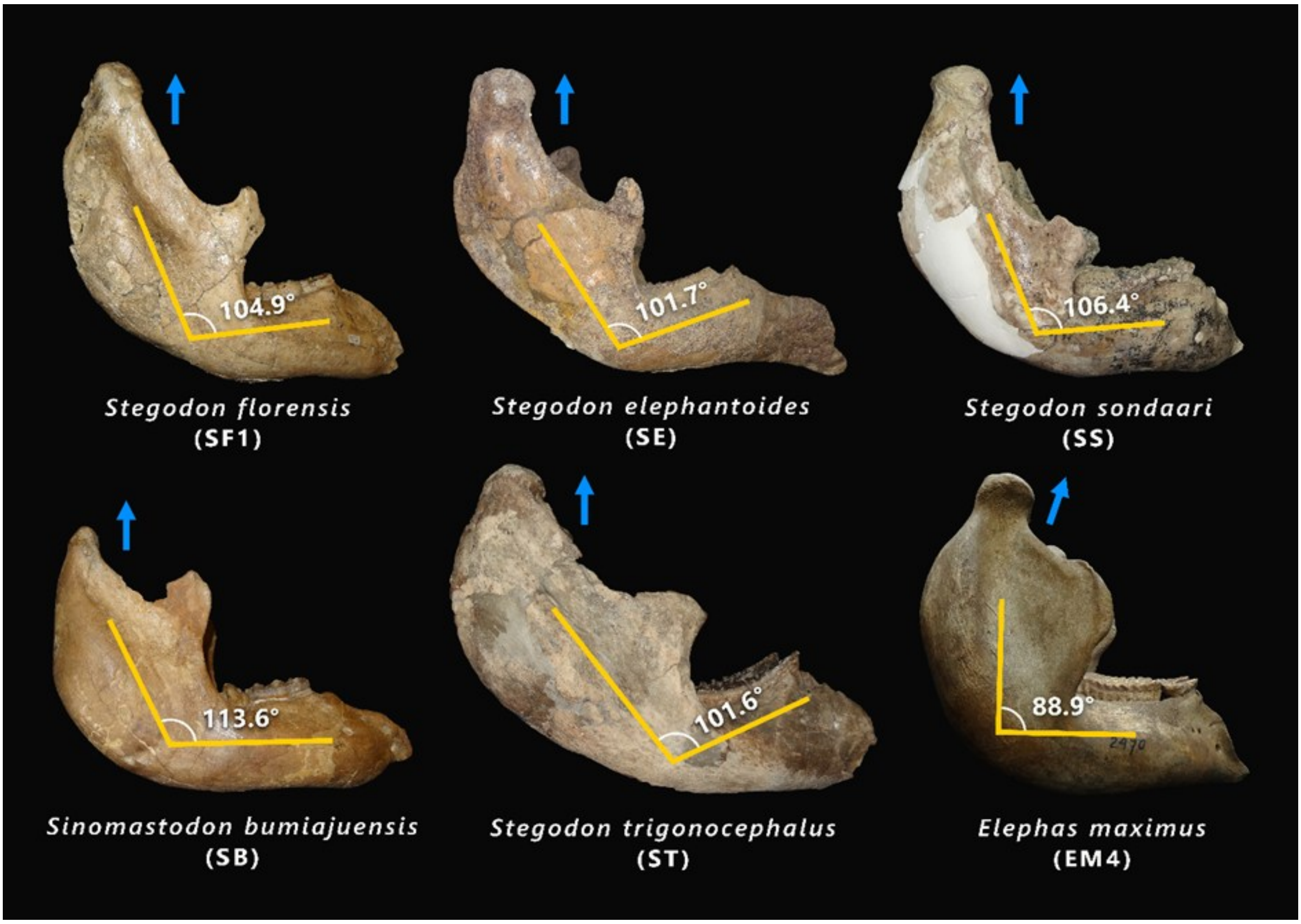

Figure 6. Mandibular angle (yellow lines) and mandibular condyles orientation (blue arrows) of six Quaternary proboscideans observed in this study. In specimens SE and SS, the photos used are of the flipped left buccal side due to the incomplete right buccal side. Specimens are not to scale.

The next observed characters of the genera were the curvature of the mandibular notch, which is the groove between the condylar process and the coronoid process (Figure 8). The genus *Sinomastodon* has a short curve and slightly curved upwards at the tip of the coronoid process. In the genus *Stegodon*, the curve tends to be longer. The direction of the curve at the tip of the coronoid process in the genus *Stegodon* also showed variations. In *Stegodon trigonocephalus*, the curve points directly to the anterior side, while in *S. elephantoides*, *S. sondaari*, and *S. florensis*, the curve points upwards and tends to form a "hook". Several specimens of *Stegodon* sp. from Sangiran (S1, S2, S3, and S4) also showed variations between the two forms. Meanwhile, the curve in the genus *Elephas* is short and tends to curve directly to the anterior side. Although most members of the genus *Stegodon* possess a "hook-shaped" coronoid process, one modern *Elephas maximus* specimen (EM6) also has this character (Figure 9). Therefore, the "hook" shape of the coronoid process most likely could not be used as a distinguishing characteristic between the genera.

The characters mentioned above can already be used to distinguish *Sinomastodon bumiajuensis* and *Elephas maximus*. However, further descriptions are needed to confirm the diagnostic characters of the genus *Stegodon* at the species level due to its diversity. Based on our morphological observations on four species of the genus *Stegodon*, characters that can be used as diagnostic characters are the mandibular symphysis and specimen size.

According to van den Bergh (1999), the mandible of *Stegodon elephantoides* is very distinctive and can be distinguished from other members of the genus *Stegodon* by its elongated and downward-curved mandibular symphysis. *Stegodon elephantoides* is also suspected to be the largest *Stegodon* species found in Indonesia (van den Bergh 1999). In contrast, *S. sondaari* is the smallest member of the genus *Stegodon* discovered in Indonesia to date (van den Bergh 1999; van den Bergh et al. 2008; Meijer et al. 2010). Additionally, van den

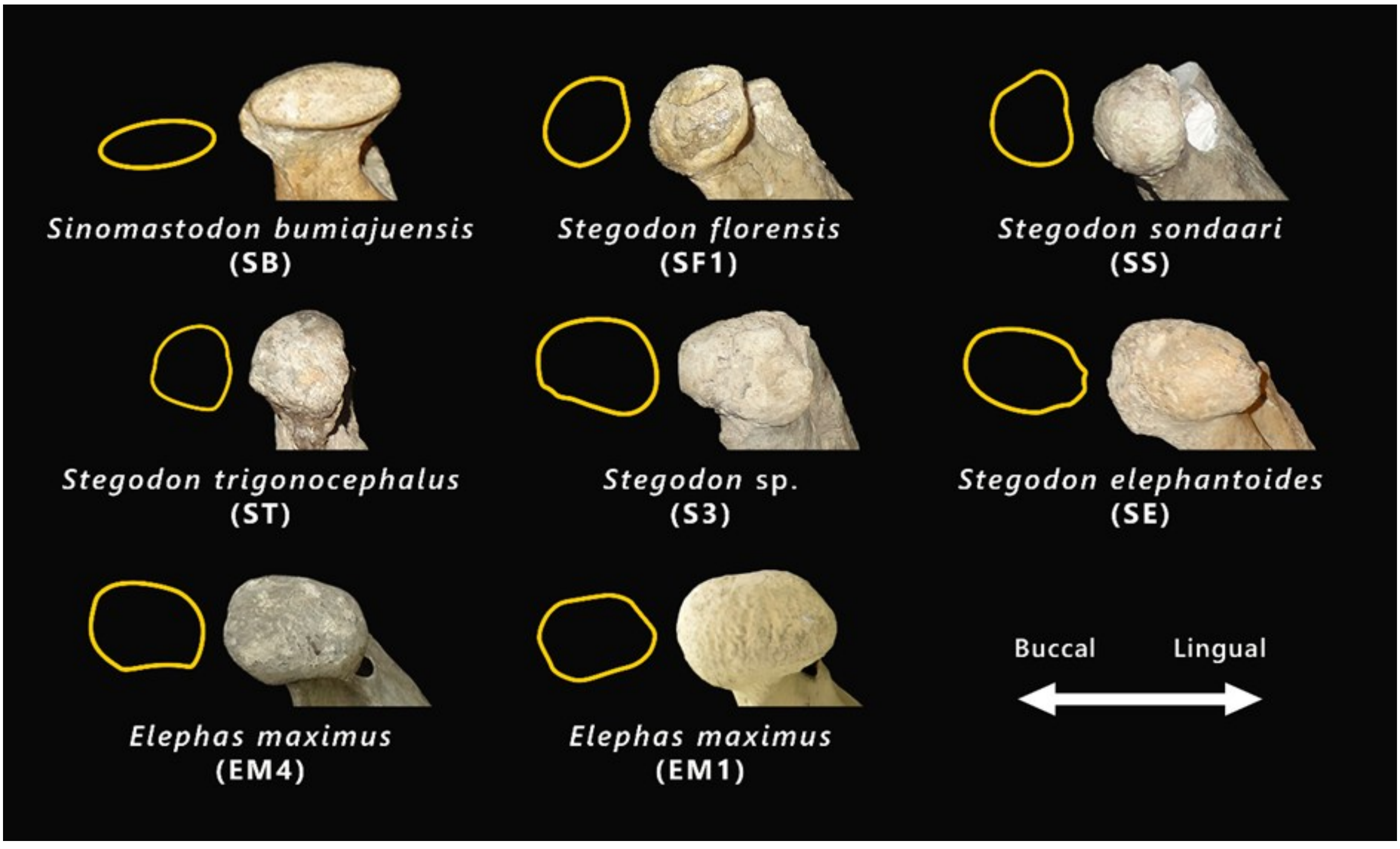

Figure 7. The shape of the mandibular condyles of six Quaternary proboscideans observed in this study. In specimens SS, SE, and EM1, the photos used are of the flipped left condyle due to the damaged right condyle. Specimens are not to scale.

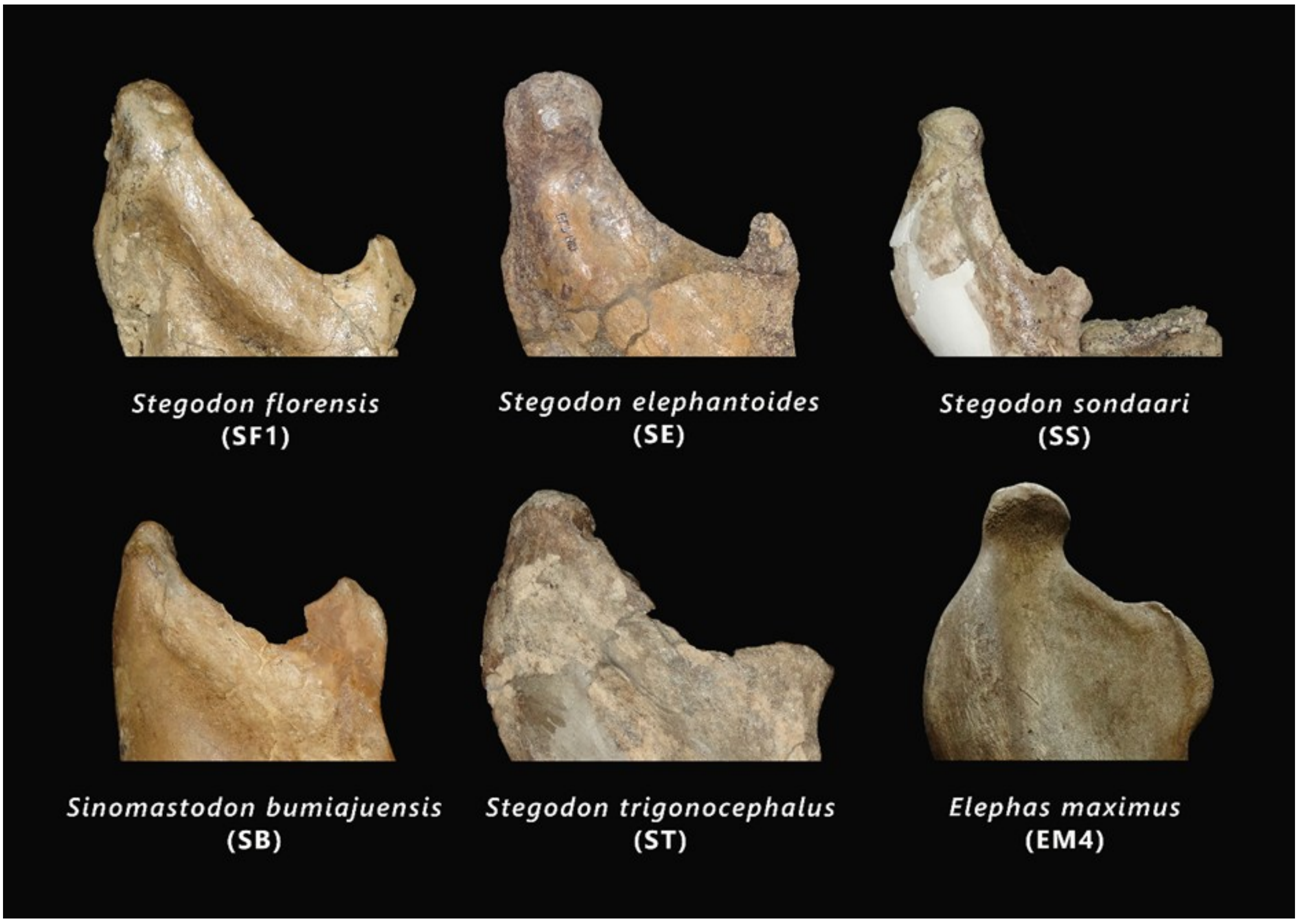

Figure 8. The curvature of the mandibular notch of six Quaternary proboscideans observed in this study. Specimens are not to scale.

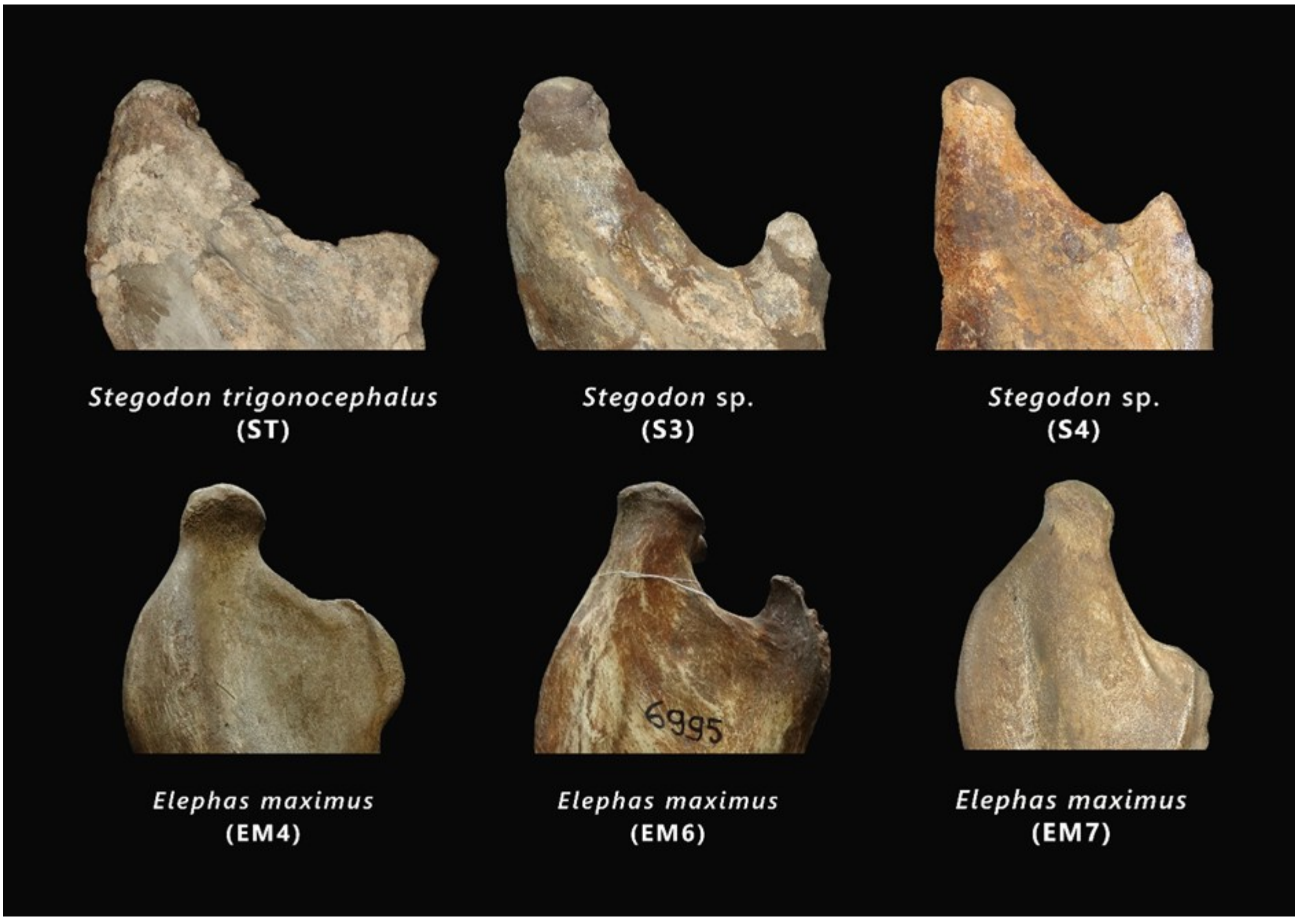

Figure 9. Variations on the curvature of the mandibular notch in *Stegodon trigonocephalus*, *Stegodon* sp. from Sangiran, and *Elephas maximus* observed in this study. Specimens are not to scale.

Bergh (1999) stated that the mandibular symphysis of *S. sondaari* is very short, since its anterior border is located right in between the anterior border of the alveoli, lacking the protrusion observed in other *Stegodon* species.

The mandibles of the last two members of the genus *Stegodon* in this study, namely *S. trigonocephalus* (including *Stegodon* sp. from Sangiran) and *S. florensis*, were difficult to distinguish, except for their size. Based on the observation, both species have a relatively short mandibular symphysis with a small protrusion to the anterior side, as stated in van den Bergh (1999). However, *S. florensis* is smaller than *S. trigonocephalus*, particularly *S. t. trigonocephalus*, at the same age range (van den Bergh 1999; van den Bergh et al. 2008). The smaller body size of *S. florensis* was the result of insular dwarfism, although not to the extreme degree as *S. sondaari*. When comparing the two species, it is important to ensure that the specimens belong to the same age range. Therefore, it is necessary to examine the molar characters first to determine their relative ages before comparing the size of the mandibles.

Diagnostic Characters of the Mandibles for Each Taxon

Based on the quantitative morphometrical measurements and qualitative morphological observations that have been conducted, it can be concluded that there are several characters which can be used as diagnostic characters of the mandibles for Quaternary proboscideans found in Indonesia. The characters can be seen in Table 3.

Based on the diagnostic characters in Table 3, we constructed a dichotomous key for a more efficient way in identifying Quaternary proboscideans of Indonesia. Since all the materials in this study were from complete or near-complete specimens, the dichotomous key is best be applied to specimens with similar conditions.

Table 3. List of mandibular diagnostic characters for each taxon observed in this study.

No.	Character	**Gomphotheriidae**	**Stegodontidae**				**Elephantidae**
		Sinomastodon bumiajuensis	***Stegodon elephantoides***	***Stegodon trigonocephalus* and *Stegodon* sp. (Sangiran)**	***Stegodon florensis***	***Stegodon sondaari***	***Elephas maximus***
1.	The size of the mandible in general	Small	Very large	Medium to Large	Small	Very small	Medium
2.	The width of the mandible	Narrow	Wide	Wide	Wide	Wide	Intermediate
3.	The height of the mandibular corpus	Low	Low	Low	Low	Low	High
4.	The angle between the mandibular ramus and the mandibular corpus	Blunt angle (±110°)	Blunt angle (±100°)	Blunt angle (±100°)	Blunt angle (±100°)	Blunt angle (±100°)	Right angle (±90°)

Table 3. Contd.

No.	Character	Gomphotheriidae	Stegodontidae				Elephantidae
		Sinomastodon bumiajuensis	***Stegodon elephantoides***	***Stegodon trigonocephalus* and *Stegodon* sp. (Sangiran)**	***Stegodon florensis***	***Stegodon sondaari***	***Elephas maximus***
5.	The orientation of the mandibular condyles from lateral view	Straight upwards	Straight upwards	Straight upwards	Straight upwards	Straight upwards	Tilt slightly to the anterior side
6.	The shape of the mandibular condyles	Oval and flattened antero-posteriorly	Oval and relativelywide antero-posteriorly	Rectangular (latero-medially) with blunt corners (antero-posteriorly wider at the lingual side), relatively circular or oval	Relatively circular	Relatively circular	Rectangular (latero-medially) with blunt corners (antero-posteriorly wider at the buccal side)
7.	The curvature of the mandibular notch	Short	Long	Long	Long	Long	Short
8.	The mandibular symphysis	Short; small anteriorly protruding rostrum	Elongated; long anteriorly protruding and curved downward-cuved rostrum	Short; small anteriorly protruding rostrum	Short; small anteriorly protruding rostrum	Very short; no protruding rostrum	Short; small anteriorly protruding rostrum

Dichotomous Key to the Mandibles of Quaternary Proboscideans Found in Indonesia

1a. Narrow mandibular width; mandibular condyles oval and flattened antero-posteriorly...*Sinomastodon bumiajuensis* **(Gomphotheriidae)**

1b. Intermediate to wide mandibular width; mandibular condyles oval, circular, or rectangular (latero-medially) with blunt corners...***2***

2a. Blunt angle (±100°) between the mandibular ramus and the mandibular corpus; low mandibular corpus; long curve on the mandibular notch; mandibular condyles face straight upwards...***3* (Stegodontidae)**

2b. Right angle (±90°) between the mandibular ramus and the mandibular corpus; high mandibular corpus; short curve on the mandibular notch; mandibular condyles tilt slightly to the anterior side..***Elephas maximus* (Elephantidae)**

3a. Very small to small mandible size..**4**
3b. Medium to very large mandible size **5**

4a. Very short mandibular symphysis; no protruding rostrum...***Stegodon sondaari***
4b. Short mandibular symphysis; small anteriorly protruding rostrum...***Stegodon florensis***

5a. Elongated mandibular symphysis; long anteriorly protruding and downward-curved rostrum.........................***Stegodon elephantoides***
5b. Short mandibular symphysis; small anteriorly protruding rostrum.......................................***Stegodon trigonocephalus***

CONCLUSIONS

This research brings a novel approach to fossil identifications in Indonesia through mandible observations, especially for Quaternary proboscideans. Based on the results of this study, the diagnostic characters for identifying the mandibles of Quaternary proboscideans found in Indonesia are the size of the mandible in general, the width of the mandible, the height of the mandibular corpus, the angle between the mandibular ramus and the mandibular corpus, the orientation of the mandibular condyles from lateral view, the shape of the mandibular condyles, the curvature of the mandibular notch, and the mandibular symphysis. Further studies with more specimens from other proboscidean taxa not mentioned in this study are needed to make a complete identification key to all known Quaternary proboscideans from Indonesia and other parts of the world.

AUTHOR CONTRIBUTION

A.D.A. designed the research, collected and analyzed the data, and wrote the manuscript. D.S.Y. supervised the research process, proofread the manuscript, and gave advice during the research process.

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CONFLICT OF INTEREST

All authors declare that there is no conflict of interests.

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APPENDICES

Appendix 1. List of materials observed in this study. YO: years old; AEY: African Elephant Years.

No.	Taxa	Code	Institution	Collection Number	Bone/Fossil	Specimen's Age
	Family Elephantidae					
1	*Elephas maximus*	EM1	MB-UGM	-	Bone	29 YO
2	*Elephas maximus*	EM2	MGB	-	Bone	15 YO
3	*Elephas maximus*	EM3	MGB	VR. 2080801	Bone	47±2 AEY
4	*Elephas maximus*	EM4	MZB-BRIN	2470	Bone	26±2 AEY
5	*Elephas maximus*	EM5	MZB-BRIN	6989	Bone	26±2 AEY
6	*Elephas maximus*	EM6	MZB-BRIN	6995	Bone	47±2 AEY
7	*Elephas maximus*	EM7	MZB-BRIN	6990	Bone	28±2 AEY
8	*Elephas maximus*	EM8	MZB-BRIN	-	Bone	15± AEY
9	*Elephas* sp.	E	MMPS	ELP/1489/BPSMPS/2013	Fossil	47±2 AEY
10	*Elephas hysudrindicus*	EH	MGB	-	Fossil	49±2 AEY
	Family Stegodontidae					
11	*Stegodon elephantoides*	SE	MMPS	1487/ELP/BPSMPS/2013	Fossil	49±2 AEY
12	*Stegodon trigonocephalus*	ST	MGB	VR. 1070501/1070601	Fossil	28±2 AEY
13	*Stegodon florensis*	SF1	MGB	BL2012/T13/F562	Fossil	47±2 AEY
14	*Stegodon florensis*	SF2	MGB	MM2011/T24A/F174	Fossil	49±2 AEY
15	*Stegodon sondaari*	SS	MGB	TT2014/T1/F122-123	Fossil	47±2 AEY
16	*Stegodon* sp.	S1	MMPS	1195/ELP/BPSMPS	Fossil	45± AEY
17	*Stegodon* sp.	S2	MMPS	-	Fossil	45± AEY
18	*Stegodon* sp.	S3	MMPS	ELP/0293/BPSMPS/10	Fossil	47±2 AEY
19	*Stegodon* sp.	S4	MMPS	3234/ELP/BPSMPS/18	Fossil	70+ AEY
20	*Stegodon* sp.	S5	LBP-UGM	21409 (0101300)	Fossil	18±2 AEY
	Family Gomphotheriidae					
21	*Sinomastodon bumiajuensis*	SB	MGB	K.135	Fossil	18±2 AEY