



The Characters of The Hippopotamidae from Java (Indonesia) Based on Skull and Tooth Analyses

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Manuscript received: August, 23, 2024; revised: April, 21, 2025;
approved: December, 08, 2025; available online: April, 14, 2026

Abstract - Hippopotamidae are known to have lived in the island of Java based on the presence of their fossils. Several researchers have described and concluded that there are three species of Hippopotamidae in the island of Java, but there are also those who argue that the three types of Hippopotamidae are of the same species. These differences give rise to further discussion regarding what species lived in the island of Java in the past. Twenty Hippopotamidae fossil specimens including twelve specimens recently discovered, and previously undescribed specimens collected from stratigraphic context from Java were analyzed in this study and compared with previous literature. This study of Hippopotamidae fossils is based on skulls and teeth where the number of incisor teeth is one of the distinguishing characters which shows that all Hippopotamidae fossils in Java Island are from the genus *Hexaprotodon*. Our evidence shows that there are two types of *Hexaprotodon* in Java, namely the relatively small *Hexaprotodon* in The Gelasian-Calabrian-Chibanian Pleistocene, and a larger *Hexaprotodon* of Late Chibanian-Late Pleistocene age. Based on its anatomy, the small *Hexaprotodon* from Java is called *Hexaprotodon sivajavanicus*, while the large *Hexaprotodon* from Java is called *Hexaprotodon megakendengensis*

Keywords: fossil, Hippopotamidae, *Hexaprotodon*, Java

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How to cite this article:

Wibowo, U.P., Zaim, Y., Aswan, and Puspaningrum, M.R., 2026. The Characters of The Hippopotamidae from Java (Indonesia) Based on Skull and Tooth Analyses. *Indonesian Journal on Geoscience*, 13 (1), p.107-127. DOI:10.17014/ijog.13.1.107-127

INTRODUCTION

Based on the anatomy of the skull bones and teeth, Boisserie (2005) identified six genera within Hippopotamidae: *Saotherium*, *Choeropsis*, *Archaeopotamus*, aff. *Hippopotamus*, *Hippopotamus*, and *Hexaprotodon*. Of these six, only two genera are still alive today: the pygmy hippo genus *Choeropsis*, which lives in West Africa, and *Hippopotamus* which lives in East Africa.

The existence of Hippopotamidae in Indonesia is evidenced by fossil discoveries on Java Island (Dubois, 1908; von Koenigswald, 1933; 1934; Hooijer, 1950) and Sumatra (Smith, *et al.*, 2021). However, their exact taxonomic position within the family remains a subject of ongoing debate. In Java Island, the first *Hippopotamus* fossil was scientifically reported by Dubois (1908). Dubois proposed that The Javan *Hippopotamus* fossil was different from previously described as Asian hippopotamids. Despite its

similarities to *Hexaprotodon sivalensis*, he classified it as a distinct species called *Hexaprotodon sivajavanicus*. This interpretation diverges from von Koenigswald (1933, 1934) classification, which recognized three successive species based on their morphology and chronological occurrence: *Hexaprotodon simplex* in The Late Pliocene, *Hexaprotodon antiquus* from The Late Pliocene to Early Pleistocene, and *Hippopotamus namadicus* in The Middle and Late Pleistocene. The interpretations of Dubois and von Koenigswald study were later criticized by Hooijer (1950), who proposed that all Hippopotamidae in Java belonged to the genus *Hippopotamus*. However, Boisserie (2005) later suggested a different perspective, indicating that Indonesian Hippopotamidae were likely of the *Hexaprotodon* type. This ongoing debate underscores the uncertainty regarding the exact taxonomic identity of these extinct Hippopotamidae. Additionally, newly discovered specimens have not been formally identified or incorporated into comparative analyses with older collections. The lack of comprehensive comparative analyses, including newly discovered specimens, has hindered definitive resolution of this taxonomic issue.

The existence of *Hippopotamus* fossils in Indonesia is important to be studied further because of their position as one of the characteristic fauna elements in Indonesian vertebrate biostratigraphy (von Koenigswald, 1935; Aziz *et al.*, 1995; Hooijer, 1975; Sondaar, 1984). Taxonomic identification of *Hippopotamus* species is primarily based on dental and cranial morphology. This study attempts to characterize the morphological features of the teeth and skull bones, employing both qualitative and quantitative methods, to distinguish Hippopotamidae taxa in Java. The primary objective is to determine whether the Javan Hippopotamidae represent *Hexaprotodon*, *Hippopotamus*, or whether both genera have existed in Java. The current analysis intends to clarify the taxonomic position and biogeographic relationships of Javan Hippopotamidae within the broader context of Asian Hippopotamidae.

Hippopotamidae Dental Anatomy

Among fossil remains, teeth are often the most informative elements for taxonomic analysis. Consequently, the morphological characteristics of incisors, canines, premolars, and molars are crucial for differentiating between *Hippopotamus* taxa. Previous studies have highlighted the number of incisors as a key distinguishing feature between *Hexaprotodon* and *Hippopotamus*. *Hexaprotodon* possesses six incisors, while *Hippopotamus* has four incisors. The anatomical position of Hippopotamidae teeth causes distinctive wear facet patterns on its incisors. The wear facet of the first mandibular incisor is located on its labial surface, whereas the first and second maxillary, as well as the second mandibular, incisors display wear facets at their apical tips.

Within The Hippopotamidae, the shape of the mandibular canines exhibits a more pronounced curvature compared to the maxillary canines. The maxillary canines tend to be oval in cross-section, while mandibular canines are typically triangular. Regarding the incisors, mandibular incisors are generally straight, whereas maxillary incisors are curved (De Visser, 2008). The canine morphology of *Hippopotamus* differs significantly from that of *Hexaprotodon*. *Hexaprotodon* maxillary canines possess a more defined and deeper groove than those of *Hippopotamus* (Coryndon, 1977). Conversely, *Hippopotamus* mandibular canines exhibit prominent linear ridges along the curvature of the canine surface, while *Hexaprotodon* mandibular canines display less pronounced ridges. These canine surface characters are also found in The *Hippopotamus* fossil from the Malagrotta site, Italy, where the maxillary canine of MCZR PV 2010.269 exhibits relatively shallow grooves, and the mandibular canine presents a rough enamel surface due to prominent linear ridges along the canine arch (Martino *et al.*, 2024).

Dental characters include the presence of a hypoconulid exclusively on the mandibular third molar in *Hippopotamus* or in *Hexaprotodon*. Additionally, mandibular premolars and molars exhibit a more rectangular shape compared to

their maxillary teeth. As noted by Mazza (1995) and Martino *et al.* (2024), dental accessories, such as the lingual cingulum, are more pronounced than the labial cingulum in Hippopotamidae. *Hippopotamus* possesses larger and more prominent premolar and molar accessories, including the posterior cingulum, side cingulum, and anterior cingulum, compared to *Hexaprotodon*. Premolar and molar fossil specimens of *Hippopotamus* from the Barrac de la Boella site in Spain exhibit a strong and thick posterior and anterior cingulum (Fidalgo *et al.*, 2023).

MATERIALS AND METHODS

Material

In this study, twenty-one Hippopotamidae fossil specimens from Java were used for qualitative observations and biometric measurements. The material includes cranial, mandibular, and dental elements from Hippopotamidae fossils recovered from various vertebrate paleontological sites in Java (Figure 1 and Table 1). All selected specimens represent individuals whose third molars had erupted and were worn, which ensures that all specimens had reached the adult stage. This selection was done to ensure that the morphometric measurements were not biased due

to the different ontogenetic stages. The age of the fossils is obtained from the absolute age dating and the geological age of the rock formations, as determined by previous studies.

The oldest *Hexaprotodon* fossil in Java is from the Cijolang site, Ciarnis, West Java (von Koenigswald, 1935). Colbert (1943) noted that von Koenigswald places the Cijolang fauna of Java in The Upper Pliocene age. At the time of von Koenigswald publications, The Pliocene-Pleistocene boundary was often taken at 1.8 Ma. For this this reason The *Hexaprotodon* fossils from Cijolang should be older than 1.8 Ma. According to the modern consensus, the earliest Pleistocene or Gelasian Stage starts at 2.58 Ma. Therefore, considering this clasification, The Cijolang *Hexaprotodon* should have lived around The Gelasian. Younger than The Cijolang *Hexaprotodon* are the *Hexaprotodon* fossils from Calabrian sites, such as The *Hexaprotodon* from Subang, Sumedang, Bumiayu, Sangiran, Ngawi, Gunung Butak, and Mojokerto. Early Middle Pleistocene or Early Chibanian Stage *Hexaprotodon* were found at Kedungbrubus, Watualang, and Tritik. Furthermore, *Hexaprotodon* was also found in The Late Middle Pleistocene or Late Chibanian Stage fluviatile sedimentary rock layers in Sambungmacan and Grobogan, as well as in The Late Pleistocene Bengawan Solo Terrace in Ngandong. Based on the geological proximity

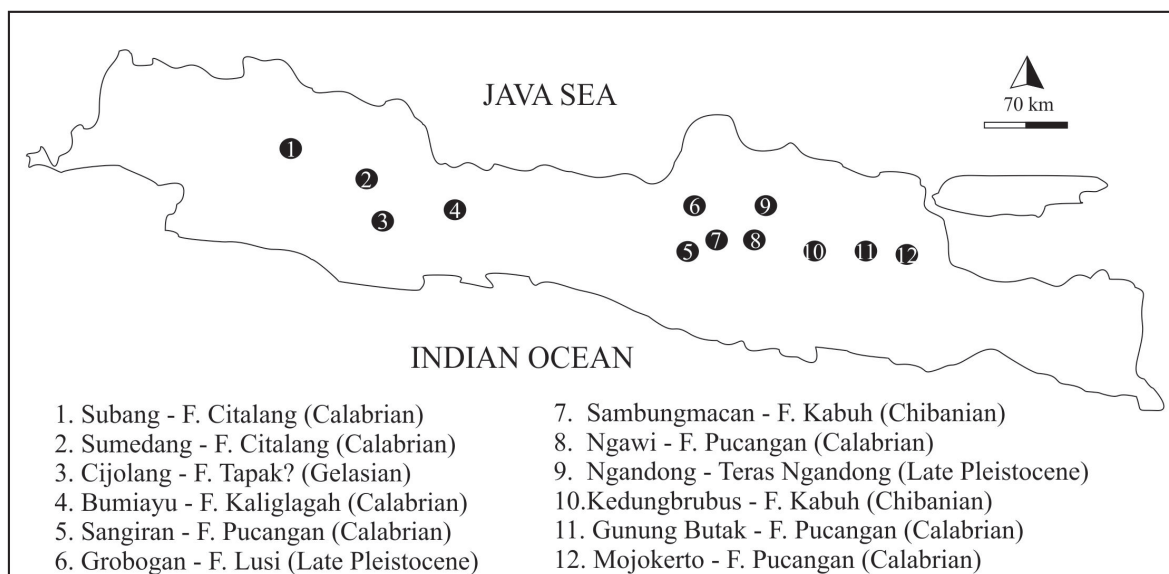


Figure 1. Discovery locations and ages of Javanese Hippopotamidae fossils.

Table 1. Qualitative Morphological Comparison Between *Hexaprotodon* And *Hippopotamus* Used in This Study

Characteristic Anatomy		<i>Hexaprotodon</i>	<i>Hippopotamus</i>	
Dentary	Incisor (Colbert, 1935)	Amount	6 pairs	4 pairs
	Lower incisor (Boisserie, 2005)	Size	I ₁ and I ₃ almost the same, I ₂ usually smaller than the other	I ₁ larger than I ₂
	Upper canine (Coryndon, 1977)	Posterior groove deep	Deep	Shallow
	Lower canine (Coryndon, 1977)	Enamel surface	Smooth enamel	Ridged enamel
	Premolar	Cingulum lingual	Least prominent (Hooijer, 1950)	Prominent (Fidalgo <i>et al.</i> , 2023)
			Posterior cingulum	Least prominent (Hooijer, 1950)
	Molar	Cingulum lingual	Least prominent (Hooijer, 1950)	Prominent (Fidalgo <i>et al.</i> , 2023)
Anterior cingulum			Moderate (Hooijer, 1950)	Prominent (Fidalgo <i>et al.</i> , 2023)
Mandible	Premolar position (Colbert, 1935)		Widens anteriorly	Tends to be parallel
	The position of the symphysis on a flat plane (Boisserie, 2005)		Oblique	Sloping
	The shape of sagittal symphysis (Boisserie, 2005)		Like a pear fruit	Oval egg
Cranial	Sagittal crest (Boisserie, 2005)		High	Low
	Anterior premaxilla (Colbert, 1935)		Fused	Separately
	Position of the lacrimal bone relative to the nasal bone (Colbert, 1935)		Not contacted	Contacted

of their ages, these Javan *Hexaprotodon* can be grouped into three geological stages, from oldest to youngest: The Gelasian and Calabrian group, The Early Chibanian group, and The Late Chibanian to Late Pleistocene group.

Methods

This study focuses on observations of the cranial, mandibular, and dental aspects (Figure 2). For the qualitative morphological analysis of the cranium and mandible, the diagnostic features provided by Colbert (1935), Coryndon (1977), Hooijer (1950), and Boisserie (2005) were used (Table 2). Colbert (1935) described differences in the number of incisors, tooth position, and cranial morphology. Coryndon (1977) focused on canine characters, while Hooijer (1950) noted the differences of premolars and molars between teeth of both genera. Boisserie (2005) identified several cranial and mandibular diagnostic features of both taxa. Individual age assessments were determined using The Hippopotamus age table, which is based on the degree of tooth wear, as described by Laws (1968). Dental biometric measurements were conducted using the biometric point guide for anatomical measurements of Hippopotamidae provided by De Visser (2008).

For the quantitative biometric analysis, the anatomical measurements were used for Hippopotamidae established by de Visser (2008). The measurement results were subjected to linear regression analysis, coefficient of variation analyses, and T-Test analysis to identify factors influencing shape variation and to differentiate between Hippopotamidae taxa. Based on the available material, a total of seven mandibles with molars and one isolated molar were suitable for the regression analysis. The linear regression analysis employed data on the maximum length and width of mandibular molars from the Javan specimens (Table 3). PAST software (Hammer and Harper, 2006) was used for the statistical analysis to assess the correlation between these two tooth variables.

RESULTS

Specimen

The number of incisors is a key distinctive character between *Hexaprotodon* and *Hippopotamus*. Based on observations of mandible specimens from Java, both from literature and direct examination, all specimens exhibit six

Table 2. List of Specimens Used in This Study, for Which The Geological Age References have been converted from The Series Scale to Stage Scale of The Geological Time Scale

NO	SPECIMEN	LOCATION	AGE	FORMATION	STORE	ANATOMY
1	22G	Cijolang, Ciamis	Gelasian	Cijolang Bed	MGB	Mandible with a complete tooth series
2	GR05	Grobogan	Late Chibanian, (Hascaryo, 20218; Putra et al., 2023)	Lusi	MBR	Mandible with a dextral canine, a sinistral I ₂ and a set of sinistral premolars and molars
3	GR07	Grobogan	Late Chibanian, (Hascaryo, 20218; Putra et al., 2023)	Lusi	MBR	Dextral mandible with set of premolars and molars
4	VR1030603	Sangiran	Calabrian (Matsu'ura et al., 2020)	Samgiran	MGB	Mandible with a missing dextral half of the corpus-ramus
5	BU-MGB	Bumiayu	Calabrian (Zaim, 1978)	Kaliglagah	MGB	Mandible and cranium
6	SM2014	Sambung -Macan	Late Chibanian (Indriati et al., 2011)	Kabuh	MGB	Anterior part of mandible with a sinistral I ₁ and dextral I ₁ and I ₃
7	NG-MGB	Ngandong	Late Pleistocene (Rizal et al., 2020)	Terrace	MGB	A cranium and mandible with a sinistral I ₂ and set of premolars and molars
8	NG2-K727	Ngandong	Late Pleistocene (Rizal et al., 2020)	Terrace	MGB	Sinistral mandible with M ₁ and M ₃
9	NG3-K726	Ngandong	Late Pleistocene (Rizal et al., 2020)	Terrace	MGB	Dextral mandible with M ₁ , M ₂ and M ₃
10	K728	Gunung Butak	Calabrian (Bandet et al., 1989)	Pucangan	MGB	Dextral mandible with M ₂ and M ₃
11	F50	Delu, Ngawi	Calabrian (Watanabe & Kadar., 1985)	Pucangan	MGB	Dextral M ₃
12	F52	Delu, Ngawi	Calabrian (Watanabe & Kadar., 1985)	Pucangan	MGB	Dextral P ₄
13	SB2012	Subang	Calabrian (Djuhaeni annd Martodjojo, 1989)	Citalang	MGB	Premaxilla with a dextral canine, I ³ and a sinistral I ¹
14	SBK	Subang	Calabrian (Djuhaeni annd Martodjojo, 1989)	Citalang	MGB	Sinistral mandibular canine
15	KDB	Kedung-brubus	Calabrian (Sartono, 1961)	Kabuh	MGB	Dextral maxilla with a M ¹ , M ² and M ³
16	TMB2	Cijolang, Ciamis	Gelasian	Cijolang Bed	MTS	Dextral M ²
17	TMB9	Cijolang, Ciamis	Gelasian	Cijolang Bed	MTS	Dextral M ¹ , M ²
18	TMB10	Cijolang, Ciamis	Gelasian	Cijolang Bed	MTS	Premaxilla with a dextral canine
19	TMB11	Cijolang, Ciamis	Gelasian	Cijolang Bed	MTS	Dextral mandibular canine
20	SUM1	Sumedang	Calabrian (Djuhaeni annd Martodjojo, 1989)	Citalang	MLC	Tip of the dextral mandibular canine
21	MJK1	Mojokerto	Calabrian (Morwood et al., 2003)	Pucangan	ITB	Cranium with its anterior and posterior parts missing

Abbreviation: MGB: Museum Geologi Bandung; MBR: Museum Banjarejo; MTS; Museum Tambaksari; MLC: Museum Lembah Cisaar; ITB: Laboratorium Paleontology ITB; I: Incisor; P: Premolar; M: Molar.

incisors with a dental formula of I₁, I₂, I₃ from the symphysis towards the canine. An exception is specimen SM2014 from Sambungmacan, which has a defect with the right I₂ failed to erupt, while the left I₂ developed normally (Figure 3). The six-incisor configuration is also observed in the premaxilla specimen SB2012 from Subang and the NG-MGB skull from Ngandong.

The maxillary canine specimens TMB10 from Cijolang and SB2012 from Subang show *Hexaprotodon* canine characteristics, indicated by distinct grooves on the canine surface. Similarly, the mandibular canine specimens 22G, GR05, SBK, and TMB11 also show *Hexaprotodon* characteristics due to the presence of subtle linear ridges along the curvature of the canine (Table 4).

Molars and Premolars

All observed isolated premolar specimens exhibit *Hexaprotodon* characteristics, as indicated by their less prominent posterior cingulum and cingulum (Table 4). Likewise, all molar specimens possess a less pronounced anterior cingulum, further indicating *Hexaprotodon* characteristics.

Quantitative Analysis of Javan Hexaprotodon Molar Tooth Specimens

Regression Analysis

Regression analysis was carried out on the molar tooth measurement data in this study, which were combined with data from previous studies (Table 3). The regression of the maximum length versus width of mandibular molars was performed. The regression of length vs.

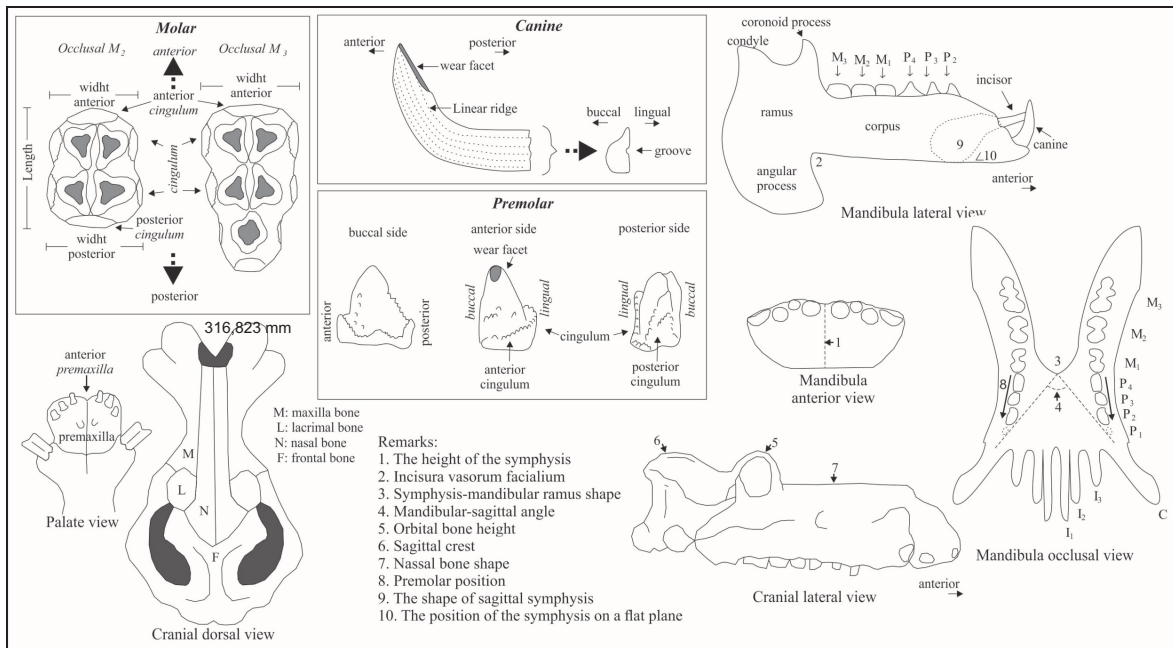


Figure 2. Teeth, cranial and mandibular character states

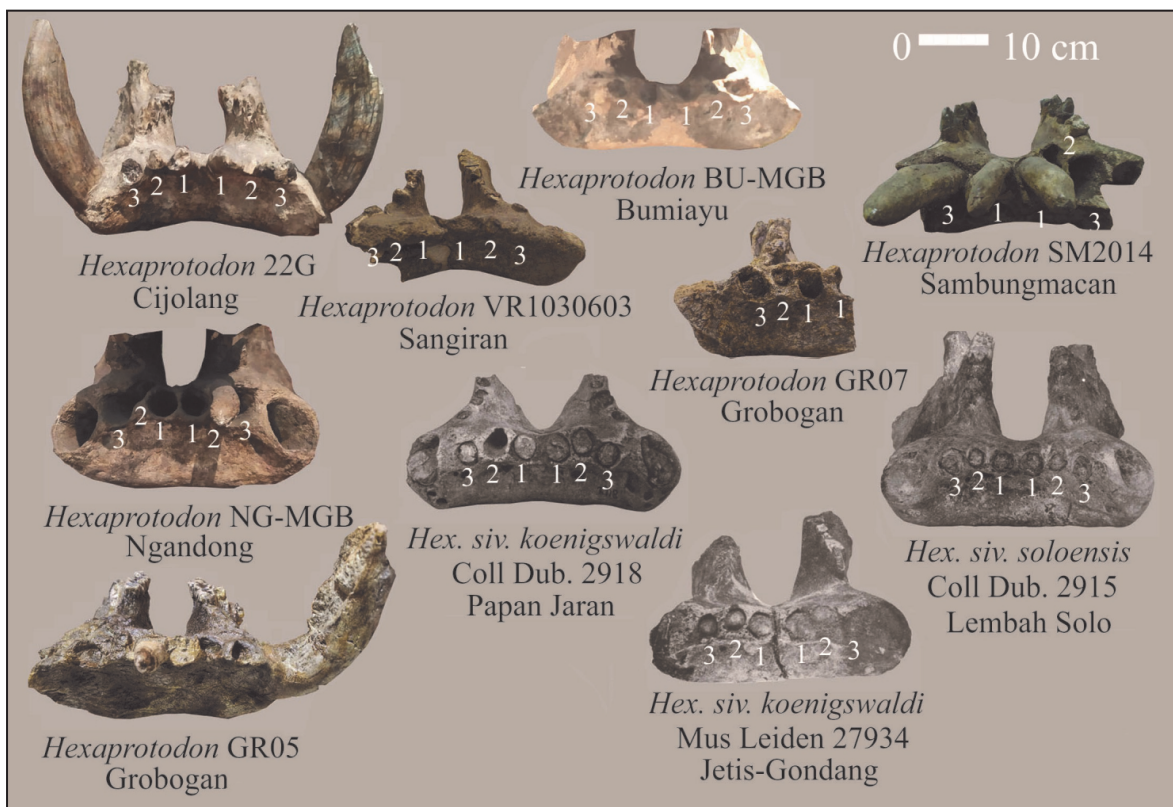


Figure 3. View of the incisor alveoli of several mandibles from Java shows a six-incisor pattern, photos from the Coll. Dub. 2915, Coll. Dub. 2918 and Mus Leiden 27934 collections were sourced from Hooijer (1950).

width of the M_1 , M_2 , and M_3 demonstrates a moderate correlation between these two vari-

ables, with r values varying between 0.63 and 0.69. This is not a very strong linear correlation,

Table 3. Measurement of mandibular molars, length and width (size in mm)

No	Collection ID	S/D	Site	Origin	M ₁		M ₂		M ₃		Age	References
					L	W Post	L	W Post	L	W Ant		
1	22G	S	Cijolang	Java	33.9	28.1	42.8	31.2	51.4	31.3	Gelasian Pleistocene	Present work
2	22G	D	Cijolang	Java	35.5	27.6	41.9	30.7	52.5	32.2	Gelasian Pleistocene	Present work
3	VR1030603	S	Sangiran	Java	29.2	23.7	41.4	30.6	51.9	32.5	Calabrian Pleistocene	Present work
4	VR1030603	D	Sangiran	Java	29.4	23.8	-	-	-	-	Calabrian Pleistocene	Present work
5	BU-MGB	S	Bumiayu	Java	39.4	26.6	41.1	30.5	49	29.8	Calabrian Pleistocene	Present work
6	BU-MGB	D	Bumiayu	Java	37.3	26.4	42.5	31.9	50	31	Calabrian Pleistocene	Present work
7	F.50	D	Ngawi	Java	-	-	-	-	54.5	29.8	Calabrian Pleistocene	Present work
8	K707	S	Gn. Butak	Java	-	-	-	-	57.4	30.6	Calabrian Pleistocene	de Visser, 2008
9	K 731	S	Sangiran	Java	33.7	28.8	-	-	-	-	Calabrian Pleistocene	de Visser, 2008
10	K 742/1	S	Sangiran	Java	33.7	26.4	-	-	-	-	Calabrian Pleistocene	de Visser, 2008
11	K 746	D	Watualang	Java	-	-	-	-	61.4	34.8	Chibanian Pleistocene	de Visser, 2008
12	K728	D	Kedung Brubus	Java	29.9	28.1	38.1	30.2	50.2	28.8	Chibanian Pleistocene	Present work
13	SA 040979-20N/1	S	New Pb Site	Java	37.3	28.1	-	-	-	-	Calabrian Pleistocene	de Visser, 2008
14	Dub. 310	S	Kedung Brubus	Java	-	-	-	-	54	31.7	Chibanian Pleistocene	de Visser, 2008
15	Dub. 2903	D	"Trinil"	Java	33.3	24	42.3	34	-	-	Chibanian Pleistocene	de Visser, 2008
16	Dub.2916	D	Kedung Brubus	Java	20.2	26.4	42.6	31.6	60.2	34.5	Chibanian Pleistocene	de Visser, 2008
17	Dub.2916	S	Kedung Brubus	Java	-	-	42.5	32.1	-	-	Chibanian Pleistocene	de Visser, 2008
18	Dub. 99	S	Tritik	Java	27.9	26.3	42.3	31.5	54.1	31.1	Chibanian Pleistocene	de Visser, 2008
19	Dub. 99	D	Tritik	Java	-	-	43.3	32.1	52.5	30.8	Chibanian Pleistocene	de Visser, 2008
20	Dub. 323a/1	D	Kedung Brubus	Java	-	-	41	30.6	58.8	30	Chibanian Pleistocene	de Visser, 2008
21	Dub. 323a/2	S	Kedung Brubus	Java	-	-	-	-	56.6	28.8	Chibanian Pleistocene	de Visser, 2008
22	Dub. 2013	S	Kedung Brubus	Java	-	-	41.8	29.2	-	-	Chibanian Pleistocene	de Visser, 2008
23	Dub. 2910	S	Tritik	Java	-	-	37.2	29	60.6	34.5	Chibanian Pleistocene	de Visser, 2008
24	GR05	S	Grobogan	Java	40.5	30.1	44.2	35.6	64.2	39	Late Pleistocene	Present work
25	GR05	D	Grobogan	Java	41.4	30.3	47.9	38.6	65.1	39.2	Late Pleistocene	Present work
26	GR07	D	Grobogan	Java	39.8	29.1	46.1	37.1	62.6	37.6	Late Pleistocene	Present work
27	NG-MGB	S	Ngandong	Java	42.5	30	47	38	66.1	40.8	Late Pleistocene	Present work
28	NG-MGB	D	Ngandong	Java	42.8	31.1	48.9	39.4	65.8	40.4	Late Pleistocene	Present work
29	K 727	S	Ngandong	Java	-	-	-	-	49.9	35.4	Late Pleistocene	Present work
30	K 726	D	Ngandong	Java	-	-	-	-	49	35.1	Late Pleistocene	Present work
31	K 657	S	Ngandong	Java	-	-	-	-	53.9	36.9	Late Pleistocene	de Visser, 2008
32	K 723/1	S	Ngandong	Java	-	-	-	-	58.5	36.8	Late Pleistocene	de Visser, 2008
33	K723/2	S	Grobogan	Java	-	-	-	-	65.4	36.3	Late Pleistocene	de Visser, 2008
34	Hex. iravaticus NMMP-KU-IR 0449	D	Yebyu-Letma	Myanmar	35.6	26.5	35.9	29.8	50.8	29.8	Pliocene	Htike and Takai, 2016
35	Hex. iravaticus NMMP-KU-IR 0191	D	CHZ20	Myanmar	36.1	26	41	30.2	51.5	31.2	Pliocene	Htike and Takai, 2016
36	Hex. iravaticus MGW 0001	S	-	Myanmar	35	26	42.3	29.3	51	28	Pliocene	Htike and Takai, 2016
37	Hex. sivalensis subsp. nov NMM HBG 19	D	Near Tabingyaung Village	Myanmar	-	-	44.8	31.6	-	-	Mio-Pliocene	Htike and Takai, 2016
38	Hex. palaeindicus subsp. nov NMM HBG 20	S	Near Tabingyaung Village	Myanmar	-	-	46	32	57	32.8	Late Pliocene	Htike and Takai, 2016
39	Hex. iravaticus MUDG-V 1003	S	-	Myanmar	-	-	43	31.7	55.8	31.2	Pliocene	Htike and Takai, 2016
40	Hex. iravaticus YUDG HBG 56	D	-	Myanmar	-	-	42.5	30.2	-	-	Pliocene	Htike and Takai, 2016
41	Hex. iravaticus NMMP-KU-IR-0326	D	-	Myanmar	-	-	-	-	51.9	31.2	Pliocene	Htike and Takai, 2016
42	Hex. iravaticus No number from Yenangyaung	S	Yenang yaung	Myanmar	-	-	41.5	26.1	-	-	Pliocene	Htike and Takai, 2016
43	Dub. 3147	D	Siwaliks	India	-	-	36.8	34.1	64.3	38.7	Late Miocene	de Visser, 2008

Remarks: S : Sinistral; D : Dextral; L : Length; W ant: Widht anterior side; W post: Widht posterior side

and may indicate that size variability in the larger Late Pleistocene specimens is quite large (Figures 4, 5, 6).

Coefficient of Variation Analysis

The regression analysis results indicate that The Late Chibanian to Late Pleistocene *Hexaprotodon* in Java are considerably larger than The Gelasian-Calabrian-Chibanian *Hexaprotodon*. To confirm the diversity of *Hexaprotodon* in Java, their molar measurements were compared with the coefficient of variation (CV) based on the measurements for recent *Hippopotamus amphibius* molars provided by Avedik and Clauss (2023) (see Table 5). The CV was

calculated using the standard deviation of the sample type (Formula 1).

$$CV = \frac{s}{\mu} \times 100$$

$$s = \sqrt{\frac{\sum (x_i - \mu)^2}{N - 1}} \dots\dots\dots (1)$$

Remarks:

- CV : Coefficient of variation
- S : Sample Standard deviation
- μ : Mean
- X_i : Sample
- N : Total sample

Table 4. Comparative Qualitative Morphology of Observed Dental, Maxillary, And Mandibular Specimens of Javan Hippopotamidae

No	Code	Location	Canine	Incisor	Premolar		Molar		Conclusion
					Cingulum	Posterior Cingulum	Cingulum	Anterior Cingulum	
Maxilla	KDB	Kedungbrurus	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	TMB2	Cijolang	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	TMB9	Cijolang	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	TMB10	Cijolang	Upper canine has a deep groove	Small	?	?	?	?	<i>Hexaprotodon</i>
	NG-MGB	Ngandong	?	?	Least prominent	Least prominent	Least prominent	Moderate	<i>Hexaprotodon</i>
	SB2012	Subang	Upper canine has a deep groove	Small	?	?	?	?	<i>Hexaprotodon</i>
	MJK1	Mojokerto	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	22G	Cijolang	Least prominent linear ridges	Small	Least prominent	Least prominent	Least prominent	Moderate	<i>Hexaprotodon</i>
	GR05	Grobogan	Least prominent linear ridges	Large	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	GR07	Grobogan	?	Large	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
Mandible	VR1030603	Sangiran	?	Small	Least prominent	Least prominent	Least prominent	Moderate	<i>Hexaprotodon</i>
	BU-MGB	Bumiayu	?	Small	Least prominent	Least prominent	Least prominent	Moderate	<i>Hexaprotodon</i>
	SM2014	Sambungmacan	?	Large	Least prominent	Least prominent	?	?	<i>Hexaprotodon</i>
	NG-MGB	Ngandong	?	Large	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	NG2-K727	Ngandong	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	NG3-K726	Ngandong	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	K728	Gunung Butak	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>
	TMB11	Cijolang	Least prominent linear ridges	?	?	?	?	?	<i>Hexaprotodon</i>
	SUM1	Sumedang	Least prominent linear ridges	?	?	?	?	?	<i>Hexaprotodon</i>
	SBK	Subang	Least prominent linear ridges	?	?	?	?	?	<i>Hexaprotodon</i>
F50	Delu, Ngawi	?	?	?	?	Least prominent	Moderate	<i>Hexaprotodon</i>	
F52	Delu, Ngawi	?	?	Least prominent	Least prominent	?	?	<i>Hexaprotodon</i>	

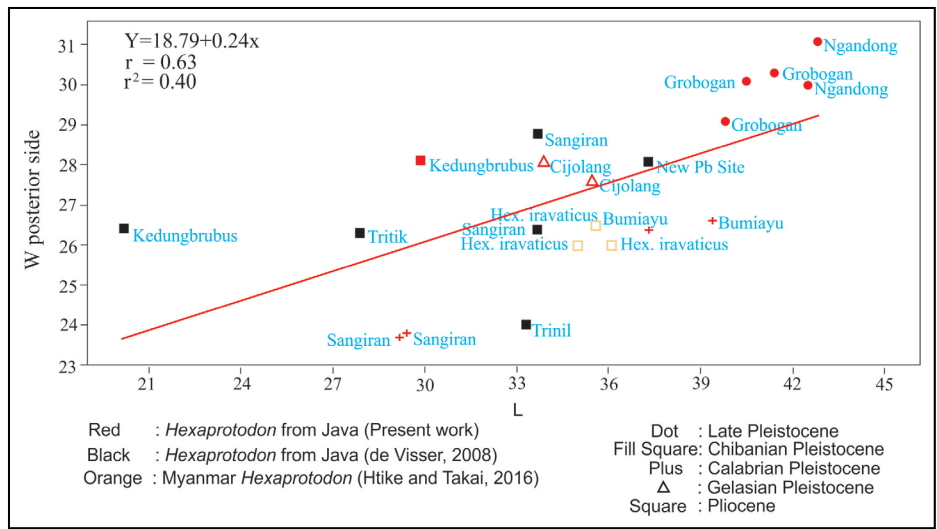


Figure 4. Linear regression graph of lower M_1 specimen.

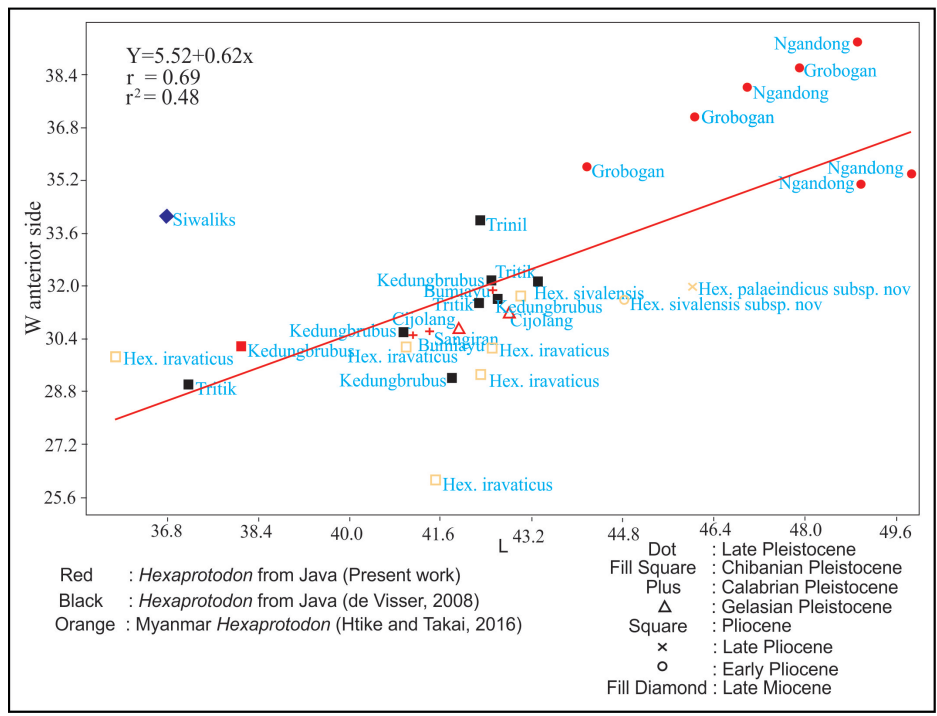


Figure 5. Linear regression graph of lower M_2 specimen.

With all Javan *Hexaprotodon* molars included, the CV values are larger than the CV of recent *Hippopotamus amphibius*, with only the M_1 showing a slightly smaller value. This indicates that the entire Javan *Hexaprotodon* sample population is more diverse in molar size than the recent *Hippopotamus amphibius*. When The *Hexaprotodon* are separated by geological age, the CV values are all smaller than that of the combined Javan

Hexaprotodon sample (Table 6). This suggests a size difference between *Hexaprotodon* from the Gelasian-Calabrian-Chibanian and those from the Late Chibanian to Late Pleistocene.

T-Test Analysis

To determine if there is a significant difference in the mean molar size of Javan *Hexaprotodon*, an independent samples T-Test was performed. The

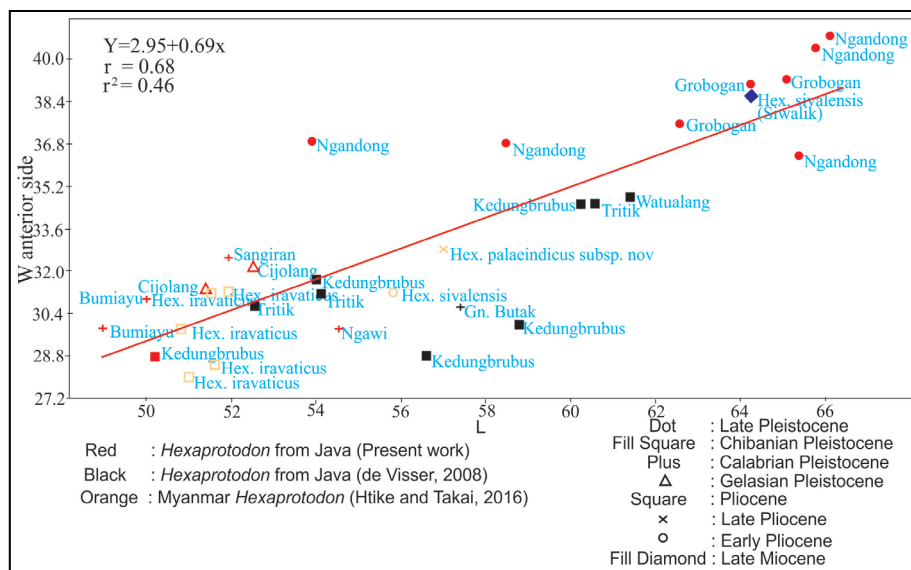


Figure 6. Linear regression graph of lower M_3 specimen.

analysis was conducted with a significance level of $\alpha = 0.05$, and the proposed hypotheses are:

First sets of hypotheses:

1. The null hypothesis (H_0) is that there is no difference in the mean molar size between The Gelasian-Calabrian Javan *Hexaprotodon* and The Chibanian Javan *Hexaprotodon*.
2. The alternate hypothesis (H_a) is that there is a difference in the mean molar size between The Gelasian-Calabrian Javan *Hexaprotodon* and The Chibanian Javan *Hexaprotodon*.

Second sets of hypotheses:

1. The null hypothesis (H_0) is that there is no difference in the mean molar size between The Gelasian-Calabrian-Chibanian Javan *Hexaprotodon* and The Late Chibanian-Late Pleistocene Java *Hexaprotodon*.
2. The alternate hypothesis (H_a) is there is a difference in the mean molar size between The Gelasian-Calabrian-Chibanian Javan *Hexaprotodon* and The Late Chibanian-Late Pleistocene Javanese *Hexaprotodon*.

In the T-Test hypothesis testing, if the calculated t-statistic or t-count is greater than the critical t-value or t-table, the null hypothesis is rejected. Conversely, if the calculated t-value is less than or equal to the critical t-table, the null hypothesis is not rejected or "is accepted". The results of the T-Test analysis are given in Table 7.

DISCUSSION

The results of this study indicate that all examined mandible and maxilla specimens of fossil Hippopotamidae possess six incisors, a diagnostic characteristic suggesting that all Hippopotamidae fossils from Java belonged to the genus *Hexaprotodon*. This finding supports De Visser (2008) assertion that all Javan Hippopotamidae were *Hexaprotodon* and answers Boisserie (2005) query regarding the specific genus of extinct Hippopotamidae of Java. Furthermore, these results refute the statement of von Koenigswald (1933, 1934) who claimed that in addition to *Hexaprotodon*, *Hippopotamus namadicus* also once lived in Java. This study result also negates Hooijer (1950) statement that all Hippopotamidae in Java were *Hippopotamus*. However, neither von Koenigswald (1933, 1934) nor Hooijer (1950) provided clear morphological evidence to support their classification of these fossils as *Hippopotamus*.

As indicated by linear regression analysis, the observed fossils are grouped into two size groups. A *Hexaprotodon* with smaller molars is represented by The Gelasian-Calabrian-Chibanian specimens such as Subang SB2012, Cijolang 22G, Bumiayu BU-MGB, Sangiran VR1030603, Ngawi F5, Kedungbrubus KDB, Gunung Butak

Table 5. Mandibular molars measurement of *Hippopotamus amphibius* from Avedik and Clauss (2023)

No	Collected in	Age	Origin	Collection ID	Sex	S/D	M ₁ Widht post	M ₂ Widht post	M ₃ Widht ant
1	Zurich	adult	unknown	13619	-	S	3	3.5	3.6
2	Zurich	adult	unknown	13619	-	D	3	3.7	3.6
3	Zurich	adult	unknown	14509	-	S	2.9	3.5	3.4
4	Zurich	adult	unknown	14509	-	D	2.8	3.6	3.2
5	Zurich	adult	unknown	14508	-	S	3.2	3.2	3.7
6	Zurich	adult	unknown	14508	-	D	3.5	3.2	3.4
7	Zurich	adult	unknown	17912	-	S	3.4	4	3.7
8	Zurich	adult	unknown	17912	-	D	3.3	4	3.6
9	Basel	adult	unknown	6498	-	S	3.4	3.6	3.8
10	Basel	adult	unknown	6498	-	D	3.4	3.6	3.6
11	Basel	adult	unknown	C286i	-	S	3.1	3.4	3
12	Basel	adult	unknown	C286i	-	D	3.1	3.4	3.2
13	St. Gallen	adult	unknown	6285	-	S		3.3	3.6
14	St. Gallen	adult	unknown	6285	-	D	2.7	3.4	3.7
15	St. Gallen	adult	unknown	6286	-	S	3.3	4.2	3.5
16	St. Gallen	adult	unknown	6286	-	D	3.3	3.9	3.3
17	Stuttgart	adult	Sudan	1640	Female	S	3.5	3.5	3.3
18	Stuttgart	adult	Sudan	1640	Female	D	3.6	3.4	3.3
19	Stuttgart	adult	unknown	32105	-	S			3.6
20	Stuttgart	adult	unknown	32105	-	D		3.6	3.1
21	Stuttgart	adult	unknown	17524	-	S	3.3	3.7	3.9
22	Stuttgart	adult	unknown	17524	-	D	3.2	3.8	3.6
23	Stuttgart	adult	unknown	17523	-	S	3.2	3.3	3.3
24	Stuttgart	adult	unknown	17523	-	D	3.2	3.3	3.3
25	Stuttgart	adult	unknown	17526	-	S	3.4	4.2	3.9
26	Stuttgart	adult	unknown	17526	-	D	3.3	4.2	4.1
27	Stuttgart	adult	unknown	17525	-	S	4	4.3	4.2
28	Stuttgart	adult	unknown	17525	-	D		4.2	3.8
29	Stuttgart	adult	Tanzania	7320	-	S	2.9	3	3.3
30	Stuttgart	adult	Tanzania	7320	-	D	2.9	3.3	3.4
31	Stuttgart	adult	Cameroon	17522	-	S	3.4	4	4.3
32	Stuttgart	adult	Cameroon	17522	-	D	3.4	4.2	4.2
33	Stuttgart	adult	unknown	17521	-	S	3.4	3.2	3.6
34	Stuttgart	adult	unknown	17521	-	D	3.1	3.3	3.6
35	Bonn	adult	Cameroon	2014728	-	S	3.4	3.9	4.1
36	Bonn	adult	Cameroon	2014728	-	D	3.5	4.1	3.7
37	Bonn	adult	unknown	B1	-	S	3.2	4	3.9
38	Bonn	adult	unknown	B1	-	D	3.2	3.9	3.9
39	Bonn	adult	unknown	B10	-	S	3.2	3.5	3.7
40	Bonn	adult	unknown	B10	-	D	3.1	3.9	3.8
41	Bonn	adult	unknown	B2	-	S		4.3	4.6
42	Bonn	adult	unknown	B2	-	D	3.3	4.2	4.6
43	Bonn	adult	evtl. engl. Kolonie	20160745	Female?	S	3.4	3.9	3.8
44	Bonn	adult	evtl. engl. Kolonie	20160745	Female?	D	3.4	4.2	4.1
61	Jena	adult	Africa	1663	-	S	3.5	3.7	3.9
62	Jena	adult	Africa	1663	-	D	3.6	3.7	3.7
63	Jena	adult	Africa	1667	-	S	3.6	4.1	4
64	Jena	adult	Africa	1667	-	D	3.5	4.3	4
65	Jena	adult	Africa	1664	-	S	3.2	3.5	3.2
66	Jena	adult	Africa	1664	-	D	3.5	3.6	3.4
67	Frankfurt	adult	unknown	480	-	S	3.5	3.9	3.9
68	Frankfurt	adult	unknown	480	-	D	3.5	4.3	4
69	Frankfurt	adult	Kongo	482	-	S	3.1	3.8	3.8
70	Frankfurt	adult	Kongo	482	-	D	2.9	3.9	3.7
71	Frankfurt	adult	Tanzania	483	-	S	3.3	3.7	4.1
72	Frankfurt	adult	Tanzania	483	-	D	3.5	3.9	3.9
73	Frankfurt	adult	Chad	6426	Female	S		4.3	4.1
74	Frankfurt	adult	Chad	6426	Female	D		4.2	4.5
75	Frankfurt	adult	unknown	22061	-	S	3.2	3.7	3.4
76	Frankfurt	adult	unknown	22061	-	D	3.2	3.8	3.3
77	Frankfurt	adult	Chad	6427	Male	S	3	3.6	4.3
78	Frankfurt	adult	Chad	6427	Male	D	2.9	3.8	4.4
79	Frankfurt	adult	unknown	35452	-	S	3.6	4.1	4.6

Table 5. Continued ...

No	Collected in	Age	Origin	Collection ID	Sex	S/D	M ₁ Widht post	M ₂ Widht post	M ₃ Widht ant
80	Frankfurt	adult	unknown	35452	-	D	3.6	4.5	4.1
81	Frankfurt	adult	Tansania	35448	-	S	3.7	4	3.8
82	Frankfurt	adult	Tansania	35448	-	D	3.8	3.9	4.2
83	Frankfurt	39 years	Zoo Fankfurt	53506	Male	S	3.5	4.5	4.3
84	Frankfurt	39 years	Zoo Fankfurt	53506	Male	D	3.2	4.2	4.4
85	Hamburg	adult	unknown	8389	-	S	3.8	4.1	4.1
86	Hamburg	adult	unknown	8389	-	D	3.8	4.5	4.2
87	Hamburg	adult	unknown	1068	-	S	3.5	3.8	3.7
88	Hamburg	adult	unknown	1068	-	D	3.5	3.5	3.6
89	Hamburg	adult	unknown	9589	-	S	3.4	4.1	3.7
90	Hamburg	adult	unknown	9589	-	D	3.3	4.4	4.1
91	Hamburg	adult	unknown	4261	-	S	3	4.1	3.5
92	Hamburg	adult	unknown	4261	-	D	2.9	3.7	3.4
93	Hamburg	adult	unknown	8395	-	S	3.3	3.5	3.5
94	Hamburg	adult	unknown	8395	-	D	3.3	3.5	3.4
95	Karlsruhe	adult	unknown	26623	-	S	2.9	4.1	3.9
96	Karlsruhe	adult	unknown	26623	-	D	3.1	3.9	4
97	Karlsruhe	adult	unknown	26619	-	S	3.8	4.2	4.1
98	Karlsruhe	adult	unknown	26619	-	D	3.8	4.3	4.4
99	Karlsruhe	adult	unknown	26617	-	S	3.6	3.8	3.8
100	Karlsruhe	adult	unknown	26617	-	D	3.5	3.7	3.6
101	Karlsruhe	29 years	Zoo Karlsruhe	11894	Male	S	3	3.6	3.6
102	Karlsruhe	29 years	Zoo Karlsruhe	11894	Male	D	2.9	3.7	3.7
103	Berlin	adult	unknown	32132	-	S	3.5	3.7	3.5
104	Berlin	adult	unknown	32132	-	D	3.5	3.6	3.5

Table 6. Coefficient of Variation in molar widht between *Hippopotamus amphibius* and Javan *Hexaprotodon*

Molar	Group	n	Coefficient of Variation Calculation Results	Sample Data Source
M ₃	<i>Hippopotamus amphibius</i>	104	9.85	Avedik and Clauss, 2023
	All Javan <i>Hexaprotodon</i>	26	10.66	Present Work
	Gelasian-Calabrian Javan <i>Hexaprotodon</i>	8	4.11	Present Work
	Chibanian Javan <i>Hexaprotodon</i>	8	7.17	Present Work
	Late Chibanian to Late Pleistocene Javan <i>Hexaprotodon</i>	10	5.32	Present Work
	Gelasian-Calabrian-Chibanian Javan <i>Hexaprotodon</i>	16	6.08	Present Work
	Chibanian-Late Pleistosen Javan <i>Hexaprotodon</i>	18	7.48	Present Work
M ₂	<i>Hippopotamus amphibius</i>	103	9.88	Avedik and Clauss, 2023
	All Javan <i>Hexaprotodon</i>	19	9.97	Present Work
	Gelasian-Calabrian Javan <i>Hexaprotodon</i>	6	1.87	Present Work
	Chibanian Javan <i>Hexaprotodon</i>	8	5.06	Present Work
	Late Chibanian to Late Pleistocene Javan <i>Hexaprotodon</i>	5	3.87	Present Work
	Gelasian-Calabrian-Chibanian Javan <i>Hexaprotodon</i>	14	4.12	Present Work
	Chibanian-Late Pleistosen Javan <i>Hexaprotodon</i>	13	10.70	Present Work
M ₁	<i>Hippopotamus amphibius</i>	96	8.32	Avedik and Clauss, 2023
	All Javan <i>Hexaprotodon</i>	18	8.15	Present Work
	Gelasian-Calabrian Javan <i>Hexaprotodon</i>	6	7.21	Present Work
	Chibanian Javan <i>Hexaprotodon</i>	7	6.03	Present Work
	Late Chibanian to Late Pleistocene Javan <i>Hexaprotodon</i>	5	2.38	Present Work
	Gelasian-Calabrian-Chibanian Javan <i>Hexaprotodon</i>	13	6.51	Present Work
	Chibanian-Late Pleistosen Javan <i>Hexaprotodon</i>	12	4.96	Present Work

Table 7. Results of T-Test analysis on molar size samples of Javanese *Hexaprotodon*

Molar	Sample Test	t-table	t-count	H0	Result
M ₃	Gelasian-Calabrian VS Chibanian	±2.14	-0.65	Accepted	There is no difference in M ₃ mean size between The elasian-Calabrian Javanese <i>Hexaprotodon</i> and The Chibanian <i>Hexaprotodon</i>
	Gelasian-Calabrian-Chibanian VS Late Chibanian-Late Pleistocene	±2.07	-8.72	Rejected	There is a difference in the mean size of M ₃ between The Gelasian-Calabrian-Chibanian Javanese <i>Hexaprotodon</i> and The Late Chibanian-Late Pleistocene <i>Hexaprotodon</i>
M ₂	Gelasian-Calabrian VS Chibanian	±2.17	0.70	Accepted	There is no difference in M ₂ mean size between The Gelasian-Calabrian Javanese <i>Hexaprotodon</i> and The Chibanian <i>Hexaprotodon</i>
	Gelasian-Calabrian-Chibanian VS Late Chibanian-Late Pleistocene	±2.10	-9.64	Rejected	There is a difference in the mean size of M ₂ between The Gelasian-Calabrian-Chibanian Javanese <i>Hexaprotodon</i> and the late Chibanian-Late Pleistocene <i>Hexaprotodon</i>
M ₁	Gelasian-Calabrian VS Chibanian	±2.20	-0.86	Accepted	There is no difference in M ₁ mean size between The Gelasian-Calabrian Javanese <i>Hexaprotodon</i> and The Chibanian <i>Hexaprotodon</i>
	Gelasian-Calabrian-Chibanian VS Late Chibanian-Late Pleistocene	±2.11	-4.50	Rejected	There is a difference in the mean size of M ₁ between The Gelasian-Calabrian-Chibanian Javanese <i>Hexaprotodon</i> and The Late Chibanian-Late Pleistocene <i>Hexaprotodon</i>

K728, and Mojokerto MJK1, while a group with large-sized molars is represented by specimens of Grobogan GR05, GR07, Sambungmacan SM2014, and Ngandong NG-MGB with a Late Chibanian-Late Pleistocene age. Although differences in mammalian body size can be caused by sexual dimorphism, the results of the comparison of the CV value of Javan *Hexaprotodon* molar homology with data sets from combined female and male *Hippopotamus amphibius* from Avedik and Clauss (2023) study suggest otherwise. The T-Test on The Gelasian-Calabrian-Chibanian Javan *Hexaprotodon* population, when compared to The Late Chibanian-Late Pleistocene Javan *Hexaprotodon*, also supports the hypothesis of a size difference. The Gelasian-Calabrian-Chibanian Javan *Hexaprotodon* are significantly smaller than The Late Chibanian-Late Pleistocene Javan *Hexaprotodon*.

De Visser (2008) showed that the canines of female Hippopotamidae are smaller than in males, but for other teeth it is difficult to distinguish between males and females by size. Christensen *et al.* (2023) concluded that body size and molar size are linked, and this relationship can be used to estimate body size from molar measurements. However, referring to a *Hippopotamus* body mass study, it was suggested that there is no significant difference between adult male and female body

masses (Sadler, 2019). Based on these findings, the differences in molar size in this study were more indicative of body size than sexual dimorphism.

In the regression graph of M₁, M₂, and M₃ (Figures 3, 4, and 5) large *Hexaprotodon*, such as specimens from Grobogan (GR05, GR07) and Ngandong (NG-MGB) cluster towards the upper size limit and are generally above the regression line. In contrast, *Hexaprotodon* specimens smaller than those from Grobogan and Ngandong are generally scattered close to the regression line. The presence of data points above the regression line, such as those from the Grobogan and Ngandong specimens, indicates that factors other than the independent variable (x-axis) affect the dependent variable (y-axis), causing its value to be higher than predicted. Given that all specimens are adult *Hexaprotodon*, this suggests that the large *Hexaprotodon* from Grobogan and Ngandong indeed represents a different group from the smaller *Hexaprotodon*. The molars of the Grobogan and Ngandong specimens are relatively wide in buccolingual direction compared to their width, which indicates that these specimens have wider occlusal surfaces than the smaller specimens. A wider occlusal surface increases the effectiveness of chewing food. This suggests that The *Hexaprotodon* from Grobogan and Ngandong were more effective at chewing food than the smaller *Hexaprotodon*.

The wider molar shape in the buccolingual direction would also affect the space accommodation in the corpus and, consequently, the shape and characteristics of the mandible.

Based on morphological observations and comparisons between the large *Hexaprotodon* and small *Hexaprotodon*, several distinct characters in mandible and cranium were identified, as shown in Table 4 and Appendix 1. The existence of small *Hexaprotodon* raises questions about its potential relationship with the extant *Choeropsis*, a dwarf *Hippopotamus* found in East Africa. However, based on dental formula and geographical distribution, it is unlikely that small *Hexaprotodon* in Java shares an evolutionary relationship with *Choeropsis*. *Choeropsis* itself is distinguished from other Hippopotamidae by its distinct dental formula, with two upper incisors and one lower incisor (Flacke and Decher, 2019). This significant difference in dental formula clearly separates *Choeropsis* from *Hexaprotodon*, which possesses three incisors in both upper and lower jaws.

The incisors of the small *Hexaprotodon* group exhibit relatively small mandibular incisors compared to their canines. This is observed in the mandibular specimens Bumiayu BU-MGB, Sangiran VR1030603, and Cijolang 22G. In contrast, the large-bodied *Hexaprotodon*, represented by specimens Grobogan GR05, GR07, and Ngandong NG-MGB, possess larger mandibular incisors relative to their canine size. All of these mandibular specimens show worn third molars or M_3 , indicating that they represent adult individuals. Based on these observations, it can be concluded that two distinct morphological variants of *Hexaprotodon* existed in Java, characterized by either small or large incisors in comparison to their canines.

For an assessment of the symphysis position relative to a flat plane of the horizontal ramus, seven specimens were chosen due to their completeness. A flatter symphysis position or smaller angle between the dorsal surface of the symphysis and the horizontal plane defined by the ventral borders of the horizontal ramii of the mandible (see Appendix 1 Remarks 10) was found in

smaller *Hexaprotodon* from Bumiayu BU-MGB, Cijolang 22G, and Sangiran VR1030603. In contrast, the large *Hexaprotodon* from Grobogan GR05, Grobogan GR07, Ngandong NG-MGB, and Sambungmacan SM2014 exhibited a bigger angle between the dorsal surface of the symphysis and the horizontal plane defined by the ventral borders of the horizontal ramii of the mandible. Small and large *Hexaprotodon* also exhibit differences in symphysis shape and the sagittal angle of the mandible (see Appendix 1 Remarks 4). The small *Hexaprotodon* has a U-shaped symphysis with a mandibular sagittal angle of approximately 90° , whereas the larger *Hexaprotodon* has a V-shaped symphysis with a sagittal angle of the mandible exceeding 90° . The larger sagittal angle in the large *Hexaprotodon* is associated with the increased size of their incisors and canines, along with the widening of the premaxilla tooth row and ramus. This suggests that the larger jaw morphology of the large *Hexaprotodon* group is better adapted to accommodate their relatively larger canines and incisors.

The angular process also shows differences in shape between small and large *Hexaprotodon* (Figure 7). The angular process of the small *Hexaprotodon* has a rounded shape, whereas that of the large *Hexaprotodon* has an angled shape (Table 8). Although fragmentary, the Gunung Butak K728 specimen is estimated to have a rounded angular process based on the preserved portions. Similarly, the Ngandong K727 and K726 specimens likely had an angled angular process, based on the available remains (Figure 8). The angular process is a crucial part for muscle attachment in the mandible and for jaw mechanics. An angled shape of the angular process provides a stronger muscle attachment than a non-angled shape. This suggests that *Hexaprotodon* with an angled angular process had a stronger jaw for biting and chewing compared to *Hexaprotodon* with a non-angled angular process. In the context of diet, it is possible that the large *Hexaprotodon* group may have consumed plants with strong root systems attached to the bottom of water bodies or grass on land. Modern *Hippopotamus*, which

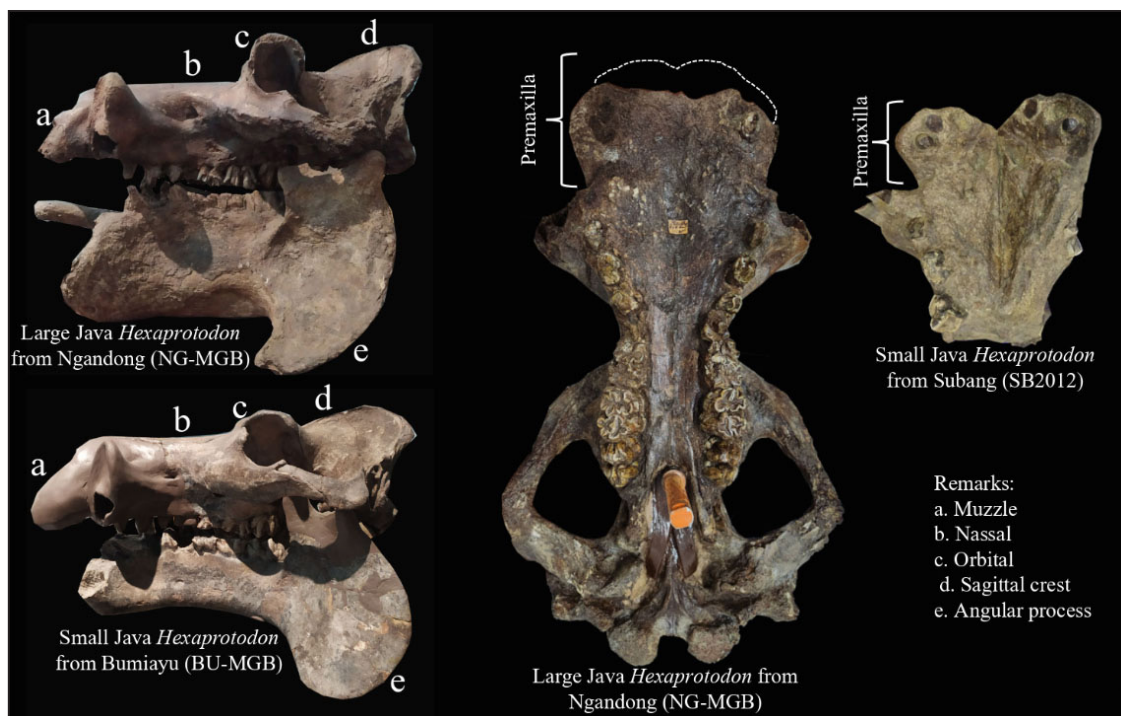


Figure 7. Comparison of the distinct morphological features from the skull and mandible of large and small Javan *Hexaprotodon*.

Table 8. Differences between small *Hexaprotodon* and large *Hexaprotodon*

Characteristic Anatomy		Small <i>Hexaprotodon</i> (<i>Hexaprotodon sivajavanicus</i>)	Large <i>Hexaprotodon</i> (<i>Hexaprotodon megakendengensis</i>)
	Relative size of the lower incisor to the lower canine	Small	Large
Mandible	The height of the symphysis	low	high
	Angular process	Rounded	Angled
	Symphysis-mandibular ramus shape	U	V
	Mandibular sagittal angle	Around 90°	>90°
Cranial	Orbital bone height	Moderate	High
	Sagittal crest	Curve	Rise
	Nasal bone shape	Relatively slender	Relatively broader
	Muzzle	Relatively short	Relatively long

also have an angled angular process, are grazers (Fritsch, 2020).

Comparative analysis of the crania of small and large *Hexaprotodon* reveals further morphological differences. The small *Hexaprotodon* is represented by Bumiayu BU-MGB and Mojokerto MJK1, while the large *Hexaprotodon* is represented by Ngandong NG-MGB. The large *Hexaprotodon* possesses a taller orbital bone and a more prominent sagittal crest than the small *Hexaprotodon* (Figure 7). These cranial features suggest that the large *Hexaprotodon* was better

adapted to an aquatic lifestyle. The elevated position of the orbital bone would have allowed the large *Hexaprotodon* to maintain visual accuracy while its body was submerged and its eyes remained above the water surface. This interpretation aligns with the jaw morphology, which is well-suited for the consumption of aquatic plants. Modern *Hippopotamus* also have this protruding eye sockets. They come to land at night (to avoid burning their skin) to graze on grasses.

Additionally, the nasal bone of the small *Hexaprotodon* appears more slender compared to the

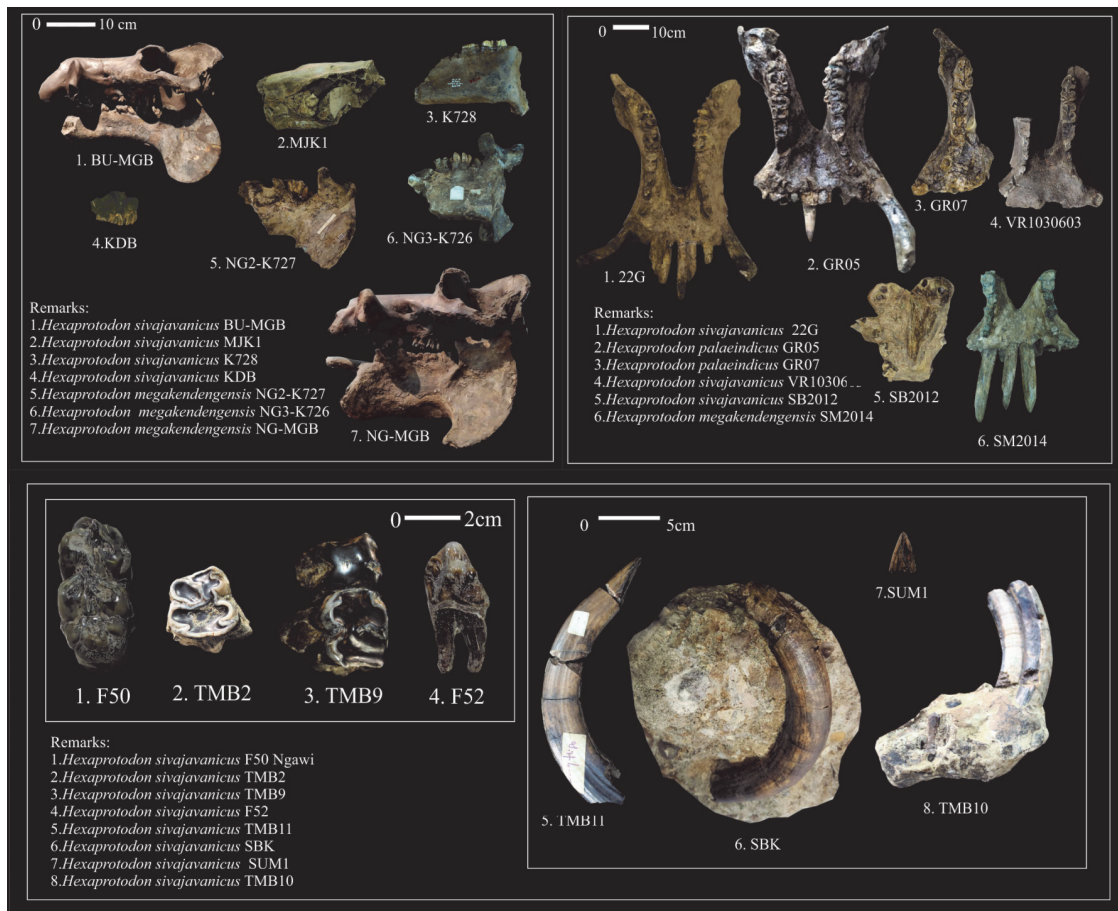


Figure 8. Photos of specimens used in this study

broader nasal bone of the large *Hexaprotodon*. Furthermore, the shape of the premaxilla is also of interest. To analyze it, the premaxilla and muzzle shape of a small Javan *Hexaprotodon* specimen were compared with that of a large Javan *Hexaprotodon*. Unfortunately, the skull muzzle of the small Javan *Hexaprotodon* from Bumiayu (BM-MBG) is a reconstruction, and thus can not be used for comparison. Fortunately, the premaxilla of a small Javan *Hexaprotodon* can still be observed in the collection from Subang (SB2012), which allows for comparison with the large Javan *Hexaprotodon*. The premaxilla of the small Javan *Hexaprotodon* from Subang appears shorter than that of the large one from Ngandong (NG-MGB), leading to the conclusion that the muzzle of the small Javan *Hexaprotodon* is shorter than that of the large Javan *Hexaprotodon* (Figure 7). Van der Geer *et al.* (2018) and Pandolfi *et al.* (2020) state that insular dwarfing in Hippopotamidae

also tends to lead to relatively shorter muzzles in dwarfed island species.

The differences in characteristics and size among Javan Hippopotamidae have long been a subject of scientific inquiry. De Visser (2008) acknowledged that size differences existed between different types of Hippopotamidae that once lived in Java. However, De Visser (2008) overlooked significant anatomical differences between small and large *Hexaprotodon*, attributing this oversight to the limited availability of large *Hexaprotodon* specimens, with only one cranium (Ngandong NG-MGB) available for the study. As a result, De Visser (2008) concluded that small and large *Hexaprotodon* were all one type, *Hexaprotodon sivajavanicus*, neglecting the apparent morphological distinction.

Referring to the calvarium specimen of *Hippopotamus sivalensis koenigswaldi* (Coll. Dub. No. 2919) in Hooijer (1950) Appendix, Plate

IV and Plate II, Figure 3, it exhibits a medium-height orbital bone with a curved sagittal crest. Similarly, Plate II, Figure 4 of the *Hippopotamus sivalensis sivajavanicus* holotype (Coll. Dub. No. 2908) from Kedungbrubus shows a medium-height orbital bone and a curved sagittal crest. This characteristic aligns with the small *Hexaprotodon* from Bumiayu BU-MGB, which von Koenigswald classified as *Hexaprotodon simplex*. Furthermore, Plate V, Figure 2, showcasing the *Hippopotamus sivalensis koenigswaldi* mandible specimen (Coll. Dub. No. 2916) from Kedungbrubus, and Plate X, Figures 1, and 3, depicting *Hippopotamus sivalensis koenigswaldi* (Coll. Dub. No. 99) from Tritik (a Middle Pleistocene site), show a U-shaped symphysis-mandibular ramus configuration. This morphology is similar to that observed in small mandible specimens such as Bumiayu BU-MGB, Cijolang 22G, and Sangiran VR1030603 in this study.

According to Hooijer (1950), *Hippopotamus sivalensis koenigswaldi* is a revised name for *Hexaprotodon antiquus* von Koenigswald. Based on all the available data, *Hexaprotodon simplex*, *Hippopotamus sivalensis sivajavanicus*, *Hexaprotodon antiquus*, and *Hippopotamus sivalensis koenigswaldi* all appear to represent the same small *Hexaprotodon* in Java. The shared characteristics of the orbital bone and sagittal crest morphology are somewhat similar to *Hexaprotodon sivalensis* from India. Therefore, the appropriate name for this small Javan *Hexaprotodon* is *Hexaprotodon sivajavanicus*, as it was the first name assigned to this taxon by Dubois (1908).

The large size of the Javanese *Hexaprotodon* can also be observed in Hooijer (1950) publication Figure 9. In Plate II, Figure 1, of Hooijer (1950) publication the holotype calvarium specimen (Coll. Dub. no. 2908) from Tinggang, Bojonegoro, is shown, and Plate VI, Figure 2, shows Coll. Dub. No. 2909 from the same locality, both referred to as *Hippopotamus sivalensis soloensis*. These specimens show a high orbital bone with a raised sagittal crest, similar to the Ngandong NG-MGB specimen. The mandible specimen of *Hippopotamus sivalensis soloensis* (Coll. Dub. No. 2915)

from the Solo Valley, in Plate VI, Figure 3, and Plate VI, Figure 2, also shows an angled angular process with a V-shaped symphysis-mandibular ramus, consistent with the characteristics of the large *Hexaprotodon* in this study. *Hippopotamus sivalensis soloensis* is a revised name for *Hippopotamus namadicus* von Koenigswald. It is noteworthy that all skull and mandible specimens of large Javan *Hexaprotodon* possess six incisors, which supports their assignment to the genus *Hexaprotodon* rather than *Hippopotamus*.

The high orbital bone character of large Javan *Hexaprotodon* exhibits similarities to *Hexaprotodon palaeindicus* from India and Myanmar (Htike and Takai, 2016). However, the index ratio of the distance between the mandibular premolars P_2 - P_4 to the distance between the mandibular molars M_1 - M_3 , as defined by Boisserie (2005), falls outside the range of *Hexaprotodon palaeindicus*. According to Boisserie (2005), this index ratio for *Hexaprotodon palaeindicus* is approximately 70, whereas the large Javan *Hexaprotodon* shows a range of around 80. Therefore, the assumption that the large Javanese *Hexaprotodon* is a *Hexaprotodon palaeindicus* can not be accepted.

Based on the regression graph, particularly the M_3 , The Gelasian-Calabrian Javan *Hexaprotodon* specimens from Cijolang, Bumiayu, and Sangiran generally exhibit smaller M_3 sizes compared to their Chibanian counterparts, such as those from Kedungbrubus, Tritik, and Watualang, as well as The Late Chibanian-to-Late Pleistocene *Hexaprotodon* (Figure 5). This pattern indicates an evolutionary change in the size of *Hexaprotodon* in Java. Consequently, it is plausible that the large Javan *Hexaprotodon* evolved from the smaller specimens that inhabited the island since The Gelasian. This finding supports de Visser (2008) assertion that the *Hexaprotodon* in Java underwent an increase in size since its initial arrival.

Because it exhibits distinct morphological features distinguishable from *Hexaprotodon sivajavanicus*, The Javan Late Chibanian-Late Pleistocene *Hexaprotodon* is concluded to be a distinct species resulting from the evolution of *Hexaprotodon sivajavanicus*. Because it is

larger than *Hexaprotodon sivajavanicus* and is found in the Kendeng Zone, a new species name, *Hexaprotodon megakendengensis* nov. spec., is proposed for this taxon.

Based on the aforementioned analysis, the proposed name for the small *Hexaprotodon* in Java Island is:

Hexaprotodon sivajavanicus Dubois, 1908

Holotype: Calvarium from Dubois' collection (Coll. Dub. 2908)

Synonyms:

Hippopotamus sivalensis sivajavanicus (Dubois, 1908)

Hexaprotodon simplex (von Koenigswald, 1933)

Hippopotamus sivalensis koenigswaldi (Hooijer, 1942)

Paleogeography range: West, Central and East Java

Age: Gelasian-Calabrian-Chibanian

Diagnosis:

The lower incisor is relatively small compared to the mandibular canine, and the height of the symphysis is great. The molars are relatively smaller and narrower compared to the large Javan *Hexaprotodon*. The angular process part is rounded, while the symphysis-mandibular ramus exhibits a U-shaped configuration. Mandibular sagittal angle around 90°. The height of the orbital bone is moderate, the sagittal crest is curved, the nasal bone is slender and the muzzle is short.

The proposed name for the large *Hexaprotodon* in Java Island is:

Hexaprotodon megakendengensis nov. spec.

Holotype: Skull from Museum Geologi Bandung NG-MGB

Synonyms:

Hippopotamus namadicus (von Koenigswald, 1933)

Hippopotamus sivalensis soloensis (Hooijer, 1950)

Paleogeography range: Central and East Java

Age: late Chibanian-Late Pleistocene

Diagnosis:

The lower incisors are relatively large compared to the mandibular canine, the height of the sym-

physis is low. The angular process part is angled, while the symphysis-mandibular ramus exhibits a V-shaped configuration. Mandibular sagittal angle greater than 90°. The height of the orbital bone is high, the sagittal crest is raised, the nasal bone broad and the muzzle is long.

The chronology of the existence of *Hexaprotodon* on the island of Java can be explained as follows. *Hexaprotodon sivajavanicus* first appeared in The Gelasian. Its fossils were found along The Cijolang River and its tributary at the Rancah area of West Java. Specifically, the fossils were discovered in a sedimentary rock layer known as The Cijolang Bed, which is also the location where a fossil of *Merycopotamus* was found (von Koenigswald, 1935). Fossils at the tributary in the Rancah area could be younger than those found on The Cijolang River itself.

Merycopotamus is an artiodactyl with a distribution exclusive to Asia (Lihoreau *et al.*, 2007). It existed from The Middle Miocene to The Pliocene-Pleistocene boundary or the Gelasian-Calabrian boundary according to the modern consensus (Hussain *et al.*, 1992; Lihoreau *et al.*, 2007). The age of The Gelasian-Calabrian boundary is also supported by the characteristics of The Cijolang Llyer, which shows evidence of erosion products from The Kumbang Formation. These include andesitic breccia lenses within the Cijolang sandstone layers. The Kumbang Formation itself is composed of volcanic materials, specifically breccia, andesite lava, and tuff, indicating significant volcanic activity during its formation. The Kumbang Formation was deposited in a deep marine environment from The Late Miocene to The Early Pliocene (Sulistyo, 2016; Rizal *et al.*, 2017). Therefore, considering these facts, the lithology of The Kumbang Formation must have been uplifted in The Late Pliocene, then eroded and redeposited in the Plio-Pleistocene.

During The Gelasian-Calabrian, *Hexaprotodon sivajavanicus* spread across Java, with fossils found in Cijolang, Bumiayu, Sangiran, Gunung Butak, and Mojokerto (see Figure 1). This species then evolved to become larger in The Chibanian. The discovery of larger *Hexapro-*

todon sivajavanicus specimens from Chibanian layers, such as those from Watualang and Kedung Brubus, confirms this evolutionary trend. Later, at the end of The Chibanian or during The Late Chibanian-Late Pleistocene, *Hexaprotodon megakendengensis* from Sambungmacan, Grobogan, and Ngandong replaced *Hexaprotodon sivajavanicus*. The presence of *Hexaprotodon megakendengensis* at these sites represents the end of the existence of *Hexaprotodon sivajavanicus* in Java.

CONCLUSION

All Hippopotamidae fossils discovered in Java belong to the genus *Hexaprotodon*; no *Hippopotamus* fossils have been identified in either old or new collections. This study recognizes two distinct *Hexaprotodon* lineages in Java: a relatively small form from The Gelasian-Calabrian-Chibanian and a larger form from The Late Chibanian-Late Pleistocene. Based on anatomical comparisons and biogeographic considerations, the small Javan *Hexaprotodon* is identified as *Hexaprotodon sivajavanicus*, which descended from *Hexaprotodon sivalensis*. The large Javan *Hexaprotodon* is named *Hexaprotodon megakendengensis*, and it likely derived from *Hexaprotodon sivajavanicus*.

ACKNOWLEDGEMENTS

This research is funded by P2MI Research Programme of Faculty of Earth Sciences and Technology, Bandung Institute of Technology, number FITB.PPMI-1-06-2024 given to Dr. Aswan.

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